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CEPHALOPODS OF THE WORLD

AN ANNOTATED AND ILLUSTRATED CATALOGUE OF CEPHALOPOD SPECIES KNOWN TO DATE

Volume 3. Octopods and Vampire Squids

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Volume 3

Octopods and Vampire Squids

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The Third Volume of this New Edition of the Cephalopods of the World Catalogue

is warmly dedicated to the memory of

Katharina Mangold Wirz

an extraordinary brilliant scientist and teuthologist,
an unforgettable lady
and a cherished friend and colleague.

photo: F.G. Hochberg

PREPARATION OF THIS DOCUMENT

This document has been prepared by the Marine and Inland Fisheries Service, Fisheries and Aquaculture Resources Use and Conservation Division, FAO Fisheries and Aquaculture Department. It is part of the regular programme activities and a partial fulfillment of the Organization’s role with regard to the marine fisheries resources identification and biodata. It received support through contributions from the Ministry of Agriculture and Forestry Policies of the Government of Italy and from the Ministry of Foreign Affairs of the Kingdom of Norway to the FAO Global Partnerships for Responsible Fisheries (FISHCODE).

This publication is the third of three volumes of the second edition of the original FAO Catalogue of Cephalopods of the World (Roper *et al.*, 1984), and it constitutes Volume 3 of Number 4 in the new series: *FAO Species Catalogue for Fisheries Purposes*, that evolved as an independent series in 2001 from the former *FAO Fisheries Synopsis* No. 125.

Because the new Catalogue has expanded apace with recent research and fisheries information and revisions, it now is necessary to publish it as three free-standing volumes. Each volume has separate pagination, terminology/glossary, systematic sections, list of species and a volume-specific bibliography. This allows readers to use each volume independently without having to consult the other volumes for technical terms, measurements or bibliographic purposes. We hope that this added flexibility will provide convenience and utility for users of the Catalogue.

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Technical and editorial assistance: Ingrid Roper (Smithsonian Institution, NMNH, Volunteer, Washington D.C., USA).

Scientific assistance: Michael J. Sweeney (formerly Smithsonian Institution, NMNH, Washington D.C., USA).

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Page composition: Cinzia Lucini (Litografica Doria snc, Rome).

Distribution maps: Fabio Carocci (FAO, Rome).

Cover illustration: Emanuela D’Antoni (FAO, Rome).

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Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids by P. Jereb, C.F.E Roper, M.D. Norman, and J.K. Finn (eds)

FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. 2016. 370 p. 11 colour plates.

ABSTRACT

This is the third volume of the entirely rewritten, revised and updated version of the original FAO Catalogue of Cephalopods of the World (1984). The present Volume is a multiauthored compilation that reviews 13 families, i.e. (in alphabetical order), *Alloposidae, Amphitretidae, Argonautidae, Bolitaenidae, Cirroctopodidae, Cirroteuthidae, Octopodidae, Ocythoidae, Opisthoteuthidae, Stauroteuthidae, Tremoctopodidae, Vampyroteuthidae, Vitreledonellidae,* with 56 genera and the 280 species known and named to the date of the completion of the volume. It provides accounts for all families and genera, as well as illustrated keys. Information under species accounts includes: valid modern systematic name and original citation of the species (or subspecies); synonyms; English, French and Spanish FAO names for the species; illustrations of dorsal aspects of the whole animal (as necessary) and other distinguishing illustrations; field characteristics; diagnostic features; geographic and vertical distribution, including GIS map; size; habitat; biology; interest to fishery; local names when available; a remarks section (as necessary) and literature. The Volume is fully indexed and also includes sections on terminology and measurements, an extensive glossary, an introduction with an updated review of the existing biological knowledge on octopods and Vampire squids (including fisheries information and main catch data for recent years) and a dedicated bibliography.

Distribution
Authors
FAO Fisheries Officers
Regional Fisheries Councils and Commissions
Selector SC

For bibliographic reference the different sections should be quoted as follows:

AAVV 2016. Illustrated glossary of technical terms and measurements. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn, eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 22-32.

Finn, J.K. 2016. Family Alloposidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn, eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 225-228.

Finn, J.K. 2016. Family Argonautidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 228-237.

Finn, J.K. 2016. Family Ocythoidae. *In* P. Jereb, C.F.E. Roper, M. D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 237-239.

Finn, J.K. 2016. Family Tremoctopodidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 240-243.

Hochberg, F.G., Norman, M.D. & Finn, J.K. 2016. Family Cirroctopodidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 245-247.

Hochberg, F.G., Norman, M.D. & Finn, J.K. 2016. Family Cirroteuthidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 262-265.

Hochberg, F.G., Norman, M.D. & Finn, J.K. 2016. Family Opisthoteuthidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 248-261.

Hochberg, F.G., Norman, M.D. & Finn, J.K. 2016. Family Stauroteuthidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 266-267.

Jereb, P. & Roper, C.F.E. 2016. Introductory remarks. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 1-2.

Jereb, P. & Roper, C.F.E. 2016. General remarks on cephalopods. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 3-5.

Norman, M.D. 2016. General remarks on octopods. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J. K Finn, eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 6-9.

Norman, M.D. & Finn, J.K. 2016. World octopod fisheries. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J. K Finn, eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 9-14.

Norman, M.D. & Finn, J.K. 2016. Family Amphitretidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 217-219.

Norman, M.D. & Finn, J.K. 2016. Family Bolitaenidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 221-224.

Norman, M.D. & Finn, J.K. 2016. Family Vampyroteuthidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 268-270.

Norman, M.D. & Finn J.K. 2016. Family Vitreledonellidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 219-221.

Norman, M.D., Finn, J.K. & Hochberg, F.G. 2016. Family Octopodidae. *In* P. Jereb, C.F.E. Roper, M.D. Norman & J.K. Finn eds. *Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 3. Octopods and Vampire Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 3. Rome, FAO. pp. 36-215.

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From the Series Editors

We wish to gratefully acknowledge the contributions of colleagues who have supplied information, help and support to enable completion of the updated version of the Cephalopods of the World FAO Catalogue, first published in 1984 (Roper, Sweeney and Nauen, 1984). We appreciate their good efforts to help us make the 3-volume Catalogue a comprehensive and useful tool.

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Our deepest thanks to the members of the FAO technical staff who so efficiently worked to produce the 3-volume series and contributed to the preparation of this third Volume: **Emanuela D'Antoni** for her excellent accomplishments in creating many of the illustrations needed for the Catalogue and for greatly enhancing many illustrations from the literature; **Nicoletta De Angelis** for her skilful collaboration during the first phases of the preparation of this document; **Fabio Carocci** for the careful preparation of the distribution maps. All are premier representatives of their professions. Deep, sincere thanks also to **Michèle S. Kautenberger-Longo** (formerly FAO), for her valuable and precious professional contribution to the preparation of the first two Volumes of the series. Our special thanks to **Nicoletta**, for her valuable and constant support during the entire production of this 3-volume Cephalopods of the World Catalogue project.

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Last, but not least, very special thanks are due to **Ingrid H. Roper**, for her technical assistance and invaluable support during all stages of the preparation of this Catalogue.

We are aware that oversights occurred in Volumes 1 and 2. These will be amended on the on-line versions available on the FAO website (http://www.fao.org/fishery/fishfinder/ publications/en).

Also, some changes in cephalopod terminology have occurred in the past 15 years. These may create discrepancies in the Glossary definitions used among the three volumes. We recommend that users refer to the Glossary that applies to the specific group/taxon being discussed in each volume.

Recent reviews of the geographic distributions of some European species were conducted during a cooperative research project with several European colleagues (Jereb *et al.*, 2015). This study confirmed the existence of strong fluctuations in marine conditions in some geographic areas, such as the North Sea. In turn, this phenomenon may strongly influence the geographic distribution of cephalopod species, which may result in geographic fluctuations. Such a situation is difficult to represent on a map. A map best illustrates the normal distributions, while details about potential fluctuations or extensions and reductions in the distribution observed over time, are best described in the text. We are aware that some of the maps in Volumes 1 and 2 may not adequately reflect the complexity of actual distributions.

We sincerely appreciate the contributions, effort and support of colleagues around the world who have made it possible for us to complete this 3-volume work.

From the Authors

The authors gratefully acknowledge the contributions of colleagues who supplied references, species-specific information, and/or read drafts of text for this volume. In particular we would like to thank **Michael J. Sweeney** (formerly Smithsonian Institution, National Museum of Natural History, Washington, DC, USA). His comprehensive listing of cephalopod taxa, type localities, and repositories of type specimens was extremely helpful. Additional valuable feedback on this volume was provided by **Christine L. Huffard** (Monterey Bay Aquarium Research Institute). Thanks also to **Richard E. Young** for his Cephalopoda treatment in the Tree of Life website (http://tolweb.org/Cephalopoda), an excellent resource for all cephalopod researchers.

The volume was extensively reviewed and edited by **Patrizia Jereb** (Istituto Superiore per la Protezione e la Ricerca Ambientale, Rome, Italy) and **Clyde F. E. Roper** (Zoologist Emeritus, Smithsonian Institution, National Museum of Natural History, Washington, DC, USA), with assistance from **Ingrid Roper**. We warmly thank all for their considerable efforts and patience.

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The authors would especially like to thank the support of our wives and families over the lengthy production process of this volume, **Karen Zipkas**, **Lena** and **Adel Hochberg**, and **Prema Finn**.

Table of Contents

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* At the time of going to press, Strugnell *et al.* (2013) published a major revision of the familial level classification of the incirrate octopods. They establish six families: Octopodidae, Bathypolypodidae, Eledonidae, Enteroctopodidae, Megaleledonidae and Amphitretidae, the latter containing three subfamilies Amphitretinae, Bolitaeninae and Vitreledonellinae (see that work for new taxonomic structure).

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* The generic placement of this species requires review.

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* At the time of going to press, Strugnell *et al.* (2013) published a major revision of the familial level classification of the incirrate octopods. They propose a single ctenoglossan family Amphitretidae, containing three subfamilies Amphitretinae, Bolitaeninae and Vitreledonellinae (see that work for new taxonomic structure).

1. INTRODUCTION

1.1 INTRODUCTORY REMARKS

by Patrizia Jereb and Clyde F. E. Roper

The increasing exploitation of finfish resources and the depletion of a number of major fish stocks that formerly supported industrial-scale fisheries, force increased attention on the formerly-named ‘unconventional marine resources’, which include numerous species of cephalopods. Cephalopod catches have grown steadily in the last 40 years, from about 1 million metric tonnes in 1970 to around 3.6 million metric tonnes in 2010 (FAO, 2012) .

This increase confirms the potential development of the fishery predicted by G.L. Voss (1973) in the first general review of the world’s cephalopod resources prepared for FAO. The rapid expansion of cephalopod fisheries in the decade or so following the publication of Voss’s review meant that a more comprehensive and updated compilation was required, particularly for cephalopod fishery biologists, zoologists and students. The FAO Species Catalogue, ‘Cephalopods of the World’ by Roper, Sweeney and Nauen (1984) was published to meet this need.

The number of cephalopod species that enter commercial fisheries has continued to expand significantly since 1984, as a result of the still-growing market demand and the expansion of fisheries operations to new fishing areas and to deeper waters. Formerly, it was suggested that the cephalopod ‘life-strategy’ may guarantee survival against environmentally stressful conditions, including those caused by heavy fishing. However, as cephalopod fisheries experienced further intensive development, parallel concern developed regarding potential overexploitation (see discussion of World Octopod Fisheries below).

In an effort to avoid possible failures in cephalopod exploitation, a broad consensus emerged among cephalopod fishery biologists to apply the experience gained from earlier errors in finfish management. To help prevent these potential failures, refined species identification capabilities are required, as well as a more detailed and accurate compilation of information on cephalopod species, their distribution, biology, fisheries and catch statistics.

Consequently, FAO recognized that a new edition of the ‘Cephalopods of the World’ catalogue was required. To achieve this expanded goal, several authors with particular areas of specialization were assembled to enhance the accuracy, coverage and utility of this revised catalogue.

The magnitude of information currently available on cephalopod biology, taxonomy and fisheries made it necessary and convenient for specialized interests, to divide the Catalogue into three volumes: Volume I, on Chambered Nautiluses and Sepioids, published in 2005, Volume II, on Myopsid and Oegopsid squids, published in 2010, and Volume III, on octopods and Vampire squids (current volume).

In our attempt to make this document as comprehensive and as useful as possible for the variety of potential users, the taxonomic coverage of the catalogue is organized into 3 levels of interest:

Level 1: species of cephalopods currently exploited commercially and species utilized at the subsistence and artisanal levels;

Level 2: species of occasional and fortuitous interest to fisheries. This includes species considered to have a potential value to fisheries based on criteria such as edibility, presumed abundance, accessibility, marketability, fin fishery bait, etc. Species of actual or potential interest to researchers or the wider public also are considered under this level, as is at least one representative of every octopod genus;

Level 3: species with no current interest to fisheries. These species are listed only with basic systematic and distributional information.

The inclusion of such a wide range of species is necessary to provide the most comprehensive inventory of species, regardless of their current commercial status. For example, this work should be useful in the ever-expanding search for development and utilization of ‘natural products’, pharmaceuticals, etc., as well as for fisheries and biology.

The catalogue is based primarily on information available in published literature. However, yet-to-be-published reports and working documents also have been used when appropriate, especially from geographical areas where published information and data are limited. Many of these documents are the result of the research of the current authors.

We are particularly grateful to colleagues worldwide who have provided us with fisheries information, as well as with bibliographies of local cephalopod literature. The fishery data reported herein are taken from the FAO official database, FishStat Plus 2009, now replaced by FishStatJ.

During the 20-plus years separating the two editions of the Catalogue, the rapid development of worldwide cephalopod fisheries and the simultaneous increase in the population of fisheries scientists through their research and publications, have produced an enormous amount of new data. Sometimes it is difficult to evaluate the reliability of published data, especially with regard to the identification of species in areas where the cephalopod fauna has not been sufficiently studied taxonomically. It is entirely understandable that field workers isolated from comprehensive library and museum/collection facilities find it difficult to correctly identify the species they encounter in the field. Moreover, the discovery of new species, the more accurate delimitation of known species, or even the introduction of nomenclatural changes, may cause confusion and lead to the use of scientific names that are incorrect by modern standards. Although great care has been exercised to evaluate and correct the published information used in the preparation of this catalogue, some incorrect interpretations may have occurred. Another potential limitation, in the taxonomic literature especially, is that information on the economic importance of species is either scarce or of a very general nature. Further, important information may have been overlooked if published only in local fisheries literature that is unavailable on an international scale. All of these potential limitations, however, have been significantly mitigated during the preparation of the new edition because of the availability of on-line fisheries databases and bibliographic search capabilities.

With regard to the limitations mentioned above, we heartily request that readers who detect any errors in the information presented, or who have additional information and data that will enhance the accuracy and utility of this book, please contact and inform one of the authors or FAO FishFinder, the Species Identification and Data Programme of the Marine Resources Service, Fisheries Resources Division, Fisheries Department, FAO, Rome [FI-inquiries@fao.org].

For further reading and information on cephalopod biology, fisheries and resources, several references to websites are listed at the end of the references section (page 333).

1.2 PLAN OF THE CATALOGUE*

This catalogue is organized by families and their included genera within major cephalopod groups. The type genus within each family is treated first, then all remaining genera are listed alphabetically. The type species within each genus is treated first, then all remaining species are listed alphabetically.

Level 1, includes the most important species for fisheries utilization, and it consists of detailed information in all 12 categories listed below. Level 2, which comprises those species of occasional, fortuitous or potential interest to fisheries, consists of whatever information is available and appropriate for the 12 categories. Level 3, those species for which there is no current interest to fisheries, consists of basic information (i.e. scientific name, size, geographical distribution, literature). Within this volume the first two level of treatment (Level 1 and Level 2) are not differentiated. Species included in Level 3 are presented at the end of each genus.

Each major group and family is introduced with general descriptive remarks, illustrations of diagnostic features, highlights of the biology and relevance to fisheries. The information that pertains to each species in Levels 1 and 2 is arranged by categories as follows: (1) scientific name; (2) synonymy; (3) misidentifications; (4) FAO names; (5) diagnostic features with illustrations; (6) maximum known size; (7) geographical distribution, including map; (8) habitat and biology; (9) interest to fisheries; (10) local names; (11) remarks (12) literature.

(1) Scientific Name: Reference to author, date and publication citation is given for the original description of each species.

(2) Frequent Synonyms: Principal synonyms and name combinations are listed.

(3) Misidentifications: Misidentifications are reported here and discussed in detail when appropriate, along with other nomenclatural points, in section 11, Remarks.

(4) FAO Names: English, French and Spanish names for each species, used primarily in FAO statistics and literature, are selected on the basis of the following criteria: (i) each name must apply to only one species, in a worldwide context; (ii) the name must conform to FAO nomenclatural spelling; (iii) the name should apply only to a cephalopod species, and it should not lead to confusion with species names in other major animal groups. Wherever possible, these names are selected based on vernacular names (or parts of names) already in existence within the geographical areas where the species is fished. FAO species names, of course, are not intended to replace local species names, but they are considered necessary to overcome the considerable confusion caused by the use of a single common name for many different species, or several names for the same species.

(5) Diagnostic Features: Distinctive characters of the species are given as an aid for identification, accompanied by pertinent illustrations. Species identifications should be attempted only after verification of the family through use of the illustrated key to families. Morphological characters in bold are considered primary diagnostic features to aid identification.

(6) Size: The known mantle length (or total length in some cases) of both males and females is provided where possible. Sizes or measurements might not be completely comparable, because they often were taken from preserved or fixed specimens. Measurements of commercially important species often come from fresh material. Because of the elasticity of arms, total length is not a very accurate measurement. Where both total length and mantle length are given, the accompanying illustrations were not necessarily illustrated from the same specimen but may have been obtained from different sources. The information available on the size attained by some species often is meagre, so the maximum size cited herein might be smaller than the actual maximum size. Maximum weight is given when available.

(7) Geographical Distribution: The entire known geographic range of the species, including areas of seasonal occurrence, is given in the text and shown on an accompanying map. In cases where only scattered records of occurrence are available, question marks have been used to indicate areas of suspected or unconfirmed distribution.

(8) Habitat and Biology: The known depth range of the species and information on salinity and temperature of its habitat are given where available. For the sake of precision, actual depth of capture data are reported, as given in the referenced literature. Information on biological aspects, such as migration, spawning season and area, longevity, prey, and predators, also is included.

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* According to FAO standards

(9) Interest to Fisheries: This paragraph gives an account of the areas where the species is fished and of the nature of the fishery. Its importance either is qualitatively estimated (minor, moderate, major or potential) or actual figures of annual landings are provided. Data on utilization (fresh, dried, cooked, frozen, canned, etc.) also are given when available. Here, too, the quality and quantity of the available information varies considerably among the species, and it is reported in as much detail as possible in relation to the species significance to the fisheries.

(10) Local Names: These are the names used locally for the topic species. The present compilation is necessarily incomplete, since only a fraction of the local names applied to specific entities actually is published. In many cases, local names are available only for species that support traditional fisheries. Apart from possible omissions due to limitations of literature available, some of the names included may be somewhat artificial, e.g. through transliteration of indigenous words into English. The local species name is preceded by the name of the country concerned in capital letters and, when necessary, by geographical specifications in lower case letters.

(11) Remarks: Important information concerning the species, but not specifically linked to any of the previous categories, is given here. For example, in some cases the taxonomic status of certain scientific names requires further discussion. Other nomenclatural problems are discussed in this section, such as the use of subspecies names.

(12) Literature: This category includes references only to those publications cited in the text. For many uncommon species, only systematic papers are available.

1.3 GENERAL REMARKS ON CEPHALOPODS

by Patrizia Jereb and Clyde F.E. Roper

The group known as cephalopods (class Cephalopoda) is one of the most highly derived in the phylum Mollusca, and indeed, in all of the invertebrate phyla. Cephalopods include exclusively marine animals that live in all oceans of the world with the exception of the Black Sea, from the Arctic Sea to the Antarctic Ocean and from the surface waters down into the abyssal zone of the deep sea.

Cephalopods first appeared as a separate molluscan taxonomic entity, the nautiloids, in the Upper Cambrian period (over 500 million years ago), but more than half of these ancestors were already extinct by the end of the Silurian, 400 million years ago, when only the nautiluses survived. Meanwhile, other forms arose in the late Palaeozoic (between 400 and 350 million years ago), including those of the Subclass Coleoidea, but most of them became extinct by the end of the Mesozoic, about 150 million years ago. The only members of the subclass Coleoidea that exist today are the forms that developed in the Upper Triassic and Lower Jurassic (between 200 and 150 million years ago).

Although there is a long fossil record of many different groups, all living cephalopods belong to two 'subclasses'**:** the **Coleoidea**, which includes the major groups known as squids, cuttlefishes *sensu lato*, octopods and vampire squids, and the **Nautiloidea**, containing two genera, *Nautilus* and *Allonautilus*(1), the only surviving cephalopods with an external shell.

At the present time the status and understanding of the systematics and classification of the Recent Cephalopoda are under considerable discussion. The families of living cephalopods are, for the most part, well resolved and relatively well accepted. Species-level taxa usually can be placed in well-defined families. The higher classification, however, still is not resolved. The classification above the family level is controversial and a broad consensus still needs to be achieved. This situation is not unexpected for a group of organisms that has undergone explosive research attention in recent decades.

Consequently, rather than accept and promote any particular scheme of classification, before consensus and stability are achieved, we will use an 'operational breakdown' that is satisfactory for the objectives of this Catalogue. For practical purposes we separate the cephalopods into several groups, without assigning or implying taxonomic relationships. **Figure 1** diagrams several of the classification schemes currently under discussion.

In this work the following groups are used, as illustrated in **Figure 2**(2):

Nautiluses
Cuttlefishes
Bobtail squids
Bottletail squids
Pygmy squids
Ram's horn squid
Myopsid squids
Oegopsid squids
Vampire squids
Cirrate octopods
Incirrate octopods

Unresolved taxa:
Spirula
Chtenopteryx

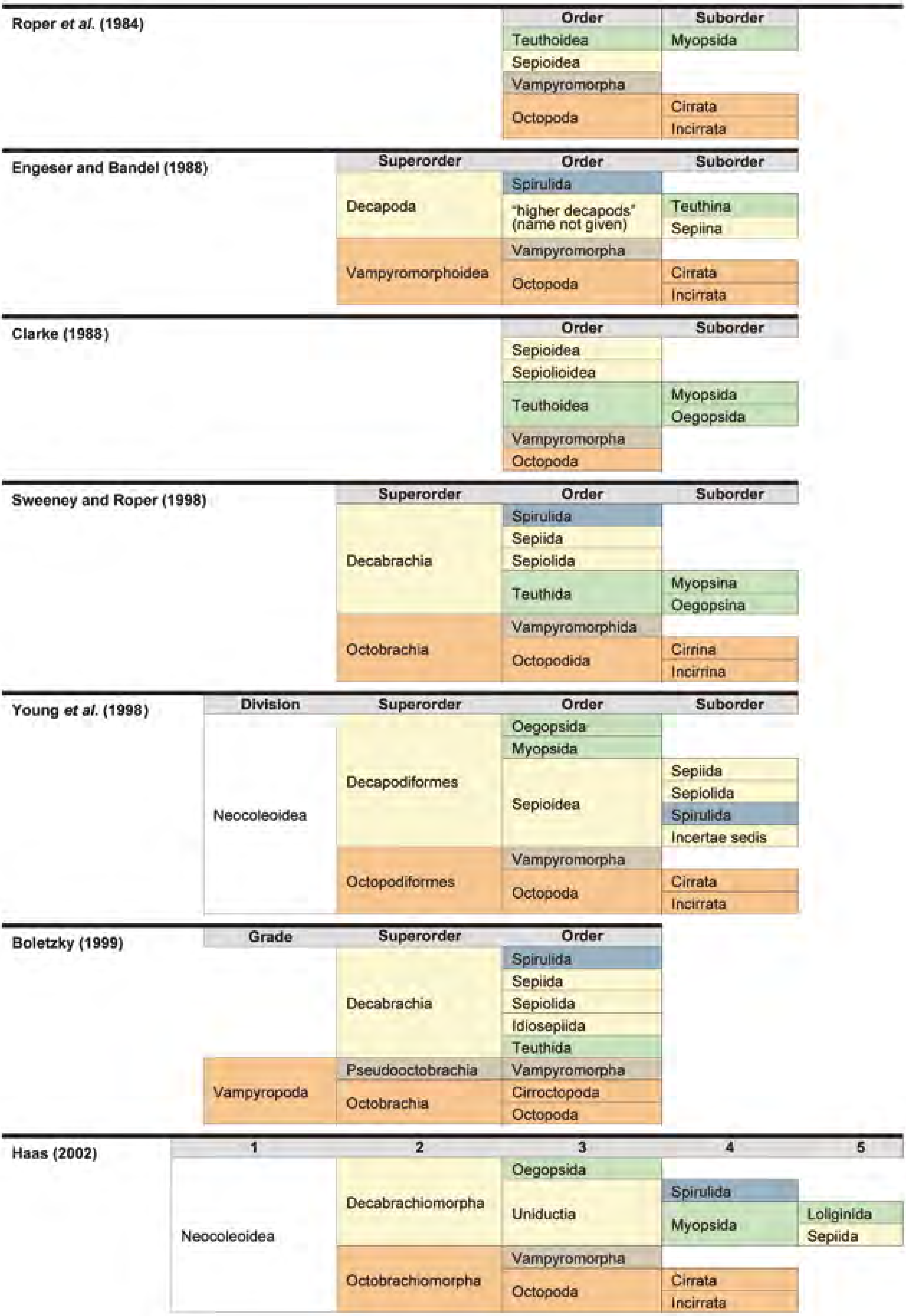
Plural versus singular usage of cephalopod common group names is standardized as follows: **squid, cuttlefish, octopod, octopus, vampire squid, nautilus** refer to one individual or one species; **squids, cuttlefishes, octopods, octopuses, vampire squids, nautiluses** refer to two or more individuals and/or species. These terms also are used to indicate the major groups.

We differentiate between the members of the family Octopodidae, which are called **octopus/octopuses**, and the members of the whole group (Incirrate and Cirrate or any combination of non-Octopodidae taxa), which are called **octopod/octopods**.

Cuttlefishes, along with Nautiluses, were treated in Volume I. Squids were treated in Volume II. This third Volume of the Catalogue is focused on octopods.

1/ Harvey *et al.* (1999) questioned the validity of the genus *Allonautilus*. However, the majority of the scientific community still considers the genus as valid (e.g. Ward, 1999; Bonnaud *et al.*, 2004; Klug *et al.*, 2004, 2007; Davis, 2005; Crook, 2008; Kruta and Landman, 2008; Turek, 2008; Young, 2010; Dunstan *et al.*, 2011).

2/ The endings used in the group names do not imply any particular level of classification.



Roper *et al.* (1984)

Order	Suborder
Teuthoidea	Myopsida
Sepioidea	
Vampyromorpha	
Octopoda	Cirrata
	Incirrata

Engeser and Bandel (1988)

Superorder	Order	Suborder
Decapoda	Spirulida	
	"higher decapods" (name not given)	Teuthina
		Sepiina
Vampyromorphoidea	Vampyromorpha	
	Octopoda	Cirrata
		Incirrata

Clarke (1988)

Order	Suborder
Sepioidea	
Sepiolioidea	
Teuthoidea	Myopsida
	Oegopsida
Vampyromorpha	
Octopoda	

Sweeney and Roper (1998)

Superorder	Order	Suborder
Decabrachia	Spirulida	
	Sepiida	
	Sepiolida	
	Teuthida	Myopsina
		Oegopsina
Octobrachia	Vampyromorphida	
	Octopodida	Cirrina
		Incirrina

Young *et al.* (1998)

Division	Superorder	Order	Suborder
Neocoleoidea	Decapodiformes	Oegopsida	
		Myopsida	
		Sepioidea	Sepiida
			Sepiolida
			Spirulida
			Incertae sedis
	Octopodiformes	Vampyromorpha	
		Octopoda	Cirrata
			Incirrata

Boletzky (1999)

Grade	Superorder	Order
	Decabrachia	Spirulida
		Sepiida
		Sepiolida
		Idiosepiida
		Teuthida
Vampyropoda	Pseudooctobrachia	Vampyromorpha
	Octobrachia	Cirroctopoda
		Octopoda

Haas (2002)

1	2	3	4	5
Neocoleoidea	Decabrachiomorpha	Oegopsida		
		Uniductia	Spirulida	
			Myopsida	Loliginida
				Sepiida
	Octobrachiomorpha	Vampyromorpha		
		Octopoda	Cirrata	
			Incirrata	

Fig. 1 Some conflicting suprafamilial classifications of living coleoid cephalopods

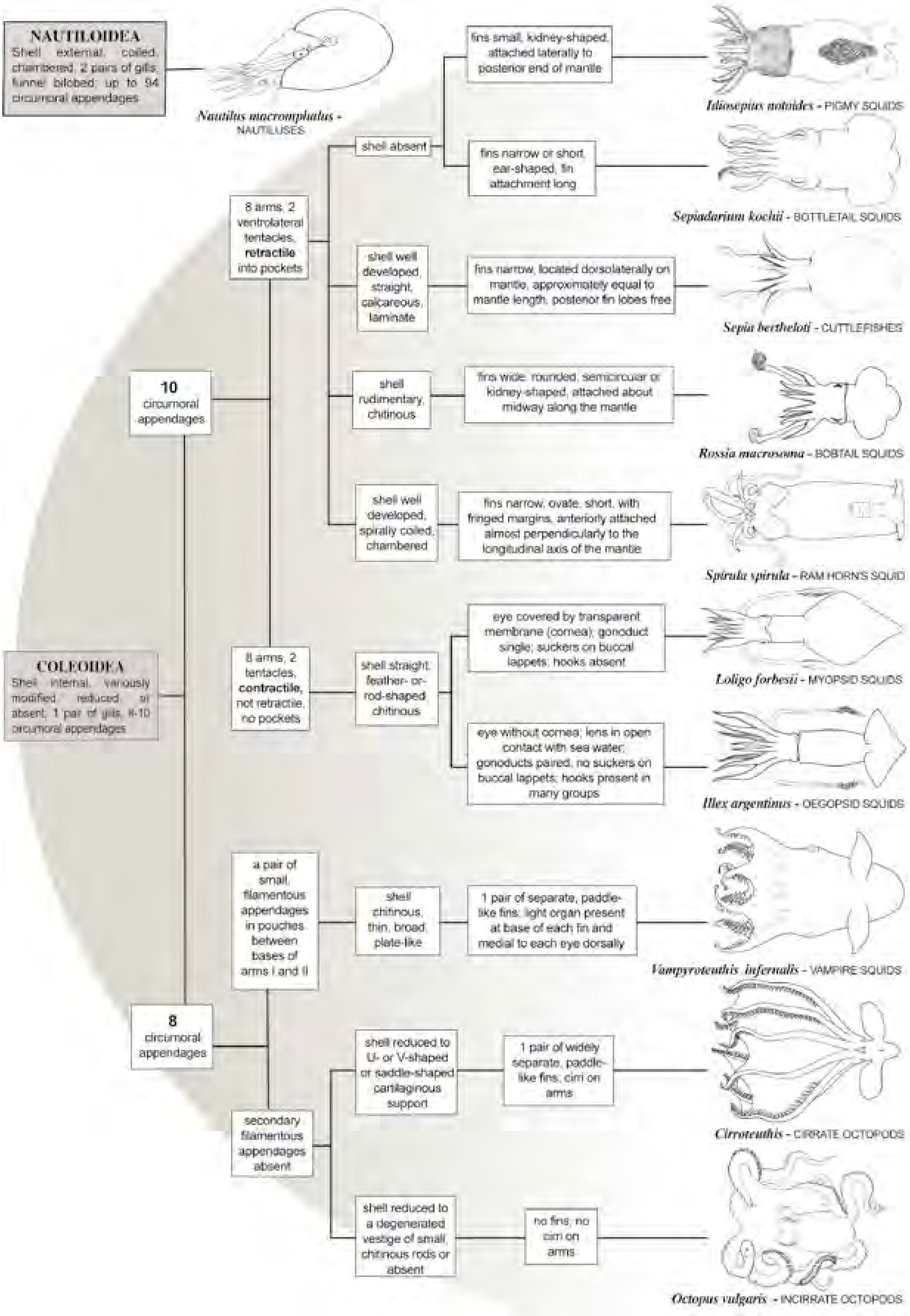


Fig. 2 Living cephalopods

1.4 GENERAL REMARKS ON OCTOPODS

by Mark D. Norman

Distribution, habitats and diversity

Octopods are exclusively marine in habit. None have colonized fresh water habitats, as this group shares the poor tolerance to low salinities found in the vast majority of cephalopods. The only potential octopod exceptions may be tolerance to high and low salinity by intertidal octopuses (such as members of the genus ***Abdopus***). Periodic high temperature evaporation versus heavy rainfall on exposed intertidal reefs and pools can cause large variation in salinity levels.

Octopods occur at all latitudes from the equator to the polar waters. They also occur over a huge depth range from intertidal habitats to at least 5 000 m deep in the deep sea. There are two major groups, the finless incirrate octopuses (including the familiar benthic octopuses) and the semi-gelatinous finned cirrate octopods (and the related vampire squid). These two groups show different distributional trends.

Incirrate octopods exist in all habitat types and at all depths from coral and rocky reefs, to seagrass meadows, sponge gardens, soft substrates, open waters and into the deep sea. By contrast, the cirrate octopods and related vampire squids are restricted to the deep sea, rarely found shallower than 600 metres, except at high latitudes.

The highest diversity of octopods occurs amongst the shallow-water benthic octopuses of the family Octopodidae, likely to total more than 300 species worldwide. Many of these lack formal scientific description. In common with many marine animal groups, the highest diversity of the octopods occurs in the tropical Indo-West Pacific region, particularly the Indo-Malayan Archipelago.

Life mode and locomotion

Octopods exhibit diverse life styles. Most species are associated with the seafloor, with further division of these benthic species into those with free-swimming planktonic juvenile stages and those with well-developed crawl-away young.

Other groups of octopods are free-swimming in the water column for their entire life cycle (*holopelagic*). Two groups, the ctenoglossans and the argonautoids, occupy the middle to upper levels of the water column (above approximately 600 m). The ctenoglossans include the families Bolitaenidae, Vitreledonellidae and Amphitretidae*, characterised by transparent soft bodies and reduced organs oriented to minimise their silhouettes from predators below in the twilight zone of the open ocean. The argonautoids include the argonauts (also known as ‘paper nautiluses’) and their relatives. These muscular animals typically reside in near-surface waters and are united by extreme sexual dimorphism (i.e. dwarf males).

In deeper waters (typically greater than 600 m), vampire squid and some cirrate octopods are holopelagic. Other cirrate octopods are associated with the ocean layer immediately above the seafloor and are capable of settling on the substrate (i.e. they are *benthopelagic*).

Locomotion of octopods varies from walking on the substrate with all limbs (or a subset, i.e. bipedal walking), jet swimming using the funnel, and/or a form of pulsating swimming consisting of rhythmic opening and closing of the arms and webs (medusoid swimming).

Cirrate octopods and vampire squids also use the fins to power (or assist) swimming locomotion (juvenile vampire squids have two pairs of fins). Swimming is aided in some groups by a gliding motion achieved by spreading the lateral arms as wings (e.g. benthic octopuses such as ***Enteroctopus***) or by full spread of the arms and webs as a disk (e.g. cirrate octopods such as ***Grimpoteuthis***).

Octopods are primarily solitary in nature. As for all cephalopods there is no parental care or association beyond hatching. Like many other cephalopods, there is a prevalence of cannibalism. Only a few octopods appear to group in large numbers (outside breeding aggregations), namely the pelagic argonauts and members of the family Bolitaenidae.

General external characteristics

There are two major forms of octopods: 1) incirrate octopods, and 2) the deep-sea cirrate octopods and vampire squids. The incirrate octopods contain the greatest number of species including the familiar, muscular, bottom-dwelling (benthic) octopuses that are popular as fisheries targets (family Octopodidae).

Most incirrate octopods are bottom dwelling and occur from intertidal habitats to the deep sea floor. This group also includes a few strange free-swimming (pelagic) octopuses of the open ocean, such as the argonauts and the Glass octopus (***Vitreledonella richardi***). Mature animals range in size from pygmy octopuses at under one gram to the Giant Pacific octopus (***Enteroctopus dofleini***) and the pelagic Seven-arm octopus (***Haliphron atlanticus***) with arm spans likely to exceed 3-4 metres.

The primary external characteristics of incirrate octopods are:
- Generally muscular, spherical bodies that lack fins;
- Skin that is typically coloured and often sculptured in regular or irregular textures, with or without larger raised papillae;
- A wide opening on the underside of the head/body into the mantle cavity, from which the tubular funnel protrudes;
- Short to long arms that bear one to two longitudinal rows of suckers;
- Typically moderate to deep web sectors between the arms;
- Suckers with wide bases and soft cup linings (never with the horny sucker ring found in squid and cuttlefish);
- Most species possess an ink sac;
- All except several transparent pelagic forms have males with a modified arm tip on one of the third arms (right arm in most species);
- A well-developed beak and radula.

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* At the time of going to press, Strugnell *et al.* (2013) published a major revision of the familial level classification of the incirrate octopods. They establish six families: Octopodidae, Bathypolypodidae, Eledonidae, Enteroctopodidae, Megaleledonidae and Amphitretidae, the latter containing three subfamilies Amphitretinae, Bolitaeninae and Vitreledonellinae (see that work for new taxonomic structure).

By contrast the cirrate octopods and vampire squids are exclusively residents of the deep sea. They are soft, semi-gelatinous animals that are rarely encountered. None are commercially harvested. Mature animals range in size from around 10 cm to at least two metres in total length. The primary external characteristics of cirrate octopods and vampire squids are:

- Body and arms semi-gelatinous;
- Body bears a pair of round to elongate fins (two pairs in juvenile vampire squids), supported under the skin by a cartilaginous support (shell);
- Skin is typically uniform in colour (white to dark red-brown), lacking any skin sculpture;
- A narrow opening on the underside of the head/body into the mantle cavity, tightly fitting around the protruding tubular funnel;
- Short to long arms that bear a single longitudinal row of suckers between two longitudinal rows of thin digits of skin (cirri);
- Vampire squids possess a pair of long, thin, sensory filaments, which can retract into pits in the web between the bases of arms 1 and 2;
- Typically possess deep and thin web sectors between the arms, as a double inflatable layer in some groups;
- Small suckers embedded within the flesh with small soft-lined cups (never with the horny sucker ring found in squid and cuttlefish). Mature males of some groups possess enlarged suckers in their single sucker row;
- All species lack an ink sac;
- No male arm tip modifications as found in incirrate octopods;
- A well-developed beak;
- Radula present, reduced or absent, depending on the group.

Nervous and sensory systems

Cephalopods in general, and octopods in particular, are renowned for their well-developed brain and nervous system. The brain of octopods (and cephalopods) has a unique floor plan, having evolved as a neural ring around the oesophagus. The majority of the octopod brain consists of the optic lobes. For example, the brain of ***Octopus vulgaris*** contains around 130 million nerves in the optic lobes and only 40 million for all the other portions of the brain. The paired optic lobes are primarily concerned with vision, regulating visual behaviour and learning, storing visual memory and controlling skin displays.

Almost all octopods have well-developed eyes and excellent vision. The eye typically contains a two-part lens consisting of two half spheres. Evidence from retinal structure and behavioural experiments indicates that octopods (and all cephalopods) are colour blind – their colour change abilities are responding to tonal differences rather than colour wavelengths. Species have also been demonstrated as discriminating the plane of polarization of polarized light, proposed as aiding detection of prey or predators in sunlit surface waters.

Eye form becomes more diverse in deep-water octopods. The deep-sea cirrate octopod, ***Cirrothauma murrayi***, is unique amongst all cephalopods, as its eyes are simple open cups that lack lens or iris. It is unlikely to be able to form a focused image. As the name suggests, the telescope octopus (***Amphitretus pelagicus***) has vertically-oriented, tubular eyes used to search the waters above for the silhouettes of its prey in the twilight zone between around 200-800 metres.

The skin of octopods

Octopods are most famous for the complex skin in many species and their capacities for rapid pattern and texture changes. The skin contains two main components that carry out these changes: chromatic and sculptural.

The chromatic components produce the colour of the skin and are under direct neural control. There are three classes of organs within the skin that produce and change colour: 1) chromatophores, 2) iridocytes and reflector cells, and 3) leucophores. In a general sense these can be considered as the colour pixels, the reflective cells and the white markings (respectively).

Chromatophores are like small elastic balloons of coloured pigment surrounded by the spokes of radial muscles. The balloon is stretched by contraction of the radial muscles so that the colour is displayed as a circular or polygonal spot. When the muscles relax, the elastic balloons contract to a tiny dot so that the colour is not visible. This is how the coloured dots can be turned on and off, much like the colour pixels in a television screen. Chromatophores come in different colours, grading through yellow to orange, red, dark brown and black. They can be less than 0.3 mm across and can occur in very high densities, resulting in high-resolution body patterns.

Iridocytes and reflector cells cause the iridescent sheen in the skin of many octopods, especially around the eyes. These structures selectively reflect and refract light, causing green, blue or violet shades. Some species concentrate these iridescent structures in rings within false-eye spots (i.e. some ocellate members of the genus ***Amphioctopus*** and all species of the blue-ringed octopuses, genus ***Hapalochlaena***).

Leucophores wholly reflect white light, forming the high contrast white markings found in many well-camouflaged benthic octopuses, e.g. the transverse pair of bright white spots on the dorsal mantle.

The sculptural components of the skin can include large individual papillae of skin (particularly over the eyes), overall textures of regular/irregular rounded warts or patches (patch and groove system), and longitudinal flaps or ridges. Some benthic octopuses, particularly those from soft sediment substrates, also may possess a longitudinal raised ridge around the lateral and posterior mantle (the lateral mantle ridge).

Used in combination, these skin components can produce dynamic and complex visual displays. When coupled with appropriate postures and motion, complex camouflage and even mimicry can be effected.

Circulatory system

The blood of cephalopods contains the respiratory pigment haemocyanin, a copper-based pigment that causes the blood to be blue to green in colour. This pigment is less efficient at capturing and transporting oxygen compared with human iron-based respiratory pigment, haemoglobin, and as such requires higher blood pressures and flow rates to maintain the high metabolic rate of active predators. The circulatory system is made up of three hearts, a central systemic heart and paired branchial (gill) hearts, one above each gill. The gills consist of multiple fleshy plates (8-30 per gill), each plate is known as a *gill lamella*. Besides the gills, there is some evidence that oxygen also can be directly absorbed through the skin.

Digestive and excretory systems

Beginning from the mouth, the primary components of the digestive system of octopuses (Fig.15) are the buccal mass (a muscular ball containing the two beak halves and the toothed radula), one or two pairs of salivary glands, an oesophagus, a crop (with or without a side-branch diverticulum), a muscular stomach, a coiled caecum joined by paired ducts into a large digestive gland (the vertebrate liver equivalent in cephalopods), and an intestine culminating in the anus. An ink sac, if present, is typically embedded in the ventral surface of the digestive gland and connected to the intestine (or at the level of the anus) via the ink duct. Many species, particularly those with an ink sac, possess a pair of small paddle-shaped appendages on each side of the anus, known as *anal flaps*. The well-developed beak and toothed tongue (*radula*) of all cephalopods may have evolved as a consequence of the oesophagus passing through the centre of the donut-shaped brain. This configuration probably requires prey to be macerated into a semi-liquid state in order to pass through the centre of the brain. Thus octopods (and cephalopods in general) are not able to swallow whole, large prey, compared to most fishes, birds and mammals. This has direct consequences for studies of cephalopod diets as stomach contents are macerated in comparison to many fishes.

Cephalopods have a protein-based metabolism - there is no lipid digestion or storage. Muscles can act as an energy store, with females of some squid species digesting so much of their own musculature as they approach spawning that their bodies literally start falling apart. The primary by-product of protein consumption in these carnivores is ammonia, which is excreted via two organ types. The first is the paired renal appendages, enclosed within membranes to form the renal sacs. These spongy tissues release ammonia directly from the blood and also are home to a unique phylum of highly specialized parasites – the dicyemids. Waste ammonia is then released through the paired renal pores. Octopus studies also have found that additional ammonia is excreted directly through the gill membranes.

Reproduction

The reproductive strategy of most octopods consists of males using a modified arm, or in a few groups the terminal organ of the male reproductive tract (penis), to pass encapsulated packages of sperm (spermatophores) to females. Processes prior to and after copulation vary between the major groups.

For benthic incirrate octopuses (family Octopodidae), the third arm (*hectocotylus*) of mature males (typically on the right hand side) is modified (Fig. 13) with a curled groove along the length of the arm on the ventral edge (the *spermatophore groove*), leading to a triangular to spoon-shaped tip (*ligula*) with a small triangular process at the base of a central groove (the *calamus*). During mating, males either mount the mantle of the female or simply place the tip of the extended hectocotylized arm into the female's oviduct opening within the gill (mantle) cavity.

Egg fertilization occurs within the oviducts, oviducal glands or ovary (depending on the species) and then the female lays eggs singly or in strings (festoons). Eggs are typically attached to substrate or shells, or are carried in the web in some species (e.g. blue-ringed octopuses). All incirrate octopods are egg brooders, with the females tending, cleaning, jetting and protecting the eggs until they hatch.

Pelagic incirrate octopods vary their strategy from brooding within the arm crown and webs, to carrying the eggs within a shell (genus ***Argonauta***), to ovovivipary where brooding and hatching occurs from within elongate oviducts (genus ***Ocythoe***).

The vast majority of incirrate octopods appear to be semelparous - having a single egg-producing event and dying around the time of egg hatching. One of the possible exceptions is the pelagic argonautoids where egg spawning may be a prolonged process (see treatment for Family Argonautidae).

In stark contrast, the deep-sea finned cirrate octopods and vampire squids lack arm tip modifications in the males, instead they appear to pass small barrel-shaped spermatophores directly to the female using the terminal organ of the male tract (penis). Females deposit their eggs directly on the seafloor and also may produce eggs over a prolonged period.

The mature males of many octopods (both groups) may possess distinctly enlarged suckers on the arms. In benthic incirrate octopods, these suckers are thought to be visual cues to females of a male's reproductive viability. The function in deep-sea cirrate octopods remains unknown but may be a tactile equivalent.

Growth and life history

As for most cephalopods, the majority of octopods probably are fast growing and relatively short-lived. Some polar species are estimated to live for at least 6 years, but lifespan for most warmer-water species is probably only 1 to 2 years. Longevity of deep-sea cirrates and vampire squids is less well known.

At hatching, octopods tend to take one of two developmental paths: either by direct development (taking on the habit and behaviours of the adult) or via a free-swimming planktonic stage (termed *paralarva*). For benthic incirrate octopods egg size relative to mantle length can be an indicator of hatchling form. Species with eggs less than 10% of mantle length tend to have planktonic paralarvae while species with eggs greater than 12% of mantle length tend to be well-developed, benthic, crawl-away young. There is no post-hatching parental care in octopods. All hatchlings fend for themselves from hatching.

Diet and feeding behaviour

Like all cephalopods, octopods are carnivores, preying on diverse prey but particularly on crustaceans, fishes and shelled molluscs. Prey are gripped by the suckers and may be seized directly, enveloped in ensnaring webs, extracted from burrows or crevices by single arms, or flushed from the sand using the arm tips.

The radula and salivary toxins play a large role in prey immobilisation and manipulation. Active prey such as crabs and fishes are rapidly immobilized and partially digested by a combination of salivary neurotoxins and digestive enzymes. Commercially harvested lobsters that have been bitten by octopuses have semi-liquified flesh, so they have no sale value. With shelled mollusc prey, many benthic octopuses may prise shells apart or use a combination of the toothed salivary papillae adjacent to the radula and salivary chemicals to drill and dissolve through shells to paralyse the occupant and gain access. Some octopuses also use this technique to extract hermit crabs from their gastropod shell homes.

Defensive behaviours

The primary defense of most octopods is concealment or crypsis. Many benthic incirrate octopods have excellent camouflage capacities, matching both tonal and textural components of their backgrounds. In a few species, mimicry of distinct models (e.g. poisonous animals) also has been reported.

Benthic octopods often construct dens or occupy cave lairs. These refuges can be supplemented by barricading the entrances with rock, coral or shells. Some species on soft substrates, such as ***Amphioctopus marginatus***, will carry coconut or bivalve shells as portable shelter to be assembled as required. Other species bury directly into the substrate.

Once disturbed or attacked, many species release ink either as a congealed decoy or a diffuse smoke screen. Many long-arm benthic octopuses also are able to sever an arm at a basal weak point, leaving a wriggling decoy for attackers. This is known as *arm autotomy* and the stump of the severed arm will regenerate a replacement arm within weeks to months.

The blue-ringed octopuses (genus ***Hapalochlaena***) use the powerful neurotoxin, tetrodotoxin, for both prey immobilisation and as defence against their attackers. They advertise this toxicity using brilliant iridescent blue rings and/or lines distributed across their body.

Classification and taxonomic status

The largest group of octopods is the benthic octopuses of the family Octopodidae*, containing over 300 species. The taxonomy and classification of this group are undergoing considerable revision and many new species (>150) await formal scientific description, particularly in the tropical Indo-West Pacific. The higher-level classification (family level and above) and knowledge of the evolutionary history of these animals currently are under review*, aided by recent developments in molecular phylogeny and analysis tools.

Concluding remarks

The octopods are a very large and important group in marine environments, playing significant roles as top-level predators in all ecosystems. Many species have a very high fisheries profile and value, worth more than $US1.5 billion in annual trade. Overall, the group is poorly studied, particularly away from the primary research centres of the US, Europe and east Asia. The group requires considerable further research, particularly into diversity, roles in ecosystems, reproductive biology, fisheries impacts and management, and conservation status (see Fisheries chapter below).

1.5 WORLD OCTOPOD FISHERIES

by Mark D. Norman and Julian K. Finn

Octopus fishery techniques

Benthic octopuses of the family Octopodidae are harvested throughout the world, being highly valued both for human consumption and, to a lesser degree, as bait (Boyle and Rodhouse, 2004). Diverse techniques are used to capture octopuses, ranging from small-scale subsistence and artisanal harvests to large-scale commercial fisheries. The primary techniques employed are: (1) direct capture by hand, hook, or spear; (2) line capture (using lures and/or baits); (3) use of weighted pots (baitless or baited); and (4) use of nets, including trawls (e.g. otter, seine, beam), cast, and static nets (e.g. fyke). In many regions of the world, hand, line, and cast net capture can include the use of lights at night to harvest nocturnally active species. A number of papers have summarized octopus harvest techniques (e.g. Pennington, 1979; Voss, 1985; Rathjen and Voss, 1987; Paust, 1988; Rathjen, 1992; Guerra, 1997; Lang and Hochberg, 1997; Roper, 1997; Gillespie *et al.*, 1998).

Octopus harvests occur across diverse environments - from exposed intertidal habitats (e.g. ***Octopus cyanea*** collection from coral reef flats throughout the tropical Indo-West Pacific region), to continental shelf (e.g. trawl harvests of ***O. vulgaris*** off northwest Africa and ***Amphioctopus*** species from the Gulf of Thailand) and from the continental slope (e.g. ***Enteroctopus dofleini*** trawling off northern Japan).

In the last decade, a number of aquaculture trials for octopuses have been undertaken (e.g. ***Octopus vulgaris*** in Spain, see Vae-Pires *et al.,* 2004; ***Enteroctopus megalocyathus*** in Chile, see Pérez, 2006; ***O. maya***

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* At the time of going to press, Strugnell *et al.* (2013) published a major revision of the familial level classification of the incirrate octopods. They establish six families: Octopodidae, Bathypolypodidae, Eledonidae, Enteroctopodidae, Megaleledonidae and Amphitretidae, the latter containing three subfamilies Amphitretinae, Bolitaeninae and Vitreledonellinae (see that work for new taxonomic structure).

in Mexico, FIS, 2009; and up to eight species in China, Liao *et al.*, 2006, Lv *et al.,* 2007, Cai *et al.,* 2009), although none have reached commercial operation. The biggest challenges for octopus aquaculture are high mortality rates where stocking densities are high (including the prevalence of cannibalism), requirement for low cost and high quality feed, and raising the earliest life stages (particularly for species with planktonic young).

Octopus ongrowing, where wild caught small animals are fed in captivity to attain profitable sizes, has been investigated for ***Octopus vulgaris*** (e.g. Rodriguez *et al.,* 2006; Pham and Isidro, 2009). As with full life cycle aquaculture, the issues of high mortality rates at higher stocking densities, along with cost and quality of feed, are challenges for the economic viability of this practice.

Parasites of octopods are reviewed by Hochberg (1983, 1989).

Global catch statistics

Octopuses form the basis of major and valuable fisheries throughout the world. The most recent global catch statistics for octopuses placed the 2010 total world octopus production (catch and culture of all species) as exceeding 350 710 tonnes (FAO, 2011). In 2009, world exports of this catch was valued at $US1.07 billion dollars, while import value was $US1.33 billion (FAO, 2011). The scale and value of this catch exceeds that of many valuable finfish fisheries. Despite this high value and profile, little synthesis of the composition and nature of the world octopus harvests has been made to date.

Commodity data for 2009 places export value at an average of $US4.48 per kilogram and import value at an average of $US4.38 per kilogram (FAO, 2011). In many regions of the world octopuses are more valuable per kilogram than many valued finfishes. In 2009, octopus commodity values per kilogram significantly exceeded those of the FAO commodities finfish category “tuna, bonito, billfish” (import $US3.19/kg, export $US3.02/kg, FAO, 2011).

Figure 3 presents the total reported global production of octopuses over the past three decades, indicating a relatively steady increase in catch, almost doubling from 179 042 tonnes in 1980 to 350 710 tonnes in 2010 (FAO, 2011). Economic value for this world octopus catch (using export sales as an indicator, Fig. 4) has increased almost sixfold over this timeframe, rising from $US231 million in 1980 to $US1.33 billion in 2009 (FAO, 2011). The trend in global octopus catch presented in Fig. 3 suggests a gradual rise in catch, potentially stabilising over the past seven years. This trend suggests sustained catches. However, a number of inherent attributes of the data that underpin this trend may be masking real trends in global production.

Production data attributes

Available summary statistics for world octopus harvests come from two sources: (1) production estimates provided by nation states to 2010 (‘Global Production’, FAO, 2011); and (2) estimates based on fishery commodities data to 2009 (i.e. export and import data, ‘Fisheries Commodities and Trade’, FAO, 2011). For many fisheries, these data sources can differ significantly from each other. Major issues associated with this data include poor species taxonomy, poor catch resolution, the failure of many regions of the world to collect (or provide) any cephalopod catch statistics, the lumping of octopus catch under the broader generic categories of ‘cephalopod’ or ‘squid, etc.’, and various failures to include subsistence/artisanal harvests, domestic consumption of commercial catches, bycatch, and/or harvests of octopuses used for bait. Three issues are discussed individually below.

Poor taxonomy

The single largest impediment to accurate catch statistics is the historically poor state of octopus taxonomy and the limited identification tools available. As a result there is little or no discrimination of catch composition for all but a handful of octopus harvests worldwide. Little is known of the biology, ecology, distributions and stocks of the vast majority of harvested species. Norman and Hochberg (2005a) estimated that there are likely to be more than 300 species of benthic octopuses in the world, many of them lacking formal description. Of these, we estimate that more than 100 species are likely to be taken in human harvests, yet global summary statistics list only four species: common octopus (***Octopus vulgaris***), Mexican four-eyed octopus (***O. maya***), horned octopus (***Eledone cirrhosa***) and musky octopus (***E. moschata***). The remaining species, at most, are treated as ‘unidentified octopus’.

Unreported catches

Many countries with octopus fisheries provide no specific catch statistics. Few countries from the northern and western Indian Ocean (including the Red Sea) report any cephalopod (and thus octopus) catch, for example, the Islamic Republic of Iran and Iraq. Other nation states such as India, Pakistan, Somalia, and Madagascar include octopuses within general cephalopod categories, preventing specific estimations of octopus catch.

The majority of island nations of the tropical Pacific Ocean harvest octopuses in subsistence and/or small-scale commercial fisheries (mainly ***Octopus cyanea*** and members of the genus ***Callistoctopus***), yet few report catch statistics. For half the tropical Pacific Ocean (FAO area 77: central and eastern Pacific), only the Cook Islands and Mexico provided octopus catch statistics (FAO, 2011), while other island groups known to harvest octopuses provide no statistics (e.g. Hawaii, Tonga and the Society Islands). Other notable absences from broader Pacific Ocean octopus catch statistics include Papua New Guinea, Vanuatu, and New Caledonia. The combined harvest of the many island nations around the tropical Pacific and Indian Oceans could prove to be very high.

Catch underestimates

Throughout the world, reported statistics of octopus catch also fail to include the majority of subsistence and artisanal harvests. These catches are very difficult to monitor due to their dispersed and small-scale nature, localized consumption, and rapid sale through small local markets. For many countries with limited fishery management resources, the result is that such catches go unreported. In addition, the octopus catch statistics provided by many nation states appear to be based primarily on estimates from export data. Export data often are equivalent to, or even larger than, total production estimates. Such rough estimates of octopus production exclude domestic consumption, which for some countries is extremely significant.

Bycatch of octopuses by fisheries that target other species, particularly trawl, line and pot fisheries, also are largely unreported. One study in Western Australia estimated that more than 250 tonnes of octopus were caught each year as bycatch in the Western Australian rock lobster pot fishery alone, all of which were killed and discarded or used as bait (Joll, 1977). This non-target byproduct of a single fishery is not reported and constitutes almost half the reported harvest of all octopuses for all of Australia in 2010 (548 tonnes, FAO, 2011).

As a result of these inherent attributes and problems, global catch data for octopuses should be considered a very rough estimate of total harvest, and likely to be a considerable underestimate. Watson and Pauly (2001) highlighted the inherent difficulties in amassing and interpreting global catch statistics, stating that "(the) FAO must generally rely on the statistics provided by member countries, even if it is doubtful that these correspond to reality" (p. 534). These authors suggest that inaccuracies and underestimates can cause globally spurious trends that "influence unwise investment decisions by firms in the fishing sector and by banks, and prevent the effective management of international fisheries" (p. 534). We agree that statistics such as the available global octopus production data should be used and interpreted with caution.

World catch composition

The aim of this volume is to review the octopus species of highest fisheries value, profile or potential, and to present representatives of all world octopus genera for comparison/discrimination. The previous scarcity of information on taxonomy and biogeography has severely impeded species identification for many regions, particularly the Indo-West Pacific region, where octopus diversity is highest (Norman and Hochberg, 2005a).

Catch statistics reported by FAO currently are listed under just four octopus species names (***Octopus vulgaris***, ***O. maya***, ***Eledone cirrhosa***, and ***E. moschata***), the remainder being classified as unidentified octopuses. While the "Common octopus", ***Octopus vulgaris***, and closely related taxa (see ***O. vulgaris*** species treatment below) are high-value, targeted species in a number of regions of the world, a much larger number of species is harvested throughout the world, particularly throughout Asia and the western Pacific Ocean. Table 1 presents a preliminary list of more than 50 octopus species collected in small-scale to large-scale harvests around the world. Catch varies significantly by region and may target single species or consist of multi-species catches (targeted or incidental).

Major producers and consumers

Producers

Asia reported the highest octopus production for 2010, at 217 506 tonnes, primarily as unidentified octopus species. This catch is highly diverse and consists of a large number of species. In tropical and subtropical regions of Asia, the most common species harvested are members of the genera ***Amphioctopus***, ***Callistoctopus***, and ***Cistopus***, along with members of the '***Octopus***' ***minor*** group. In cooler latitudes (e.g. Japan), the catch shifts to the northern Pacific ***Octopus vulgaris*** (see ***O. vulgaris*** species treatment), ***Enteroctopus dofleini***, '***O.***' ***conispadiceus***, and members of the '***Octopus' minor*** group. The seven largest reported producers of octopuses in Asia in 2010 were China (125 776 t), Japan (41 700 t), the Republic of Korea (20 759 t), Indonesia (10 860 t), Thailand (10 315 t), Philippines (5 506 t), and Malaysia (1 936 t).

Octopus production from Africa for 2010 was reported as 57 982 tonnes, the vast majority of which is the octopus harvest from off the northwest coast of Africa (for ***Octopus vulgaris*** with a small proportion of ***Amphioctopus burryi***). Four countries take the majority of this harvest (Morocco, 32 006 t), Mauritania (15 801 t), Tunisia (3 764 t) and Senegal (3 317 t).

European production of octopuses for 2010 was 42 945 tonnes, which is primarily ***Octopus vulgaris***, with some ***Eledone cirrhosa*** and ***E. moschata***, from the western and central Mediterranean Sea and the Atlantic coasts of Spain and Portugal. The five largest producers are Spain (16 470 t), Portugal (10 934 t), Italy (9 884 t), Greece (2 676 t), and France (1 744 t).

The reported octopus catch from the Americas for 2010 was 31 546 tonnes, which is primarily of ***Octopus vulgaris*** and related species ***O. maya***, ***O. mimus***, and ***O. insularis***. The largest American producers are Mexico (***O. vulgaris*** 15 325 t, ***O. maya*** 5 713 t), Brazil (2 069 t), Chile (1 895 t), Venezuela (1 420 t) and Peru (1 030 t).

Importers and exporters

Based on commodities data, a total of 303 428 tonnes of octopuses were reported as being imported globally in 2009, worth $US1.33 billion (FAO, 2011). The two biggest importing regions were Europe (import value $US716 million) and Asia ($US538 million). For the same year, global octopus exports were reported as 239 314 tonnes, worth $US1.07 billion. The largest exporters by region were Asia (exports worth $US417 million), Africa ($US358 million) and Europe ($US247 million). The 20% discrepancy between global import and export figures is further evidence of the inaccuracies in current octopus catch estimates worldwide.

Octopuses as sustainable fishery targets

Many cephalopod species, including octopuses, may be better suited as targets for fisheries exploitation than finfishes and other harvested marine groups. Their fast growth rates, high escapement (through speed and/or cryptic behaviour) and high fecundity (for small-egg species) have led to them being considered 'weed-like' species that are able to: (1) recover quickly from disturbance or overfishing; (2) occupy niches vacated by overexploited finfish stocks; and/or (3) flourish under 'predator release', where natural predators have been removed by fisheries (Caddy and Rodhouse, 1998; Chotiyaputta *et al.*, 2002; Rigby and Sakurai, 2005). Some studies have suggested that the behavioural flexibility of octopuses may enable further resilience to fishing pressures. For example, Rigby and Sakurai (2005) found that ***Enteroctopus dofleini*** in northern Japan reduced normal home ranges to target and feed on finfishes captured in gill nets.

Octopus fisheries also are promoted as ecologically sustainable due to the low-impact fishing techniques that can be used for harvests, such as the use of baited or unbaited pots. Baeta *et al.* (2005) found baited octopus pots were the most sustainable fishery of seven estuary fisheries in the Tagus region of Portugal. Unbaited pots are considered even more sustainable as they collect no bycatch and cause negligible environmental disturbance. Due to such perceptions, octopuses historically rated higher on seafood sustainability indices than other marine seafood resources. However, more recent concerns about overfishing and the environmental impacts of trawl harvests have lowered the rating of octopuses with some conservation agencies (e.g. SeaChoice, Canada; Seafood Watch, Monterey Bay Aquarium; Environmental Defence Fund, USA).

Increasingly environmental impacts and sustainability issues such as "food miles" are being considered in seafood harvests. Vasquez-Rowe *et al.* (2011) assessed the environmental impact of ***Octopus vulgaris*** captured in Mauritanian waters and exported frozen to Japan, finding discard and seafloor impacts as high during capture, while associated energy use post-harvest was low, due to the slow maritime transport of the frozen product to Japan.

For most harvested octopus species, the perception of octopuses as sustainable fishery targets is not backed up by detailed knowledge of the biology, ecology, distributions, stock assessments, and/or impacts of fisheries on stocks or reproductive cycles.

Interpreting catch trends

The relatively stable total catch trend in world octopus fisheries as presented in Figure 3 appears to run contrary to that of finfish catch trends worldwide over the same time period (e.g. total finfish catch, Fig. 5; shark and ray catch, Fig. 6). However, reported world octopus captures over recent years contain data attributes that may be clouding real trends in global harvest.

Recent contribution of catch statistics from China

The single largest impact on global octopus catch statistics has been the relatively recent inclusion of fishery statistics from China (see Fig. 7 for total Southeast Asian and Japanese production). Prior to 1987, China reported no octopus production figures to the Food and Agriculture Organisation. Over the 16 years between 1987 and 2003, Chinese octopus production figures reported to FAO consisted solely of catch from the west coast of Africa (***Octopus vulgaris***) and did not exceed 7 500 tonnes in any one year. Between 2003 and 2007, reported production jumped to around 100 000 to 140 000 tonnes and primarily represents catch in the western central Pacific Ocean. It is not considered here that the Chinese catch rapidly increased 20 fold in one year, but, rather, that FAO requests for global fisheries data around this time led to submission of Chinese octopus production data to these global statistics. Due to the high profile and value of octopuses in China, harvests in this country very likely are to have been at high levels for a considerable time. If Chinese catch data are considered (Fig. 8), the global trend appears less sustained and suggests that global octopus catch (as reported) may have peaked in 1999 (when excluding Chinese data) at around 350 000 tonnes.

Regional catch trends

When catch trends are examined on a regional scale, it is evident that the majority of octopus fisheries as reported are now in decline. By region, it is clear that catches have peaked for many octopus fisheries. Comparisons of the most recent production data with historical peaks show distinct declines (FAO, 2011):

- Africa: 57 982 t (2010), peak: 140 476 t (1999).
- Europe: 42 945 t (2010), peak: 107 902 t (1983).
- Americas: 25 833 t (2010), peak: 37 505 t (1996).
- Oceania: 731 t (2010), peak 1990: 3 161 t (1990)*
  (* 1995 record of 11 547 t from New Zeland is an error, New Zeland Ministry of Fisheries, pers. comm.).

The only region to have the highest octopus harvest within the past decade is Asia, where the 2007 production was the highest at 247 196 tonnes (two-thirds of the global catch), with a 2010 production of 217 506 tonnes. As discussed above, the relatively recent inclusions of data from China (i.e. 100 000+ tonnes per annum since 2003) means that the scale of harvests through unreported years remain unknown.(Fig. 7).

Specific fishery examples

If two specific fisheries are examined in more detail, the same post-peak trends emerge. To date, the largest octopus fishery for a single species in the world has been the ***Octopus vulgaris*** fishery off northwest Africa, harvested primarily by Senegal, Mauritania and Morocco. Historically, the Republic of Korea and the Democratic People's Republic of Korea, the Russian Federation and two Central American nations, Honduras and St. Vincent, also targeted what has been identified as this species up until the early 1990's. Figure 9 shows the total catch data by all nations for this fishery, demonstrating peaks of 112 461 tonnes and 137 722 tonnes in 1991 and 1999 respectively, compared with around 49 259 tonnes in 2010 (FAO, 2011). Studies by individual nations support this trend. Sato and Hatanaka (1983) assessed Japanese 'distant-water' exploitation of this fishery and diagnosed the stock as over-exploited. Gascuel *et al.* (2007) reported declines of ***O. vulgaris*** harvests from Mauritania from 70 000 to 15 000 tonnes between 1982 and

2006. Using commodity data, Yagi *et al.* (2009) plotted four stages of resource exploitation for ***O. vulgaris*** in Morocco: (1) the underexploited stage from 1970 to 1987 of small catch and low prices; (2) the maximum sustainable yield stage from 1988 to 1998 of moderate catch and intermediate prices; (3) the overexploited stage from 1999 to 2001 of large catch and intermediate prices; and (4) the reduced stock stage after 2002 of small catch and high prices.

The second example is the trawl harvests of members of the genera ***Amphioctopus*** and ***Cistopus*** by Thailand from the Gulf of Thailand that have supplied markets worldwide with frozen octopus for decades, members of the first genus being marketed as 'baby octopus'. Figure 10 represents this regional catch, similarly showing a peak harvest of around 32 000 tonnes in 1998 versus 10 315 tonnes reported in 2010 (FAO, 2011). Chotiyaputta *et al.* (2002) reported that these octopus stocks have been fully exploited since 1989.

Catch per unit effort data

Reported catch trends also should be considered both in relation to increasing fishing effort globally and effort shift to cephalopod harvests from other fisheries (e.g. finfishes). Although some catch-per-unit-effort data (CPUE) have been collected for selected species (see individual species treatments), there have been few long-term or large-scale studies of CPUE for octopus fisheries.

Octopus fisheries management

For most octopus harvests worldwide, there is little or no direct fisheries management. For those fisheries that are managed, measures can include seasonal closures, area closures, size and catch limits, effort restrictions, and/or gear restrictions. For example, since 2001, Spain has instigated a range of management measures for the ***Octopus vulgaris*** fishery off Asturias (NW Spain), including establishment of a closed season, minimum capture weight of 1 000 grams and the restriction of permitted fishing gear to baitless traps (Fernandez-Rueda, 2007). The Republic of Korea established gear limits on its octopus trap fishery (Kim, 2008), establishing maximum fishing gear usage per fishery type and proposing a vessel buyback program in order to maximise fishery viability and profit. Increasingly, different sectors of fisheries (e.g. artisanal versus industrial fleet) can compete for the same valued octopus resource, requiring management intervention (e.g. for ***O. vulgaris*** in Morocco; Faraj and Bez, 2007, Veguilla, 2009).

In order to achieve sustainable management of octopus fisheries, it is crucial that biological attributes of target species are considered. Two factors in particular are critical: reproductive output (recruitment) and breeding behaviour.

Egg size and recruitment

Benthic octopus species are relatively fixed in possessing one of two broad life history strategies (Boletzky, 1977): (1) production of numerous small eggs (<10% of mantle length) that hatch into abundant planktonic hatchlings; or (2) production of few large eggs (>10% of mantle length) that hatch as less abundant benthic 'crawl-way' young. As a consequence, fisheries that target large-egg species have much lower recruitment potential than for small-egg species with their abundant planktonic young (i.e. production of hundreds to thousands of offspring per female versus 10 000's to millions of offspring per female). Regional depletions are much more likely for fisheries targeting large-egg octopus species, which should be managed on much smaller scales than small-egg species (see Narvarte, 2006 for ***'Octopus' tehuelchus*** in Argentina; Leporati *et al.,* 2009 for ***'O.' pallidus*** in Australia).

Breeding behaviour

Breeding behaviour also must be taken into account as harvest techniques often inappropriately target breeding stocks. Octopus pot harvests typically target octopus species of soft-sediment substrates, as the pots provide rigid refuge from predators and are used by both sexes and all growth stages. However, mature females also use pots as a substrate/refuge in which to lay and brood their eggs, leading to this harvest technique depleting the reproductive output of populations (particularly for low fecundity, large-egg species, Leporati *et al.,* 2009). As females reduce or cease feeding at the commencement of egg brooding, fisheries that target feeding animals, by contrast, may catch fewer breeding females.

For some fisheries, the problems of overexploitation, low fecundity (e.g. large-egg species) and the targeting of breeding aggregations have merged. For example, the harvest of an undescribed large-egg octopus species from the ***'Octopus' minor*** group on the Peng-hu Islands of Taiwan peaked in the mid-2000's when high demand by the live-octopus restaurant trade resulted in sale prices of up to $US80 per kilogram (C.C. Lu, pers. comm.). This species aggregates to spawn on shallow coral reef flats in February each year, where it is targeted at night by long lines of walking fishers using headlamps and gaffs to hook active octopuses. In 2005, dramatic catch declines led to implementation of a one-month seasonal closure each year to protect spawning females.

It is critical for all octopus fisheries (current, developing, and potential) to both understand the biological attributes of the target species and to take these attributes into account in effecting appropriate and precautionary management regimes.

Impacts of climate change

In addition to the many factors discussed above, octopus fisheries around the world are likely to be significantly impacted by climate change. Several studies propose that observed population declines are strongly linked with the climatic fluctuations associated with climate change, declines correlating directly with increasing seawater temperatures (e.g. for ***Eledone cirrhosa*** in the Ligurian Sea, Italy, Relini *et al.* 2006; and ***Octopus vulgaris***, from the northern Alboran Sea, southwestern Mediterranean, Vargas-Yáñez *et al.,* 2009). It is anticipated that distributions of octopus species will expand towards the poles as climatic conditions (particularly seawater temperature) displace species from their historical distributions. Resulting impacts could include extinctions, invasion of adjacent biomes, resultant competition with resident octopus faunas, and disrupted broader ecosystem structure and function. Species may variously be overwhelmed, be preyed upon or act in an equivalent manner to invading marine pests. As for all habitats and wildlife, potential larger-scale impacts of climate change on these animals remain poorly known.

Table 1. Harvested octopus species by region

Species	**Region**	**Scale of catch**
Family Octopodidae		
Genus *Octopus*		
Octopus bimaculatus	Southern California to Mexico	Minor artisanal harvests for food and bait (Ambrose, 1997). Collected live for aquarium trade (C. Huffard, pers. comm.).
Octopus bimaculoides	Southern California to Mexico	Minor artisanal harvests for food and bait (Lang, 1997). Collected live for aquarium trade (C. Huffard, pers. comm.).
Octopus hubbsorum	West coast of Mexico	Moderate artisanal harvests (Aguilar Chavez and Godínez-Domínguez, 1997; Espino-Barr *et al.,* 2007; Alejo-Plata *et al.*, 2009).
Octopus insularis	Brazil	Minor artisanal harvests (Leite, 2008).
Octopus maya	Gulf of Mexico	Major line fishery using bait or lure (Arocha, 1989; Solís-Ramirez, 1997; Arreguín-Sánchez *et al.,* 2000; Juarez *et al.,* 2010).
Octopus mimus	Western South America	Major commercial line harvest off Chile (Guerra and Fernández, 1990; Rocha and Vega, 2003).
Octopus oculifer	Galapagos Islands	Minor small-scale harvests for human consumption (Norman, unpubl. data).
Octopus tetricus	Temperate eastern Australia/New Zealand	Minor bycatch/small-scale target harvest for human consumption and as bait (Norman, 1998; Nottage, 2007).
Octopus cf. *tetricus*	Temperate western Australia	Minor lobster pot bycatch primarily for bait (Joll, 1983, as *O. tetricus*).
Octopus vulgaris	Mediterranean and North Atlantic	Major trawl, pot and trap harvests (Sánchez and Obarti, 1993; Guerra, 1997; Murphy *et al.,* 2002; Jouffre, 2002; Katsanevakis, 2006).
Octopus "*vulgaris*" I	Caribbean and Gulf of Mexico	Minor to moderate harvest (Cabello, 2004).
Octopus "*vulgaris*" II	Brazil	Moderate scale pot harvest (Haimovici and Perez, 1992; Moreira *et al.,* 2011).
Octopus "*vulgaris*" III	South Africa	Minor artisanal catch and minor bycatch in lobster potting (Smale and Buchan, 1981; Oosthuizen, 2004).
Octopus "*vulgaris*" IV	Japan, Korean Peninsula, Taiwan Province of China and China, Hong Kong SAR	Major trawl harvest off western Japan. Scale of catch elsewhere not reported (Voss and Williamson, 1971; Okutani *et al.,* 1987).
Genus *Abdopus*		
Abdopus aculeatus	Philippines, Indonesia	Collected alive for aquarium trade (C. Huffard, pers. comm.).
Genus *Amphioctopus*		
Amphioctopus aegina	China, Philippines to India	Major commercial trawl harvests for human consumption, particularly Gulf of Thailand (Norman and Sweeney, 1997, Nateewathana, 1997; Norman, 1998; Chotiyaputta *et al.*, 2002).
Amphioctopus burryi	East and west Atlantic Ocean	Minor bycatch in *O. vulgaris* fisheries off NW Africa (A. Caveriviere, unpubl. data).
Amphioctopus exannulatus	Taiwan to northern Australia	Minor bycatch in trawl fisheries at least in Taiwan and Australia (Norman, 1993b).
Amphioctopus fangsiao	Japan to China, Hong Kong SAR and Taiwan Province of China	Major commercial trawl harvests for human consumption (Okutani *et al.,* 1987, under the name *O. ocellatus*; Norman, 1998).

Table 1. Harvested octopus species by region

Species	Region	Scale of catch
Amphioctopus kagoshimensis	Japan to Taiwan Province of China	Minor to moderate trawl bycatch (Okutani *et al.,* 1987, under the name *O. aegina*; Norman and Kubodera, 2006).
Amphioctopus cf. *kagoshimensis*	Temperate eastern Australia	Minor trawl bycatch for human consumption and as bait (Nottage, 2007).
Amphioctopus marginatus	Tropical Indian Ocean to Japan	Major commercial trawl harvests for human consumption (Nateewathana, 1997; Norman, 1998).
Amphioctopus cf. *marginatus*	At least Taiwan Province of China	Minor trawl bycatch (C.W. Ho, unpubl. data).
Amphioctopus neglectus	Kerala, India to Taiwan Province of China	Major trawl harvest at least in Thailand (Nateewathana and Norman, 1999, Sreeja *et al.,* 2012).
Amphioctopus rex	Andaman Sea to Gulf of Thailand	Minor trawl harvest in Gulf of Thailand (Nateewathana and Norman, 1999).
Amphioctopus siamensis	Andaman Sea to Gulf of Thailand	Major trawl harvest at least inThailand (Nateewathana and Norman, 1999) and minor bycatch in northern Australia (Norman, unpubl. data).
Genus *Callistoctopus*		
Callistoctopus graptus	Northern Australia	Minor trawl bycatch, primarily for bait (Norman, 1993a).
Callistoctopus luteus	Gulf of Thailand to Philippines	Subsistence to significant commercial harvest for human consumption (Norman and Sweeney, 1997; Nateewathana, 1997; Norman, 1998).
Callistoctopus nocturnus	Philippines	Historical records of subsistence harvest for human consumption (Norman and Sweeney, 1997).
Callistoctopus ornatus	Tropical Indo-West Pacific	Subsistence and small-scale harvests (Norman, 1993c; Young and Harman, 1997).
Genus *Cistopus*		
Cistopus indicus	At least Philippines	Scale of harvest unknown (Norman and Sweeney, 1997).
Cistopus chinensis	Emerging fishery and acquaculture interest	Zheng *et al.,* 2012
Cistopus taiwanicus	Taiwan Province of China	Moderate trawl capture, often sold alive (Liao and Lu, 2009).
Cistopus sp.	India to China, Hong Kong SAR	Major trawl harvest throughout range, particularly Thailand (Nateewathana, 1997; Chotiyaputta *et al.,* 2002).
Genus *Eledone*		
Eledone cirrhosa	Mediterranean Sea, North Atlantic	Moderate trawl harvests for human consumption (Boyle, 1997; Sànchez, 2004; Relini, 2006; Fonseca *et al.,* 2008).
Eledone massyae	Eastern South America	Minor trawl bycatch in Brazil and Argentina (Haimovici and Perez, 1992).
Eledone moschata	Mediterranean Sea	Minor trawl bycatch in Mediterranean Sea for human consumption (Mangold, 1983b).
Genus *Enteroctopus*		
Enteroctopus dofleini	Northern Pacific Ocean	Major trawl harvest (>20 000 t) off Hokkaido, Japan (Kubodera, 1992). Minor harvest, primarily by divers as bait for halibut fishery in Northeast Pacific (Mottet, 1975; Hartwick and Barriga, 1997).
Enteroctopus magnificus	South Africa	Minor trawl harvest (Villanueva *et al.,* 1992; Groeneveld *et al.* 2006).
Enteroctopus megalocyathus	Southern South America	Minor catch by hooks in the intertidal zone and by diving in the subtidal zone (Re, 1980; Rocha and Vega, 2003; Ibáñez, 2008; Ortiz *et al.,* 2011).

Table 1. Harvested octopus species by region

Species	Region	Scale of catch
Genus *Hapalochlaena*		
Hapalochlaena lunulata	Philippines, Indonesia	Collected alive for aquarium trade (C. Huffard, pers. comm.).
Genus *Thaumoctopus*		
Thaumoctopus mimicus	Indonesia, Philippines	Collected live for aquarium trade (C. Huffard, pers. comm.).
Genus *Wunderpus*		
Wunderpus photogenicus	Indonesia	Collected live for aquarium trade (C. Huffard, pers. comm.).
Unplaced '*Octopus*'		
'Octopus' alecto	Mexico to Ecuador	Minor subsistence harvest (Roper *et al.,* 1995).
'Octopus' australis	Temperate eastern Australia	Minor trawl bycatch for human consumption and as bait (Norman, 1998; Nottage, 2007).
'Octopus' berrima	Southern Australia	Minor pot fishery for human consumption (Stranks and Norman, 1993).
'Octopus' briareus	Gulf of Mexico, Caribbean Sea	Minor fishery using spears, hooks and pots (Voss, 1971b), popular in aquarium trade (C. Huffard, pers. comm.).
'Octopus' californicus	Mexico to Gulf of Alaska	Minor trawl bycatch (Hochberg, 1997a, 1998).
'Octopus' conispadiceus	Off northern Japan	Minor incidental catch in *Enteroctopus dofleini* harvests off northern Japan (Okutani *et al.,* 1987; Gleadall, 1993).
'Octopus' cyanea	Tropical Indo-West Pacific	Minor to moderate subsistence and local catch with spears or lures for human consumption. Minor commercial harvests in Indonesia, Philippines and Hawaii (Norman, 1992a; Young and Harman, 1997); Tanzania (Guard and Mgaya, 2002); Rodrigues (Sauer *et al.* 2011).
'Octopus' hongkongensis	Japan	Minor trawl harvest (Okutani *et al.,* 1987; Gleadall, 1993).
'Octopus' maorum	Southern Australia/New Zealand	Minor bycatch in lobster and trawl fisheries primarily as bait, with some targeted operations for human consumption (Stranks, 1988a; Brock and Ward, 2004; Brock, 2006; Harrington *et al.,* 2006).
'Octopus' microphthalmus	Strait of Malacca and Singapore	Historical records from fish markets in Singapore (Norman, unpubl. data).
'Octopus' minor	Japan to Korean Peninsula and Taiwan Province of China	Minor to moderate trawl bycatch (Okutani *et al.*, 1987; Kim, 2008); species name may represent multiple species.
'Octopus' pallidus	Southern Australia	Minor harvest in pot fisheries (Stranks, 1988b; Leporati *et al.,* 2009).
'Octopus' rubescens	NE Pacific Ocean	Minor trawl bycatch (Hochberg, 1997b).
'Octopus' tehuelchus	Brazil to Argentina	Minor intertidal artisanal fishery on North Patagonian coast, by hooks (Iribarne, 1991a; Narvarte, 2007).
'Octopus' vitiensis	Tropical Indo-West Pacific	Historical records from fish markets in Thailand (Norman, unpubl. data).
Family Argonautidae		
Genus *Argonauta*		
Argonauta argo	Indo-West Pacific	Historical collection and market sales following mass strandings (Okutani and Kawaguchi, 1983).

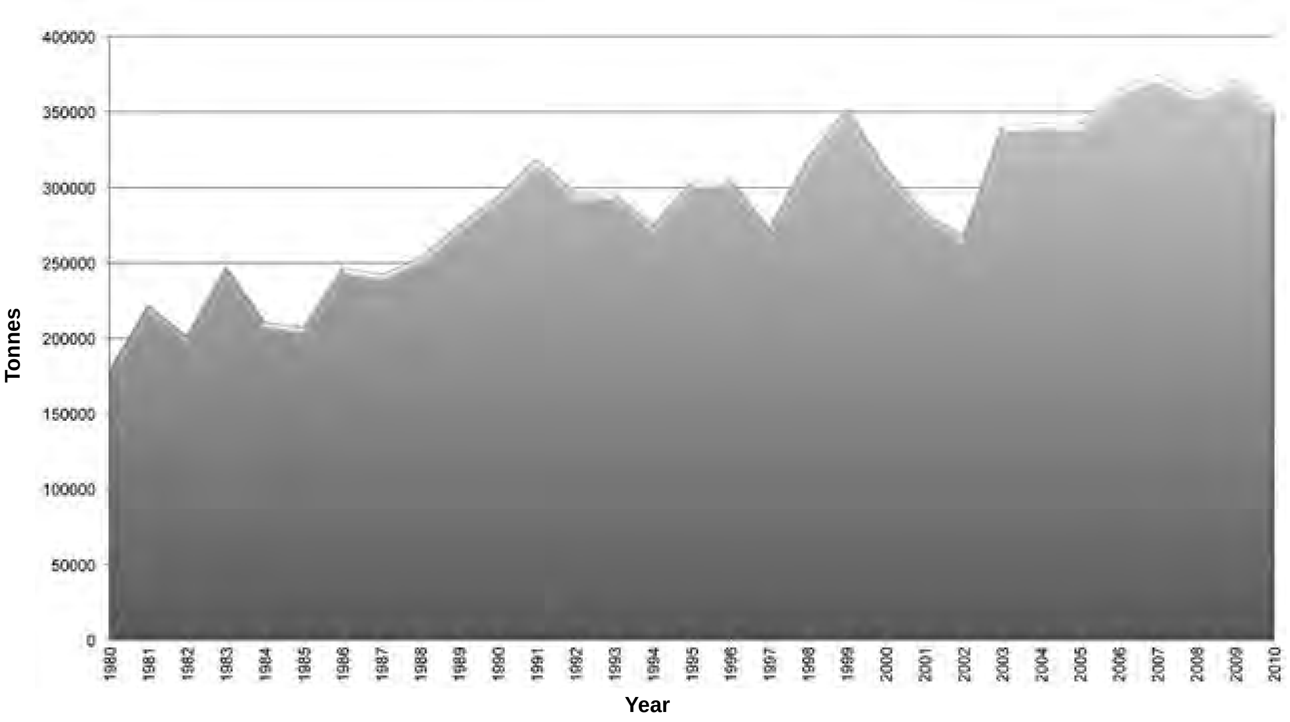


Fig. 3 Total world octopus production 1980 to 2010

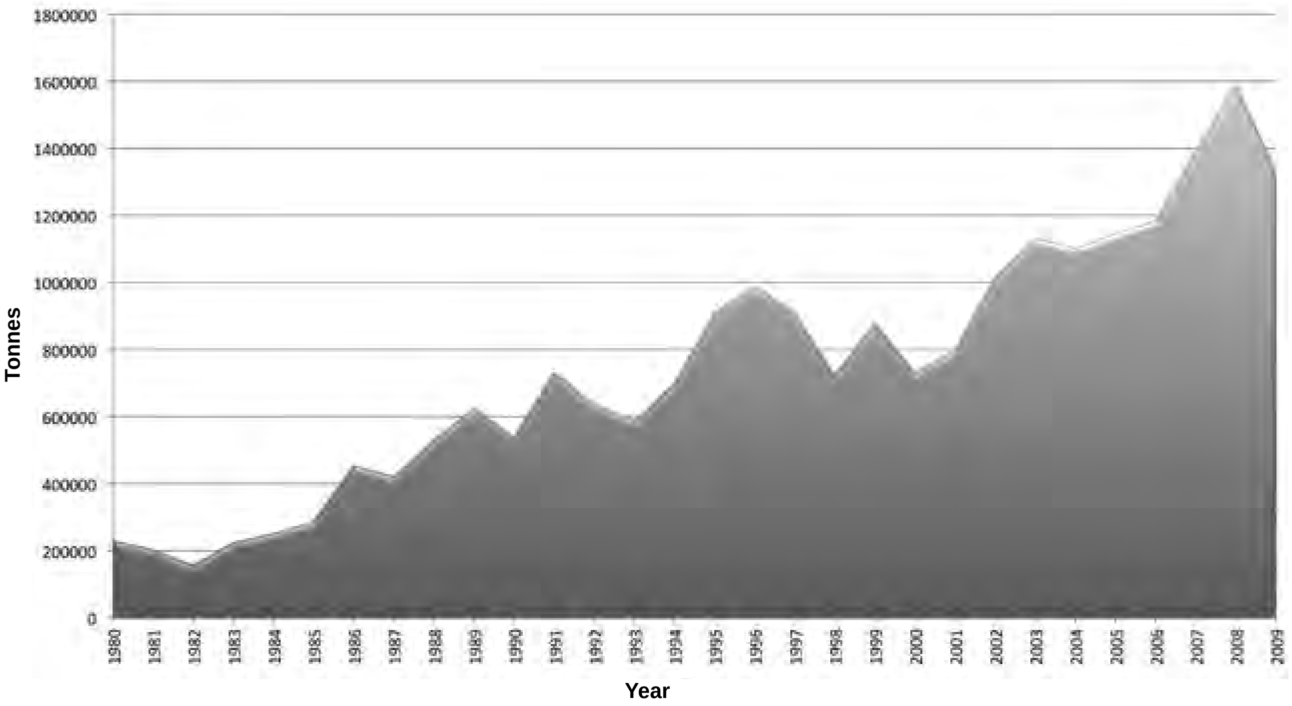


Fig. 4 Total world export value for octopus fisheries 1980 to 2009

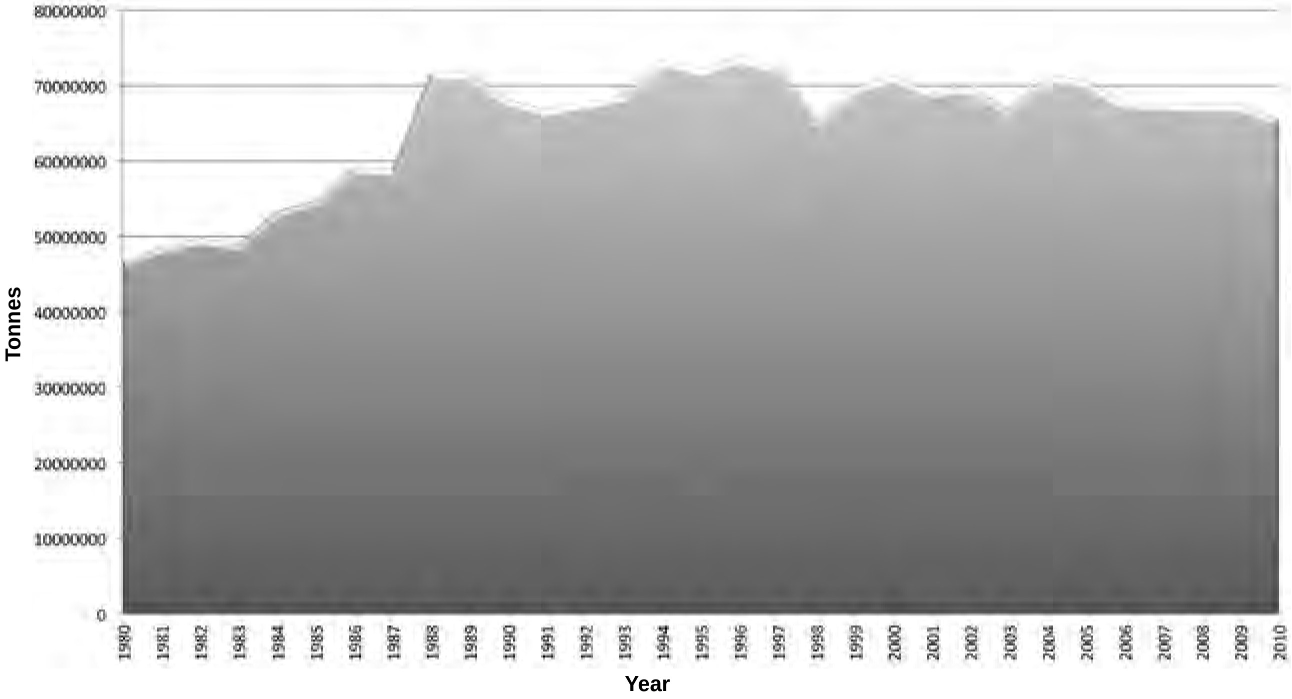


Fig. 5 Total world fishery production - all marine fishes 1980 to 2010

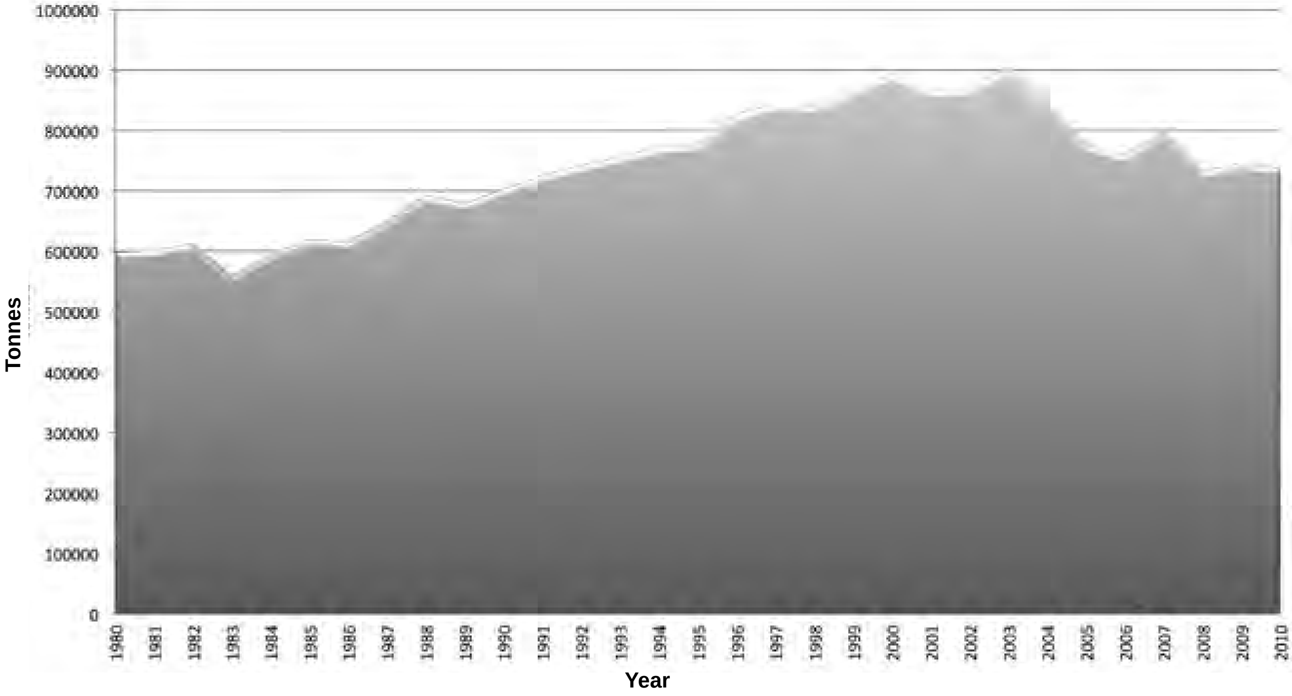


Fig. 6 Total world chondrichthyan production 1980 to 2010

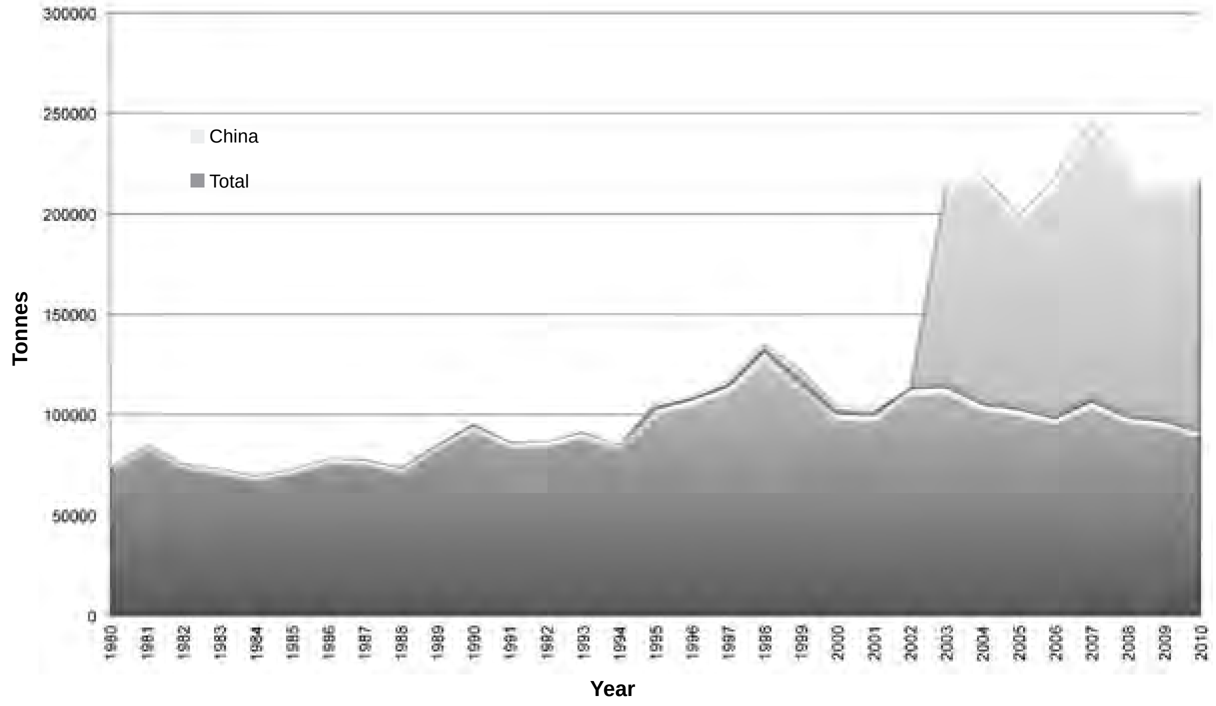


Fig. 7 Total southeast Asia octopus production 1980 to 2010

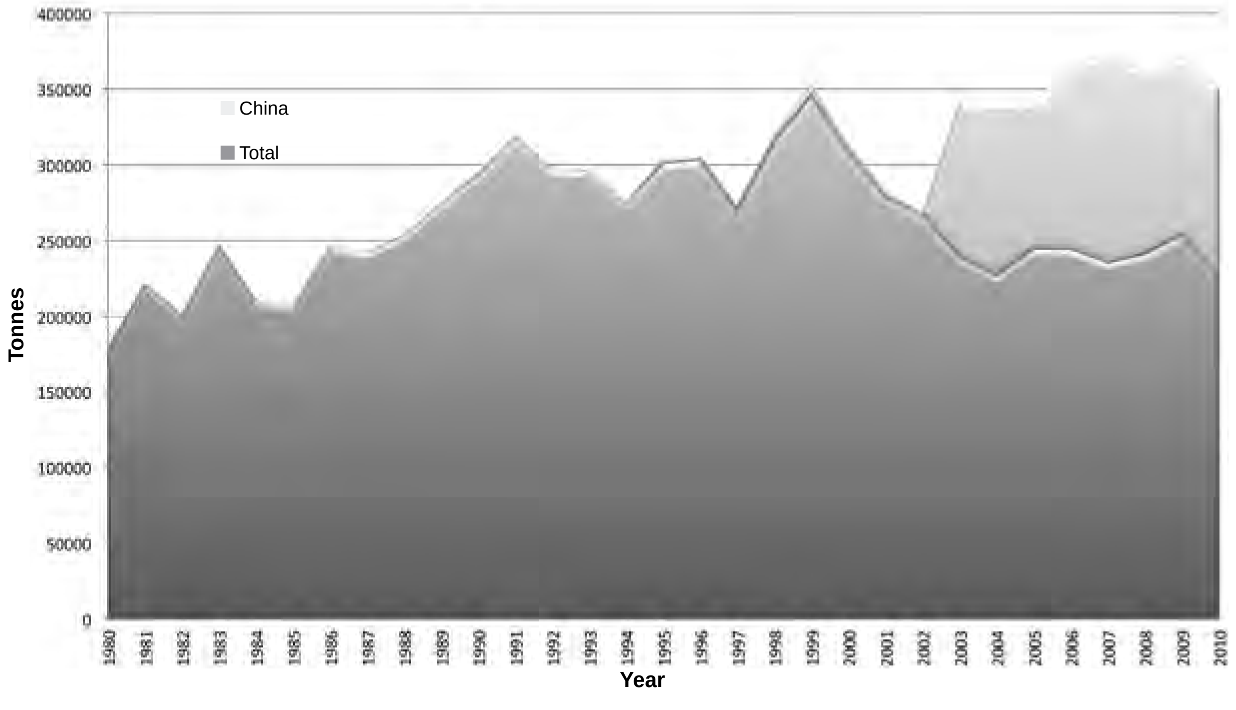


Fig. 8 Total world octopus production 1980 to 2010

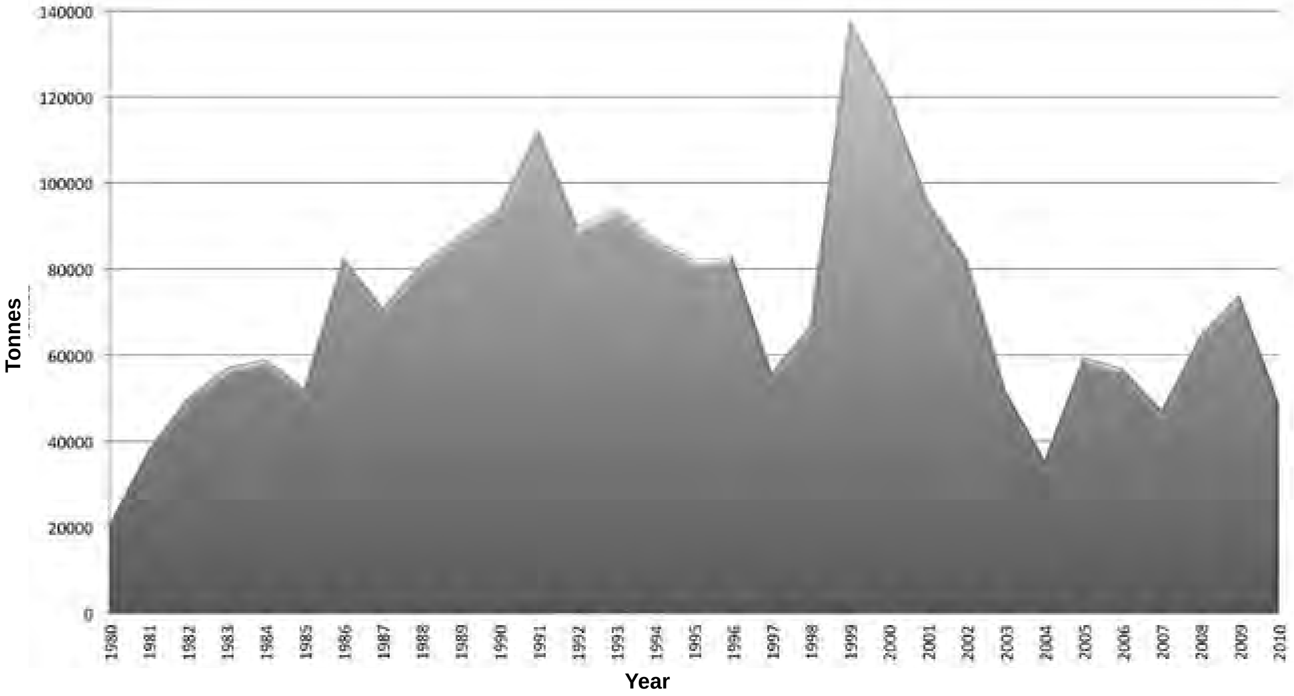


Fig. 9 West Africa octopus production 1980 to 2010

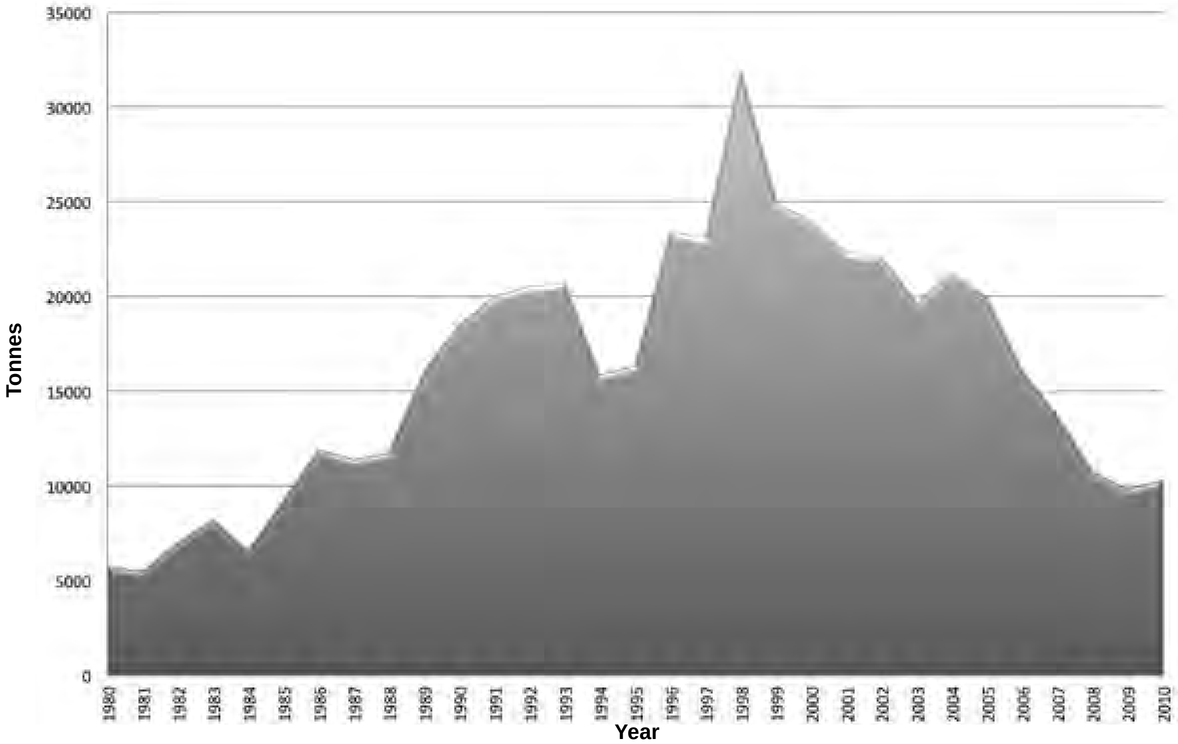
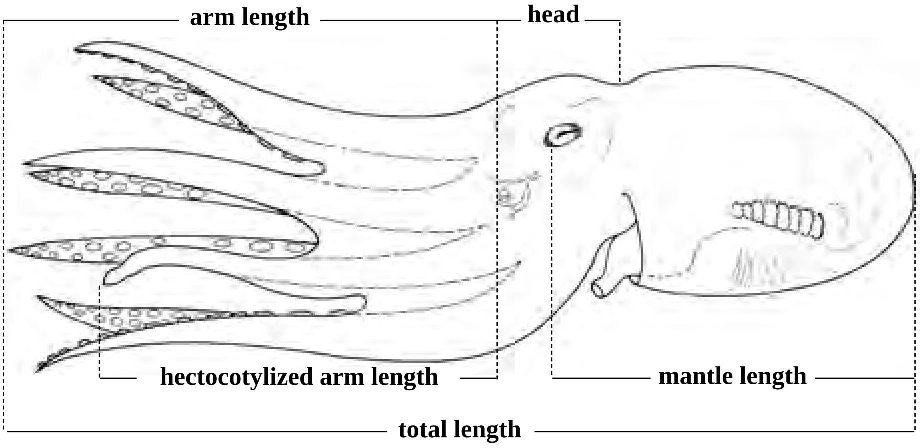
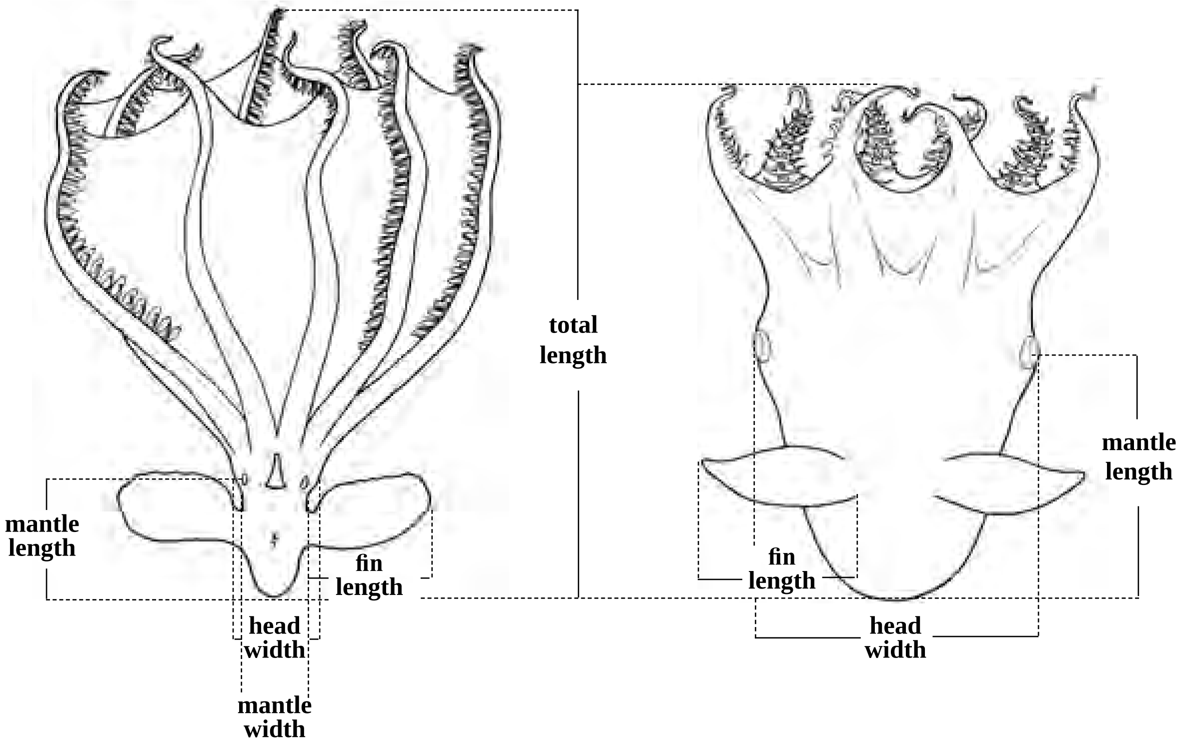


Fig. 10 Gulf of Thailand octopus production 1980 to 2010

1.6 ILLUSTRATED GLOSSARY OF TECHNICAL TERMS AND MEASUREMENTS*



a) Schematic illustration of an incirrate octopod



b) Schematic illustration of a cirrate octopod

c) Schematic illustration of a vampire squid

Fig. 11 Schematic illustration of octopods and vampire squids

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* According to cephalopod scientific terminology standards (see Roper and Voss, 1983; Norman and Sweneey, 1997).

Abdominal septum – Median septum that internally bisects the mantle cavity parallel to the body axis. It extends from the ventral surface of the visceral mass to the dorsal surface of the ventral mantle wall. The ventral mantle artery runs along the dorsal edge of this septum.

Aboral – Away from, or on the opposite side to, the mouth.

Abyssal – The great depths of the ocean: from 2 000 to 6 000 m.

Acetabulum – The central, open, water-filled cavity or cup of cephalopod suckers, responsible for suction on muscular expansion. Surrounded by an outer rim (**infundibulum**), often flared in incirrate octopods (Fig. 29).

Adult – A female whose ovary is filled with mature eggs or a male that has spermatophores present in the spermatophore storage sac (=**Needham's sac**).

Anal flaps – A pair of small conical or paddle-like appendages, one on each lateral edge of the anus, present in octopod species that produce ink. The flaps function to direct releases of ink (Figs. 15).

Anterior – Toward the head-end or the arm-tips of cephalopods.

Anterior salivary glands – Glands on, or in, the buccal mass that aid in preliminary digestion (Fig. 15**;** see also **Posterior salivary glands**).

Anus – Terminal opening of the digestive tract in the anterior mantle cavity, occasionally extends to inside of the funnel, through which digestive waste products, as well as ink, are expelled (Fig. 15).

Apomorphic – Derived from a more ancestral condition. Loosely considered the 'advanced' condition.

Arm(s) – Recommended term for the circumoral appendages of coleoid cephalopods. Arms are designated by numbers or Roman numerals, i.e. 1 to 4 or I to IV, starting with 1 or I as the dorsal (or upper) pair (Fig. 16). Arms also are designated as being on either the right or left side (R1, R2, etc.). In vampire squids, a pair of long filamentous structures emerge from pits situated between arms I and II. Cirrate and incirrate octopods have only eight arms.

Arm crown – In octopods the ring of 8 arms that surround the mouth, including the webs. Also known as the **Brachial crown.**

Arm formula – Comparative length of the four arm pairs expressed numerically in decreasing order: the longest arm is indicated first and the shortest last, e.g. 4>3>2>1. If 4>3=2>1, then arm pair 4 is the longest, followed by arm pair 3 which is the same length as arm pair 2 and both are longer than arm pair 1. In octopods, the non-hectocotylized arm 3 (right or left) is used in this formula.

Armature – **(1)** For limbs, the grappling structures of the arms and tentacular clubs, including suckers, sucker rings, and/or hooks. **(2)** For spermatophores, the internally facing teeth found within the ejaculatory apparatus of some octopod species (e.g. ***Eledone moschata*** or ***Amphioctopus aegina***) that are splayed on the external surface of the everted spermatophore and aid in penetration into the female's oviducts and/or ovary.

Bathypelagic – Descriptor of mode of life or habitat for midwater within the deep sea. Often refers to pelagic species that occur at great depths, e.g. greater than 1 000 m.

Beaks – The chitinous jaws of cephalopods, comprising of two halves bound in powerful muscles. The dorsal beak component is referred to as the 'upper' beak and it inserts within the 'lower' (ventral) beak. The two components act in concert to cut tissue with a scissors-like action.

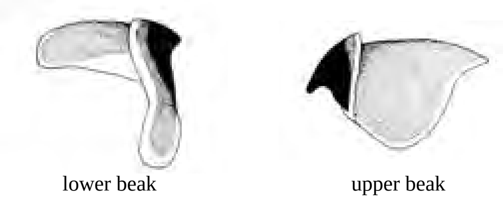


Fig. 12 Beaks

Benthopelagic – A free-swimming animal that lives just above the ocean floor but rarely rests on the substrate.

Bilateral symmetry – The symmetry exhibited by an organism or organ where one plane can divide the form into two halves that are mirror images of each other.

Bioluminescence – The production of light by living organisms, sometimes called 'living light'. The light is produced through a chemical reaction that generally takes place in complex organs called photophores or light organs.

Brachial – Pertaining to the arms.

Brachial crown – The combination of arms that surrounds the mouth. Also known as the **Arm crown**.

Branchial – Pertaining to the gills.

Branchial canal – A large opening at the base of each gill lamella and between the primary afferent and efferent blood vessels of the gill. A branchial canal is absent in cirrate octopods.

Branchial gland – Elongate or spheroidal gland adjacent and parallel to the gill's attachment to the mantle wall.

Branchial heart(s) – Accessory hearts located at the base of each gill that function to pump blood to the gills.

Brooding – Incubation of eggs by the female. The eggs are attached to a substrate or held in the arms of the female. Characteristic feature of incirrate octopods.

Buccal – Pertaining to the mouth.

Buccal mass – Muscular bulb at the anterior-most part of the digestive system that consists of the mouth, beaks, radula, muscles, and anterior pair of salivary glands (Fig. 15).

Buoyancy (neutral, positive, negative) – The tendency to float in seawater. A neutrally buoyant object does not rise or sink but maintains its position in the water; a positively buoyant object will rise; and a negatively buoyant object will sink.

Calamus – The conical projection at the base of the ligula at the distal tip of the hectocotylized arm of octopods. Located at the distal terminus of the spermatophore groove, distal to the last sucker (Fig. 13) (see **Ligula**).

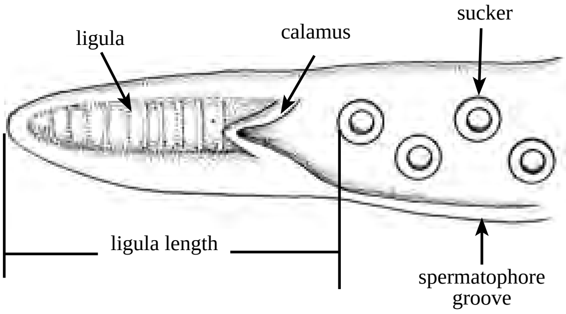


Fig. 13 Distal tip of the hectocotylized arm in octopuses

Calcified – Chalky, calcareous material of calcium salts (calcium carbonate), formed through deposition.

Cement body – Structure within spermatophores that draws the sperm cord into a bulb during spermatophore eversion (Fig. 26).

Cephalic cartilage – Cartilage-like tissue that envelops the posterior part of the brain of cephalopods and encompasses the statocysts. The cartilage has a large central opening through which the oesophagus passes and minor foramina channels for nerves and blood vessels.

Cephalopoda – The Class within the **Mollusca** characterized by bilateral symmetry, internal 'shell' or absence of shell (except nautiluses and female argonauts), anterior head appendages and funnel, posterior mantle, mantle cavity with organs, and fins when present.

Character state – A particular condition of a morphological character of taxonomic value. For example, the character 'sucker' may include the two states: sucker with a chitinous or horny ring; or sucker without a horny ring.

Chemotactile – Sensory capacity to 'taste' chemicals through direct touch contact, e.g. as in octopus suckers (see also **Olfactory organ**).

Chitin(ous) – A horny, polysaccharide substance (fingernail-like) that forms the sucker rings, hooks, beaks, and stylets of octopods and other cephalopods.

Chorion – A tough secreted membrane that encapsulates the egg.

Chromatophores – Pigment-filled, muscular sacs in the skin under individual nervous control that collectively provide the background colour, colour patterns, and colour dynamics of cephalopods.

Circumoral appendages – Collective term for the limbs of cephalopods, e.g. the eight arms of **Octopodiformes**. All arise from the head and encircle the mouth (see **Arm crown**).

Cirri (singular **cirrus**) – Elongate, fleshy, finger-like projections that are present along the lateral edges of the sucker row in cirrate octopods and vampire squids squid (Fig. 14). Terms formerly used with reference to erected papillae on the skin of incirrate octopods, usually over the eyes.

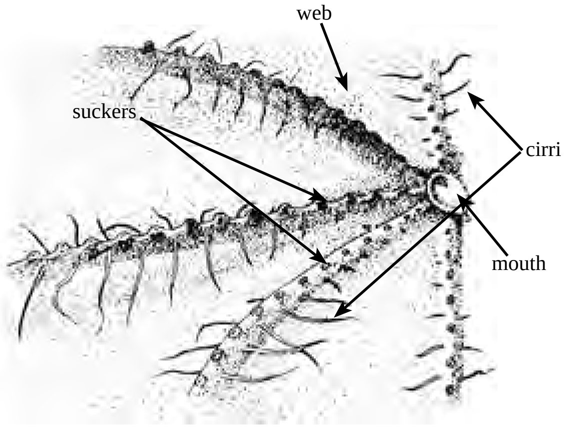


Fig. 14 Cirri on arms of cirrate octopods (oral view)

Coelom – An internal body cavity of mesodermal origin that is lined by an epithelium. Cephalopods have two coeloms: the viscero-pericardial (body organs and heart) coelom; and the nephridial (renal or kidney) coelom.

Coleoid – Cephalopods from the subclass Coleoidea, which includes the major living groups of squids, cuttlefishes, octopods and vampire squids. Nautiluses and extinct shelled cephalopods such as the ammonites belong in the subclass Nautiloidea (see Fig. 2).

Cornea – Smooth, thin, turgid, transparent skin without muscles that covers the eyes to protect the eye lenses of incirrate octopods.

Counter shading – Body pigmentation in cephalopods that is darker on the dorsal and lateral surfaces of the mantle, head, and arms, and lighter on the ventral mantle and arms. It allows an animal to conceal its body from predators looking up towards lighter shallow water or down against a dark bottom (see also **Reverse counter shading**).

Crop – Expansion (i.e. a broadening or a side pocket) of the oesophagus for storing ingested food, prior to its entering the stomach. Present in nautiluses and most octopods (Fig. 15).

Crop diverticulum – A distinct side-branch of the crop section of the gastrointestinal tract found in many octopod groups (Fig. 15).

Decapods (Decapodiformes) – Cephalopods with ten limbs, namely squids and cuttlefishes. As opposed to octopods (**Octopodiformes**) that have eight arms but lack the additional two feeding tentacles.

Demersal – Organisms that live close to the ocean floor.

Diel vertical migration – Vertical animal migration during twilight periods. Many mesopelagic animals migrate at sunset to shallow depths where they spend the night feeding. At sunrise they descend from near-surface waters to spend the day hiding at greater, darker depths. Some animals migrate vertically over 1 000 m, others migrate less than 100 m.

Digestive gland – The liver equivalent of cephalopods. The primary organ that secretes digestive enzymes and plays roles in digestion, absorption, and excretion (Fig. 15).

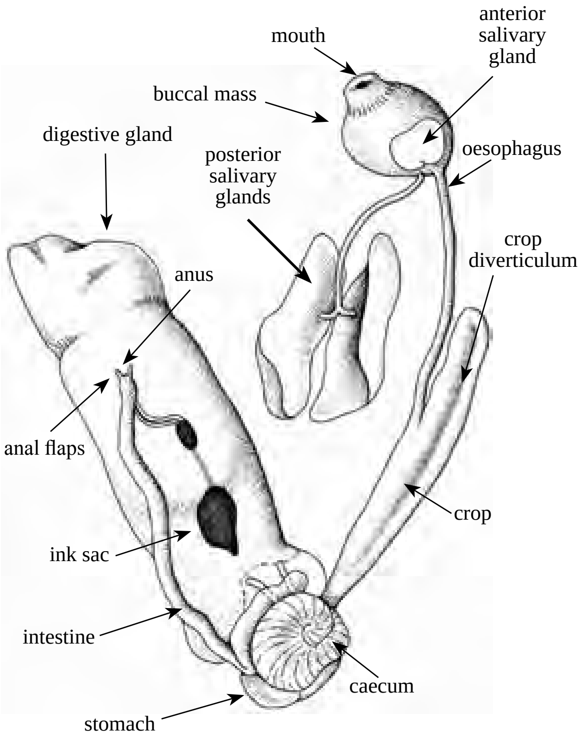


Fig. 15 Digestive system terminology

Distal – Away from the central region of the body or point of origin; toward the peripheral or outer parts (opposite of proximal).

Dorsal – The uppermost surface of a cephalopod, opposite to the ventral surface where the funnel is located (Fig. 16).

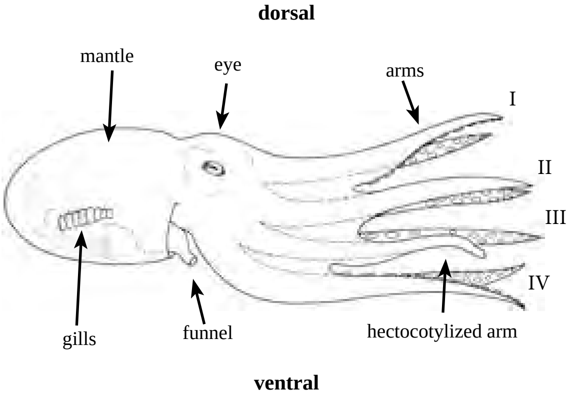


Fig. 16 Schematic lateral view of octopus features

Ejaculatory apparatus – Portion of the spermatophore (distinct from the sperm reservoir) that performs the eversion of the spermatophore and extrusion of the sperm mass (Fig. 26).

Epipelagic zone – The uppermost pelagic zone of the ocean, typically considered the upper 200 m.

Epithelial pigmentation – The pigmentation contained in epithelial cells that are unable to change their shape/expression in the absence of muscles and nerves. Colour in most cephalopods, however, is created by pigment granules contained in specialized organs, the chromatophores, that can change shape rapidly, by muscular action under nervous control (see **Chromatophores**).

Eye (**position** and **size**) – Eyes are the primary sensory organs of cephalopods; they usually are large and located one on each side of the head (Fig. 16). In contrast, some species have small eyes, eyes on stalks, or telescopic eyes.

Family – The group (taxon) above the genus level, comprised of the most closely related genera.

Fin(s) – The pair of muscular flaps that arise along the dorsolateral surface of the mantle of vampire squids and cirrate octopods. Used for locomotion, steering, and stabilization (Figs. 11, 17).

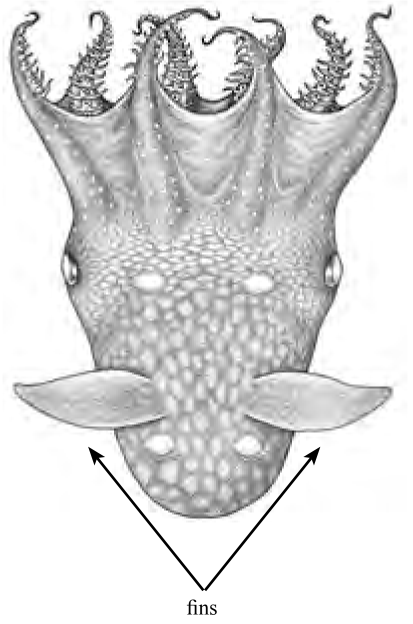


Fig. 17 ***Vampyroteuthis infernalis*** **(dorsal view)**

Fin attachment – Point of attachment to the mantle, the opposite fin, or combination of both.

Fin cartilage – Cartilage associated with the fins of all fin-bearing cephalopods, including cirrate octopods and vampire squids.

Fin length – Length from anterior lobe, or anterior-most attachment of fin lobe, to posterior-most attachment of fin to mantle or tail (Fig. 11).

Foot – See **Molluscan foot**.

Funnel – The ventral, subconical tube through which water is expelled from the mantle cavity during locomotion and respiration. Ink and waste products also pass through the funnel (Fig. 16). Archaic term: siphon.

Funnel-adductor muscles – Muscles that support the lateral attachment of the funnel to the head.

Funnel organ – Glandular pad(s) on the internal surface of the funnel. In octopodiformes the form is species-specific and varies from a single W-shape, to a double V-shape, to three or four separate components (Fig. 18).
Indistinct in frozen or poorly preserved material. Soluble dyes such as methylene blue can help to make the outline of this structure more obvious.

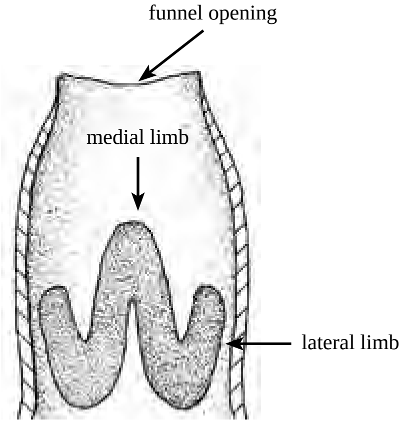


Fig. 18 Funnel organ of incirrate octopod (W-shaped)

Funnel-retractor muscles – Large muscles that attach to the corners of the funnel and run posteriorly to attach to the sides of the shell sac (generally near the base of the gills) or, in some species, insert on the interior mantle wall.

Genus – The taxon (group) below the family level and above the species level.

Gill – Primary organ for the exchange of respiratory gases with seawater. Composed of multiple gill lamellae (Fig. 22).

Gill lamella (pl. **lamellae**) – The leaf-like, convoluted, individual components of the gill through which gas exchange occurs. Forms inner and outer rows on the gill with a medial terminal lamella (Fig. 22).

Gonoduct(s) – Tubular structure(s) of the reproductive system which serve to transport reproductive products from the gonad(s) to the exterior (see **Oviducts**).

Hatchling – Young cephalopod, newly hatched from the egg.

Head-mantle fusion – Zone of fusion of head and mantle; varies among groups/families; of systematic and biological significance.

Hectocotylized arm(s) – One (or more) modified arm(s) in male cephalopods used to transfer spermatophores to the female. In octopods, refers to the entire arm, typically the third right or third left arm (Figs. 11, 16). Often called the **Hectocotylus**. (See also **Calamus**, **Ligula**) (Fig. 13). In some octopods (e.g. ***Argonauta***), the entire arm is detached and left in the mantle cavity of the female. (Fig. 19) .

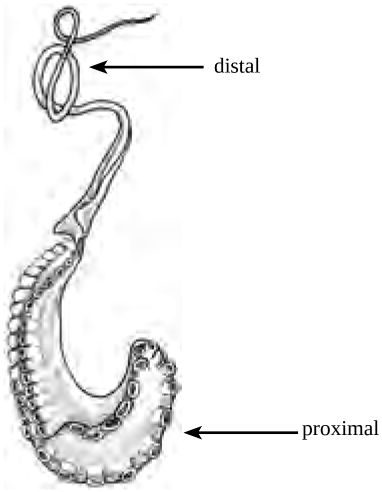


Fig. 19 *Argonauta hians* - detached hectocotylized arm

Hectocotylus – See **Hectocotylized Arm.**

Holotype – The single specimen designated by the original author in formal taxonomic descriptions to represent a new species name. An international standard of reference that provides objectivity and stability for species names (see also **Type material**).

Horizontal arm septa – Septa that extend the length of the arms (i.e. parallel to the arm axis), that roughly divide the arms into oral and aboral regions (Fig. 20). This feature is characteristic of the arms of cirrate octopods as well as incirrate octopods of the family Bolitaenidae. The functional significance is unknown.

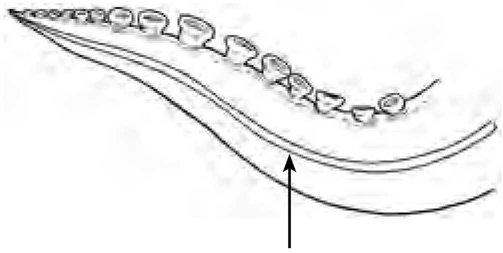


Fig. 20 Horizontal arm septa

Inferior frontal lobe system – A system of lobes in octopod brains: the paired posterior buccal; lateral inferior frontal and subfrontal lobes; and the single median inferior frontal lobe. They form a functional unit concerned with processing chemotactile information from the arms.

Infundibulum – The disc (or plate-like) rim of cephalopod suckers that surrounds the opening to the **acetabulum** (Fig. 29).

Ink sac – The structure that manufactures and stores the ink of cephalopods. The sac is situated on (or embedded in) the ventral surface of the digestive gland. It is oriented parallel with the intestine and empties via the ink duct into the rectum (or at the level of the anus) (Fig. 15).

Intestine – Distal region of the alimentary canal between the stomach/caecum complex and the anus (Fig. 15).

Iridophores – Platelet-like components of the skin that form an iridescent or reflective sheen in cephalopods. May be concentrated in particular skin regions, as in the iridescent blue rings of some ocellate octopuses and members of the genus ***Hapalochlaena***, or may be dispersed throughout the skin to produce a general body iridescence.

Iteroparous – A reproductive strategy in which females spawn repeatedly over a period of years as in ***Nautilus***. Most extant cephalopods are semelparous and spawn only once towards the end of their lives (see **Semelparous**).

Juvenile – Immature life history stage between the hatchling and the nearly mature subadult stages.

Keel – A raised ridge of skin around the lateral margin of the mantle in incirrate octopods (also referred to as **Lateral ridge)** (Fig. 21).

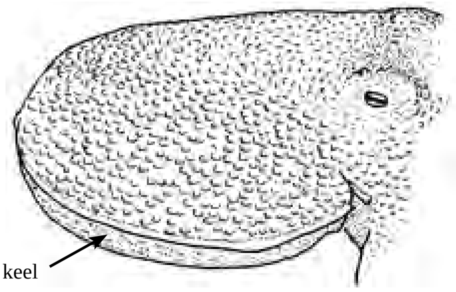


Fig. 21 Lateral view of mantle of an incirrate octopod

Lateral – Pertaining to the side(s) of an organism or structure, away from the centre or midline.

Lateral-line analogue – Sensory structure analogous to the lateral-line of fishes. The lateral-line analogue, which senses vibrations transmitted by seawater, is located along a series of lines on the dorsal surface of the head. Some sensory cells extend onto the bases of the arms.

Lateral ridge – A narrow, horizontal, ridge of skin along the lateral sides of the mantle of incirrate octopods (also referred to as a **Keel**) (Fig. 21).

Lectotype – See **Type material**.

Leucophores – The white-reflecting components of the skin of some octopods, particularly shallow-water members of the family Octopodidae.

Light organ – A simple or complex structure that produces bioluminescence by intrinsic (self-generated) or extrinsic (bacterial) means (also referred to as a **Photophore**).

Ligula – The spatulate or spoon-shaped terminal structure at the tip of the **hectocotylized arm** in males of most species of incirrate octopods. Used to hold spermatophores as they are inserted into the female's oviducts (Fig. 13).

During mating, spermatophores are transferred from the terminal organ within the mantle cavity to the spermatophore groove that runs along the edge of the hectocotylized arm, then gripped by the ligula when they are transfered to the female. (see **Calamus**, **Hectocotylized arm**).

Mantle – The fleshy (muscular), tubular, or sac-like body of cephalopods; provides propulsion through jet-like expulsion of water through the funnel; contains the viscera (Fig. 11, 16).

Mantle cavity – Space enclosed by the mantle. In cephalopods, the mantle cavity contains the visceral organs, gills, anus, openings of the gonoducts, nephridial pores, plus various muscles and septa (Fig. 22).

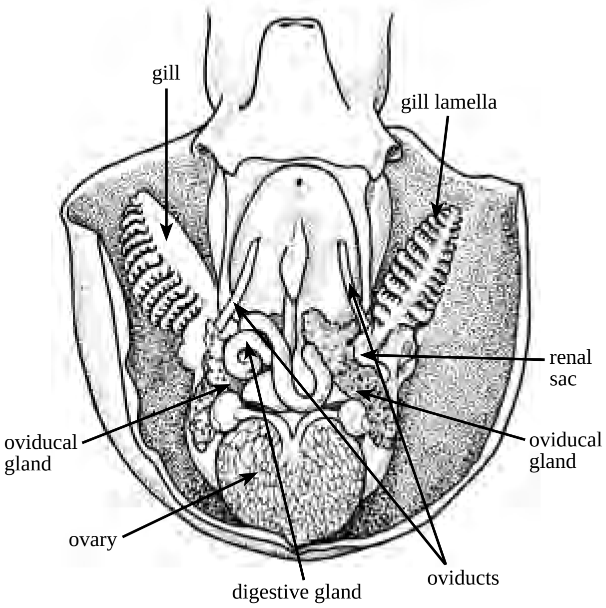


Fig. 22 Internal organs of female octopus

Mantle length (ML) – The standard measure of length in coleoid cephalopods. In octopods**,** mantle length is measured from a line joining the mid-point of the eyes (rather than the anterior mantle margin, since the latter is obscured by the head/mantle fusion, as used in squid and cuttlefishes) to the posterior-most margin of the mantle (Fig. 11).

Mature – In cephalopods this term refers to sexual maturity, which is determined for females by the presence of mature eggs in the ovary or free in the oviducts (Fig. 22), and for males by the presence of spermatophores in the spermatophore storage (formerly Needham's) sac (Fig. 27) (see **Adult**).

Medial (Median) – Pertaining to a structure located toward, on, or along the dorsal or ventral midline.

Mesopelagic zone – The middle-depth zone of the pelagic realm of the ocean, generally considered to be from 200 to 1 000 m deep.

Mollusca – One of the major invertebrate phyla. Some of the more common molluscs are snails and clams. The Cephalopoda is a class within the Mollusca.

Molluscan foot – A major structure in molluscan morphology. In gastropods the foot is the muscular sole that the animal crawls with. In cephalopods the funnel, and possibly the arms and tentacles are derived from the molluscan foot. The evolutionary origin of the latter is still uncertain. They may represent outgrowths of the head (favoured by anatomical evidence of the nerve connections) or modifications of the molluscan foot that have migrated around the mouth (favoured by embryological evidence, the migration of arm primordia).

Monophyletic group – A natural group (taxon) that shares a common ancestor, compared to a polyphyletic group where members with multiple ancestry are artificially grouped.

Needham's sac – See **Spermatophoric storage sac.**

Neocoleoid – The neocoleoids are a division of cephalopods within the subclass **Coleoidea** that contain the Recent cuttlefishes, squids, and octopods.

Neotype – See **Type material**.

Nephridial coelom – The cavity of the renal (kidney) sac. It connects with the exterior via the renal or nephridial pore and with the viscero-pericardial coelom via a pair of slender ducts. In incirrates two separate renal cavities are present.

Nephridial papillae – Small raised openings to the mantle cavity from the renal cavities (also referred to as **renal pores**).

Neritic – The region of the ocean that overlies the continental shelf.

Nominal species – A species that has been formally described and is based on a morphological type specimen. It is an available name but not necessarily a valid species.

Nuchal organ – Small sensory organ with photoreceptor-like sensory cells that is located in the nuchal (neck) region of **coleoid** cephalopods.

Nuchal region – The dorso-lateral area around the posterior part of the head in cephalopods and the area immediately posterior to it (the neck analogue). Normally covered by the anterior mantle wall.

Ocellate – Referring to octopuses that possess false eyespots (see **Ocellus**).

Ocellus (pl. **ocelli**) – A pigmented spot or patch, used in alarm displays to give the appearance of the head of a larger animal. An ocellus usually consists of a dark round or ovoid spot of concentrated chromatophores, but also may possess an additional outer concentric dark or light ring. Ocelli occur in some octopus species (one each on the lateral arm crown in members of ***Octopus*** *sensu stricto* and ***Amphioctopus***, or as a pair on the dorsal mantle in ***Euaxoctopus***). Some species possess an iridescent blue, purple, gold, or green ring within the dark ocellus spot (also called False eyespot).

Octopodiformes – Higher-level taxon that includes all eight-limbed cephalopods: vampire squids, cirrate octopods, and incirrate octopods. Because of the long history of referring to these cephalopods by the common name '**octopods**', this term is used as the common name for all members of the Octopodiformes (see Fig. 2 - Living Cephalopods).

Octopods – Common name for **Octopodiformes**.

Oesophagus – The portion of the digestive tract between the buccal mass and the stomach (Fig. 15). In some species the distal or posterior region of the oesophagus is expanded to form a crop for food storage (see **Crop**).

Olfactory organ – A chemosensory organ. In octopods in the form of a shallow rimmed pit, one each present at the inside of the lateral margins of the mantle aperture (also referred to as olfactory papilla or olfactory pit).

Optic lobes of brain – Large lobes of the brain associated with the eyes. In octopods and some squids the optic lobes may be separated from the rest of the brain by an optic stalk of varying length.

Oral – Toward, or pertaining to, the mouth.

Order – The taxonomic category above the family level.

Oviduct(s) – Female gonoduct(s). The oviduct(s) conduct eggs from the ovary to the mantle cavity. In octopods each oviduct is divided into proximal and distal portions on either side of the **oviducal gland**. Incirrate octopods and vampire squids have two oviducts while cirrate octopods possess a single oviduct (Fig. 23).

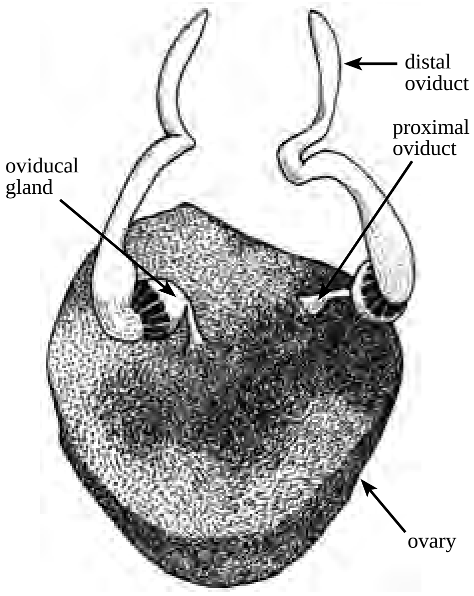


Fig. 23 Female octopus reproductive tract

Oviducal gland – Swollen glandular structure that surrounds the middle of the oviduct and secretes the external coating of the spawned eggs and produces the cement for egg or egg string attachment. This gland divides the oviduct into proximal and distal portions. It can also contain seminal receptacles for sperm storage (Fig. 23).

Papilla (pl. **papillae**) – Conical or flattened projections of skin present on the dorsal and lateral mantle, head, and arms of many incirrate octopods used in camouflage and other body displays. May consist of a single, simple digit or may possess side branches to form a tree-like structure. Depending on size and location papillae typically are defined as primary (1°), secondary (2°), tertiary (3°), etc. Large papillae over each eye are referred to as supraocular papillae, and, formerly were referred to as "cirri" (e.g. ***Eledone cirrhosa***, ***Octopus tetracirrhus***, ***Scaeurgus unicirrhus***).

Paralarva (pl. **paralarvae)** – The term for the first free-living life history stage (typically planktonic) for those cephalopods that differ in morphology and ecology from later growth stages (Fig. 24).

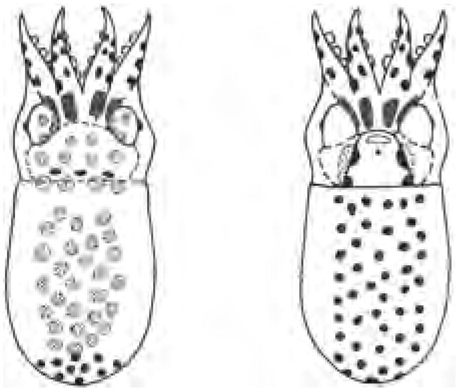


Fig. 24 Octopus paralarvae

Pelagic – **(1)** Free swimming in open ocean; **(2)** The region of the ocean away from the ocean floor.

Penis – (See **Terminal organ).**

Photocytes – Cells that produce bioluminescence in photophores.

Photophore – An organ that produces and distributes bioluminescence or 'living light', either intrinsically through biochemical reaction or extrinsically through culture of luminescent bacteria. For octopods, photophores are only known in the vampire squid, ***Vampyroteuthis infernalis***, the cirrate octopod, ***Stauroteuthis syrtensis***, and females of the pelagic octopod family Bolitaenidae (also referred to as **Light organ**).

Phylogeny – The deduced evolutionary relationships that connect living and extinct creatures. The study of the tree of evolutionary origins.

Phylum – The major, formative, principal taxonomic level; above 'Class'.

Polarity (evolutionary) – The direction of evolution. That is, one state is 'primitive' (plesiomorphic) and another is 'derived' (apomorphic).

Polarize (evolutionary) – To determine the direction, or polarity, of evolution. That is, to determine which state is 'primitive' (plesiomorphic) and which is 'derived' (apomorphic).

Posterior – Toward the closed end of the mantle; away from the head and arms.

Posterior salivary glands – Second pair of salivary glands located posterior to the buccal mass; typically much larger than the anterior salivary glands (Fig. 15).

Proximal – Situated nearest or next to the centre of the body or nearest the point of origin or attachment of a muscle or appendage (opposite of **distal**).

Pseudomorph – An ejected mass of ink and mucous that approximates the size and shape of the cephalopod that released it; i.e. a false body that fixes the attention of a predator while the cephalopod escapes.

Pseudoocellus – The term given to the pair of white oval spots, one each on the lateral arm crown between arms 2 and 3, formed by dense leucophores in the skin of certain octopuses, e.g. ***'Octopus' micropyrsus***.

Pseudophallus – (See **Terminal organ**).

Radula – The chitinous, ribbon-like band in the mouth of cephalopods (tongue equivalent), containing up to seven longitudinal rows of teeth that aid in the tearing and transport of food into the oesophagus (Fig. 25). Note: the radula is not used for drilling, this is done by the toothed **Salivary proboscis**.

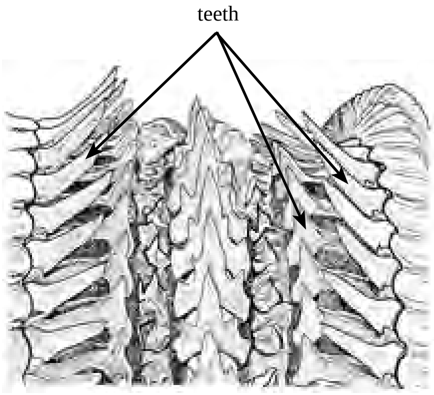


Fig. 25 Octopus radula

Recent – Geological term referring to an organism or species that is living or has lived within the past 10 000 years, or to an object formed or events that have occurred within the past 10 000 years.

Renal appendages – Structures that form the nephridium kidney. The renal appendages are out-pockets of the veins within the renal sac that are covered with renal epithelium. The renal sac empties into the mantle cavity via the renal (or nephridial) pore.

Renal pore – The opening(s) of the renal cavities into the mantle cavity, through which urine is discharged.

Reverse counter shading – Body pigmentation in some incirrate octopods that is darker on the ventral and lateral surfaces of the mantle, head, and arms, and lighter on the dorsal mantle and arms. Considered an adaptation for life on light-coloured substrates in deep waters (see also **Counter shading**).

Salivary gland(s) – Paired glands that produce salivary enzymes and, in some octopod species, paralysing toxins. Typically consists of a pair of anterior salivary glands attached to the buccal mass and a pair of larger posterior salivary glands adjacent to the oesophagus/crop (Fig 15).

Salivary proboscis – A muscular papilla that lies just below the radula in incirrate octopods. The anterior tip is covered with very small teeth. Functions as an accessory radula to drill tiny holes in mollusc shells and crustacean carapaces in order to administer paralysing or muscle-relaxing toxins.

Secondary fin – A non-muscular, fin-shaped structure found in juvenile vampire squids; lost with growth.

Secondary web – The narrow membrane that connects the primary web to the arms in some cirrate octopods; e.g. Cirroteuthidae.

Semelparous – A reproductive strategy in which females spawn once then die. Sometimes called terminal or 'big-bang' spawners. Many octopods are semelparous but in some species reproduction is prolonged (up to 50% of the ontogenesis).

Seminal receptacle – A cavity or invagination for deposition/storage of spermatangia. Present within the oviducal glands of some incirrate octopods (see **Spermatheca**).

Sepioid gills – Gills of some cirrate octopods that take the form of a swollen half orange that is superficially like the gills of sepioid cephalopods. Contrasts to the tree-like shape of typical octopod gills.

Species – Populations of animals that interbreed or are potentially capable of interbreeding in nature. Considerable debate exists over the general definition of a species and how the theoretical definition should be applied in practice.

Cephalopod species generally are defined by distinct morphological traits not exhibited by any other species. This practice is valid if interbreeding does not occur. However, the amount of interbreeding (i.e. hybridization) that actually occurs in nature and contributes to or diminishes speciation is virtually unknown in cephalopods.

Sperm bulb – See **Spermatangium.**

Sperm cord – The coiled rope of sperm that lies within the sperm reservoir of the spermatophore (Fig. 26).

Spermatangium (pl. **spermatangia**) – The encapsulated mass of sperm formed on eversion of spermatophores, often in the form of a round bulb.

Spermatheca (pl. **Spermathecae**) – Specialized structures for deposition and storage of sperm; found as pockets or invaginations of the oviducal gland in octopods. (Also referred to as **Seminal** or **Sperm receptacles**).

Spermatophore – A complex tubular structure produced by male cephalopods for encapsulating and transferring sperm to the female (Fig. 26). It typically consists of two parts: a **sperm reservoir** containing a coiled sperm cord; and an **ejaculatory apparatus** (often coiled) responsible for everting the spermatophore. On eversion the sperm cord is drawn out into an expanded bulb (**spermatangium**) that is placed on or in the female's skin or implanted in special receptacles (**spermathecae**), oviducts, oviducal glands, or the ovary.

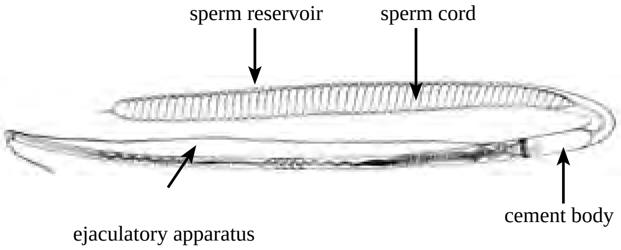


Fig. 26 Spermatophore

Spermatophore groove – Groove (sulcus) along the ventral edge of the hectocotylized arm in which spermatophores are gripped and transferred (Fig. 13).

Spermatophore storage sac – The elongate, membranous organ of males where mature, functional spermatophores are stored. It opens into the mantle cavity or directly into the water through the terminal organ (Fig. 27). **(Needham's sac** is an obsolete equivalent term not currently used to describe octopod anatomy).

Spermatophoric complex – The unit formed by the sperm duct, the spermatophoric gland, the spermatophoric duct, the accessory spermatophoric gland, the spermatophore storage sac, and the terminal organ (Fig. 27).

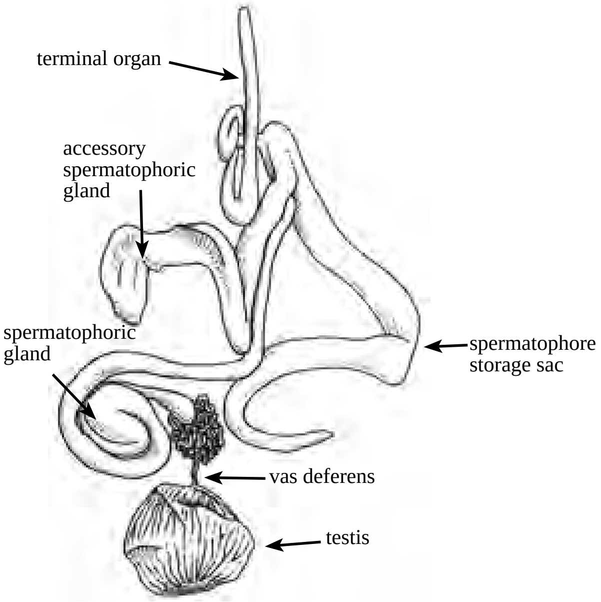


Fig. 27 Male reproductive tract in octopuses

Spermatophoric gland – Tubular organ in the male reproductive tract where the spermatophores are formed (Fig. 27).

Spermatophoric reaction – The evagination of a spermatophore with the extrusion of the sperm mass, caused by the penetration of water inside the spermatophoric cavity, where the osmotic pressure is higher.

Stalked eyes – See **Eye** (**position** and **size**).

Statocyst – A sense-organ that detects gravity, angular accelerations, and low-frequency sound. The statocyst is embedded within the cephalic cartilage and contains the **statoliths**.

Statolith – A tiny calcareous concretion in the **statocyst** that detects linear acceleration, angular acceleration, and orientation. Statoliths of many species can be ground down and used to estimate age on the basis of internal rings.

Stellate ganglion – Pair of major ganglia of the peripheral nervous system of **neocoleoid** cephalopods that controls nerves to the mantle muscles, located inside of the lateral mantle walls.

Stomach – The muscular organ of the digestive system where primary digestion occurs (Fig. 15). The stomach generally is lined with cuticular ridges to aid in grinding food, and is supplied with digestive enzymes from the digestive gland.

Stylets – A pair of rod-like, chitinous, structures considered remnants of the molluscan shell in incirrate octopods. Generally in the form of a slender, pointed rod tightly surrounded by the shell sac and buried in the mantle muscle at a dorso-lateral position. Possess a mineralized or calcareous core in some species (e.g. ***Scaeurgus***) (Fig. 28).

Fig. 28 Stylet in incirrate octopods

Subadult – Stage of maturity at which all of the characters that typically define the species are present, but the reproductive system is not mature and functional. It follows the immature stage and precedes the adult stage. A subadult stage is defined in cephalopods since the adult phase frequently is abbreviated.

Subequal – Nearly equal. Generally refers to the length of the arms when these appear to be approximately the same length.

Sucker – Muscular, suction-cup structure on cephalopod arms and tentacles (occasionally on the buccal membrane in some squids). It consists of a cup-shaped portion, the **acetabulum**, and a flat, distal ring, the **infundibulum**, which contacts the substrate or prey. Suckers can be stalked, placed on muscular rods that contract (squids and cuttlefishes), or sessile, embedded without stalks on the oral surface of the arms (octopods) (Fig. 29). In octopods suckers are counted in longitudinal rows, i.e. 1 or 2 rows.

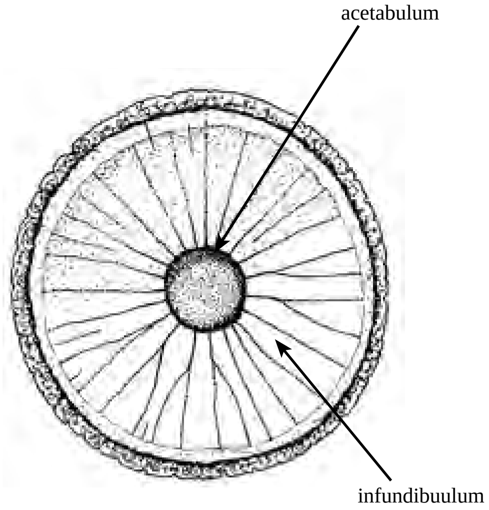


Fig. 29 Sucker

Sucker rows – The number of longitudinal rows of suckers on octopod appendages, sometimes called ‘series’. Typically 1-2 in octopods.

Superior buccal lobes – Lobes of the central nervous system that occur dorsal to the oesophagus where the latter enters the buccal mass.

Swimbladder – Gas-filled structure found in the dorsal visceral mass of the pelagic octopod, ***Ocythoe***.

Synonym – One of two or more names applied to the same taxon/species. Senior synonyms are the older valid names and junior synonyms are more recent names.

Syntype – See **Type material**.

Systematics – The classification of organisms into hierarchal groups based on evolutionary (phylogenetic) relationships.

Taxon (**Taxa**) – A taxonomic group, or unit, of any rank.

Terminal organ – The muscular, terminal portion of the male reproductive tract that transfers spermatophores to the female or into the spermatophore groove on the hectocotylized arm of the male. Alternative name for penis, as the true definition of a penis is ‘organ of insertion’ (Fig. 27).

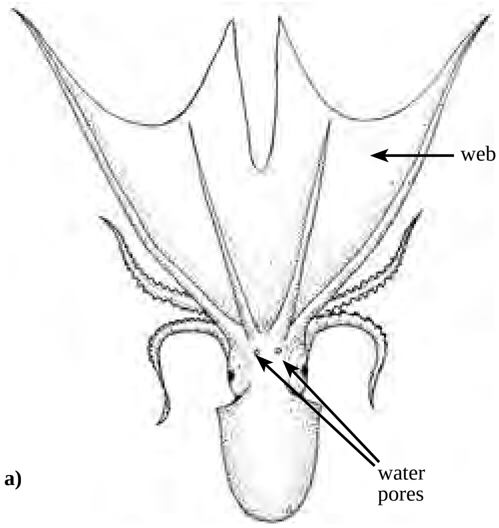
Total length (**TL**) – Length measured from the posterior margin of the mantle to the anterior or distal tip of the longest of the outstretched arms (octopods) (Fig. 11).

Type material – Formal taxonomic term referring to the original specimens (one or more) on which a scientific name of a species is formally based. **Holotype** refers to the primary specimen to which the scientific name attaches. **Paratypes** are a supporting series of specimens for the same species. **Syntypes** refer to multiple specimens that are presented in an original species descriptions as a series without a specific holotype. **Lectotype** refers to a specimen from a type series that is designated by subsequent authors as the equivalent of a holotype, where none had been designated in the original description. **Neotype** refers to a specimen designated by subsequent authors where the original type material has been lost, or destroyed.

Ventral – The lowermost or belly surface of a cephalopod, i.e. the surface on which the funnel is located. Opposite to the dorsal surface (Fig. 16).

Visceral sac – The body region posterior to the head surrounded by the mantle. The body wall that encases the viscera usually is rather thin-walled, hence the name ‘visceral sac’. Also called the ‘visceral dome’.

Water pores – **(1)** Large cephalic orifices at base of the arms of some pelagic octopods, e.g. ***Tremoctopus*** (Fig. 30a); **(2)** Historical name for eight small openings to the web pouches located at the base of the arms on the oral web of the incirrate octopod genus ***Cistopus*** (Fig. 30b).



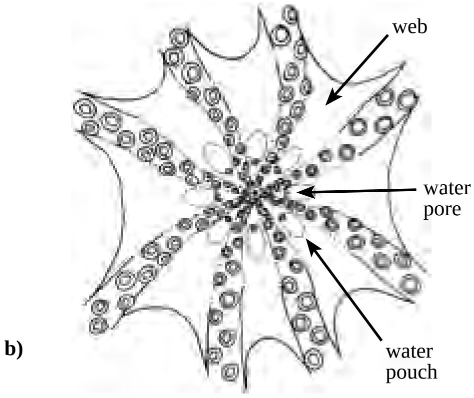


Fig. 30 Water pores

a) Tremoctopus - b) Cistopus

Web – The membranous skin and muscle sector that extends between the arms of many **octopods**, giving an umbrella-like appearance when the arms are spread out, especially conspicuous in cirrate octopods (Fig. 11b).

Web pouches – Glandular pouches, each with a muscular pore or opening situated in the oral webs between the base of each arm in the incirrate octopods genus ***Cistopus***. When full, these pouches contain mucous-like liquids. Historically called “water pouches”. There is no evidence that these pouches contain water (Fig. 30b).

Web nodule (cirrates) – A muscular spherical nodule attached to the webs of some deep-sea cirrate octopods.

White spots - Conspicuous spherical white spots consisting of dense leucophores on the dorsal mantle and head of some octopod species. The presence or absence, and location helps to define genera and species especially of octopuses.

2. OCTOPODS AND VAMPIRE SQUIDS

by Mark D. Norman, Frederick G. Hochberg and Julian K. Finn

This group contains 13 families and over 300 species including all the bottom-living (benthic) and free-swimming (pelagic) octopods, as well as the unusual vampire squid, ***Vampyroteuthis infernalis***. These cephalopods share eight arms and lack the pair of elongate feeding tentacles of the true squids and cuttlefishes. Vampire squids possess a pair of long filament-like appendages that retract into pouches between the first and second arm pair. These structures have been considered by some researchers as limb homologues (see Young, 2014), placing the vampire squid in an intermediate position between the octopods and the decapodiform cephalopods (cuttlefishes and squid). Octopodiforms lack the buccal crown found in many other cephalopods. The suckers are symmetrically rounded and lack a horny ring. They never possess hooks as found in some squid groups (e.g. family Gonatidae). Female octopodiforms lack nidamental glands, the glands that produce the jelly-like coatings of eggs in squids and cuttlefishes. The deep-sea cirrate octopods and the vampire squid have fins on the body and rows of finger-like cirri adjacent to the suckers.

This group has representatives in all oceans, from intertidal reefs to depths of at least 7 000 m.

Key to incirrates, cirrates and vampire squids

1a. Fins present on mantle . . . . → **2**
1b. Fins absent. . . . . **Incirrate octopods**

2a. Always a single pair of fins. Pits containing thread-like filament absent. Light organs absent or as highly modified suckers. Only left oviduct present in females . . . . **Cirrate octopods**
2b. Two pairs of fins in juveniles. One pair of fins in adults. Pair of pits on external (aboral) web between bases of arms 1 and 2, each contains a long thread-like filament. Pair of large light organs on posterior mantle. Both oviducts present in females . . . . **Vampire squids**

2.1 Incirrate octopods

by Mark D. Norman, Frederick G. Hochberg and Julian K. Finn

Incirrate octopods contain the familiar benthic octopuses (family Octopodidae) and seven less familiar families of pelagic octopods. They are united by 8 arms with 1 to 2 rows of sessile suckers and the absence of fins or cirri. Females of all members of this order brood their young, tending and remaining with the eggs until hatching.

Key to families

1a. Eyes telescopic, situated close together on dorsal surface of head; body and arms soft, semi-gelatinous; funnel fused to ventral mantle to form two openings to the mantle cavity (Fig. 31) . . . . . . **Family Amphitretidae (Ctenoglossan octopods)***
1b. Eyes lateral, round to oblong, not telescopic; body and arms muscular or semi-gelatinous; funnel free from ventral mantle, single opening to mantle cavity. . . . . → **2**

2a. Body and arms very soft and semi-gelatinous, transparent in all life stages . . . . → **3**
2b. Body and arms muscular, transparent only in smallest juveniles . . . . → **5**

dorsal view

Fig. 31 Amphitretidae (*Amphitretus*)

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* At the time of going to press, Strugnell *et al.* (2013) published a major revision of the familial level classification of the incirrate octopods. They propose a single ctenoglossan family Amphitretidae, containing three subfamilies Amphitretinae, Bolitaeninae and Vitreledonellinae (see that work for new taxonomic structure).

3a. Suckers in single row . . . . → **4**

3b. Suckers in double row for at least some portion of each arm (Fig. 32) . . . . **Family Alloposidae (Argonautoid octopods)**

4a. Arms longer than mantle length (Fig. 33) . . . . **Family Vitreledonellidae (Ctenoglossan octopods)**

4b. Arms shorter than mantle length (Fig. 34) . . . . **Family Bolitaenidae (Ctenoglossan octopods)**

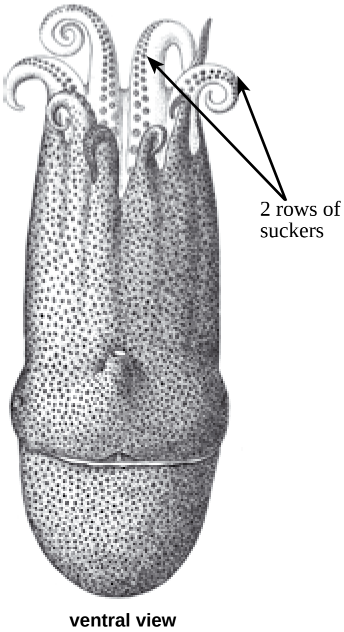

Fig. 32 Alloposidae (*Haliphron*)

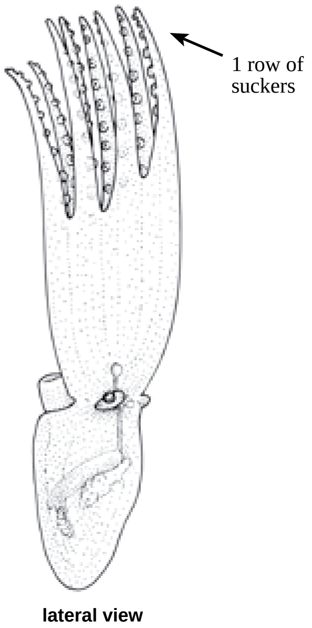

Fig. 33 Vitreledonellidae (*Vitreledonella*)

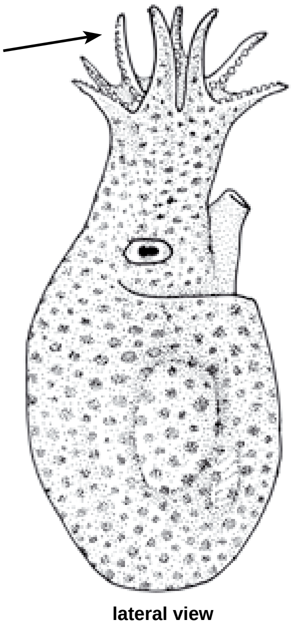

Fig. 34 Bolitaenidae (*Bolitaena*)

5a. Distinct locking apparatus present, joining inner edge of lateral mantle to funnel base. . . . . → **6**

5b. Distinct locking apparatus absent (Fig. 35) . . . . **Family Octopodidae**

6a. Female specimens . . . . → **7**

6b. Male specimens . . . . → **9**

7a. Females with drastic web modifications on dorsal arms, either joined and greatly elongated or as large flared flanges off the distal end of the dorsal arm pair; network of cartilaginous structures absent from skin . . . . →**8**

7b. Females with no obvious web modifications; network of semi-rigid cartilaginous rods present under skin on ventral mantle. (Fig. 36). . . . . **Family Ocythoidae (Argonautoid octopods)**

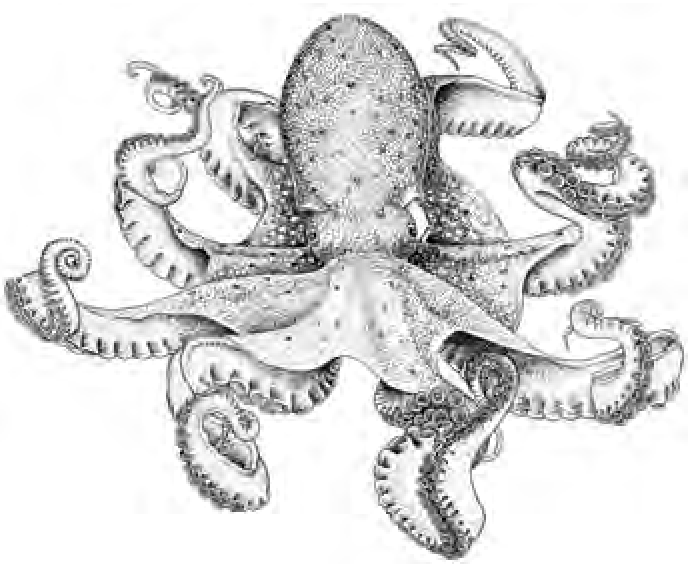

Fig. 35 Octopodidae (*Octopus*)

8a. Two dorsal arm pairs joined by greatly expanded webs that extend beyond arm tips as semi-translucent banners; external shell absent (Fig. 37) . . . . **Family Tremoctopodidae (Argonautoid octopods)**

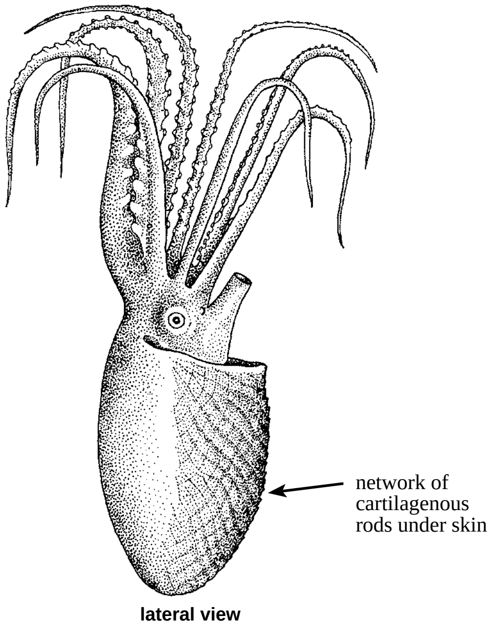

Fig. 36 Ocythoidae (*Ocythoe*)

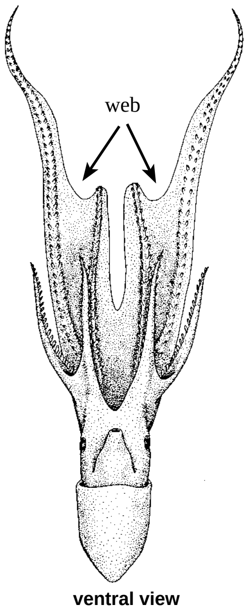

Fig. 37 Tremoctopodidae (*Tremoctopus*)

8b. Wide flange of web present on distal half of dorsal arm pair; live animal produces and resides within brittle white shell known as "paper nautilus" shell (Fig. 38) . . . . **Family Argonautidae (Argonautoid octopods)**

9a. Male with large, modified third right arm coiled within membranous pouch . . . . → **10***

9b. Male with large, modified third left arm coiled within membranous pouch. . . . . **Family Argonautidae (Argonautoid octopods)**

(* Males of the Family Alloposidae also have a modified third right arm coiled within a membranous pouch)

10a. Dorsal arms longest, joined by deep web; other arm pairs progressively shorter to shortest ventral pair. . . . . **Family Tremoctopodidae (Argonautoid octopods)**

10b. Dorsal and ventral arm pairs longer than other arms . . . . **Family Ocythoidae (Argonautoid octopods)**

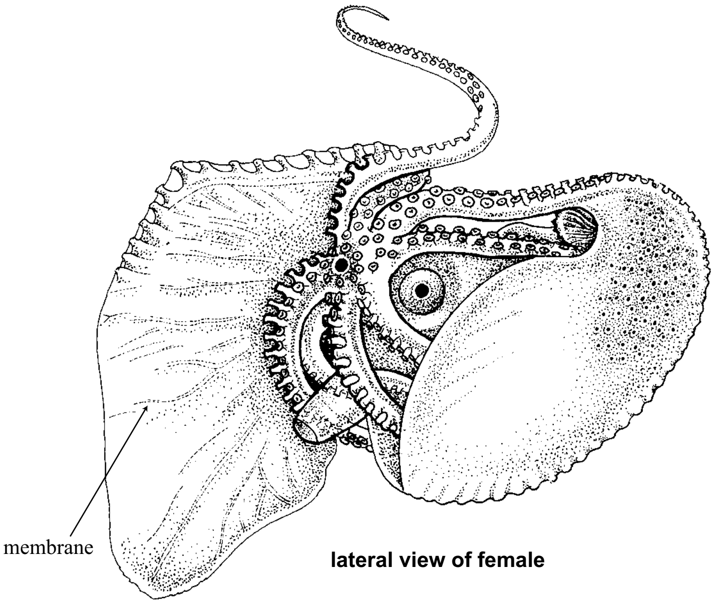

Fig. 38 Argonautidae *(Argonauta)*

2.1.1 **Family OCTOPODIDAE*** d'Orbigny, 1840 by Mark D. Norman, Julian K. Finn and Frederick G. Hochberg

Octopodidae d'Orbigny, 1840, *Mollusques Vivants et Fossils*, 1: 164.

Type Genus: ***Octopus*** *sensu stricto* Cuvier, 1797.

FAO Names: **En** — Octopuses; **Fr** — Pieuvres, Poulpes; **Sp** — Pulpitos, Pulpos.

Diagnostic Features: This family contains the vast majority of octopods, with more than 200 valid species. They are bottom-living, muscular animals with eight arms. Each arm possesses 1 or 2 rows of suckers. All species lack fins and rows of cirri adjacent to suckers. The internal shell is reduced to a pair of small rod-like stylets or is absent. One arm of the third arm pair (typically right-hand side) is modified in mature males (known as the *hectocotylized arm*). This arm bears a gutter-like groove (*spermatophore groove*) along the ventral margin of the arm and a modified arm tip (*ligula*) used to grip and pass spermatophores to the female. A funnel locking apparatus is absent.

Size: Benthic octopuses vary considerably in size from pygmy species weighing less than 1 g to giant species weighing more than 100 kg.

Geographical Distribution: Benthic octopuses occur in all oceans of the world from the equator to polar regions.

Habitat and Biology: Benthic octopuses occur from intertidal reefs to great depths (>4 000 m). The word 'benthic' means bottom-living and these octopuses live most or all of their lives on the seafloor. The juveniles of many species spend at least some time in the plankton. The adults of some species also swim in open water as a means of travelling between reefs. Octopuses occur in a wide range of habitats. Many species live on rocky or coral reefs where there is abundant cover. Some pygmy species spend most of their lives in the safety of small coral heads or kelp holdfasts. Other octopuses live on sand or mud habitats in which they can bury to hide from predators. Several groups of octopuses (particularly ***Abdopus*** and ***Ameloctopus***) forage primarily in pools on exposed reef flats during low tide. Most octopuses are night active with only a few species that emerge during daylight hours to forage. Others restrict their hunting bouts to the half light of dusk and dawn (*crepuscular*). Many octopuses are excellent at camouflage, being able to match the tones and textures of their surroundings. Some species use these colour change abilities to warn off potential predators while others mimic poisonous animals. The vast majority of benthic octopuses have well-developed salivary glands which contain strong paralysing toxins used to quickly immobilise prey. Blue-ringed octopuses (genus ***Hapalochlaena***) have salivary toxins that include tetrodotoxin, an extremely powerful toxin which has been responsible for a number of human deaths. Male octopuses possess a modified third arm, typically the third right arm. This arm, the *hectocotylus*, typically has a spoon-like tip ligula and a curved gutter or groove along its length. During mating, males insert the tip of this arm into the mantle cavity of the female and into the oviducts. Males then shunt small packets of sperm (*spermatophores*) into the proximal end of the spermatophore groove near the base of the arm; then, with muscular contractions, work them along the groove to the arm tip and thus into the female's oviduct. Females then are capable of storing one or more spermatophores until required to fertilise eggs during spawning. All female benthic octopuses brood their eggs until they hatch, diligently oxygenating and cleaning them. Most species attach eggs singly or in strings (festoons) to hard surfaces, although the females of some species (e.g. ***Hapalochlaena*** and certain ***Amphioctopus*** species) carry the egg bundles with them. The mother typically dies soon after egg hatching. Egg size in different species dictates the behaviour of the hatchlings. Species with small eggs (approximately 1 to 3 mm long) produce many tiny planktonic young which spend at least some time in the water column. Species with large eggs (10 to 40 mm long) produce few, large, "crawl-away", benthic young.

Interest to Fisheries: Octopuses are a popular food source for humans around the world, yet there is negligible information available on biology, distribution or importance to fisheries for all but a handful of species. They are harvested in a range of fisheries from subsistence catches through to valuable, large-scale commercial fisheries. The largest documented harvests are off north-west Africa and throughout Asia. They are caught by hand, with spear, on lines using baited or unbaited lures, by trawl or by using unbaited pots that the octopuses use as shelters.

Remarks: The taxonomy of this group is in a state of flux. A total of more than 350 species names have been coined but many of these are known only from their original descriptions. More recently, over 150 undescribed species have been recognized, primarily from the tropical Indian and Pacific Oceans (see Norman and Hochberg, 2005a). The majority await formal taxonomic description. In support of earlier morphological studies, recent molecular studies (e.g. Strugnell *et al.,* 2005; Guzik *et al.,* 2005) indicate that the catch-all genus ***Octopus*** contains many distinct groups, and erection (or resurrection) of numerous distinct genera is warranted. As a consequence we have presented many species under their new combinations, primarily for members of the genera ***Abdopus*** Norman and Finn, 2001 (ex "***Octopus horridus*** group"), ***Amphioctopus*** Fischer, 1882 (ex "***Octopus aegina*** group"), ***Callistoctopus*** Taki, 1964 (ex "***Octopus macropus*** group") and ***Enteroctopus*** Rochebrune and Mabille, 1889 (ex "***Octopus dofleini*** group"). The valid genus ***Octopus*** (***Octopus*** *sensu stricto*) is here considered to be restricted to members of the "***Octopus vulgaris*** group" (Guzik *et al.,* 2005). Until a detailed generic revision is undertaken, we have provisionally retained a number of unplaced taxa under the generic designation '***Octopus***', denoted by quotation marks.

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* At the time of going to press, Strugnell *et al.* (2013) published a major revision of the familial level classification of the incirrate octopods. They establish six families: Octopodidae, Bathypolypodidae, Eledonidae, Enteroctopodidae, Megaleledonidae and Amphitretidae, the latter containing three subfamilies Amphitretinae, Bolitaeninae and Vitreledonellinae (see that work for new taxonomic structure).

Literature: Robson (1929a, 1932), Norman and Hochberg (2005a).

Key to genera in the family Octopodidae†

The following key treats clearly defined or named genera within the family Octopodidae. The generic placement of many species within this family remains unresolved and thus may not be covered by this key. Such taxa are treated in the species treatments below under the general category 'unplaced ***Octopus***' (designated as '***Octopus***'). The same applies for the genus ***Eledone*** in relation to the Australian species, treated here as ***'Eledone' palari***. Genera designated with an asterisk (*) are in urgent need of revision.

Notes for key and species treatments

Measurements based on preserved material: Due to the soft-bodied nature of octopods with their absence of a significant internal skeleton, the body and arms are prone to considerable distortion when fresh (unpreserved). This often manifests as extreme arm elongation when musculature starts to decay in fresh specimens. As a result it is necessary to "fix" reference and voucher material, where the animals are chemically preserved. The best method is to place specimens in a solution of 5-10% formalin in seawater, with a liquid volume of at least five times the volume of the specimen. The specimen is kept in this solution for at least two weeks and then rinsed and transfered to 70% ethanol for long-term preservation. All measurements presented here are based on material fixed by this method.

Note: Formalin cross-bonds DNA molecules, severely limiting the capacity to extract molecular sequence data. It is recommend that tissue samples (i.e. mantle or arm muscle) are taken and preserved separately (frozen and/or placed in 100% ethanol) before fixing whole reference specimens in formalin.

Male diagnostic features: As for many cephalopod groups, octopus taxonomy relies heavily on the reproductive characters of mature males, particularly structures of the modified reproductive arm (hectocotylized arm). Female material is more difficult to identify.

Arm length: Use of relative arm lengths requires intact arms. A sudden reduction in sucker diameter at any point along an arm generally is an indicator of partial arm regeneration. Such arms should not be considered in assessing relative arm lengths.

Funnel organ: The funnel organ is a pad (or a series of pads) of glandular tissue in the skin on the inside surface of the funnel. In frozen or poorly preserved material this structure can be indistinct. A temporary dye such as methylene blue can be used to distinguish the outline and thus shape of this organ.

In the following key, an asterisk (*) shows genera requiring detailed taxonomic revision

1a Suckers in single row or as slight zigzag in live animals or contracted specimens . . . . **→2**
1b. Suckers clearly in two rows on all arms . . . . **→14**

2a. Ink sac present. . . . . **→3**
2b. Ink sac absent . . . . **→10**
[**Note:** The genus ***Bathypurpurata*** Vecchione, Allcock and Piatkowski, 2005* is a pygmy octopus from deep waters off the Antarctic Peninsula (500 m) that possesses a single row of suckers. It is not included in this key as it is known only from a single female specimen (mantle length 23 mm) and the original description does not provide details of radula and ink sac].

3a. Webs greatly enlarged at distal ends to form wing-like vanes (single species restricted to deep waters of western Indian Ocean) . . . . ***Velodona***
3b. Web margins absent or as narrow bands to arms tips, not expanded in distal portion. . . . . **→4**

4a. Mature males with distinct ligula and calamus; non-hectocotylized arm tips with or without sucker modification **→5**
4b. Mature males with hectocotylized arm tip that lacks a distinct ligula and calamus, or has a normal ligula but no calamus; suckers highly modified on tips of normal arms of mature males - as ridges, stellate suckers or frills of papillae (Atlantic Ocean) . . . . ***Eledone****
[includes ***Aphrodoctopus*** Roper and Mangold, 1992, and excludes ***'Eledone' palari*** Lu and Stranks, 1992, from Australia].

5a. Webs very deep (40-70% of arm length); body and dorsal arm crown with paired and widely spaced, large, erectile, papillae; non-hectocotylized arms of mature males with fleshy pads of spongiform tissue; thick fleshy skin ridge around lateral margin of mantle (single species from deeper Australian continental slope) . . . ***'Eledone' palari***
5b. Webs moderate to deep (<40% of arm length); paired and widely spaced, large, papillae absent; non-hectocotylized arms of mature males with suckers unmodified to arm tips; skin ridge around lateral margin of mantle present or absent. . . . . **→6**

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†At the time of going to press, Strugnell *et al*. (2013) published a major revision of the familial level classification of the incirrate octopods. They establish six families: Octopodidae, Bathypolypodidae, Eledonidae, Enteroctopodidae, Megaleledonidae and Amphitretidae, the latter containing three subfamilies Amphitretinae, Bolitaeninae and Vitreledonellinae (see that work for new taxonomic structure)."

6a. Radula normal, with 9 elements, 7 rows of teeth plus marginal plates . . . . →**7**
6b. Radula reduced to 3 elements, a single row of highly modified teeth with vane-like lateral wings plus marginal plates (single species restricted to west and southwest Atlantic Ocean) . . . . ***Vosseledone****

7a. Funnel organ as W, UU or V V-shaped pads; skin smooth or sculptured . . . . →**8**
7b. Funnel organ as four distinct short longitudinal pads (IIII); all dorsal and lateral body surfaces covered in large branched papillae (single species restricted to central western Atlantic Ocean) . . . . ***Tetracheledone****

8a. Small to moderate species, never attaining large sizes; head width close to or greater than mantle width; gills with 6 to 11 lamellae per demibranch . . . . →**9**
8b. Large species (up to 14 kg) with loose soft gelatinous skin; head distinctly narrower than mantle; gills with 10 to 11 lamellae per demibranch (single, large species restricted to Antarctic waters) . . . . ***Megaleledone***

9a. Ligula groove without transverse ridges; lower beak without sharp modified tip, rostrum curved ventrally in lateral profile; posterior salivary glands approximately equal in length with buccal mass; stylets present (Antarctic waters) . . . . ***Pareledone***
9b. Ligula groove with distinct transverse ridges; lower beak with sharp modified tip, rostrum straight or slightly turned dorsally in lateral profile; posterior salivary glands approximately twice length of buccal mass; stylets absent (single species restricted to Antarctic waters) . . . . ***Adelieledone***

10a. Skin beset with raised conical or composite papillae hardened with cartilaginous inclusions, less obvious in frozen material (deep-water species) . . . . ***Graneledone***
10b. Skin lacks hardened papillae, sculpture soft or skin completely smooth . . . . →**11**

11a. Arms short, less than 2 times mantle length; posterior salivary glands large, more than half buccal mass length . . . →**12**
11b. Arms of moderate length, approximately 2 to 3 times mantle length; posterior salivary glands small to tiny, significantly less than half buccal mass length . . . . →**13**

12a. Radula with 9 elements, 7 rows of teeth, lateral teeth flattened into broad plates; skin smooth (single species known only from deep water in the Tasman Sea) . . . . ***Microeledone***
12b. Radula with reduced number of elements, 3 to 5 rows of teeth; skin covered in low regular rounded papillae (deep-water species) . . . . ***Thaumeledone****

13a. Radula with unicuspid rachidian tooth, small first lateral teeth, wide second lateral teeth with single cusp, elongate (conical) marginal teeth and marginal plates (1 to 2 Antarctic species) . . . . ***Bentheledone****
13b. Radula with all teeth in transverse series of approximately similar size and shape, marginal plates absent (single Antarctic species) . . . . ***Praealtus****

14a. Small short-armed octopuses with repeated colour pattern of iridescent blue lines or rings over body, arms and webs, iridescent markings fade to white in preserved material (Indo-West Pacific region) . . . ***Hapalochlaena***
14b. Small to large octopuses without repeated iridescent markings over body, arms and webs (some species possess a single pair of iridescent rings within ocelli, one on each side of the arm crown on the web between the bases of arms 2 and 3) . . . . →**15**

15a. Ink sac present . . . . →**16**
15b. Ink sac absent . . . . →**33**

16a. Arms long (>4 times mantle length); arm autotomy present, evident as multiple arms severed or regenerating from set plane near arm base . . . . →**17**
16b. Arms short to long; arm damage and regeneration not at set plane at arm base . . . . →**21**

17a. Second arm pair longest; large longitudinally oriented crescent markings present on dorso-lateral posterior mantle; enlarged suckers absent (restricted to Central Americas) . . . . ***Euaxoctopus***
17b. Third or fourth arm pair longest; large longitudinally oriented crescent-shaped markings on mantle absent, enlarged suckers present or absent . . . . →**18**

18a. Fields of enlarged suckers present on arms 2 and 3 of mature males (Indo-West Pacific only) . . . . . ***Abdopus***
18b. Enlarged suckers absent in mature males . . . . →**19**

19a. Gills with 11 lamellae per demibranch (shallow-water species of Atlantic Ocean and potentially tropical Indo-West Pacific) . . . . ***Macrotritopus****
19b. Gills with less than 11 lamellae per demibranch . . . . →**20**

20a. Eyes small and stalked, mantle and arms with regular and defined colour pattern of white bands and spots over brown to red background colour; gills with 5 to 7 lamellae per demibranch; single blunt and rounded large papilla over each eye (single species, Indo-Malayan Archipelago and west Pacific) . . . . ***Wunderpus***

20b. Eyes of moderate size, not obviously stalked, colour pattern variable from banded to even coloration; white U-shape marking on posterior dorsal mantle; gills with 9 lamellae per demibranch; two elongate and sharp papillae over each eye (single species, Indo-West Pacific region) . . . . ***Thaumoctopus***

21a. Dorsal arms distinctly longer than remaining arms, arm formula 1>2>3>4 . . . . **→22**

21b. Arms approximately equal in length or lateral/ventral arms longest . . . . **→23**

22a Series of water pouches on oral web in ring around mouth, small muscular pore of each pouch opening to exterior around level of 3rd to 6th proximal suckers; ligula tiny in mature males, calamus absent or present (3 shallow-water species in Indo-West Pacific) . . . . ***Cistopus***

22b. Water pouches and pores absent; ligula and calamus well-developed in mature males (shallow-water tropical and temperate species worldwide) . . . . ***Callistoctopus***

23a. Ligula with transverse ligula groove containing small teeth-like papillae; raised skin ridge present on lateral mantle (single deepwater species from 200 to 400 m in Western Pacific). . . . . ***Galeoctopus***

23b. Ligula groove longitudinal, without teeth-like lugs; lateral mantle ridge present or absent. . . . . **→24**

24a. Left third arm of males hectocotylized . . . . **→25**

24b. Right third arm of males hectocotylized . . . . **→26**

25a. Mantle opening narrow, one third or less of body circumference, fitting close to funnel; paired narrow to elongate papillae over each eye; skin loose and semi-gelatinous with regular small, pavement-like patches; skin ridge absent from lateral mantle; body markings absent (deep water species, 200 to 800 m) . . . . left-handed species of ***Pteroctopus****

25b. Mantle opening moderate to wide, approximately one half of body circumference; single large papilla over each eye; lateral mantle skin ridge present; two pairs of dark spots visible on mantle of live and well-preserved material (deep water species, 200 to 800 m). . . . . ***Scaeurgus***

26a. Web margin extends as thin membrane along ventral face of all arms, flared towards distal tips . . . . **→27**

26b. Web margins not expanded at distal tips of arms . . . . **→28**

27a. Mantle opening narrow, significantly less than 50% of body circumference, fitting close to funnel; paired narrow elongate papillae over each eye; skin loose and semi-gelatinous with regular small, pavement-like patches; body markings absent (deep-water species worldwide, 200 to 800 m) . . . . . right-handed species of ***Pteroctopus****

27b. Mantle opening moderate to wide, around 50% of body circumference, papilla over eye single, robust, never elongate, skin firm (not semi-gelatinous), skin sculptured with evenly spaced small rounded papillae; markings over orange brown base dorsally, cream ventrally (deep-water species of western Pacific and eastern Indian Oceans, 300 to 600 m) . . . . ***Histoctopus***

28a. Giant species (to >3 m total length); skin on mantle in loose branching and coalescing longitudinal folds (as lines in preserved specimens); ligula very long (to accommodate giant spermatophores up to several times mantle length) (at least 3 species in temperate and subtropical waters worldwide) . . . . ***Enteroctopus****

28b. Small to large species; skin not in loose longitudinal folds; spermatophores small to long, never giant. . . . **→29**

29a. Skin firm, texture of regular papillae or patch and groove system, colour pattern variable, funnel organ W-shaped . . . . **→30**

29b. Skin relatively smooth without regular papillae or patch and groove system, colour pattern variable, funnel organ W-shaped or UU-shaped. . . . . **→32**

30a. Arms typically 2 to 3 times mantle length . . . . **→31**

30b. Arms typically 3 to 5 times mantle length, sculpture on oral surface of dorsal web not a continuation of mantle and aboral web sculpture; colour patterns of dark leading arm edges absent; four large primary papillae (round in cross section) in diamond arrangement on dorsal mantle; stylets present (shallow-water species typically of temperate waters worldwide) . . . . ***Octopus*** *sensu stricto*

31a. Skin sculpture of dorsal mantle, head and webs continues onto oral surface of shallow dorsal web; colour patterns often incorporate dark leading edges along dorso-lateral face of arms 1 to 3; four short longitudinal ridges of skin in diamond arrangement on dorsal mantle (shallow-water species of tropical and subtropical waters worldwide) . . . . ***Amphioctopus***

31b. Skin sculpture not extending to oral surface of web; skin texture as dense complete cover of small compound papillae over entire dorsal and ventral surfaces; dark leading edges of arms absent; larger papillae or ridges on dorsal mantle absent; (single deep-water species from northern Pacific Ocean) . . . . ***Sasakiopus***

32a. Eyes large and bulging, funnel organ W-shaped, gills with 6 to 8 lamellae per demibranch (three central American shallow-water pygmy species) . . . . ***Paroctopus****

32b. Eyes small, head relatively flush with spherical mantle, funnel organ UU-shaped, gills with 8 to 10 lamellae per demibranch (single shallow-water Indian species). . . . . ***Macrochlaena****

33a. Arms very long (6 to 10 times mantle length) and extremely thin, with regular equal width bands of brown and white, arms equal in length and thickness; webs minute (<5% of arm length); eyes tiny; branchial hearts visible through thin mantle wall, body uniform pink to brown in colour (single intertidal species, northern Australia). . . . . ***Ameloctopus***

33b. Arms unequal in length; eyes moderate to large; webs >5% of arm length; mantle walls not semi-transparent . . →**34**

34a. Skin white, lacking any pigmentation; iris of eye absent; eyes small (single species from deep-sea hydrothermal vents) . . . . ***Vulcanoctopus***

34b. Skin with at least some pigmentation (i.e. oral webs, ventral and/or dorsal surfaces); iris present; eyes moderate to large. . . . . →**35**

35a. Funnel organ with four short rounded longitudinal pads (two poorly known deep-water Indian Ocean species) . . . . ***Teretoctopus****

35b. Funnel organ W-, UU- or V V-shaped . . . . →**36**

36a. Calamus of mature males very large, over half ligula length (single species, southern Australia) . . . ***Grimpella****

36b. Calamus small to moderate, much less than half ligula length. . . . . →**37**

37a. Ligula of mature males large and spoon-shaped, deeply excavated with a number of well-defined transverse ridges (laminae) (deep-water species of Arctic and Atlantic Ocean) . . . . ***Bathypolypus***

37b. Ligula moderate to large, elongate, typically with closed ligula groove; raised laminae absent (over 25 deep-water worldwide) . . . . ***Benthoctopus**** and ***Muusoctopus**** (see **Remarks** in these genera)

Octopus *sensu stricto* Cuvier, 1797

Octopus Cuvier, 1797, *Tableau Elémentaire de l'Histoire Naturelle des Animaux*, 380.

Type Species: *Octopus vulgaris* Cuvier, 1797, by absolute tautonymy (see ICZN Opinion 233; 1954).

Diagnostic Features: Small to large shallow-water species. Mantle muscular, globose to rounded ovoid. Stylets present, long, chitinous (non-mineralized). **Arms muscular, medium length, 3 to 5 times mantle length. Lateral arms longest (typically 2>3>4>1 or 3>2>4>1).** Arm autotomy at distinct plane absent. Webs moderate to deep, deepest around 20 to 30% of longest arm. **Webs deepest on lateral arms, webs between dorsal arms shallowest (typically B=C=D>E>A).** Interbrachial web pouches absent. Suckers in two rows. **Enlarged suckers present in mature males, typically on arms 2 to 3, sometimes on arm 4.** Slightly enlarged suckers on same arms in mature females. Funnel organ W-shaped. Gills with 6 to 11 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands moderate to large. Distinct crop present as side-branch off oesophagus. **Ink sac present.** Anal flaps present. Third right arm of male hectocotylized, slightly shorter than opposite arm. Ligula and calamus present. Spermatophores unarmed. Eggs small to large, stalks twisted into chords or braids, eggs always laid in festoons. Colour patterns variable. False eye-spots (ocelli) present in some species, in several species with complex blue iridescent ring. **Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). Skin with distinct patch and groove system that forms a dark trellis or reticulate pattern. Fixed diamond pattern of four large erectile primary papillae in midregion of dorsal mantle.** One long primary papilla at posterior end of dorsal mantle, one large and two smaller primary papillae over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 400 mm; total length to around 1.8 m; body weight to over 20 kg. Common at smaller size (250 mm ML)

Geographical Distribution: Predominantly found in temperate waters of all oceans; several species found in warmer waters (Fig. 39).

Habitat and Biology: Typically subtidal, associated with rocky reefs in temperate waters and coral reefs in tropical waters.

Remarks: The genus ***Octopus*** to date has been treated as a catchall genus in which the vast majority of described octopuses have been placed; i.e. any species that possess two rows of suckers and an ink sac. Recent molecular studies (e.g. Guzik *et al*., 2005; Strugnell *et al*., 2005) have demonstrated that this genus is *polyphyletic*, meaning it is an artificial grouping of multiple groups of unrelated species. A major taxonomic revision of the classification of octopuses is currently underway. As a consequence we treat the core genus ***Octopus*** (known as "***Octopus*** *sensu stricto*", previously treated as the "***Octopus vulgaris*** group") as the group of species listed immediately below. Other species currently placed in the genus ***Octopus***, but awaiting generic revision, are treated in the later section designated by parentheses on the generic name (i.e. '***Octopus***') and are treated separately.

The species name ***Octopus vulgaris*** (meaning “common octopus”) was originally described by Cuvier (1797). No type specimen was designated and it is presumed he based his description on specimens from the Mediterranean Sea, where this species is the most commonly encountered octopus. Considered here as ***Octopus vulgaris*** *sensu stricto*, this form has a geographic range from the northeast Atlantic Ocean, south to the midcoast of western Africa, as well as to offshore central Atlantic islands. This taxon supports large commercial fisheries, particularly off northwest Africa (see World Octopod Fisheries chapter).

In addition to this form, the species name ***Octopus vulgaris*** is also currently applied to at least four additional, morphologically similar, but unresolved taxa with disjunct geographical distributions across tropical, subtropical and temperate waters worldwide. All are of high profile and high fisheries value. These species typically occur on, or in association with, reef habitats (rock and/or coral) in relatively shallow coastal waters. All taxa produce small eggs with planktonic hatchlings capable of wide dispersal across open ocean, thus potentially enabling gene flow between the disjunct distributions of at least some forms.

A number of studies have used molecular tools to seek insights into the relationships of the octopuses being treated under the name ***Octopus vulgaris***. Söller *et al.* (2000) and Warnke *et al.* (2000, 2002) analyzed COIII, RAPD and 16S sequences to examine ***vulgaris***-like taxa on both coasts of the Americas. These studies recognized ***O. mimus*** of the eastern Pacific Ocean as distinct, as well as more than one species being treated under the name ***O. vulgaris*** on the northeast coast of South America. Warnke *et al.* (2004) analyzed the mitochondrial genes 16S and COIII of taxa being treated under the name ***O. vulgaris*** in the Atlantic Ocean, South Africa and northwest Pacific Ocean (Japan and Taiwan Province of China). They concluded that two taxa occurred off northeast Brazil and that all other material examined supports a single ***O. vulgaris*** species worldwide. Leite *et al.* (2008) used morphological and molecular data to describe one of the Brazilian taxa as a new species, ***O. insularis***. Guerra *et al.* (2010) used mitochondrial genes COI and COIII to identify specimens from Amsterdam and Saint Paul islands in the southern Indian Ocean as a range extension for a single widely distributed ***O. vulgaris***.

Due to the significant geographic and temperature boundaries that exist between the geographical distributions of these forms (particularly for the east Asian “***vulgaris***”) and the absence of any plausible gene flow mechanisms, we choose to treat these forms individually below until their relationships are better resolved. This approach also enables regional knowledge and literature to be presented. The geographically disjunct forms (Fig. 39) are treated here under the following names:

Form:	**Geographical Distribution:**
Octopus vulgaris *sensu stricto*	Mediterranean Sea, central and north-east Atlantic Ocean
Octopus “***vulgaris***” type I	Tropical western central Atlantic Ocean
Octopus “***vulgaris***” type II	Subtropical south-west Atlantic Ocean: Brazil
Octopus “***vulgaris***” type III	Temperate South Africa and southern Indian Ocean
Octopus “***vulgaris***” type IV	Subtropical/temperate east Asia

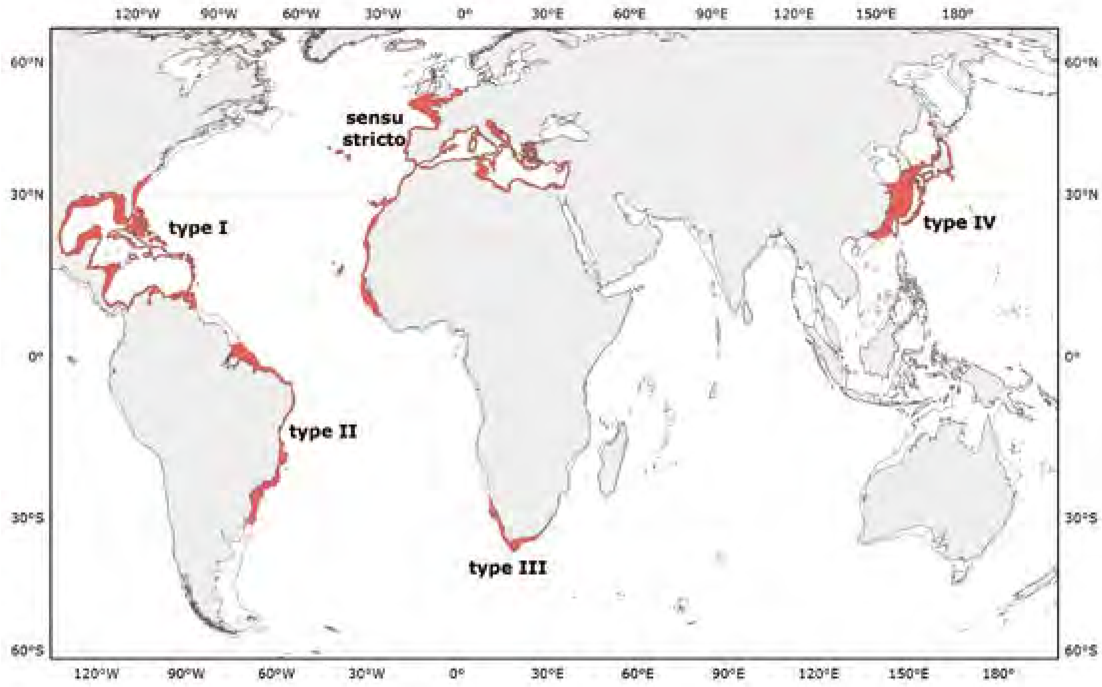


Fig. 39 Distribution of members of the *Octopus vulgaris* complex

🟥 Known distribution

As detailed morphological studies have not been undertaken on these forms for most regions, a morphological diagnosis and illustrations are presented only for ***Octopus vulgaris*** *sensu stricto*.

This species complex is in urgent need of revision, one that combines both morphological and molecular analyses, including a wider range of genes and techniques. ***Octopus insularis*** (Brazil), ***O. maya*** (Gulf of Mexico), ***O. mimus*** (western South America) and ***O. tetricus*** (eastern Australia and northern New Zealand, the latter under the synonym ***O. gibbsi***) all are closely related forms.

Literature: Söller *et al.* (2000), Warnke *et al.* (2000, 2002, 2004) Guzik *et al.* (2005), Strugnell *et al.* (2005), Leite *et al.* (2008), Guerra *et al.* (2010).

Octopus vulgaris Cuvier, 1797

Fig. 40; Plate VI, 46

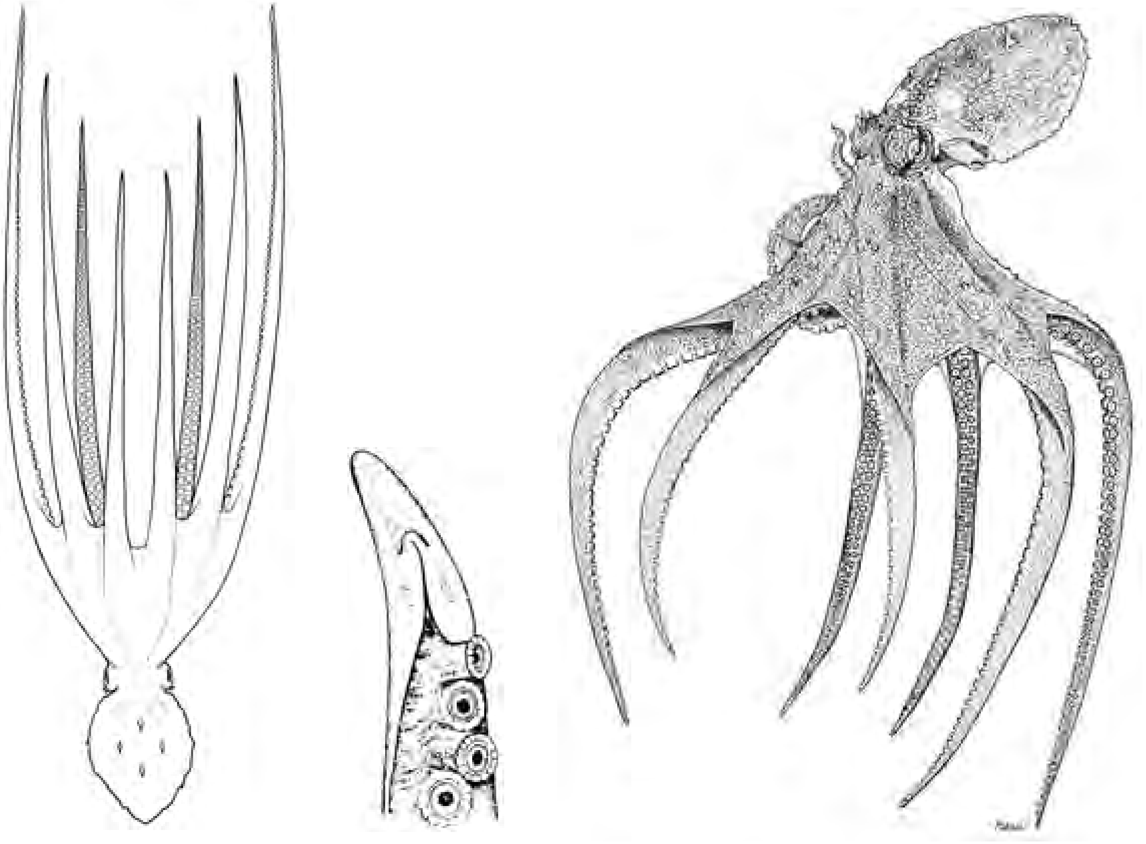
Octopus vulgaris Cuvier, 1797, *Tableau Elémentaire de l'Histoire Naturelle des Animaux*, 380. [Type locality: Presumed western Mediterranean Sea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Common octopus; **Fr** — Pieuvre; **Sp** — Pulpo común.

Diagnostic Features* : Moderate to large muscular species. Mantle broadly oval to saccular. Arms long (4 to 5.5 times mantle length), robust, taper to narrow rounded tips. Lateral arms distinctly longer than median arms; arm formula typically 3>2>4>1 or 3=2>4>1. Arm autotomy at distinct plane absent. Webs of moderate depth (deepest 15 to 20% of longest arm). Web deepest on lateral arms, typically C>D>B>E>A, often variable but sector A always shallowest.



dorsal view (outline) **hectocotylus** **dorsolateral view**

Fig. 40 *Octopus vulgaris*

Interbrachial web pouches absent. Two rows of suckers on each arm. **In larger animals, around 220 to 320 suckers on each normal arm. Both sexes with 2 to 3 enlarged suckers on lateral arms at level of 15th to 19th proximal suckers, larger in males** (males: 18 to 21% of mantle length; females: 10 to 12%). **Gills with 9 to 11 lamellae per outer demibranch.** Funnel organ W-shaped. Radula with 9 elements, 7 rows of teeth plus marginal plates. Rachidian tooth of radula with 1 to 2 lateral cusps, migrating from medial to lateral position over 2 to 5 rows. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Third right arm of male hectocotylized, shorter than opposite arm (75 to 82%), bearing 140 to 170 suckers. Ligula small to minute (1.2 to 2.1% of arm length), tip narrow, transverse striations faint. Calamus distinct, relatively long, 47 to 52% of ligula length. Terminal organ (penis) linear and moderately long (15 to 21% of mantle length), with small, rounded diverticulum. Spermatophores of moderate size (31 to 81% of mantle length). Mature eggs around 2 mm long, 1 mm wide; stalk about 2.5 times egg length. **Colour:** Colour in life variable from yellow brown, to red brown, dark brown or grey. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). False eye-spots (ocelli) absent. **Sculpture: Skin texture of regular patch and groove with small circular patches**. Four large erectile papillae in diamond arrangement on dorsal mantle; 1 to 2 supraocular papillae over each eye. Skin ridge around lateral margin of mantle absent. * Based on Mediterranean and north-east Atlantic material (see **Remarks** above).

Size: Mantle length to 400 mm; total length to around 1.8 m; body weight to over 20 kg. Common at smaller size (250 mm ML).

Geographical Distribution: Mediterranean Sea: Western and eastern basins, Adriatic Sea. Eastern Atlantic Ocean: South coast of England; north-west and west coast of Africa; Azores, Canary Islands and Cape Verde Islands. Records from western Atlantic Ocean (Caribbean Sea and northern South America), Southern Atlantc Ocean, South Africa, Indian Ocean and east Asia are discussed separately below (Fig. 39).

Habitat and Biology: This species has been reported from depths ranging from 0 to 250 m, but typically occurs shallower than 100 m. The Mediterranean and northeastern Atlantic form is typically an intertidal to shallow subtidal species that lives on the continental shelf on rocky, sandy or muddy substrates. This species is primarily night active, typically spending daylight hours within a den. Captive animals have been found to shift to at least some day activity, often in response to visual detection of prey. Dens can consist of pre-existing crevices in rocky reefs and rubble or can be constructed by the octopus in softer sediments, sometimes incorporating loose rocks or shells. Dens can be relatively permanent or temporary refuge. Behavioural studies have found high movement of individuals between lairs, often in association with mating behaviour.

This species feeds by tactile probing for prey by the dorsal arm pairs or by enveloping rocks within the arm crown and webs and using the arm tips to detect and flush prey. This species feeds on a wide range of live prey, from crustaceans (typically crabs and lobsters), to fish (when they can be caught), to a range of shelled molluscs. The latter group typically are extracted by drilling through the shell with the toothed salivary papillae to paralyse/relax the occupant. Cannibalism also has been recorded for this species.

A wide range of predators prey on this species including many fishes such as serranid groupers, wrasses and eels, as well as sharks. Seals would have been historical predators of this species across its range.

Reproductive behaviour is well documented. In a number of regions, inshore migrations occur prior to breeding (Mediterranean Sea and northwest Africa). There is no pair formation, as both sexes mate with multiple partners. Mating consists of the male approaching a female with little display or courtship, and inserts the tip of the third right arm into the female' s mantle cavity and oviduct. The male then passes small sperm packets (spermatophores) along the sperm groove gutter of this arm and deposits them in the females mantle cavity. Males produce large numbers of spermatophores (in the hundreds) from relatively early life cycle stages. Females mate while immature and can store sperm within the oviducal glands to later fertilise their eggs.

At the time of egg laying, females retreat to a sheltered den, often partially enclosing the entrance with rocks or debris. They produce between 100 000 and 500 000 eggs, which are bound together in strings (festoons) and cemented to the roof of the den. The female then remains with the eggs, constantly ventilating and stroking the eggs to provide oxygenated water and prevent algal/bacterial growth on the surface of the eggs. She typically does not feed during this entire period, which can take up to 4-5 months in cool waters. Over this period, the female digests her own musculature as an energy source and can lose a third or more of her body weight. As the hatchlings emerge, the female weakens and dies. All females die after a single brooding event.

The duration of egg development to hatching is temperature-dependent and occurs faster in warmer waters. Hatchlings emerge at around 1-2 mm in length, then immediately swim into the water column to commence a planktonic phase. The hatchlings are known as paralarvae and are transparent, with only a few, simple, large chromatophores and short arms bearing few suckers. Paralarvae swim using jet propulsion of water through the funnel and they are typically night-active, hiding in deeper waters during the day and swimming up towards surface waters at night. Paralarvae feed primarily on crustacean larvae but will also take a wide range of live and inert prey in captivity. The duration of this planktonic phase in the wild is not known but is estimated to be in the order of weeks to months, again dependent on the temperature and other environmental conditions, including availability of suitable habitat for settlement. While in this planktonic phase, oceanographic conditions can play significant roles in recruitment, dispersal and distribution of the species, which have been well documented off the northwest African coast.

On settlement, juveniles metamorphose into a form more typical of the adults, with well-developed arms equipped with numerous suckers and complex skin sculpture and chromatophores. They then commence a cryptic benthic lifestyle. Longevity of this species has been estimated in the range of one to two years.

Interest to Fisheries: This highly prized octopus is taken by amateur fishers and in small to large-scale harvests throughout its range. The greatest fishery effort occurs off northwest Africa where it constitutes the largest single species octopus fishery in the world (see World Octopus Fisheries chapter). ***Octopus vulgaris*** is one of the most valuable octopod species throughout the Mediterranean Sea, where it is marketed mostly fresh or frozen virtually in every fish market.

Local Names: GERMANY: Gemeiner Krake; GREECE: Chtapodi; ITALY: Polpo comune, Polpo verace, Polpo; PORTUGAL: Polvo; SPAIN: Pulpo.

Remarks: Microsatellite markers have been identified to aid in further investigating population/stock structure for this species complex (Greatorex *et al.,* 2000).

Due to the high economic value of this species, considerable effort has been made to investigate aquaculture potential (Vaz-Pires *et al.,* 2004). Primary challenges include housing conditions, diet and raising hatchlings. Optimum temperatures, salinities and densities have been examined in detail (Miliou *et al.,* 2005, Domingues *et al.,* 2010, Delgado *et al.,* 2011, García García *et al.,* 2011). Feeding issues include selection of appropriate diet (Aguado Giménez and García García 2002, Biandolino *et al.,* 2010, Hormiga *et al.,* 2010, Petza *et al.,* 2011), including dead fish and crustaceans (Pham. and Isidro 2009, Domingues *et al.,* 2010), and artificial diets (Valverde *et al.,* 2008, García *et al.,* 2011).

The hatchling stage has been extremely difficult to culture through to the benthic settlement phase, with considerable effort directed towards a food source for the earliest stages (Navarro and Villanueva 2003, Villanueva *et al.,* 2004, Carrasco *et al.,* 2006, Villanueva and Bustamante 2006, Iglesias *et al.,* 2007, Villanueva *et al.,* 2009, De Wolf *et al.,* 2011, Feyjoo *et al.,* 2011, García-Garrido *et al.,* 2011). The brine shrimp, *Artemia*, has been widely investigated (Villanueva *et al.,* 2002b, Iglesias *et al.,* 2004, Iglesias *et al.,* 2006, Seixas *et al.,* 2008, 2010a, b).

Perhaps due to these difficulties, rearing of wild-caught juveniles also has received considerable interest, again due to the potential for high economic returns for adult octopuses. Offshore cages suspended below rafts have been the primary method (Oltra *et al.,* 2005, Chapela *et al.,* 2006, Rodríguez *et al.,* 2006). Diet has included crabs and fishes (García García and Aguado-Giménez 2002, García García and Valverde 2006). Different stocking densities also have been trialed (García García *et al.,* 2009).

Construction of artificial reefs has been proposed as a mechanism for increasing octopus population density and hence increased harvests (Ulas *et al.,* 2002).

Literature: Wodinsky (1972), Nixon (1979), Guerra (1981), Ambrose and Nelson (1983), Mangold (1983a), Wells *et al.* (1983), Nixon and Maconnachie (1988), Whitaker *et al.* (1991), Hochberg *et al.* (1992), Nixon and Mangold (1996), Villanueva *et al.* (1997a), Hernández-García *et al.* (1998), Quetglas *et al.* (1998), Caverivière *et al.* (1999), Lefkaditou *et al.* (1999), Demarcq and Faure (2000), Domain *et al.* (2000), Faure *et al.* (2000), Hernández-García *et al.* (2000, 2002), Balguerías *et al.* (2002), Casu *et al.* (2002), Diallo *et al.* (2002),Caveriviere *et al.* (2002), Henderson *et al.* (2002), Maltagliati *et al.* (2002), Silva *et al.* (2002 a, b), Tsangridis *et al.* (2002), Carvalho and Reis (2003), Katsanevakis and Verriopoulos (2004a, b, 2006a, b), González *et al.* (2005), Rodríguez-Rúa *et al.* (2005), Otero *et al.* (2007, 2008, 2009), Villanueva and Norman (2008), Carreira and Gonçalves (2009), Moreno *et al.* (2009), Fuentes and Iglesias (2010), Garofalo *et al.* (2010), Perales-Raya *et al.* (2010), Roura *et al.* (2010a), Canali *et al.* (2011), Gristina *et al.* (2011), Hermosilla *et al.* (2011), Sobrino *et al.* (2011), Cuccu *et al.* (2013a,b).

Octopus "vulgaris" type I

Plate VI, 47

Geographical Distribution: Western central Atlantic Ocean. Throughout the Caribbean Sea and Gulf of Mexico, south to at least Venezuela and north to South Carolina (Fig. 39).

Habitat and Biology: In Venezuela, this form inhabits diverse substrates including sand, rock, mud, coral, and turtle grass (*Thalassia*) beds. It is primarily nocturnal and feeds on molluscs and crustaceans. It is caught from depths of 5 to 72 m, although high concentrations are reported around 24 to 38 m by commercial fishers. It is abundant from June until October with a peak in August-September when the animals come into shallow water to breed.

On the coral reefs of Bonaire and Bermuda, juveniles of this form forage on coral rubble substrates, being at least partially active during the day. Home range and den use have been extensively studied.

The diet consists primarily of molluscs and crustaceans. Prey middens on the island of Bonaire contained the remains of 35 species of gastropod snails, 19 bivalve species and 21 crustacean species. Drilling of shells is one strategy used to extract prey, including the drilling of crab claws.

Interest to Fisheries: Catch of this form reported through FAO includes around 10 000 to 20 000 tonnes annually, taken by Mexican fishers, primarily from the Gulf of Mexico. However many nations within the range of this form do not provide catch statistics for octopuses to FAO (or at least to the species level). This octopus is harvested on small and moderate scales throughout its range. It is harvested commercially in Venezuela, and it was proposed to be of potential commercial value in South Carolina.

Remarks: This form was first reported under the name ***Octopus vulgaris*** by d'Orbigny in 1840, although earlier records exist for this form under potentially synonymous names: ***O. americanus*** Baker *in* Denys de Montfort, 1802 and ***O. bakerii*** d'Orbigny, 1826. Through analyses of mitochondrial genes, Warnke *et al.* (2004) considered this form to be synonymous with the eastern Atlantic forms and concluded that they represent a single species.

Local Names: Unknown.

Literature: Voss (1968, 1971a), Arnold and Arnold (1969), Arocha (1989), Arocha *et al.* (1991), Mather (1991a, b, 1994), Mather and Nixon (1995), Anderson *et al.* (2008).

Octopus "vulgaris" type II

Geographical Distribution: In Brazil from Amapá (~2°00'N, 50°13'W) to Rio Grande do Sul (31°05'S, 50°32'W). Southern limits of distribution not known (Fig. 39).

Habitat and Biology: Little is reported of the biology and behaviour of this form.

Interest to Fisheries: Fished commercially in southeast and southern Brazil, where it probably constitutes the largest component of octopus catches. In 2005, the annual octopus catch in Brazil was reported as 1 783 tonnes, of which 86% was listed as ***O. vulgaris***, primarily harvested by pot trapping (Moreira *et al.,* 2011).

Remarks: This form was first reported from Brazil under the name ***Octopus vulgaris*** by d'Orbigny in 1840. In 1849, Gray described this form from Brazil under the name ***O. geryonea***. Through analyses of mitochondrial genes, Warnke *et al.* (2004) considered this form to be synonymous with the Caribbean and eastern Atlantic forms and concluded they represented a single species. Leite *et al.* (2008) described a closely related sympatric species as ***O. insularis***. Morphological studies of the paralarvae of this form showed significant differences from eastern Atlantic ***O. vulgaris*** paralarvae (Vidal *et al.*, 2010a, b), providing support for delineation of this form from ***O. vulgaris*** *sensu stricto*.

Local Names: BRAZIL: Polvo.

Literature: Haimovici and Perez (1992), Haimovici *et al.* (2009), Vidal *et al.* (2010a, b), Moreira *et al.* (2011).

Octopus "vulgaris" type III

Plate VI, 48

Geographical Distribution: Coastal waters off South Africa, from Luderitz on the west coast of Namibia in the southern Atlantic to Durban, South Africa in the east, at the boundary with the tropical Indian Ocean (Fig. 39).

Habitat and Biology: This form occurs on rocky reefs and adjacent soft substrates where it occupies/excavates dens. Male and females are found in the same or adjoining dens in all seasons, indicating mating activity year round.

Examination of stomach contents, middens and direct observation of this form found a diet dominated by the crab *Plagusia chabrus*, the abalone *Haliotis midae*, the clam *Venus verrucosa* and the mussel *Perna perna*. Mussels are extracted by pulling apart of the valves of smaller individuals and drilling of larger animals. The diet also includes other crustaceans, molluscs (gastropods, bivalves and octopuses), fishes and polychaete worms. Tests of the sea urchin

Parechinus angulosus were found in four middens. Octopuses less than 300 grams were also found to eat blenny and goby eggs off rock nests.

A population off the southeast of South Africa was found to have a higher female-bias sex ratio in intertidal animals (2:1) than for subtidal animals (1:1). There appears to be migration of mature/maturing females into subtidal habitats. Spawning activity peaks in spring to summer in the cooler southwest end of this form’s distribution and in autumn and winter on the warmer southeast coast of South Africa. Egg numbers are estimated from one population to range from 42 000 to 790 000 per female.

Octopuses on the east coast of South Africa mature at around 3 months of age and have an estimated lifespan of 12 to 15 months. Females are estimated to have the potential to reach 4 kg in 240 days, while males can attain 4 kg in 290 days. Mating appears to occur year-round with some evidence supporting seasonal migrations by females. This form has been reported in the diet of fur seals, Risso’s dolphins and squaloid sharks. It also is likely to occur in the diets of diverse fishes throughout its range.

Interest to Fisheries: Artisanal and small-scale harvests occur for this species, primarily from intertidal rock reefs. The logistics and economics of a potential subtidal pot fishery also has been investigated, although to date this fishery does not appear to have been established.

Remarks: This form occurs in the temperate waters off South Africa. Guerra *et al.* (2010) reported a member of this complex (as ***Octopus vulgaris***) from St Paul and Amsterdam Islands in the southern Indian Ocean based on analyses of COI and COIII mitochondrial genes. In these analyses this taxon was most closely aligned with South African material and may be the same or an additional member of this complex.

Local Names: Unknown.

Literature: Smale and Buchan (1981), Castley *et al.* (1991), Ebert *et al.* (1992), Cockcroft *et al.* (1993), McQuaid (1994), Smith and Griffiths (2002), Oosthuizen and Smale (2003), Smith (2003), Oosthuizen (2004), Oosthuizen *et al.* (2004), Teske *et al.* (2007).

Octopus “vulgaris” type IV

Plate VII, 49

Geographical Distribution: Coastal subtropical and temperate waters of northwest Pacific Ocean, from at least China, Hong Kong SAR and Taiwan Province of China in the south, to mid-Japan (Fig. 39).

Habitat and Biology: This form occurs on reef and soft substrate habitats where it occupies/excavates dens. On soft substrates it willingly occupies concave objects, leading to its easy capture in fisheries pot lines. It is reported as the most common octopus in middle and southern Japan. In China, Hong Kong SAR, it has been reported historically to occur in low numbers, living amongst rocks along the coast or on adjacent stony substrates at depths between 5 and 25 metres.

Eggs are produced in the hundreds of thousands and hatch into planktonic paralarvae, approximately 2-3 mm in length. Off Nanji Island, China, spawning occurs when seawater temperatures reach 13°C, with most animals spawning when seawater temperatures reach around 16°C. The spawning period occurs between April and June. Egg number ranges from 22 000 to 170 000 per female and hatching success declines at seawater temperatures above 28°C. Egg laying to hatching period ranges from 20 to 47 days and is temperature dependent.

Captive hatchlings remain in the water column for around 40 days before exhibiting settlement behaviour and associated morphological transformation. Predators of this form include sharks of the genera *Triakis*, *Hemitriakis* and *Mustelus* (family Triakidae).

Interest to Fisheries: This form is harvested in small-to moderate-scale fisheries throughout the region. Primary collection techniques include pot traps and benthic trawls. Catch statistics across its distributional range are not well reported and the total scale of the combined catch is likely to be large.

Remarks: This form occurs in subtropical to temperate waters of east Asia where it has a high fisheries and economic profile. It was first reported from the region under the name ***Octopus vulgaris*** by Appellöf (1886) from Japan. Earlier records exist for this form under a potentially synonymous name: ***O. sinensis*** d’Orbigny (1834), also from Japan. Voss and Williamson (1972) reported this form from China, Hong Kong SAR under the name ***Octopus*** sp. D. Due to the high market value of this form, Japanese catch statistics have been gathered and analyzed to investigate resource fluctuations (Boso Peninsula: Tanaka, 1958; Tokyo Bay: Shimizu, 1983; Seto Inland Sea: Uchida *et al.,* 2005; Sakaguchi *et al.,* 2000;

Sakaguchi, 2006). Distribution of planktonic juveniles also has been assessed in relation to estimating local stocks (Sakaguchi *et al.*, 1999a). In addition, considerable effort has been made to complete the life cycle in captivity (Itami *et al.,* 1963; Sakaguchi *et al.,* 1999b; Hamasaki and Takeuchi, 2001; Zhong and Ning, 2009). As the hatchlings are tiny planktonic paralarvae, the biggest challenge has been to determine suitable diet and environmental conditions. In preliminary investigations of captive propagation of this form in China, Lin *et al.* (2008) used 48 wild captured females and obtained 2 160 000 fertilized eggs, from which 1 390 000 paralarvae were hatched. Only 121 individuals were raised to settlement. Nauplii of *Artemia salina*, rotifers and copepods were assessed as early diet for this form, with the nauplii of *Artemia salina* being the most promising. In subsequent studies, brine shrimp (*Artemia*) and Pacific Sandeel (*Ammodytes personatus*) have proven effective as food in captive culturing of paralarvae (Hamasaki and Morioka, 2002; Okumura *et al.,* 2005; Arai *et al.,* 2008).

Investigations of optimum aquaculture techniques in China compared net cages versus cement tanks, raising 22,000 young (Cai *et al.*, 2007). Survival rates were between 60 and 70% over 40 days. The economic benefits of net cages were higher than those of cement tanks, with a ratio of input to output of 1:1.210, while for cement tanks the ratio was 1:1.105. Cannibalism and autotomy contributed to captive mortality rates.

Local Names: CHINA: Zhẽn-Xiāo (“True octopus”), Zhãng-Yú (“Octopus”), Bā-Zhǎo-Yú (“Eight-armed fish”); TAIWAN PROVINCE OF CHINA: Tako; CHINA, HONG KONG SAR: Sek Baat Jau Yue (“Stone Eight-legged Fish”); JAPAN: Madako.

Literature: Voss and Williamson (1971, as ***Octopus*** sp. D), Tsuchiya *et al.* (1986, 1987), Takeda (1990), Sakaguchi *et al.* (2002), Kamura and Hashimoto (2004), Cai *et al.* (2007, 2009), Cai (2009).

Octopus bimaculatus Verrill, 1883

Fig. 41; Plate V, 39

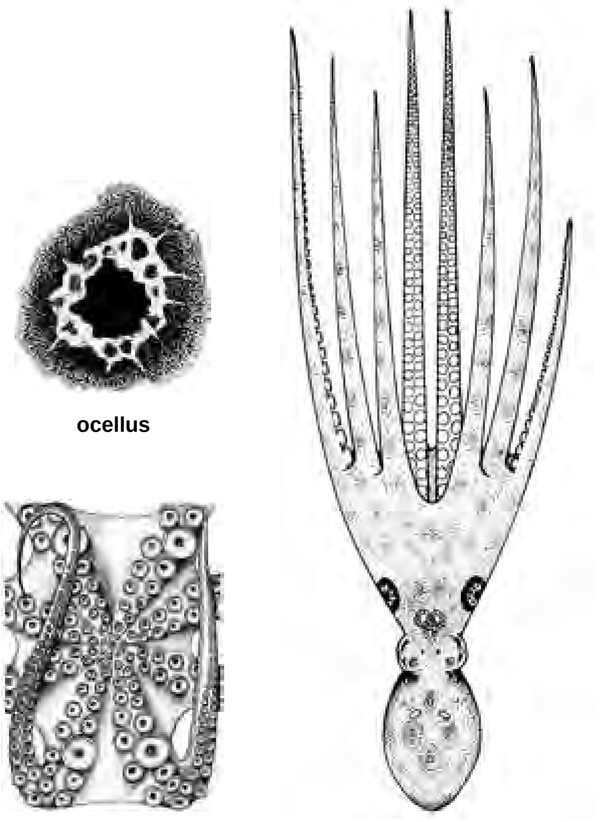
Octopus bimaculatus Verrill, 1883, *Bulletin of the Museum of Comparative Zoology*, 11(6): 121. [Type locality: Northwestern Pacific Ocean, United States, California, San Diego].

Frequent Synonyms: None.

Misidentifications: *Octopus bimaculoides* Pickford and McConnaughey, 1949.

FAO Names: En — Two-spotted octopus; **Fr** — Poulpe à deux taches; **Sp** — Pulpo con dos manchas.

Diagnostic Features: Medium-sized muscular species. Arms moderately long, 4 to 5 times mantle length. Lateral arms longest (typically 3>2>4>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 28% of arm length. Web deepest on lateral arms, webs shallowest in ventral and dorsal sectors. Narrow web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. Around 200 to 320 suckers on each normal arm in larger animals. Enlarged suckers present in mature males, 1 to 2 on arms 2 and 3, starting around the 11th proximal sucker. Gills with 8 to 10 lamellae per demibranch. Funnel organ W-shaped, outer limbs slightly shorter than medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 70% length of opposite arm. Ligula tiny, 1.2 to 2.8% of arm length. Calamus small to moderate size, 40 to 60% of ligula length. Hectocotylized arm with 134 to 157 suckers. Spermatophores of moderate size, up to 70% of mantle length. Spermatophores unarmed. **Eggs small, capsule lengths 2 to 4 mm, around 5% of mantle length.**



ocellus

oral view

dorsal view

Fig. 41 ***Octopus bimaculatus***

Colour: Dorsal surfaces variable, from dark purplish-black to yellow-green. Often mottled with dark and light patterns. **False-eye spots (ocelli) present, consisting of a dark spot containing an iridescent blue ring. Blue ring made up of broken chain links with distinct spokes radiating to the edge of a wide outer dark ring.** Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture: Skin texture of regular patch and groove with small circular patches.** Four large primary papillae in diamond arrangement on dorsal mantle, 1 to 2 supraocular papillae. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 200 mm; total length to around 1.1 m; body weight to around 3 kg.

Geographical Distribution: Northeast Pacific from California (Point Conception) south to Bahia Magdelana on the Pacific coast of the Baja California Peninsula. Also reported in Mexico from the head of the Gulf of California. Southern limits unknown (Fig. 42).

Habitat and Biology: Depths range from 0 to 50 m. ***Octopus bimaculatus*** occurs on rocky substrates from intertidal reefs to shallow subtidal depths. This species occupies temporary to moderate-term lairs in any available shelter, primarily rock crevices and assorted man-made refuse. It is most active at dusk and dawn, but is also active throughout the day and night. Crabs are the preferred prey, but their rarity leads to inclusion of chitons, snails, limpets and bivalves in the diet. Mating and spawning occur throughout the year. Females lay strands of up to 20 000 eggs in protected rock shelters. Eggs take 1 to 2 months to develop, hatching as planktonic paralarvae.

Interest to Fisheries: There is no commercial harvest of this species. Small scale harvests for personal consumption, as bait and as aquarium animals, may occur across its range.

Local Names: Unknown.

Remarks: This species is a sibling species to ***Octopus bimaculoides***. The taxonomic status of the population of ocellate octopus found in the head of the Gulf of California has not been resolved.

Fig. 42 ***Octopus bimaculatus***

🟥 Known distribution

Literature: Ambrose (1981, 1982a,b, 1983, 1984, 1986, 1988, 1997), Hochberg *et. al.* (1992).

Octopus bimaculoides Pickford and McConnaughey, 1949

Fig. 43; Plate V, 40

Octopus bimaculoides Pickford and McConnaughey, 1949, *Bulletin of the Bingham Oceanographic Collection*, 12(4): 14. [Type locality: Northeastern Pacific Ocean, United States, California, La Jolla].

Frequent Synonyms: None.

Misidentifications: *Octopus bimaculatus* Verrill, 1883.

FAO Names: En — Lesser two-spotted octopus; **Fr** — Poulpe à deux taches petit; **Sp** — Pulpito con dos manchas.

Diagnostic Features: Moderate-sized muscular species. Arms moderately long, 3-3.5 times mantle length. Lateral arms longest (typically 3>2>4>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 25% of arm length. Web deepest on lateral arms, web sectors of dorsal and ventral arms shallowest. Narrow web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 140 to 190 suckers on each normal arm. Enlarged suckers present in mature males, 1 to 2 on arms 2 and 3. Gills with 8 to 10 lamellae per demibranch. Funnel organ W-shaped, outer limbs slightly shorter than medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 80% length of opposite arm. Ligula tiny, 1.4 to 2.3% of arm length. Calamus of moderate size, 40 to 50% of ligula length. Hectocotylized arm with 102 to 116 suckers. Spermatophores small, around 50 to 65% of mantle length. Spermatophores unarmed. **Eggs large, capsule lengths 16 to 18 mm, 12 to 15% of mantle length. Colour:** Variable, from dark grey to red, brown or olive. Faintly mottled with thin dark reticulate or polygonal pattern. **False-eye spots (ocelli) present consisting of dark spot containing an iridescent blue ring. Blue ring made up of chain link pattern without radiating spokes.** Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin densely covered with papillae ("granular"), coarser on dorsal surfaces of head, mantle and arms. Four large primary papillae in diamond arrangement on dorsal mantle. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 85 mm; total length to 500 mm; body weight to at least 800 g.

Geographical Distribution: Northeast Pacific, California (San Simeon) and the California Channel Islands south to at least Guerrero Negro, on the Pacific coast of the Baja California Peninsula, Mexico (Fig. 44).

Habitat and Biology: Depths range from the intertidal zone to at least 20 m. ***Octopus bimaculoides*** lives on rocky reefs and sand and mud substrates from the intertidal zone to shallow subtidal depths. This species forms dens in a range of substrates from intertidal boulders to kelp holdfasts, rock crevices, mollusc shells or holes in the substrate lined with shells or man-made objects. Females often lay eggs within discarded aluminium cans. This species is active both day and night but appears to be more day active than ***O. bimaculatus***, which co-occurs in many regions. ***Octopus bimaculoides*** feeds on a wide range of prey from crabs and shrimp, to bivalves, gastropods and octopuses. There appears to be a peak in spawning activity between February and May. Females lay up to 800 large eggs in small clusters. Hatchlings immediately adopt a benthic lifestyle.

Interest to Fisheries: There is no commercial harvest of this species. Small-scale harvests occur in intertidal areas such as La Jolla, California for personal consumption, as bait and as aquarium animals. Sold commercially as a favoured aquarium species.

Local Names: Unknown.

ocellus **dorsal view**

Fig. 43 ***Octopus bimaculoides***

Fig. 44 ***Octopus bimaculoides***

🟥 Known distribution

Remarks: This species was originally separated from the similar, co-occurring and related ***Octopus bimaculatus*** on the basis of the large eggs and distinct assemblages of dicyemid parasites (Pickford and McConnaughey, 1949). Sucker counts, colour patterns and skin sculpture clearly separate the two species (see Lang, 1997). Packard and Hochberg (1977) and Forsythe and Hanlon (1988a) have elucidated the chromatic, textural and postural components of body patterns in this species. As discussed above for ***O. bimaculatus***, non-overlapping sucker counts on arms 2 and 3 of males and females provide an easy means of rapidly identifying preserved specimens to species. Due to its large egg size, this species has been easily reared in the laboratory and extensively utilized for experimental studies of biology and behaviour (Forsythe and Hanlon, 1988b; Boal, 1991; Boal *et al.,* 2000; Sinn *et al.,* 2001; Hvorecny *et al.,* 2007).

Literature: Pickford and McConnaughey (1949), Peterson (1959), Packard and Hochberg (1977), Hochberg and Fields (1980), Forsythe and Hanlon (1988a, b), Boal (1991), Cigliano (1993), Lang (1997), Boal *et al.* (2000), Sinn *et al.* (2001), Voight (2001a), Hvorecny *et al.* (2007), Sinn (2008).

Octopus hubbsorum Berry, 1953

Fig. 45; Plate VI, 41

Octopus hubbsorum Berry, 1953, *Leaflets in Malacology*, 1(10): 53. [Type locality: Mexico (Gulf of California), Sonora, outer Bahia San Carlos (27º05'N, 110º47'W)].

Frequent Synonyms: None.

Misidentifications: *Octopus rugosus* Bosc, 1792; *O. vulgaris* Cuvier, 1797.

FAO Names: En — Hubb's octopus; **Fr** — Poulpe de Hubb; **Sp** — Pulpo de Hubb.

Diagnostic Features: Moderate-sized muscular species. Arms of moderate length, 3 to 4 times mantle length. Lateral arms longest (typically 3>2>4>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 30% of arm length. Web deepest on lateral arms, webs between dorsal arms shallowest. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 240 suckers on each normal arm. Enlarged suckers present in mature males and females, on arms 2 and 3. Gills with 9 to 11 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 80% length of opposite arm. **Ligula tiny, around 1 to 2% of arm length.** Calamus small, around 20% of ligula length. Hectocotylized arm with around 140 suckers. Spermatophores not described. Eggs small, size unknown. **Colour:** Dorsal surfaces dark, varying from black, rusty red, purple to dark grey often with iridescent green or orange undertone, **with conspicuous dark reticulated pattern.** Patches lighter orange-brown. Ventral surfaces, especially funnel and mantle aperture, rusty orange. False-eye spots (ocelli) absent. **White dumb-bell shape on dorsal arm crown in front of eyes. Few large white spots present along midline of arms.** Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture: Skin texture of patch and groove system, patches large and irregular, generally round in shape.** Four large primary papillae in diamond pattern on mid-dorsal mantle. Two large compound ("warty") papillae above and behind each eye with 1 to 2 smaller conical simple papillae in front of these. Skin ridge around lateral margin of mantle absent.

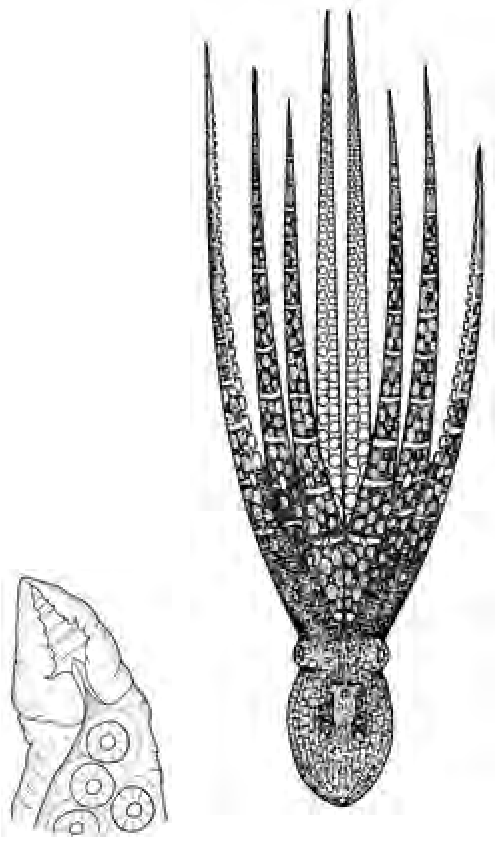

hectocotylus dorsal view

Fig. 45 ***Octopus hubbsorum***

Size: Mantle length to 220 mm; total length to over 1 m.

Fig. 46 *Octopus hubbsorum*

🟥 Known distribution

Geographical Distribution: Mexico, Pacific coast of the Baja California Peninsula from Magadelena Bay into southernhalf of the Gulf of California, south to Oaxaca and also Revillagigedo Islands. The presence of this species south into Panama and Columbia has not been confirmed (Fig. 46).

Habitat and Biology: Depths range from 0 to 30 m. The species lives in rocky areas from the intertidal to shallow subtidal. ***Octopus hubbsorum*** is a poorly known species that appears almost identical to ***O. bimaculatus*** except for the presence of the characteristic ocelli in the latter species. It is considered to be the most common medium-sized octopus in the mid-region of the Gulf of California. In general, ***O. hubbsorum*** is larger than ***O. bimaculatus*** wherever the two species co-occur.

In studies of reproductive development males were found to mature at around 140 mm and females at 160 mm ML. Eggs are small. Large numbers of eggs are laid and brooded by females throughout the year. Female fecundity ranges from about 62 500 to 425 000 oocytes per female.

Around Cabo San Lucas the species is extremely abundant in rocky areas in the intertidal and shallow subtidal zones. Animals are active during the day. They live in holes, crevices or under boulders. Den sites are often surrounded by middens of shell debris. This species is an opportunistic predator and feeds on a wide diversity of invertebrates and fishes. The diet primarily includes crustaceans (stomatopods, carideans, anomurans and brachyurans), molluscs (bivalves and gastropods [which are typically drilled] and cephalopods) and small fishes.

Interest to Fisheries: The species is fished in Mexico along the Baja California Peninsula, on both sides of the southern Gulf of California and south to Oaxaca. The species is typically fished from March to October.

Local Names: Unknown.

Remarks: ***Octopus hubbsorum*** appears to be closely related to ***O. mimus*** in South America. In turn, both are similar to ***O. bimaculatus*** and ***O. oculifer*** except for the lack of an ocellus. This is a confusing complex that needs to be carefully re-evaluated.

Literature: Fuentes (1974), Hochberg (1980), Leyva-Villarreal *et al.* (1987), González *et al.* (1990), Roper *et al.* (1995), Aguilar-Chávez and Godínez-Domínguez (1997), SAGARPA (2004), López-Uriarte *et al.* (2005), López-Uriarte and Ríos-Jara (2009), López-Uriarte *et al.* (2010), Pliego-Cárdenas *et al.* (2011).

Octopus insularis Leite and Haimovici, 2008

Fig. 47

Octopus insularis Leite and Haimovici *In* Leite, Haimovici, Molina and Warnke, 2008, *Journal of Molluscan Studies*, 74: 66. [Type locality: Southwestern Atlantic Ocean, Brazil, St Peter and St Paul Archipelago, Belmont Island (00°55’S, 29°20’W)].

Frequent Synonyms: None.

Misidentifications: *Octopus vulgaris* Cuvier, 1797.

FAO Names: En — Brazil reef octopus; **Fr** — Poulpe brésilien de récif; **Sp** — Pulpo brasileño de arrecife.

Diagnostic Features: Medium size to large muscular species. Arms moderately long, around 3 to 4.2 times mantle length. Lateral arms longest (typically 3>4>2>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20 to 30% of arm length. Web deepest on lateral arms, webs shallowest in ventral and dorsal sectors. Narrow web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 220 to 240 suckers on each normal arm. **Enlarged suckers present in mature males, 2 to 4 on arms 2 and 3, starting around the 8th to 9th proximal sucker**. Gills with 8 to 11 lamellae per demibranch. Funnel organ W-shaped, outer limbs slightly longer than medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length around 90% of opposite arm. Ligula tiny, 0.6 to 1.4% of arm length. Calamus of small to moderate size, around 40 to 60% of ligula length. Hectocotylized arm with 96 to 142 suckers. Spermatophores small, around 30 to 40% of mantle length. Spermatophores unarmed. **Eggs small, around 1.5 mm long. Colour:** Live animals yellow to reddish-brown with variable markings or patterns. False-eye spots (ocelli) absent. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture: Skin texture of irregular patch and groove system.** Four large primary papillae in diamond arrangement on dorsal mantle, 3 supraocular papillae. Other large papillae can be raised on dorsal arm crown and lateral mantle. Skin ridge around lateral margin of mantle absent.

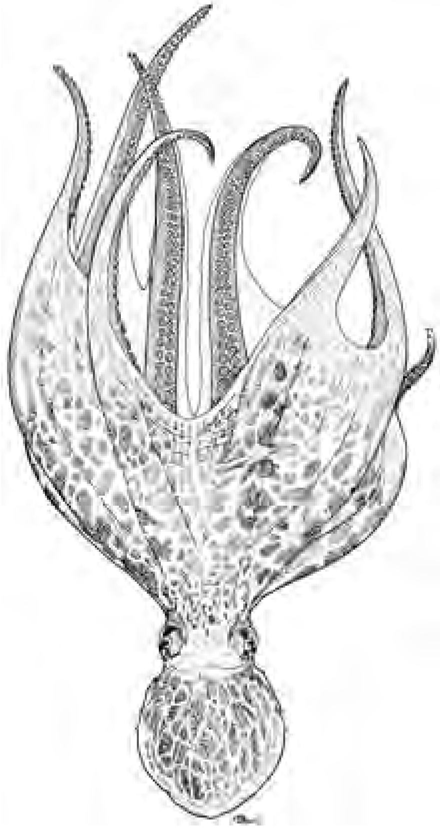

dorsal view

Fig. 47 *Octopus insularis*

Size: Mantle length to 120 mm; total length to 530 mm; body weight to 1.3 kg.

Geographical Distribution: Southeast Atlantic, off mainland Brazil (states of Rio Grande do Norte and Pernambuco) and north-east oceanic island groups: Fernando de Noronha Archipelago, Rocas Atoll, and St Peter and St Paul Archipelago (Fig. 48).

Habitat and Biology: Depths range from 0 to 45 m. The species is found on reefs, bedrock, rubble, gravel and sand beds, and rocky bottoms, regardless of the presence of algae, but never on sandy and muddy bottoms.

Interest to Fisheries: Harvested by local fishermen by hand or in traps set on coastal reefs off the mainland coast of Brazil.

Local Names: Unknown.

Literature: Leite (2007, 2008), Leite *et al.* (2008).

Fig. 48 *Octopus insularis*

🟥 Known distribution

Octopus maya Voss and Solis, 1966

Fig. 49; Plate VI, 42

Octopus maya Voss and Solis, 1966, *Bulletin of Marine Science*, 16(3): 617. [Type locality: Mexico, Campeche, off Lerma (east side of Bay of Campeche)].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Mexican foureyed octopus; **Fr** — Poulpe Mexicain; **Sp** — Pulpo mexicano.

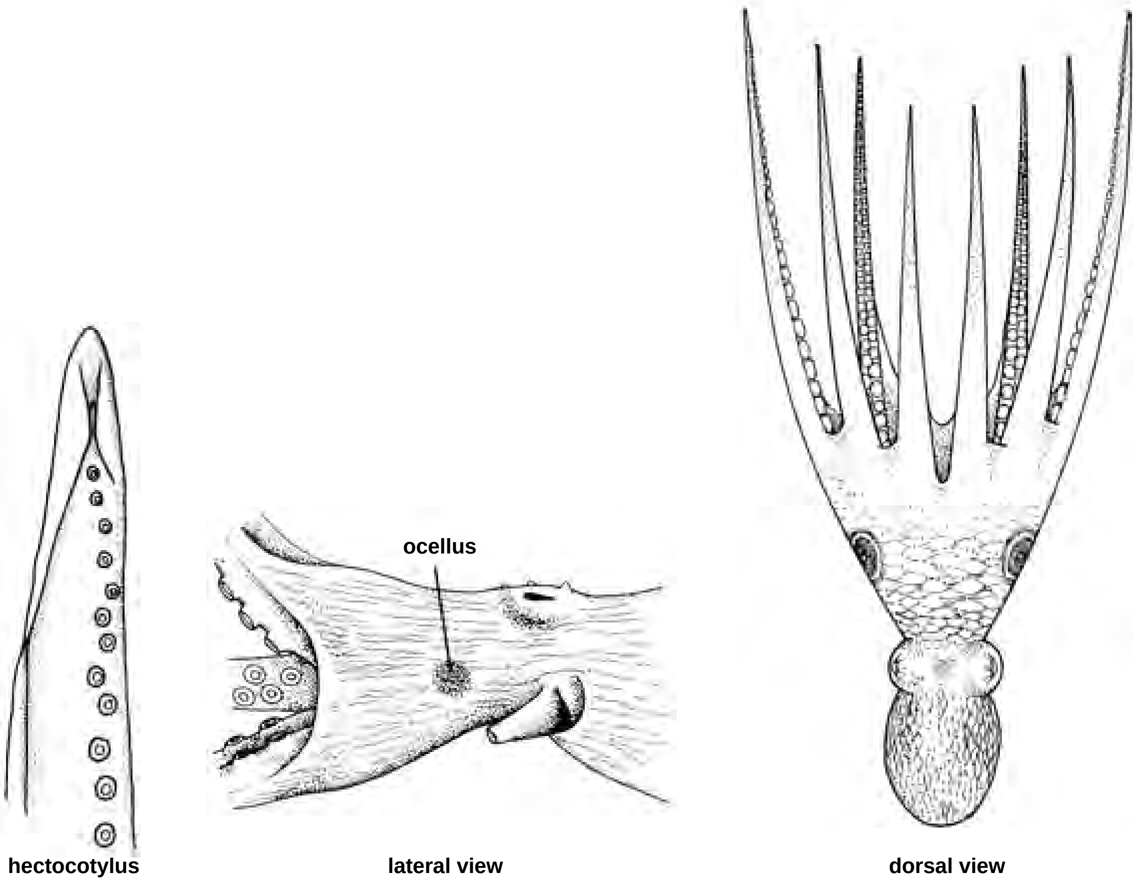


Fig. 49 *Octopus maya*

Diagnostic Features: Large, robust and muscular species. Arms moderately long, 3 to 4.5 times mantle length. Lateral arms longest (typically 3>4=2>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20 to 30% of arm length. Web deepest on lateral arms, webs between dorsal arms shallowest. Interbrachial web pouches absent. Two rows of suckers on each arm. Enlarged suckers absent. Gills with 9 to 10 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length around 80% of opposite arm. Ligula minute, 1.5 to 2% of arm length. Calamus of moderate size, around 25% of ligula length. Spermatophores of moderate size, around 60% of mantle length. Spermatophores unarmed. **Eggs large, around 17 mm and produced in relatively low numbers (~2000)**. **Colour:** Variable colour patterns from uniform dark brown, to mottled to uniform pale cream. **False-eye spots (ocelli) present, as dark spot with small central light spot, all bound in a light coloured outer ring.** Ocellus without iridescent ring. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin texture of irregular patches and grooves, capable of being raised as spiked texture aiding in camouflage against different backgrounds. Single large and several small papillae present above each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 120 mm; total length to around 1.3 m; body weight to around 5 kg.

Geographical Distribution: Gulf of Mexico along the coasts of Yucatan and Campeche, Mexico (Fig. 50).

Habitat and Biology: Depths range from 0 to 50 m. This species lives in shallow water on seagrass meadows, shell beds and reefs. The spawning season extends from September to December where females lay eggs in festoons in crevices or empty mollusc shells, brooding them for 50 to 65 days. The large hatchlings immediately settle to a benthic life. Life span is around 1 to 2 years. Diet includes crabs (such as the stone crab *Menippe mercenaria*), gastropods (such as *Nerita*), and fishes. Preyed on by groupers (Serranidae) and Spanish mackerels (Scombridae).

Interest to Fisheries: ***Octopus maya*** is harvested on a large scale using lines with bait or lures. In the late 1980's the catch of this species was reported at around 5 000 to 8 000 tonnes annually. In 2000 it was estimated at around 9 000 tonnes. FAO production statistic for 2010 placed the catch at around 8 000 tonnes.

Fig. 50 ***Octopus maya***

🟥 Known distribution

Local Names: Unknown.

Literature: Van Heukelem (1983b), Solis-Ramirez (1997), Arreguin-Sánchez *et al.* (2000), Pérez-Losada *et al.* (2002).

Octopus mimus Gould, 1852

Fig. 51; Plate VI, 43

Octopus mimus Gould, 1852, *United States Exploring Expedition during the Years 1838*, *1839*, *1840*, *1841*, *1842*, 12: 473. [Type locality: Southeastern Pacific Ocean, Peru, Callao].

Frequent Synonyms: None.

Misidentifications: *Octopus vulgaris* Cuvier, 1797.

FAO Names: En — Changos octopus; **Fr** — Poulpe des Changos; **Sp** — Pulpo de los Changos.

Diagnostic Features: Large, muscular species. Stylets present, non-mineralized. Arms long, around 4 to 6 times mantle length. Lateral arms longest (typically 2>3>4>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest 18 to 27% of arm length. Web deepest on lateral arms, webs between dorsal arms shallowest. Narrow web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. Normal arm sucker counts to around 330 in adults. Enlarged suckers present in mature males, 2 to 4 on arms 2 and 3. **Gills with 7 to 8 lamellae per demibranch**. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Right third arm of males hectocotylized, around 77% length of opposite arm. Ligula tiny, 0.7 to 1.8% of arm length. Calamus large, 30 to 60% of ligula length. Spermatophores small, around 32 to 40% of mantle length. Egg size small, 2 to 3 mm long and produced in large numbers (to 400 000). **Colour:** Live animals orange to red-purple in colour. Preserved animals dark grey to purplish brown on dorsal surfaces, lighter ventrally. Obvious false-eye spots (ocelli) absent but dark spot visible in location of ocelli in some live animal colour patterns. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Mosaic of coarse, irregular reticulations over skin, forming repeated ovoid units. Sculpture: Skin rugose, densely covered in inflated patches and with numerous papillae. 2 to 3 large papillae over each eye**. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 190 mm; total length to around 1.2 m; body weight to around 4 kg.

Geographical Distribution: Southeast Pacific, along east coast of South America from northern Peru to Valparaiso, Chile (Fig. 52).

Habitat and Biology: Depths range from 0 to at least 30 m. This species lives on rocky reefs and is common on intertidal reefs to at least 30 m. It is common on intertidal reefs where it seeks cover in crevices and under boulders. It feeds on grapsid crabs and bivalve molluscs. This species drills to open bivalve shells. Reproduction, sexual maturity and embryonic development have been studied extensively (see Literature below).

Interest to Fisheries: This species supports commercial fisheries in both Peru and Chile. In Chile the fishery occurs as intertidal hand harvest (by fishermen known as *pulperos*) and subtidal collection in the surf zone by snorkel divers and deeper by hookah divers (Defeo and Castilla, 1998).

Local Names: Unknown.

Remarks: Many earlier publications treated this species along the east coast of South America as ***Octopus rugosus*** and later ***O. vulgaris***. This was corrected in molecular studies by Söller *et al.* (2000) and Warnke *et al.* (2000, 2002, 2004).

Literature: Arancibia and Troncosco (1984), Cortez and González (1988), Guerra and Fernandez (1990), Cortez and Cotton (1992), Wolff and Perez (1992), Olivares *et al.* (1994, 1996, 2001, 2003), Cortez *et al.* (1995a,b, 1998, 1999a,b), Defeo and Castilla (1998), Talledo *et al.* (1998), Guerra *et al.* (1999), Ishiyama *et al.* (1999), Baltazar *et al.* (2000), Soeller *et al.* (2000), Villegas and Tafur (2000), Warnke *et al.* (2000, 2002, 2004), Castro-Fuentes *et al.* (2002), Pérez-Losada *et al.* (2002), Rocha and Vega (2003), Cardoso *et al.* (2004), Zamora and Olivares (2004),

dorsal view

Fig. 51 ***Octopus mimus***

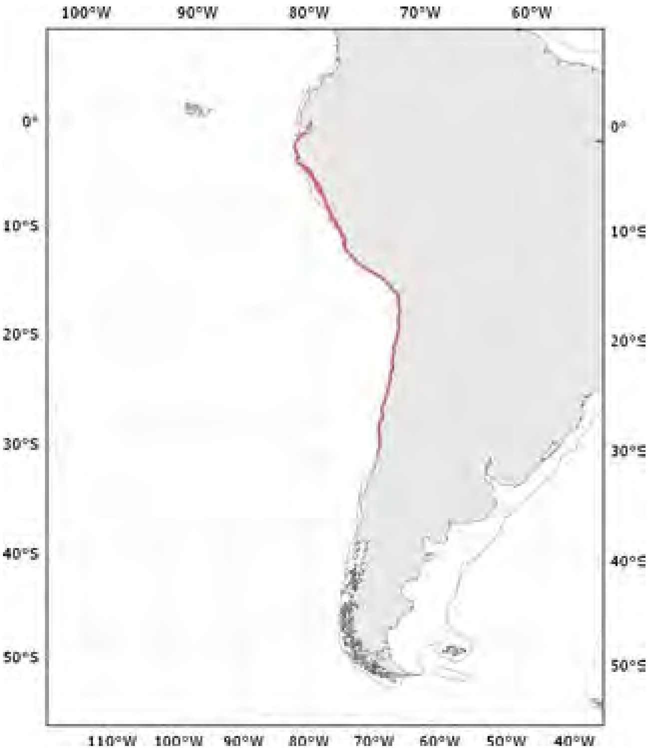


Fig. 52 ***Octopus mimus***

🟥 Known distribution

Octopus oculifer (Hoyle, 1904)

Fig. 53; Plate VI, 44

Polypus oculifer Hoyle, 1904, *Bulletin of the Museum of Comparative Zoology*, 43(1): 14. [Type locality: Southwestern Pacific Ocean, Galapagos Islands, Charles (now called Floreana) Island].

Frequent Synonyms: *Octopus roosevelti* Stuart, 1941.

Misidentifications: None.

FAO Names: En — Galapagos octopus; **Fr** — Poulpe des Galapagos; **Sp** — Pulpo de las Galapagos.

Diagnostic Features: Large muscular species. Arms moderately long, 3.5 to 4.5 times mantle length. Lateral arms longest (typically 3>2>4>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 22 to 27% of arm length. Web deepest on lateral arms, webs between dorsal arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 230 to 280 suckers on each normal arm. Enlarged suckers present in mature males, 1 to 3 on arms 2 and 3. Gills with 8 to 10 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Right third arm of males hectocotylized, length 70 to 80% of opposite arm. **Ligula tiny, 0.7 to 1.4% of arm length.** Calamus small. Hectocotylized arm with around 180 suckers. Spermatophore size unknown. Egg size unknown. **Colour:** Colour patterns variable from dark chocolate brown to mottled cream brown. Dark reticulations often displayed between light coloured patches. Regular cream coloured spots along arm tips. **False-eye spots (ocelli) present as a dark spot with small pale central spot, bound in an outer pale ring.** Ocellus without iridescent ring. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture: Skin texture of round patches of various sizes.** Four large papillae in diamond arrangement on dorsal mantle. Skin ridge around lateral margin of mantle absent.

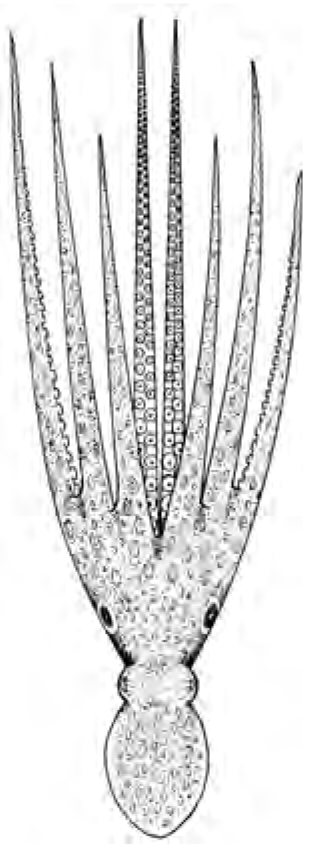


Fig. 53 ***Octopus oculifer***

Size: Mantle length to 120 mm; total length to around 420 mm.

Geographical Distribution: Galapagos Archipelago (Fig. 54).

Habitat and Biology: Depths range from 0 to 50 m. This species is common throughout the Galapagos, particularly in intertidal and shallow subtidal areas. Found on rocky shores and reefs. They feed on red shore crabs, gastropods and bivalve molluscs. Lairs in rocky reefs are surrounded by the shell remains of their prey. The flightless cormorant is one of the main predators of this octopus.

Interest to Fisheries: Small-scale commercial harvests occur for this octopus, collected primarily for human consumption and as bait.

Local Names: Unknown.

Literature: Edgar *et al.* (2004).

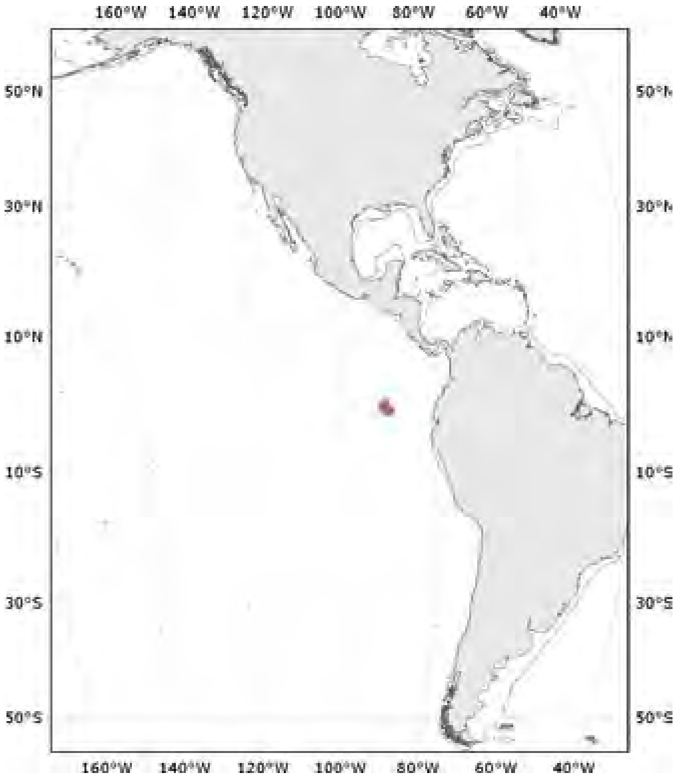


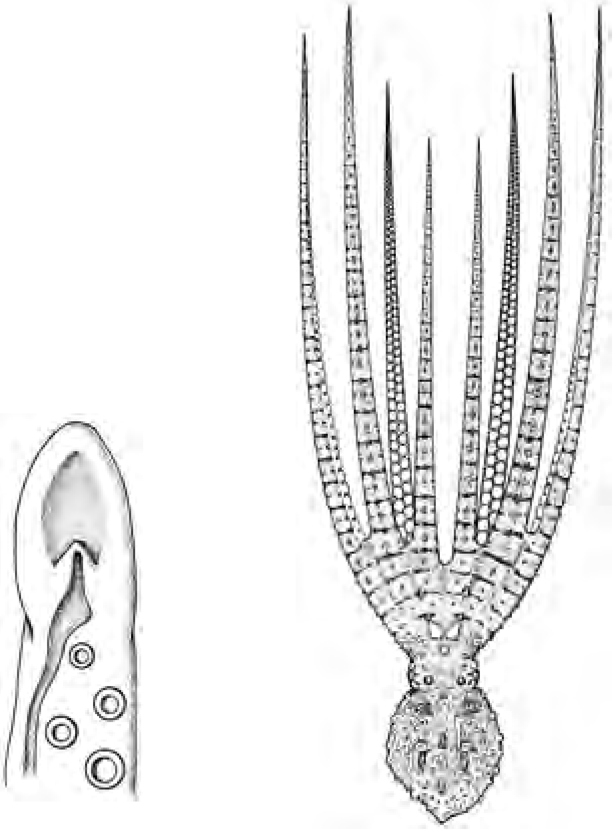
Fig. 54 ***Octopus oculifer***

🟥 Known distribution

Octopus tetricus Gould, 1852

Fig. 55; Plate VI, 45

Octopus tetricus Gould, 1852, *United States Exploring Expedition during the Years 1838, 1839, 1840, 1841, 1842*, 12: 474. [Type locality: Australia, New South Wales, Near Sydney].



hectocotylus

dorsal view

Fig. 55 *Octopus tetricus*

Frequent Synonyms: *Octopus gibbsi* O'Shea, 1999.

Misidentifications: *Octopus cyanea* Gray, 1849.

FAO Names: En — Gloomy octopus; **Fr** — Poulpe somber; **Sp** — Pulpo tétrico.

Diagnostic Features: Large, muscular species. Mantle broadly oval. Arms moderate to long, 3 to 4.5 times mantle length. Lateral arms longest, dorsal arms shortest (typically 3=2>4>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 25% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. **In larger animals, around 220 to 260 suckers on each normal arm**. Enlarged suckers present in mature males, 3 to 5 on arms 2 and 3, starting around the 13th proximal sucker. Gills with 8 to 9 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. **Third right arm of males hectocotylized, with 140 to 160 suckers.** Ligula tiny, 1 to 2% of arm length. Calamus small. Spermatophore size unknown. Eggs small, 2 to 3 mm long. **Colour:** Active animals cream to mottled orange and dark brown. Transverse narrow dark bands along arms in some colour patterns. **Resting animals within lairs show grey dorsal surfaces, orange arm faces and eyes with a white iris.** False-eye spots (ocelli) absent. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture: Skin sculptured in rounded patches separated by distinct grooves.** Capable of raising large papillae over dorsal surfaces, including four in diamond pattern on dorsal mantle and one above each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 140 mm; total length to over 600 mm; body weight to at least 1 kg.

Geographical Distribution: Eastern Australia from eastern Victoria to southern Queensland, northern New Zealand (where it is treated under the name ***Octopus gibbsi*** O'Shea, 1999). A related form occurs at similar latitudes in Western Australia (Fig. 56).

Habitat and Biology: Depths range from 0 to at least 60 m. Known from shallow coastal waters where it lives subtidally on and adjacent to rocky reefs. Active primarily at night, although alert in the mouth of lairs throughout the day. Preys primarily on crabs, but will also take shellfishes and finfishes (at least in captivity). Occupies lairs in rock crevices or excavates under rocks on sand or mud. Females lay over 150 000 eggs in festoons, each egg around 2 to 3 mm long.

Fig. 56 *Octopus tetricus*

🟥 Known distribution

Interest to Fisheries: Moderate-scale harvest as bycatch in prawn and finfish trawl fisheries. Frequently sold in fish markets in New South Wales and southern Queensland.

Local Names: AUSTRALIA: Common Sydney octopus.

Remarks: A related octopus which occurs at similar latitudes in Western Australia has been treated under the name ***Octopus tetricus*** (Joll, 1983; Roper *et al.,* 1984) and ***O.*** cf. ***tetricus*** (Norman, 2000). Preliminary molecular analyses (Guzik and Norman unpubl. data) suggest the western form is a distinct but related species. Anderson (1997) examined habitat and lair use in northern New Zealand.

Literature: Joll (1983), Anderson (1997), Stranks (1998a), Norman (2000), Nottage (2007).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Octopus filosus Howell, 1867

Octopus filosus Howell, 1867, *American Journal of Conchology*, 3(2): 240. [Type locality: (Caribbean Sea, U.S. Virgin Islands), St. Croix Island].

Synonym: *Octopus hummelincki* Adam, 1936.

Size: Mantle length to 70 mm; total length to 350 mm.

Geographical Distribution: Caribbean Sea, in shallow waters of reef areas.

Habitat and Biology: Depth range unknown.

Remarks: We agree with and follow Toll (1990) and disagree with the ICZN decision (opinion 2147, 2006) suppressing this species name.

Literature: Voss and Toll (1998).

Abdopus Norman and Finn, 2001

Abdopus Norman and Finn, 2001, *Memoirs of the Queensland Museum*, 46(2): 14.

Type Species: *Octopus horridus* d'Orbigny, 1826.

Diagnostic Features: Small to moderate-sized octopuses. Mantle muscular, ovoid to elongate amphora-shaped. Stylets present, small, chitinous (non-mineralized). **Arms muscular and long, 4 to 8 times mantle length. Lateral arms longest (typically 2>3>4>1 or 3>2>4>1). Arm autotomy at distinct plane present at a set level near the arm base. Webs of moderate depth, deepest around 15% of longest arm. Webs deepest on lateral arms, webs between dorsal arms shallowest (typically C>D>B=E>A).** Interbrachial web pouches absent. Suckers in two rows. **Enlarged suckers present in mature males, typically on arms 2 to 3, sometimes on arm 4.** Slightly enlarged on same arms in mature females. Funnel organ W-shaped. **Gills with 5 to 7 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands moderate to large. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Third right arm of male hectocotylized, slightly shorter than opposite arm. Ligula small and narrow (<6% arm length). Terminal organ (penis) linear with simple small diverticulum. Spermatophores small, narrow and unarmed with a highly coiled ejaculatory apparatus occupying one-third of spermatophore length. Eggs small to large, stalks twisted into chords or braids, eggs always laid in festoons. Colour patterns variable. False eye-spots (ocelli) absent. **Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). Skin sculptured in fine irregular patch and groove texture with large, often branched, papillae over dorsal surfaces and arms, forming bushy appearance.** Fixed pattern of four larger primary papillae in diamond pattern in midregion of dorsal mantle. Papillae often with side branches. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 70 mm; total length to 430 mm; weight to 65 g.

Geographical Distribution: Pacific region. Tropical Indo-West Pacific and the Red Sea.

Habitat and Biology: Small long-armed octopuses, typically day active on intertidal reef flats and in shallow waters.

Interest to Fisheries: Unknown.

Remarks: This group was originally treated as a subgroup within the genus ***Octopus***, under the name "***Octopus horridus*** group" (Norman, 1992c). Norman and Finn (2001) raised this group to subgeneric status, still within the genus ***Octopus***. Norman and Hochberg (2005a) raised the name to generic status. Gleadall (2004) suggests that the genus ***Tritaxeopus*** Owen, 1881 is the senior synonym for the genus ***Abdopus***. Gleadall's decision was based on superficial similarities between Owen's inadequate description of ***T. cornutus*** and preservation artefacts observed in ***A. aculeatus*** (i.e. 3 rows of suckers). Owen's holotype was collected from "Australia" and is lost (Lu *et al.,* 1995). As other Australian taxa from different genera (e.g. ***Octopus tetricus*** Gould, 1852) also show triple sucker rows on preservation as well as other morphological similarities to Owen's species, we do not support Gleadall's decision to place ***Abdopus*** in the genus ***Tritaxeopus***.

Potential public health risk - an undescribed species [***Octopus*** (***Abdopus***) sp. 5, Norman, 2000] collected at Port Hedland in the Pilbara region of northern Western Australia, was found to contain saxitoxin (STX) at a level more than three times the US, European and Australian regulatory limit for human consumption of shellfish (Robertson *et al.,* 2004).

Literature: Norman (1992c), Norman and Finn (2001), Norman and Hochberg (2005a).

Abdopus horridus (d'Orbigny, 1826)

Fig. 57

Octopus horridus d'Orbigny, 1826, *Annales des Sciences Naturelles*, Paris, series 1, 7: 144. [Type locality: Red Sea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Red Sea octopus; **Fr** — Poulpe de la Mer Rouge; **Sp** — Pulpo del Mar Rojo.

Diagnostic Features: Small long-armed octopus. Arms moderately long, 4.2 to 4.7 times mantle length. Lateral arms longer (typically 3=2>4>1). **Arm autotomy at distinct plane present at level of 7 to 10th proximal sucker**. Webs shallow, deepest to 15% of arm length. Web deepest on lateral arms, web sectors of dorsal and ventral arms shallowest. Interbrachial web pouches absent. Two rows of suckers on each arm. **In larger animals, around 130 suckers on each normal arm. Enlarged suckers present on arms 2 to 4 of males**. Gills with 6 lamellae per demibranch. Funnel organ W-shaped, lateral limbs distinctly shorter than medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Ink sac present. Right third arm of males hectocotylized, ~75% length of opposite arm. Ligula small and narrow, 3 to 4% of arm length. Calamus small. **Hectocotylized arm with around 90 suckers**. Spermatophores of moderate size, ~60% of mantle length. Eggs large type, mature eggs unknown. **Colour: Live animals with mosaic arrangement of round light patches of various sizes bound by network of dark borders**. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of irregular low papillae and fewer larger erectile papillae. Single large papilla over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 30 mm; total length to around 120 mm.

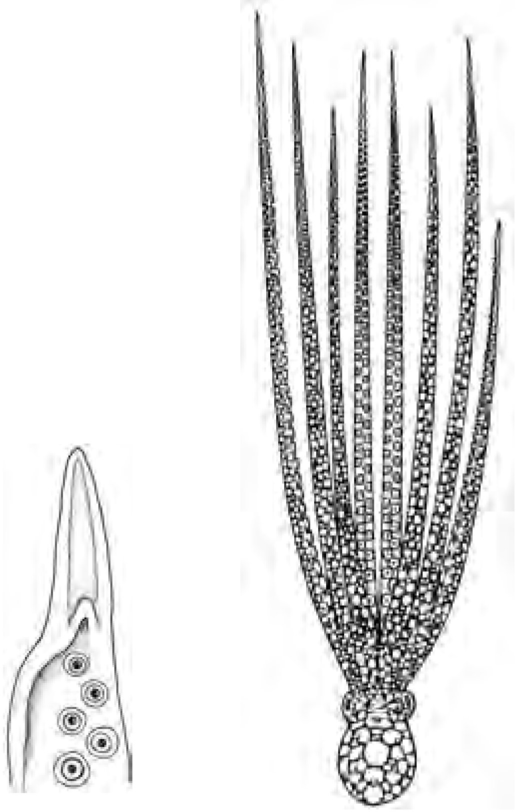
Geographical Distribution: Red Sea (Fig. 58).

Habitat and Biology: Depths range from 0 to 30 m. Poorly known. Intertidal reefs and shallow subtidal habitats.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Norman and Finn (2001), Norman and Hochberg (2005a).



hectocotylus

dorsal view

Fig. 57 ***Abdopus horridus***

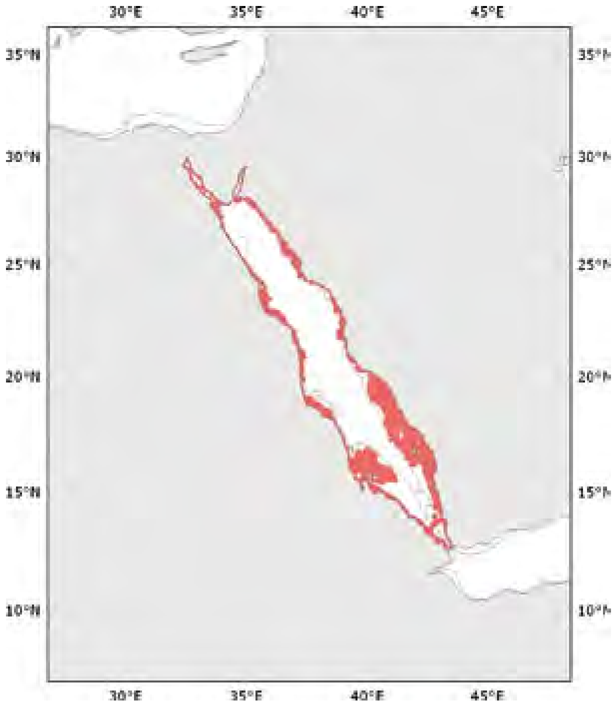


Fig. 58 ***Abdopus horridus***

🟥 Known distribution

Abdopus aculeatus (d'Orbigny, 1834)

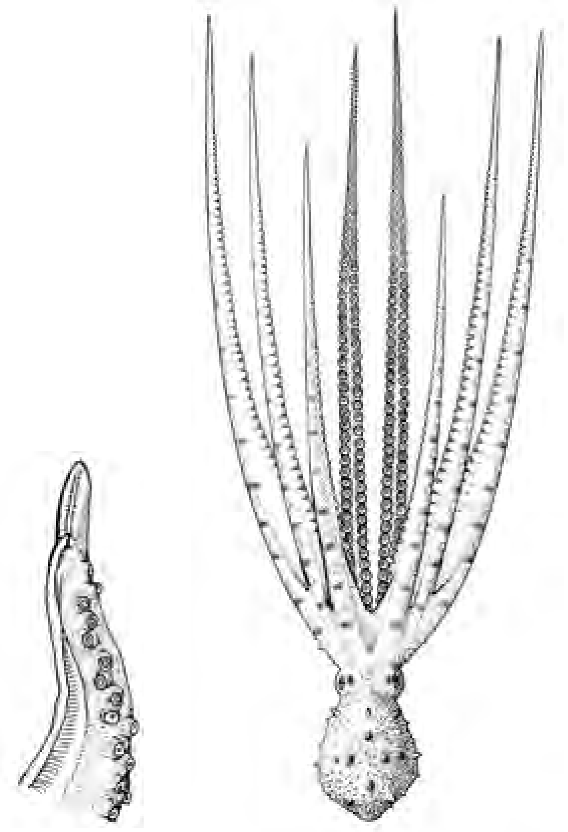
Fig. 59; Plate I, 2

Octopus aculeatus d'Orbigny, 1834, *In* Ferussac and d'Orbigny, 1834-1848, *Histoire Naturelle générale et particulière des Céphalopodes Acetabulferes vivants et fossiles*. J.B. Bailliere, Paris: 70. pls 7, 8. [Type locality: Philippines, Manila].

Frequent Synonyms: *Octopus harmandi* Rochebrune, 1882.

Misidentifications: *Octopus horridus* d'Orbigny, 1826.

FAO Names: En — Prickly octopus; **Fr** — Poulpe épineux; **Sp** — Pulpo espinoso.


hectocotylus

dorsal view

Fig. 59 *Abdopus aculeatus*

Diagnostic Features: Small to moderate-sized long-armed octopus. **Arms long, around 5 to 7 times mantle length. Lateral arms longest (typically 3>4=2>1). Arm autotomy at distinct plane present at base of arms, at level of 3rd to 7th sucker.** Webs of short to moderate depth, deepest around 15% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Web margins extend as narrow band to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. **In larger animals, around 220 to 260 suckers on each normal arm. Mature males with 3 to 6 enlarged suckers on arms 2 and 3, largest at level of around 9th to 12th proximal sucker, diameter to 16% of mantle length. Gills with 6 to 7 lamellae per demibranch.** Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length 70 to 90% of opposite arm. Ligula of moderate size and open, around 2% of arm length. Calamus small and blunt, <25% of ligula length. Hectocotylized arm with around 150 to 170 suckers. Terminal organ thin and linear with tiny diverticulum. Spermatophores short relative to mantle length, around 15 to 20 mm, around 40 to 50% of mantle length, produced in high numbers (~100 to 200). Spermatophores unarmed. Eggs small, around 3 mm, to 7% of mantle length. **Colour:** Variable in life from pale cream, to mottled, to uniform dark brown. Excellent at camouflage. False eye spots (ocelli) absent. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture: Complex skin sculpture of irregular patch and groove system over all dorsal and lateral surfaces, capable of erection and highly rugose skin capable of complex habitat camouflage, e.g. against algae.** Four primary papillae in diamond pattern on dorsal mantle. Large supraocular papilla over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 70 mm; total length to around 430 mm.

Geographical Distribution: Tropical western Pacific Ocean from Taiwan Province of China and Philippines south to northern Australia (Fig. 60).

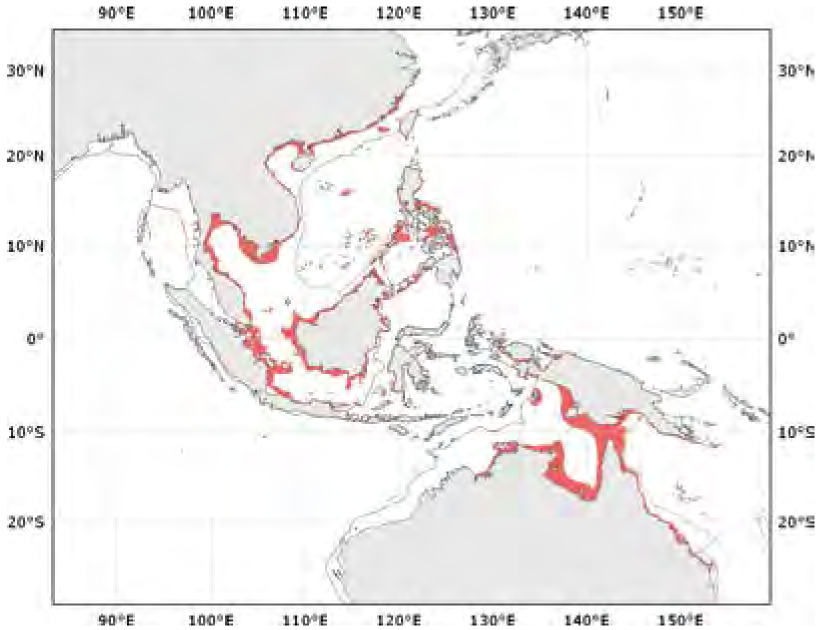


Fig. 60 *Abdopus aculeatus*

🟥 Known distribution

Habitat and Biology: Depths range from 0 to 17 m. Resident of shallow and intertidal tropical reef areas, particularly coral bedrock pools. Emerges at low tide during daylight hours to forage using excellent camouflage. Occurs in available habitat on intertidal reef flats and seagrass beds often with strong tidal currents. Typically active during diurnal mid- and low tides, although some nocturnal activity has been reported.

Interest to Fisheries: ***Abdopus aculeatus*** is one of the most common octopuses sold in the home aquarium trade worldwide. It is fished on a small scale for subsistence consumption and bait use (e.g. chum for tuna fishery) in Sulawesi, Indonesia.

Local Names: INDONESIA (north Sulawesi): Boboca popo.

Literature: Norman (2000), Norman and Finn (2001), Huffard *et al.* (2005, 2008a, 2010a), Huffard (2006, 2007b).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Abdopus abaculus (Norman and Sweeney, 1997)

Plate I, 1

Octopus abaculus Norman and Sweeney, 1997, *Invertebrate Taxonomy*, 11: 109. [Type locality: Philippines, Zamboanga del Norte Province, Solino (Selinog) Island].

Size: Mantle length to 33 mm; body weight to 21 g.

Geographical Distribution: Philippines.

Habitat and Biology: Depths range from 0 to 5 m.

Literature: Norman (2000).

Abdopus capricornicus (Norman and Finn, 2001)

Plate I, 3

Octopus capricornicus Norman and Finn, 2001, *Memoirs of the Queensland Museum*, 46(2): 24. [Type locality: Australia, Queensland, Capricorn Bunker Group, Tryon Island, 23°15’S, 151°47’E].

Size: Mantle length to 42 mm; total length to 260 mm; body weight to 65 g.

Geographical Distribution: Australia, known only from Tryon Island, Great Barrier Reef.

Habitat and Biology: Depth range intertidal.

Literature: No additional literature.

Abdopus tenebricus (Smith, 1884)

Octopus tenebricus Smith, 1884, *Report on the Zoological Collections made in the Indo-Pacific Ocean during the Voyage of H.M.S.* Alert 1881-1882: 35. [Type locality: Northeastern Australia, Queensland, Port Denison (Bowen) (20º02’S, 148º15’E)].

Size: Mantle length to 20 mm; total length to 95 mm.

Geographical Distribution: Known only from two type specimens.

Habitat and Biology: Known depth range of types from 5 to 8 m.

Literature: Norman (1992c).

Abdopus tonganus (Hoyle, 1885)

Octopus tonganus Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 15: 225. [Type locality: Tonga Islands, Tongatapu].

Size: Mantle length to 35 mm.

Geographical Distribution: Tonga.

Habitat and Biology: Depth range intertidal.

Literature: Toll and Voss (1998).

Abdopus undulatus Huffard, 2007

Abdopus undulatus Huffard, 2007a, *Molluscan Research*, 27(3): 147-170. [Type locality: Tonga, Tongatapu Island].

Size: Mantle length to 33 mm.

Geographical Distribution: Known only from islands in the Kingdom of Tonga.

Habitat and Biology: Depth range of type specimen from 7.5 to 19.5 m.

Literature: No additional literature.

Adelieledone Allcock, Hochberg, Rodhouse and Thorpe, 2003

Adelieledone Allcock, Hochberg, Rodhouse and Thorpe, 2003c, *Antarctic Science*, 15(4): 416.

Type Species: *Adelieledone polymorpha* (Robson, 1930).

Diagnostic Features: Moderate-sized octopuses, mantle length to 90 mm. Mantle saccular. Stylets absent. **Arms short, around 1.5 to 2.5 times mantle length. Arms of similar length, dorsal pair slightly shorter.** Arm autotomy at distinct plane absent. **Webs deep, deepest to 35% of longest arm.** Webs deepest on lateral arms; webs between dorsal arms and ventral arms shallowest. Interbrachial web pouches absent. **Suckers in single row. Enlarged suckers absent.** Funnel organ W-shaped. **Gills with 6 to 8 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Rachidian tooth with large central cusp. Distinct crop present as side-branch off oesophagus. Ink sac present. Posterior salivary glands very large, to twice the length of buccal mass. Third right arm of males hectocotylized with end of arm clearly differentiated into ligula and calamus. **Ligula large (10 to 16% of arm length), ligula groove long, well-marked and deep with transverse ridges.** Tips of other arms not modified. Diverticulum of terminal organ not coiled. Spermatophores of medium length (60 to 80% of mantle length) and slender. Rostral tip of lower beak sharp. **Skin loose and gelatinous with scattered low papillae. Two short, longitudinal integumentary ridges on the mid-dorsal posterior mantle. Skin ridge present around lateral margin of mantle.**

Size: Mantle length to 60 mm; total length to around 200 mm.

Geographical Distribution: Southern Ocean, Antarctica.

Habitat and Biology: Benthic species on Antarctic continental shelf and slope from 15 to over 1 500 m.

Remarks: Three Antarctic species. Allcock *et al.* (2003c) removed the species ***adelieana*** and ***polymorpha*** from the genus ***Pareledone*** Robson, 1932 and erected ***Adelieledone***, also describing a new species, ***A. piatkowski***.

Literature: Allcock *et al.* (2003c).

Adelieledone polymorpha (Robson, 1930) Fig. 61

Graneledone polymorpha Robson, 1930, Cephalopoda. I. *Octopoda, Discovery Reports*: 2: 390. [Type locality: Southern Ocean, South Georgia Island].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Antarctic knobbed octopus; **Fr** — Élédone noueux; **Sp** — Pulpo nodoso.

Diagnostic Features: Moderate-sized, robust species. **Arms short, 1.5 to 2.6 times mantle length**. Arms of similar length, dorsal arms shortest (typically 4=3>2>1). Arm autotomy at distinct plane absent. **Webs deep, deepest to 35% of arm length**. Web deepest on lateral arms, web sectors of dorsal and ventral arms shallowest. Interbrachial web pouches absent. **One row of suckers on each arm**. In larger animals, around 48 to 67 suckers on each normal arm. Enlarged suckers absent. Gills with 7 to 8 lamellae per demibranch. Funnel organ W-shaped, thick limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Ink sac present. Right third arm of males hectocotylized, length 74 to 96% of opposite arm. **Ligula robust and spoon like with 7 to 8 transverse ridges, 11 to 16% of arm length. Calamus large, 40 to 64% of ligula length**. Hectocotylized arm with 30 to 34 suckers. Spermatophores of moderate size, 68 to 79% of mantle length. Eggs large, >10 mm, >15% of mantle length. **Colour:** Live animals with dense chromatophores varying from brown to green to blue. **Sculpture:** Skin texture of loose gelatinous skin with widely scattered papillae. **Two short, longitudinal ridges present on mid-dorsal posterior mantle**. Ventral surface of mantle smooth. Single slightly larger papilla over each eye. **Skin ridge present around lateral margin of mantle**.

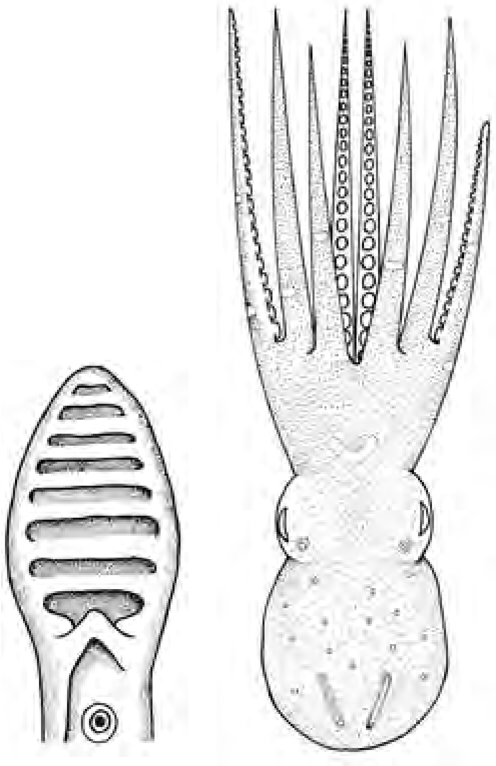

hectocotylus dorsal view

Fig. 61 *Adeleliedone polymorpha*

Size: Mantle length to 60 mm; total length to around 200 mm.

Geographical Distribution: Southern Ocean, South Georgia Island and Antarctic Peninsula (Fig. 62).

Habitat and Biology: Depths range from 15 to 365 m. Collected in trawls around South Georgia Island. Biology poorly known.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Rodhouse and Prince (1993; as ***Pareledone polymorpha***), Daly and Rodhouse (1994; as ***P. polymorpha***), Yau *et al*. (2002; as ***P. polymorpha***), Allcock *et al.* (2003c), Collins *et al.* (2004), Barratt *et al.* (2008), Strugnell *et al.* (2009a), Undheim *et al.* (2010a,b).

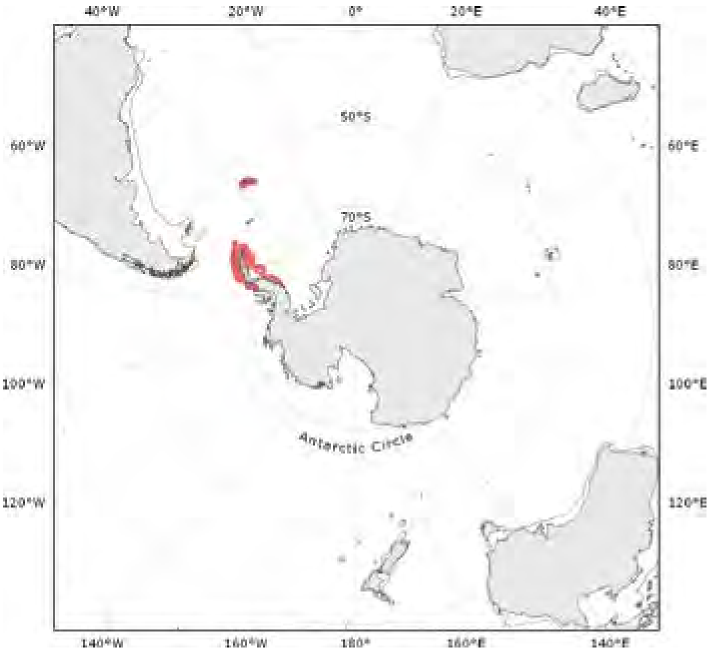


Fig. 62 ***Adelieledone polymorpha***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Adelieledone adelieana (Berry, 1917)

Moschites adelieana Berry, 1917, *Australian Antarctic Expedition Scientific Reports*, *series C*, 4(2), 1–38. [Type locality: Southern Ocean, eastern Antarctica, Adelie Land, off Mertz Glacier].

Size: Mantle length to 40 mm; total length to 160 mm.

Geographical Distribution: Antarctic continental shelf from 30°E to 90°E.

Habitat and Biology: Depths range from 139 to 680 m.

Literature: Kubodera and Okutani (1994; as ***Paraledone adelieana***), Lu and Stranks (1994, as ***P. adelieana***), Allcock *et al.* (2003b).

Adelieledone piatkowski Allcock, Hochberg, Rodhouse and Thorpe, 2003

Adelieledone piatkowski Allcock, Hochberg, Rodhouse and Thorpe, 2003b, *Antarctic Science*, 15(4): 422. [Type locality: Antarctic Peninsula].

Size: Mantle length to 55 mm; total length to 140 mm.

Geographical Distribution: Antarctic Peninsula.

Habitat and Biology: Depths range from 612 to 1 510 m.

Literature: Allcock (2005), Allcock *et al.* (2007).

Ameloctopus Norman, 1992

Ameloctopus Norman, 1992b, *Invertebrate Taxonomy*, 6: 568.

Type Species: *Ameloctopus litoralis* Norman, 1992.

Diagnostic Features: Small, elongate species with ovoid to greatly elongated mantle. **Eyes tiny. Mantle walls very thin, branchial hearts visible as dark spots on lateral mantle.** Stylets absent. **Arms greatly elongated, up to 9 times mantle length. Arms approximately equal in length when intact. Arm autotomy present at distinct plane, around level of 10th to 12th proximal sucker. Webs shallow and subequal, deepest around 7 to 16% of arm length.** Interbrachial web pouches absent. Suckers in two rows. **Enlarged suckers absent.** Funnel organ greatly reduced to four separate components, .”.-shaped, posterior two absent in some speciments. Gills with 5 to 6 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands moderate to large. Crop diverticulum present as side-branch off oesophagus. Third right arm of submature males unspecialised, copulatory organ generates from stump of autotomized third right arm in mature males only. Ligula and calamus present. Terminal organ lacks diverticulum. Spermatophores with inflated sperm reservoir, unarmed. **Colour pattern of white and red-brown transverse bands along arms.** False eye-spots (ocelli) absent. Skin smooth to fine granular texture. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 30 mm; total length to around 260 mm; body weight to at least 15 g.

Geographical Distribution: Northern Australia from southern Great Barrier Reef to north-west Western Australia.

Remarks: Single species restricted to intertidal mudflats of northern Australia.

Literature: Norman (1992b).

Ameloctopus litoralis Norman, 1992

Fig. 63; Plate I, 4

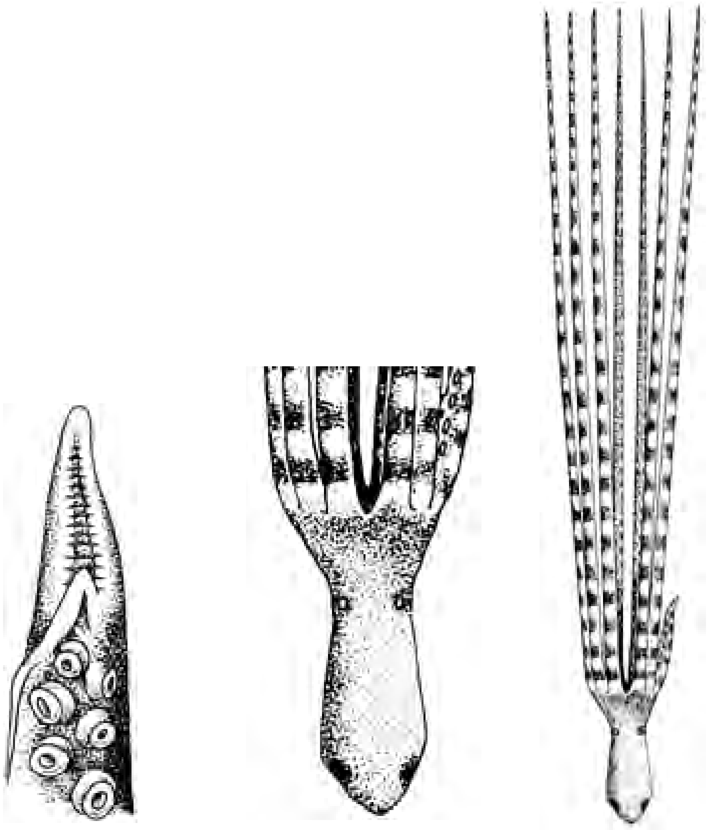
Ameloctopus litoralis Norman, 1992b, *Invertebrate Taxonomy*, 6: 569. [Type locality: Australia, Great Barrier Reef, Queensland, Orpheus Island].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Stringarm octopus; **Fr** — Poulpe à long bras; **Sp** — Pulpo brazos-largos.

Diagnostic Features: Small species with greatly elongated arms. Arms extremely long and narrow, up to 9 times mantle length. Arms approximately equal in length. Arm autotomy at distinct cleavage plane around 10th to 12th suckers. Webs very shallow, deepest around 7 to 16% of arm length. Web sectors of equal length. Web margins absent. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 180 suckers on each normal arm. Enlarged suckers absent. Gills with 5 to 6 lamellae per demibranch. Reduced funnel organ consisting of two to four small pads (typically .”.). Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off



hectocotylus **head - dorsal view** **dorsal view**

Fig. 63 ***Ameloctopus litoralis***

oesophagus. **Ink sac absent. Anal flaps absent. Young males with full length undifferentiated third right arm. Third right arm of males severed at maturity and ligula develops from stump, resulting hectocotylized arm 20 to 30% length of opposite arm.** Ligula conical, 12 to 20% of arm length. Calamus of moderate size, 22 to 38% of ligula length. Hectocotylized arm (once formed) with 21 to 38 suckers. Spermatophores short with swollen reservoir, around 6 mm, 38 to 45% of mantle length, produced in moderate numbers (up to 70). Spermatophores unarmed. Eggs large, around 10 mm, around 35% of mantle length. **Colour: Grey to purple-brown base colour on mantle and head. Regular bands of same colour against cream-grey along length of arms**. False-eye spots (ocelli) absent. **Sculpture: Skin smooth. No papillae**. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 30 mm; total length to around 260 mm; body weight to at least 15 g.

Geographical Distribution: Northern Australia from southern Great Barrier Reef to northwestern Western Australia (Fig. 64).

Habitat and Biology: Depth range appears restricted to intertidal zone. Lives in coral, on rubble, sand, or mud flats. Forages during night low tides on open sand and rubble on intertidal reef flats in pools less than 10 cm deep. Also feeds from within its lair or under rocks by extending one or more arms to forage. Small crustaceans seem to be the primary prey items. The large eggs suggest that juveniles adopt a benthic lifestyle on hatching.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Norman (2000).

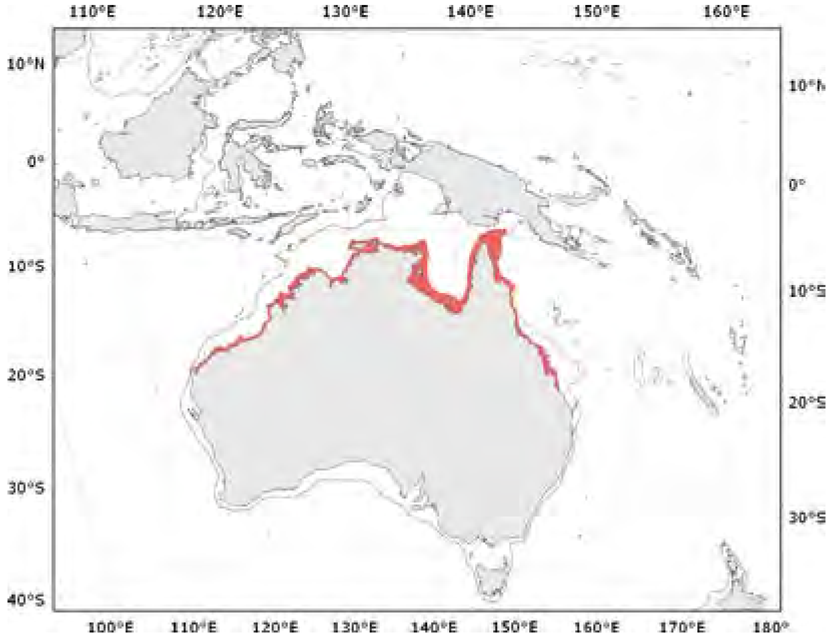


Fig. 64 ***Ameloctopus litoralis***

🟥 Known distribution

Amphioctopus Fischer, 1882

Amphioctopus Fischer, 1882, *Manuel de Conchyliologie et de Paléntologie Conchyliologique ou Histoire Naturelle des Mollusques Vivante et Fossiles. Deuxième partie, Synopsis des Genres. F. Savy: Paris, France (1880–1887)*: 333.

Type Species: *Octopus membranaceus* Quoy and Gaimard, 1832.

Diagnostic Features: Small to medium-sized species, mantle length less than 140 mm. Mantle muscular and ovoid. Stylets absent. **Arms muscular, short to medium length, 2 to 3 times mantle length. Lateral arms longest (typically 4>3>2>1 or 4=3=2>1). Dorsal arms always shortest.** Arm autotomy at distinct plane absent. **Webs moderate to deep, deepest around 25% of longest arm. Webs deepest on lateral arms, webs between dorsal arms markedly shallowest (typically B=C=D=E>A).** Interbrachial web pouches absent. Suckers in two rows. **Enlarged suckers present in mature males of many member species, on at least arms 2 and 3.** Funnel organ W-shaped. **Gills with 6 to 11 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands moderate to large. Crop diverticulum present as side-branch off oesophagus. Ink sac present. Anal flaps present. Third right arm of male hectocotylized, slightly shorter than opposite arm. Ligula and calamus present. Ligula of medium size, 5 to 9% of arm length. Spermatophores few in number (typically <10 in storage sac), armed in some species. Colour patterns: false eye-spots (ocelli) present in some species, often with blue iridescent ring. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle (‘dorsal mantle white spots’ *sensu* Packard and Sanders, 1971). **Dark leading edge occurs along dorsal face of arms 1 to 3 in many species.** 4 to 6 thick longitudinal lines present on mantle in many ocellate species. Skin on dorsal surfaces distinctly granular, patch and groove system well developed; grooves deep, patches approximately uniform in size, oval or round in shape, often visible as dark reticulations between patches, this sculpture extending to oral surface of short dorsal web. A single conspicuous primary papilla present over each eye. **Four large, longitudinally oriented, flap-like papillae arranged in diamond shape on dorsal mantle.** Continuous skin ridge around lateral margin of mantle absent. Intermittent ridge present in some species.

Size: Mantle length to 100 mm; total length to >400 mm; body weight to 400 g.

Geographical Distribution: Tropical and subtropical waters of all oceans.

Habitat and Biology: Subtidal species typically occurring on sand and mud substrates in shallow waters.

Remarks: Members of this distinctive genus of small muscular octopuses form the basis of high value commercial fisheries, particularly in southeast Asia. The type species of this genus is ***Amphioctopus membranaceus*** described by Quoy and Gaimard in 1832 from a single specimen collected from Port Dorey in current West Papua. The type specimen is still in existence in the National Museum of Natural History in Paris but is in poor condition. It clearly belongs in this genus and possesses the iridescent ringed ocellus found in many ocellate ***Amphioctopus*** species. As one of the first ocellate members of this genus to be described and illustrated (showing the iridescent ring within a dark ocellus), the name ***membranaceus*** has been used widely for almost two centuries for many Indo-West Pacific species of ocellate octopuses. As no additional animals have been attributed to the original species, it remains poorly known and defined but is considered as valid as the type species. Other better-diagnosed members of this genus are presented below as representative of this genus. Despite the extensive use of the name ***membranaceus*** in regional fisheries, we treat the species as valid but of no known commercial interest.

Literature: Huffard and Hochberg (2005), Norman and Hochberg (2005a), Norman and Kubodera (2006).

Amphioctopus aegina (Gray, 1849)

Fig. 65; Plate I, 5

Octopus aegina Gray, 1849, *Catalogue Mollusca… British Museum*: 7. [Type locality: Not stated in original description].

Frequent Synonyms: *Octopus hardwickei* Gray, 1849; *O. dollfusi* Robson, 1928.

Misidentifications: *Octopus kagoshimensis* Ortmann, 1888.

FAO Names: En — Sandbird octopus; **Fr** — Poulpe des sables; **Sp** — Pulpo reticulado.

Diagnostic Features: Moderate-sized and robust species. Arms short to moderate, 2 to 3 times mantle length. Lateral arms longest (typically 3=4>2>1). Arm autotomy at distinct plane absent. Webs deep, deepest up to 30% of arm length. Web deepest on lateral arms, webs between dorsal arms very shallow. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 110 to 130 suckers on each normal arm. Enlarged suckers present in mature males, 2 to 3 on arms 2 and 3, starting around the 6th proximal sucker. Gills with 8 to 9 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, its length 70 to 80% of opposite arm. Thin, moderate-sized ligula, 4 to 6% of arm length. Calamus small. Hectocotylized arm with around 60 to 70 suckers. Spermatophores of moderate size, around 30 to 50 mm, 50 to 90% of mantle length, produced in moderate numbers (~15 to 20). **Spermatophores armed with inward pointing teeth, exposed on eversion. Eggs small, around 3% of mantle length. Colour: Pattern of dark grooves enclosing pale round spots to form a round net mesh on dorsal and lateral surfaces, most obvious on arm bases. Cream-coloured longitudinal stripe along dorsal midline.** Cream, narrow transverse head bar sometimes present. False-eye spots (ocelli) absent. Transverse pair of white spots visible on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin with regular round patches and grooves matching colour pattern. Oral surface of dorsal web sculptured with same texture as dorsal surfaces. Diamond shape of longitudinal ridges present on dorsal mantle. No obvious supraocular papillae. Skin ridge around lateral margin of mantle absent.

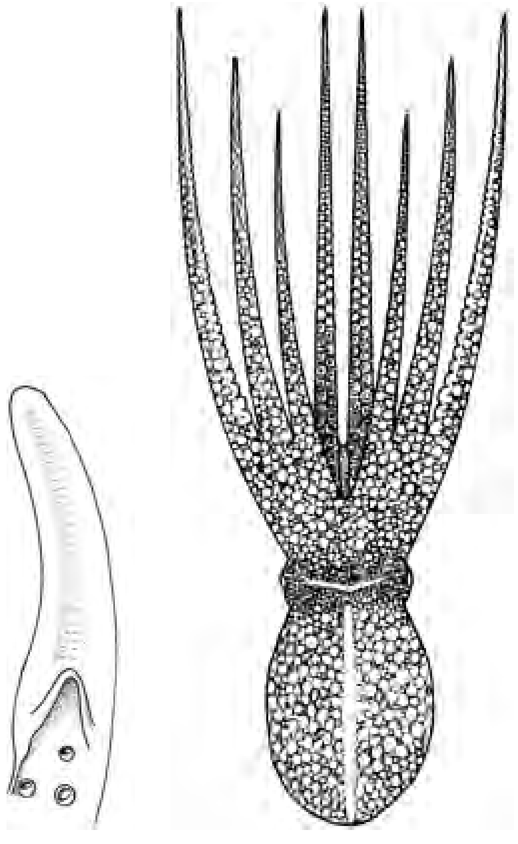


Fig. 65 ***Amphioctopus aegina***

Size: Mantle length to 90 mm; total length to around 300 mm; body weight to around 100 g.

Geographical Distribution: Coastal waters of continental Asia, from China and Taiwan Province of China, south to Malaysia and Indonesia, west to at least Chennai, India. Also reported from the Philippines (Fig. 66).

Habitat and Biology: Depths range to at least 40 m. Known from muddy coastal waters and typically found subtidally on soft substrates. Nothing known of diet or foraging behaviour. Females carry the egg strings in their webs rather than attaching the eggs to hard substrates.

Interest to Fisheries: This species forms the basis of large export trawl fisheries, particularly from the Gulf of Thailand where it is treated under the junior synonym name, ***Octopus dollfusi*** (Chotiyaputta 1993). Marketed widely around the world with other ***Amphioctopus*** species under the name 'baby octopus'.

Fig. 66 ***Amphioctopus aegina***

🟥 Known distribution

Local Names: Unknown.

Remarks: Toll and Voss (1998) designated the species name ***aegina*** as dubious due to the lack of a type locality. The type specimen exists (BMNH 1928.2.14.1) and is a mature female which clearly shows the diagnostic characters of this species. We recognise ***Amphioctopus aegina*** as a valid species name, the senior synonym of ***A. hardwickei*** and ***A. dollfusi***. Toll and Voss (1998) incorrectly treated these latter two names as synonyms of ***A. kagoshimensis***, a distinct species from further north (see treatment of that species). ***Amphioctopus kagoshimensis*** is frequently and incorrectly treated under the name ***Octopus aegina*** in Japan. Voss and Williamson's (1971) reference to the common name of ***A. aegina*** as Saa Liu (Sand Bird) refers to ***A. marginatus***. However, since "Sandbird octopus" was the name originally given to this species in FAO archives and has been used since for fisheries data and statistics, it was retained here as the official name. This species has also been treated under the common name "Marbled octopus" (e.g. Norman, 2000).

Literature: Voss and Williamson (1971; as ***Octopus dollfusi***), Nateewathana (1997), Norman and Sweeney (1997).

Amphioctopus burryi (Voss, 1950)

Fig. 67; Plate I, 7

Octopus burryi Voss, 1950, *Revista de la Sociedad Malacologia*, 7(2): 76. [Type locality: Gulf of Mexico, United States, Florida Keys, southeast of Sombrero Key Light].

Frequent Synonyms: *Octopus vincenti* Pickford, 1955.

Misidentifications: None.

FAO Names: En — Brown-striped octopus; **Fr** — Poulpe à rayures bleues; **Sp** — Pulpo granuloso.

Diagnostic Features: Moderate-sized, robust species. Arms short to moderate length, stout, 2 to 3 times mantle length. Lateral and ventral arms longest (typically 4=3>2>1). Arm autotomy at distinct plane absent. Webs deep, deepest around 30% of arm length. Web deepest on lateral arms, webs between dorsal arms the shallowest. Web margins extend at least half of arm length. Interbrachial web pouches absent. Two rows of suckers on each arm. Enlarged suckers absent. Gills with 9 to 11 lamellae per demibranch. Funnel organ W-shaped. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, ~85% the length of opposite arm. Ligula small and narrow with an open groove, 4 to 6% of arm length. Calamus of moderate size, around 30% of ligula length. Number of suckers on hectocotylized arm unknown. Spermatophores of moderate size, around 24 mm, around 60% of mantle length, produced in moderate numbers (~10). Eggs small, around 2 mm. **Colour:** Reddish brown on dorsal surfaces tending to orange on the ventral surfaces. Cream on the oral surfaces of the webs. **Conspicuous purplish brown stripe sometimes visible along entire leading edge of arms 1 to 3**. Dark eye-bar visible in some colour patterns. False-eye spots (ocelli) absent. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle (‘dorsal mantle white spots’ *sensu* Packard and Sanders, 1971). **Sculpture: Skin sculptured in regular, small, raised, round to oval patches.** Colour and sculpture of dorsal surfaces extends to mouth on oral surface of dorsal web. Single large papilla over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 70 mm; total length to around 250 mm.

Geographical Distribution: Gulf of Mexico and tropical western Atlantic from North Carolina to northern Brazil. Tropical eastern Atlantic off west Africa (Fig. 68).

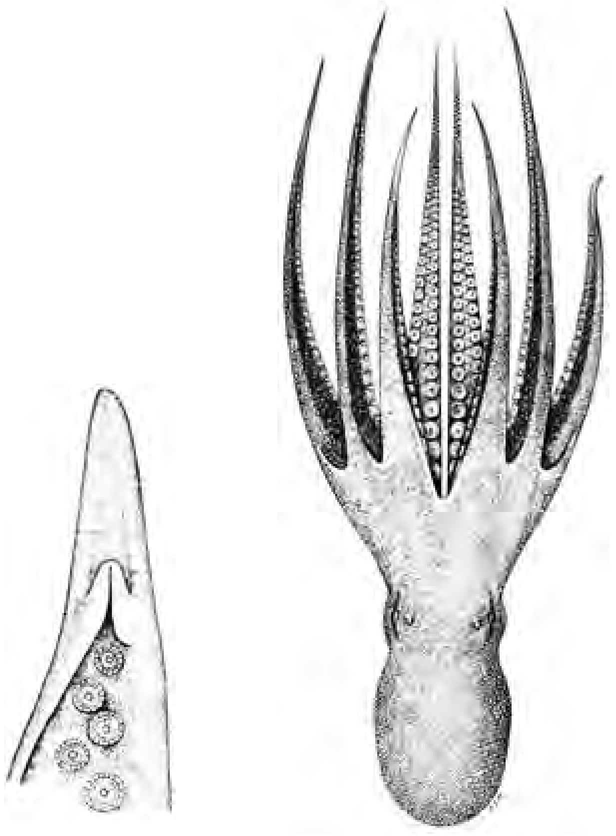
Habitat and Biology: Depths range to around 200 m. This small, shallow-water octopus is associated with substrates composed of sand, broken coral and shells. It emerges mainly at dusk and dawn to feed.

Interest to Fisheries: Taken rarely as bycatch in trawl fisheries.

Local Names: UNITED STATES OF AMERICA: Caribbean arm stripe octopus.

Remarks: The taxonomic status of this octopus is unresolved. At present it is unclear whether the eastern and western Atlantic forms are the same species. It is possible that ***Octopus granulatus*** Lamarck, 1799 from the western Atlantic is the senior synonym for this taxon.

Literature: Voss (1951b), Hanlon and Hixon (1980), Forsythe (1983), Forsythe and Hanlon (1985).



hectocotylus **dorsal view**

Fig. 67 ***Amphioctopus burryi***

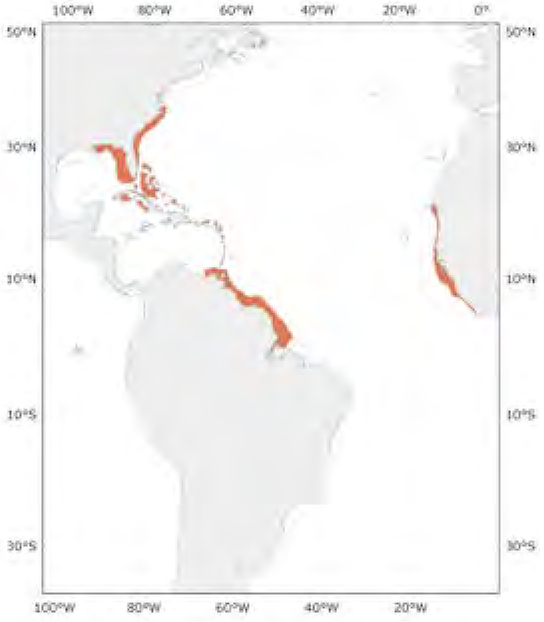


Fig. 68 ***Amphioctopus burryi***

🟥 Known distribution

Amphioctopus exannulatus (Norman, 1993)

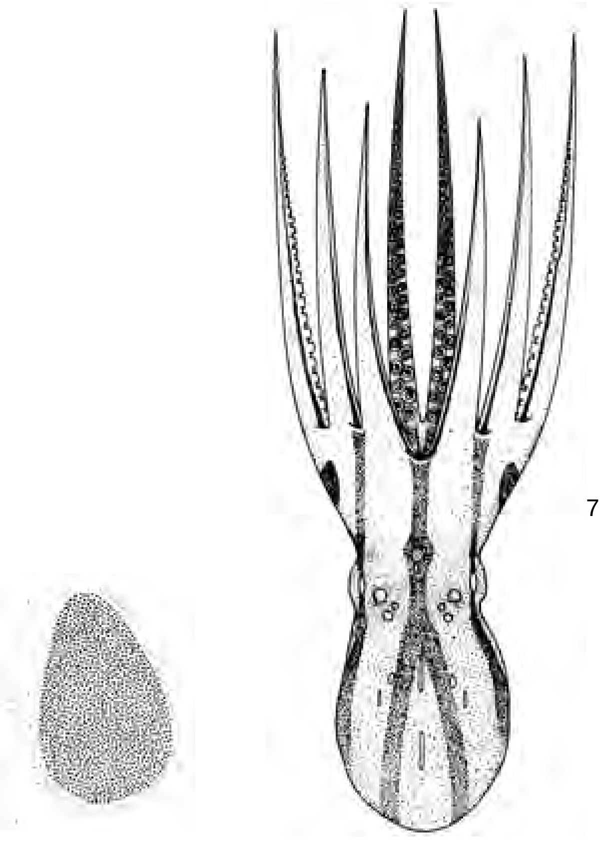
Fig. 69; Plate I, 8

Octopus exannulatus Norman, 1993b, *Memoirs of the Museum of Victoria*, 53(2): 321. [Type locality: Australia, Queensland, Moreton Bay].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Plain-spot octopus; **Fr** — Poulpe annelé; **Sp** — Pulpo ensortijado.



ocellus

dorsal view

Fig. 69 *Amphioctopus exannulatus*

Diagnostic Features: Small, muscular species. Arms of moderate length, 2 to 3 times mantle length. Lateral arms longest (typically 3>4>2>1). Arm autotomy at distinct plane absent. Webs deep, deepest around 25 to 37% of arm length. Web deepest on lateral arms; webs between dorsal arms distinctly shorter. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 120 to 190 suckers on each normal arm. Enlarged suckers present in mature males, 2 to 4 on arms 2 and 3, starting around the 6th proximal sucker. Gills with to 8 lamellae per demibranch. Funnel organ W-shaped; outer limbs slightly shorter than medial limbs (80 to 100%). Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 80% length of opposite arm. Ligula small, roughly conical, 3.5 to 6% of arm length. Calamus of moderate size, 20 to 35% of ligula length. Hectocotylized arm with 62 to 77 suckers. **Spermatophores large, around 60 mm long, 130 to 160% of mantle length,** produced in low numbers (~10). Spermatophores unarmed. Eggs small, around 4 mm long, around 7% of mantle length. **Colour:** Base colour variable from grey-white to dark chocolate brown. **Alarm pattern of four broad longitudinal stripes along mantle, extending through eye and continuing as dark lines along leading edges of arms 1 to 3. False eye-spots (ocelli) present as plain dark spot lacking an iridescent ring.** Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin texture of regular rounded papillae over all surfaces, distinctly larger on ventral mantle. Four longitudinal raised skin ridges in diamond arrangement on dorsal mantle. Single large branching papilla over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 50 mm; total length to around 200 mm; body weight to at least 75 g.

Geographical Distribution: From Philippines to northern Australia (Fig. 70).

Habitat and Biology: Depths range from 0 to 84 m. Little is known about the life history or biology of this species. It has been collected on exposed intertidal mudflats and subtidally on muddy, sandy and shelly sand substrates. This species appears to inhabit open bottom/inter-reef substrates and seagrass beds.

Fig. 70 *Amphioctopus exannulatus*

🟥 Known distribution

Interest to Fisheries: Prawn trawler operators fishing in Great Barrier Reef waters report catches of this distinctive species in fairly low numbers when trawling over sand or muddy substrata. This species was often retained for use as bait. No information is available on scale of catch.

Local Names: Unknown.

Literature: Norman (1993b), Norman and Sweeney (1997).

Amphioctopus fangsiao (d'Orbigny, 1839-1841)

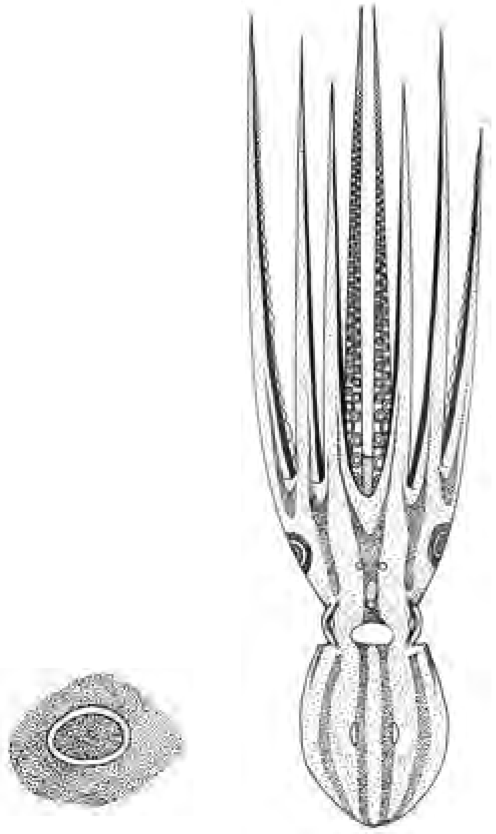
Fig. 71; Plate II, 9

Octopus fangsiao d'Orbigny, 1839-1841, *In* Ferussac and d'Orbigny, 1834-1848, *Histoire naturelle générale et particulière des Céphalopodes Acetabulferes vivants et fossiles*. J.B. Bailliere, Paris: 70. [Type locality: Japan].

Frequent Synonyms: *Octopus areolatus* de Haan, 1839-1841; *O. fangsiao typicus* d'Orbigny, 1839-1841; *O. fangsiao etchuanus* Sasaki, 1929; *O. ocellatus* Gray, 1849; ? *O. brocki* Ortmann, 1888.

Misidentifications: *Octopus membranaceus* Quoy and Gaimard, 1832.

FAO Names: En — Gold-spot octopus; **Fr** — Poulpe doré; **Sp** — Pulpo dorado.



ocellus

dorsal view

Fig. 71 ***Amphioctopus fangsiao***

Diagnostic Features: Small to moderate-sized, robust species. Arms short, 2 to 3 times mantle length. Lateral arms longest (typically 3>4=2>1). Arm autotomy at distinct plane absent. Webs deep, deepest around 20% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 150 suckers on each normal arm. Enlarged suckers present in mature males, 1 to 3 on arms 2 and 3, starting around the 5th proximal sucker. Gills with 7 to 8 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length around 80% of opposite arm. Ligula long and thin, around 6% of arm length. Calamus small and low, around 25% of ligula length. Hectocotylized arm with 75 to 95 suckers. Spermatophores small, around 30 mm, around 60% of mantle length, produced in moderate numbers (~60). Spermatophores unarmed. **Eggs large, 8 to 13 mm, around 10 to 15% of mantle length. Colour:** Generally pale in colour. **False-eye spots (ocelli) present, containing gold-coloured iridescent ring. Four to 6 dark bars shown on mantle and arm crown in some colour patterns, continuing as narrow dark lines along leading edges of arms 1 to 3. Pale oval to dumbbell-shaped patch present on head between eyes.** Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin texture of regular small patches. Sculpture and patterns extend to oral surface of dorsal web. Four short ridges of skin in diamond arrangement on dorsal mantle, several small papillae present over each eye. **Broken skin ridge present around lateral margin of mantle.**

Size: Mantle length to 80 mm; total length to at least 200 mm; body weight to at least 100 g.

Geographical Distribution: From south coast of Hokkaido, Japan south to Taiwan Province of China and China, Hong Kong SAR (Fig. 72).

Habitat and Biology: Depths to at least 100 m. Coastal species found on sand and mud substrates. Females brood large eggs in dead bivalve shells.

Interest to Fisheries: Harvested on a large scale, primarily as bycatch in coastal trawls. Popular for human consumption.

Local Names: JAPAN: Iidako.

Remarks: There is considerable confusion over standardized names for several ocellate octopus species that occur in south-east Asia. ***Amphioctopus fangsiao*** frequently is listed in fisheries statistics under the synonym names ***Octopus ocellatus*** and ***O. areolatus***, or the unresolved name ***O. membranaceus***. A thorough review of Asian ocellate octopuses is urgently required.

Literature: Voss and Williamson (1971; as ***Octopus membranaceus***), Okutani *et al.* (1987; as ***O. ocellatus***), Gleadall and Naggs (1991), Norman (1998), Furuya and Tsuneki (2005), Takumiya *et al.* (2005), Furuya (2006).

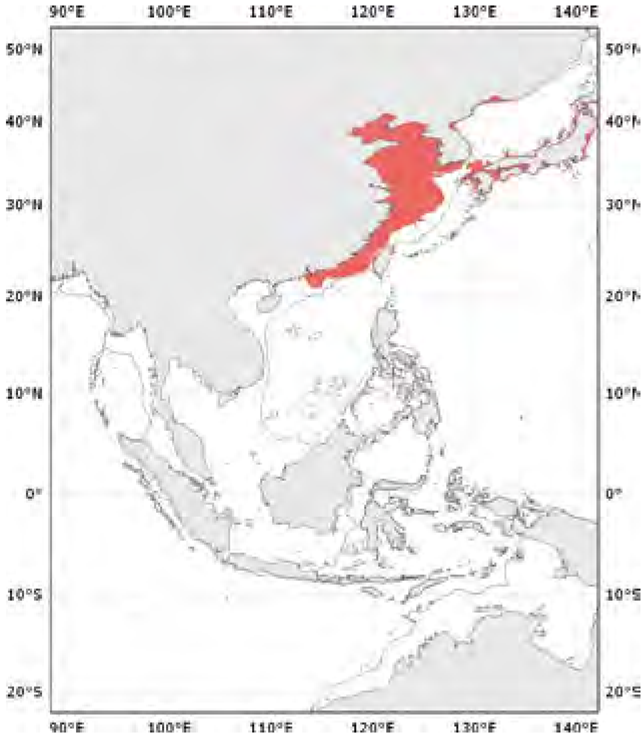


Fig. 72 ***Amphioctopus fangsiao***

🟥 Known distribution

Amphioctopus kagoshimensis (Ortmann, 1888)

Fig. 73; Plate II, 10

Octopus kagoshimensis Ortmann, 1888, *Zoologische Jahrbücher, Abteilung für Systematik. Oekologie und Geographie der Tiere*, 3: 664. [Type locality: Japan, Kagoshima Prefecture].

Frequent Synonyms: None.

Misidentifications: *Octopus aegina* Gray, 1849; *Octopus granulatus* Lamarck, 1799.

FAO Names: En — Stareye octopus; **Fr** — Poulpe étoilé; **Sp** — Poulpo estrellado.

Diagnostic Features: Small, robust species. Arms 2 to 3 times mantle length. Lateral and ventral arms longest (typically 4=3=2>1). Arm autotomy at distinct plane absent. Webs deep, deepest around 25% of arm length. Web deepest on lateral arms, webs between dorsal arms very shallow. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 150 to 170 suckers on each normal arm. Enlarged suckers absent. Gills with 8 to 9 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length 70 to 90% of opposite arm. Ligula of moderate size and open, around 6% of arm length. Calamus small and blunt, <20% of ligula length. Hectocotylized arm with 70 to 90 suckers. **Spermatophores very long, around 120 to 160 mm, much longer than mantle length (160 to 190%)**, produced in low numbers (<10). Spermatophores unarmed. Eggs small, around 4 mm, 4 to 8% of mantle length. **Colour:** Uniform pale cream to mottled orange brown. **Net-like lattice of dark lines can be displayed in grooves between skin patches. Four short white lines radiating from each eye.** Irregular dark spot visible in some colour patterns in location of false-eye spots (ocelli). Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture: Skin sculpture of regular raised polygonal patches over all dorsal and lateral surfaces. Sculpture and pattern extend to oral surface of dorsal web, visible as dark net-mesh pattern.** Four short longitudinal ridges in diamond pattern on dorsal mantle. Large supraocular papilla over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 86 mm; total length to around 300 mm.

Geographical Distribution: Northwestern Pacific from southern Japan (Sanriku coast), south to at least Taiwan Province of China (Fig. 74).

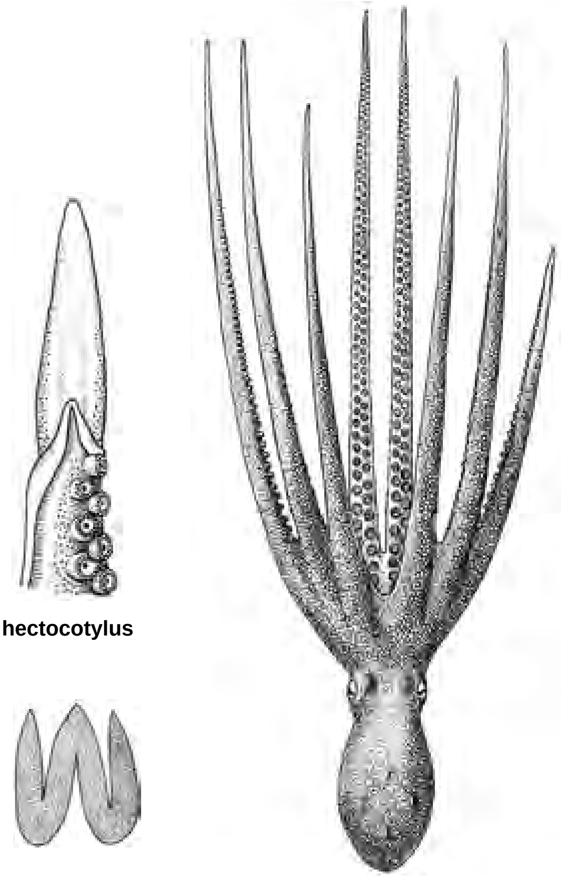
Habitat and Biology: Little is known of this octopus. It has been collected in trawls on soft sediments.

Interest to Fisheries: Minor trawl bycatch in Japanese coastal waters.

Local Names: Unknown.

Remarks: Treated in Japan under the name ***Octopus aegina***. A closely related species in eastern Australia is treated in Norman and Kubodera (2006) under the name ***Amphioctopus*** cf. ***kagoshimensis***. An unresolved member of the genus ***Amphioctopus*** is treated under the name ***O. kagoshimensis*** as an Indo-Pacific incursion into the Mediterranean Sea from the Red Sea, following the opening of the Suez Canal (Salman *et al.,* 1999; Salman *et al.,* 2005). All taxa require further investigation.

Literature: Sasaki (1929; as ***Octopus granulatus***), Okutani *et al.* (1987; as ***O. aegina***), Salman *et al.* (1999), Salman *et al.* (2005), Norman and Kubodera (2006).



hectocotylus

funnel organ

dorsal view

Fig. 73 ***Amphioctopus kagoshimensis***

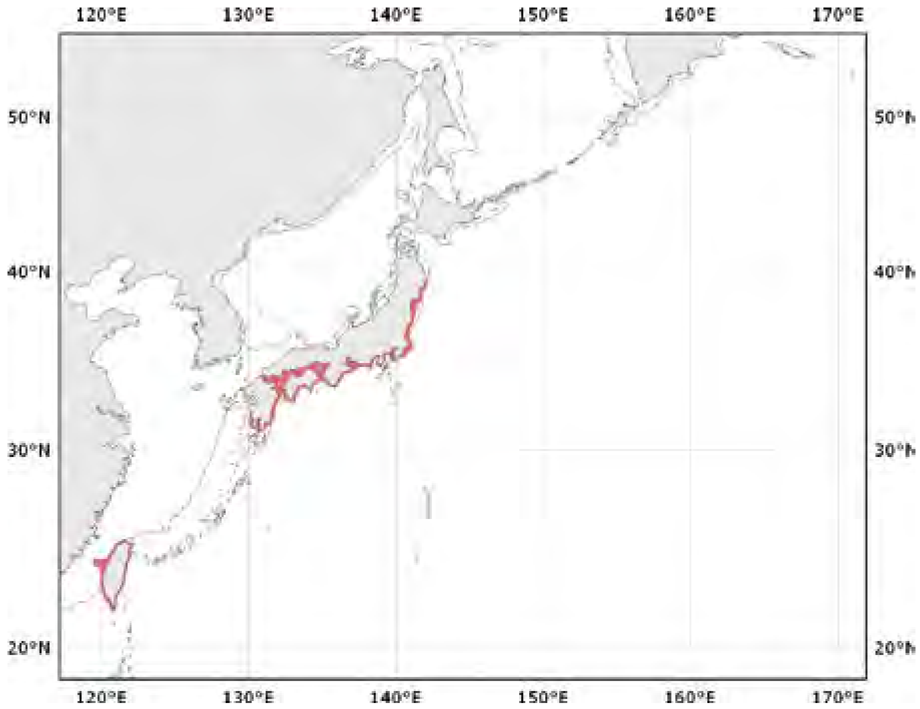


Fig. 74 ***Amphioctopus kagoshimensis***

🟥 Known distribution

Amphioctopus marginatus (Taki, 1964)

Fig. 75; Plate II, 11

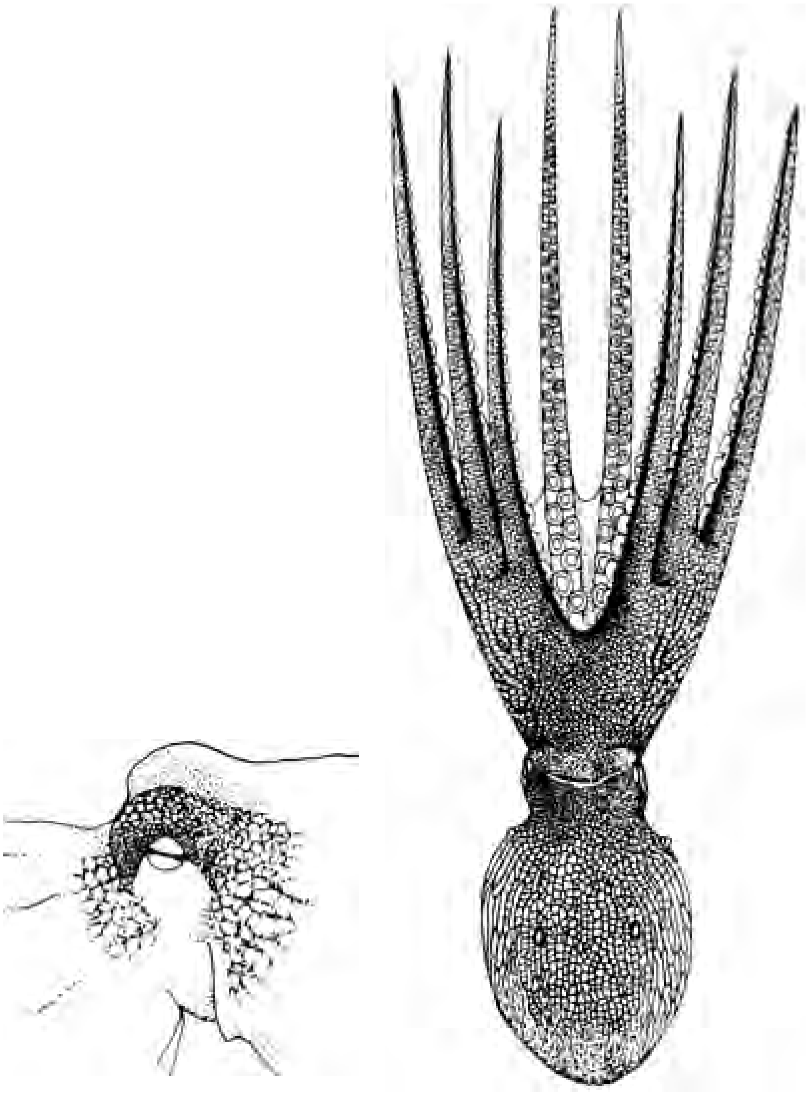
Octopus marginatus Taki, 1964, *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University*: 5(2): 304. [Type locality: Northwest Pacific Ocean, Japan, Oita Prefecture, Minami-Amabe County, near Kamae Town].

Frequent Synonyms: *Octopus striolatus* Dong, 1976.

Misidentifications: *O. aegina* Gray, 1849; *O. dollfusi* Robson, 1928.

FAO Names: En — Veined octopus; **Fr** — Poulpe veiné; **Sp** — Pulpo venoso.

Diagnostic Features: Moderate-sized, robust species. Arms of moderate length, 2 to 3 times mantle length. Lateral arms longest (typically 3>4=2>1). Arm autotomy at distinct plane absent. Webs deep, deepest around 30% of arm length. Web deepest on lateral arms; webs between dorsal arms much shallower. Web margins extend at least halfway along arms. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 150 suckers on each normal arm. Slightly enlarged suckers present in mature males, 4 to 5 on arms 2 and 3, starting around the 7th proximal sucker. Gills with 9 to 11 lamellae per demibranch. Funnel organ W-shaped; limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length around 80% of opposite arm. Ligula small and triangular, 1.5 to 3.5% of arm length. Calamus well developed, around 50% of ligula length. Hectocotylized arm with 60 to 80 suckers. Spermatophores long, around 40 to 60 mm, approximately equal to mantle length; produced in low numbers (~5). Spermatophores unarmed. Eggs small, to around 3 mm, around 4% of mantle length. **Colour:** Typical pattern of orange-brown to purple background with dark purple-brown reticulations, defining distinct patches in irregular longitudinal rows. **Suckers white to pink, contrasting against dark brown to black border along leading edge of arms 1 to 3**. Narrow transverse "head bar" visible in live animals. **White triangle below each eye. Dark vein-like reticulations distinctive on lateral arm crown in same position as false eye-spots in ocellate species**. False-eye spots (ocelli) absent. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin sculpture of regular round to elongate patches separated by distinct grooves. **Patches arranged in irregular longitudinal lines on anterior lateral edges of mantle. Diamond shape of four longitudinal skin ridges on dorsal mantle**. Single large papilla over each eye. Sculpture and colour pattern extend to mouth on oral surface of dorsal web. Skin ridge around lateral margin of mantle absent.



head - lateral view

dorsal view

Fig. 75 ***Amphioctopus marginatus***

Size: Mantle length to 100 mm; total length to around 300 mm; body weight to around 400 g.

Geographical Distribution: Found in tropical continental waters of the Indian Ocean, from Durban, South Africa, to Red Sea, India, south-east Asia, Taiwan Province of China, Philippines and Japan, as well as east to north-eastern Australia (Fig. 76).

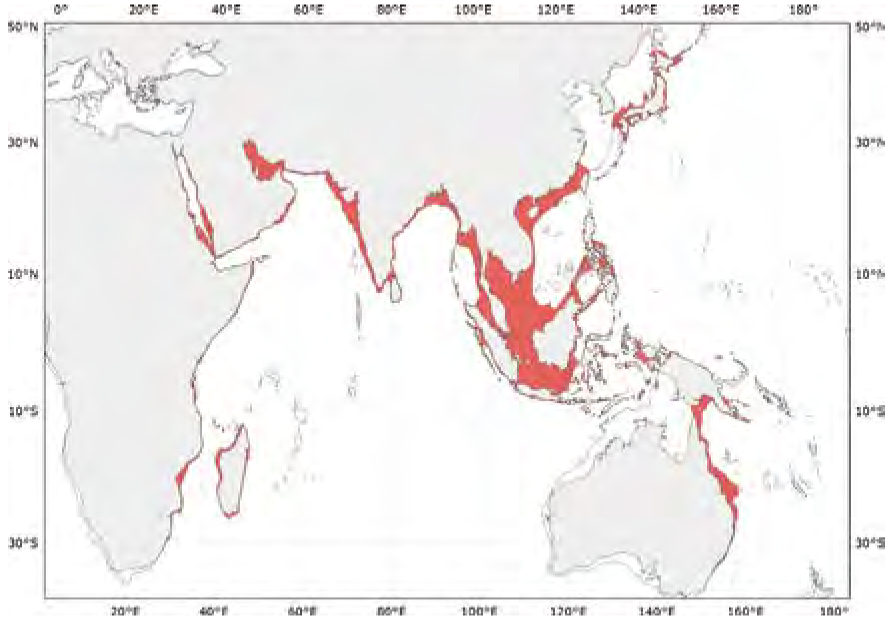


Fig. 76 ***Amphioctopus marginatus***

🟥 Known distribution

Habitat and Biology: Depths range from shallow subtidal to at least 190 m. Known from coastal muddy waters on mud and sand substrates. Little is known about the biology or behaviour of this species. It forages for crustaceans, particularly crabs (*Calappa*), and bivalves. This species makes dens in clamshells, coconut shells, bottles, and other man-made discarded objects in sand and mud. This octopus will carry one mollusc shell or a half coconut shell while searching for another shell in which to enclose itself. Females lay about 100 000 small eggs, up to 3 mm long.

Interest to Fisheries: Important fisheries species collected by trawlers, pots, and lines.

Local Names: INDONESIA: Coconut octopus; CHINA: Saa liu ("sand bird").

Remarks: This species has been confused regularly with two other related species, ***Amphioctopus aegina*** and ***A. kagoshimensis***. It is easily distinguished from these species. Taki's original description of ***marginatus*** was based on a female specimen. As Toll and Voss (1998) used spermatophore characters as the only means of distinguishing these three related species, they designated ***marginatus*** as a dubious species. We do not support this decision and recognise ***marginatus*** as a valid species (see Norman and Hochberg, 2005a).

Molecular and morphological research from Taiwan Province of China (C-W. Ho, pers. comm.) suggest that taxa treated under this species name may represent two cryptic species, at least in Taiwanese waters. Japanese type locality and records may represent vagrants of the typical tropical species carried north by the Kuroshio Current (Norman, 1992c).

Voss and Williamson's (1971) reference to the common name of ***A. aegina*** as Saa Liu (Sand Bird) refers to ***A. marginatus***. However, since "Sandbird octopus" was the name originally given to ***A. aegina*** in FAO archives and it has been used widely for fisheries data and statistics, it is retained as the official common name for ***Octopus aegina***.

Literature: Voss and Williamson (1971; as ***Octopus aegina***), Roper *et al.* (1984; as ***O. aegina***), Norman (1992c), Norman and Hochberg (1994, 2005a), Norman and Kubodera (2006), Finn *et al.* (2009), Huffard and Godfrey-Smith (2010).

Amphioctopus mototi (Norman, 1993)

Fig. 77; Plate II, 12

Octopus mototi Norman, 1993b, *Memoirs of the Museum of Victoria*, 53(2): 329. [Type locality: Australia, southern Great Barrier Reef, Queensland, Heron Island].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Poison ocellate octopus; **Fr** — Poulpe venimeux ocellé; **Sp** — Pulpo venenoso ocelado.

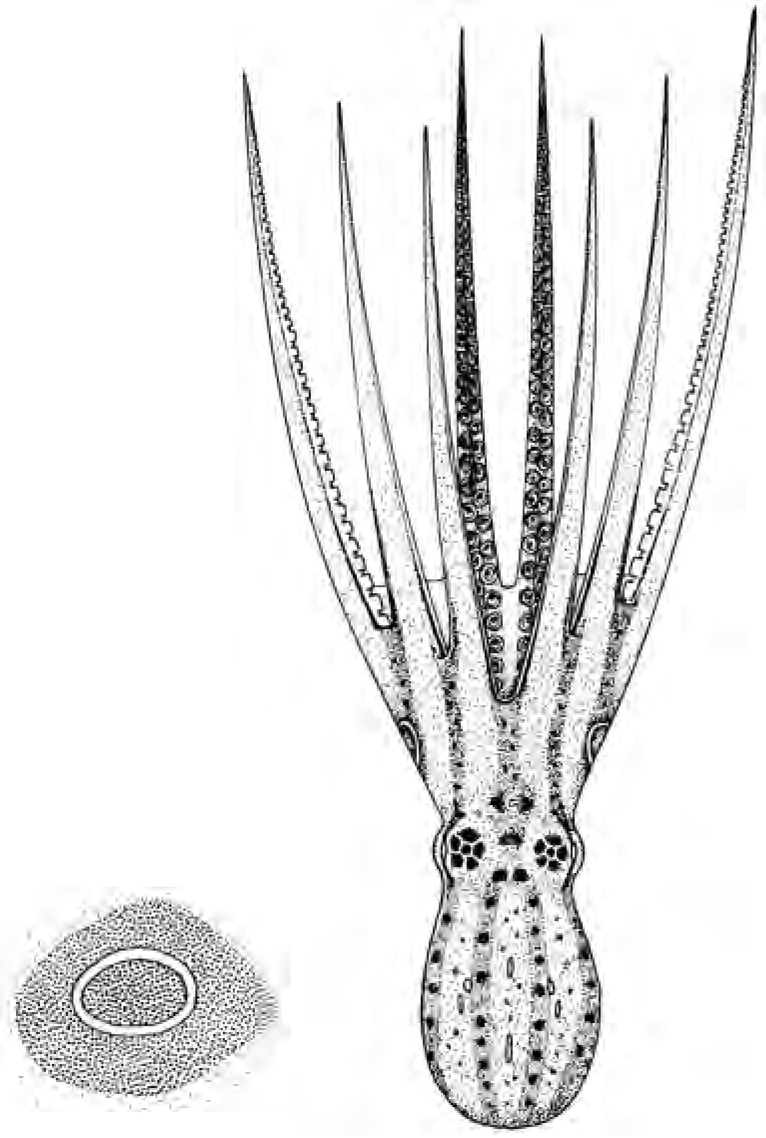


Fig. 77 ***Amphioctopus mototi***

Diagnostic Features: Muscular species. Arms of moderate length, 2.5 to 3 times mantle length. Lateral arms longest (typically 3=4>2>1). Arm autotomy at distinct plane absent. Webs deep, deepest around 25 to 40% of arm length. Web deepest on lateral arms; webs between dorsal arms distinctly shallower. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 140 to 170 suckers on each normal arm. Enlarged suckers present in mature males, 2 to 3 on arms 2 and 3, starting around the 5th proximal sucker. Gills with 9 to 11 lamellae per demibranch. Funnel organ W-shaped, length of outer limbs around 90% of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized; length 80 to 100% of opposite arm. Ligula short and broad with wide groove, 3 to 7% of arm length. Calamus of moderate size, around 40 to 50% of ligula length. Hectocotylized arm with 95 to 106 suckers. Spermatophores of moderate size, around 40 to 50 mm (= 60 to 70% of mantle length), produced in low numbers (<10). Spermatophores unarmed. Eggs of moderate size, around 6 mm, around 8% of mantle length. **Colour:** Typically orange-brown with scattered dark spots. **Petal arrangement of 5 dark spots present over each eye. Alarm colour pattern of white base colour and six dark maroon longitudinal stripes on mantle, continuing through eye and down leading edges of arms 1 to 3. False-eye spots (ocelli) present as dark spot containing simple iridescent blue ring.** Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle (‘dorsal mantle white spots’ *sensu* Packard and Sanders, 1971). **Sculpture: Skin texture of regular low rounded papillae.** Four longitudinal ridges in diamond arrangement on dorsal mantle. Single small papilla above and slightly behind each eye in centre of “flower” pattern of spots. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 100 mm; total length to at least 320 mm; body weight to at least 300 g.

Geographical Distribution: South Pacific Ocean from Great Barrier Reef and northern New South Wales, Australia to New Caledonia and Rapa Iti Island. Similar form recorded from Okinawa in the northwestern Pacific. The taxonomic status of the northern form is unresolved (Fig. 78).

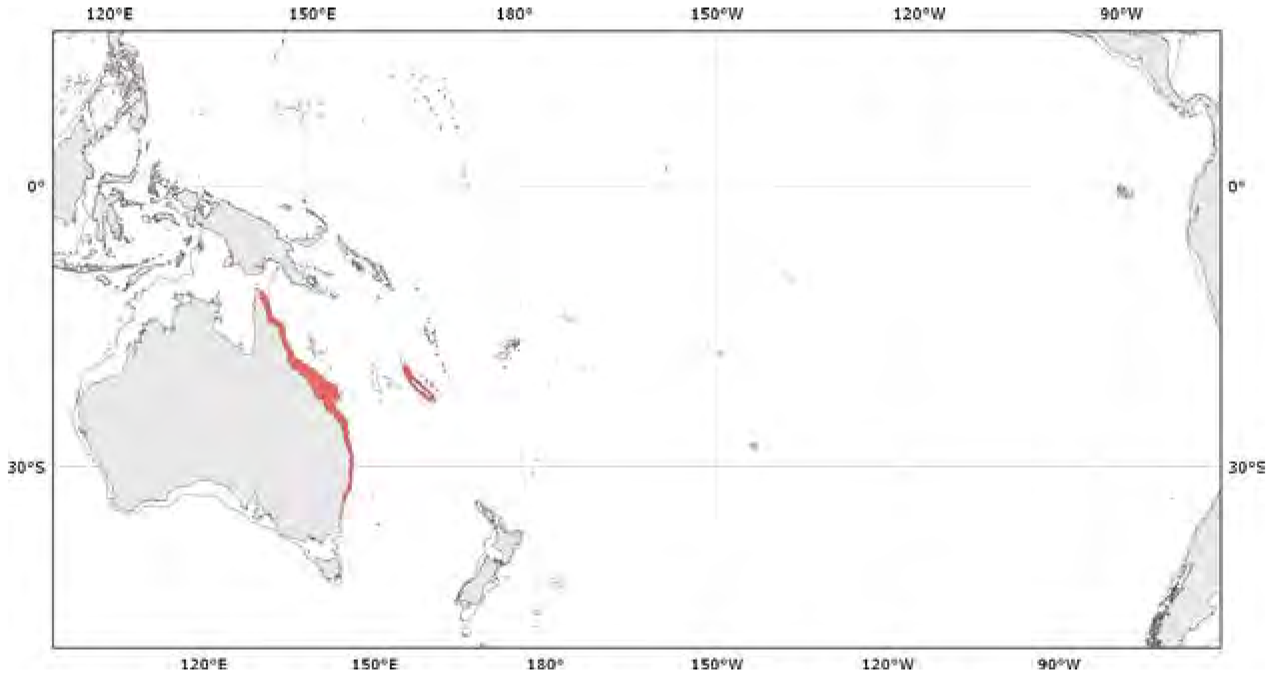


Fig. 78 ***Amphioctopus mototi***

🟥 Known distribution

Habitat and Biology: Depths range from 1 to 54 m. ***Amphioctopus mototi*** occurs on sandy substrates, often associated with coral heads or rubble. Deep lairs are excavated under coral heads or coral rubble on sand substrate. From limited observations, this species appears to have crepuscular activity patterns. Lairs are surrounded by cast off gastropod shells which may have been collected for their secondary occupants, hermit crabs. Stomach contents have a high proportion of crustacean exoskeletal fragments. Eggs are laid in large numbers in festoons. The small egg size indicates hatchlings are planktonic. This octopus may prove to be venomous. This suggestion is supported by the prominent warning coloration and the report from Rapa Iti Island that this species is known locally as the “poison octopus” (G. Paulay, pers. comm.). Live animals willingly bite objects such as aquarium nets, behaviour not normally observed in other octopus species.

Interest to Fisheries: Unknown.

Local Names: FRENCH POLYNESIA: Rapa Iti Island: Fe’e mototi.

Literature: Norman (1993b), Norman (2000).

Amphioctopus neglectus (Nateewathana and Norman, 1999)

Fig. 79

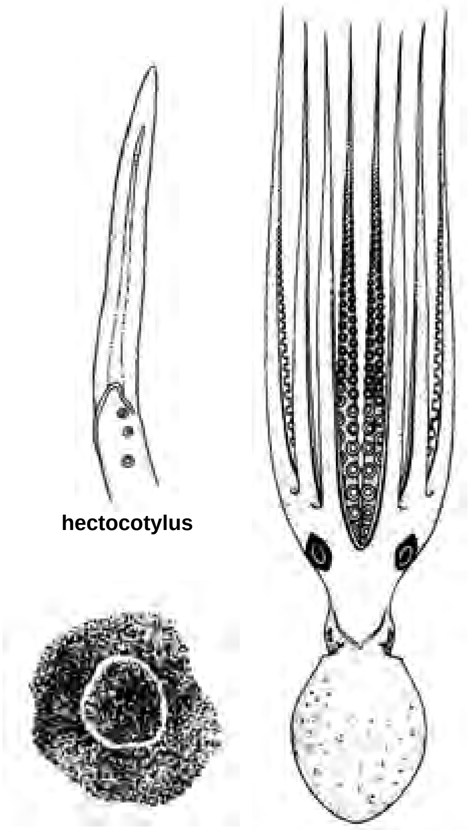
Octopus neglectus Nateewathana and Norman, 1999, *Phuket Marine Biological Center Special Publication,* 19(2): 452. [Type locality: Andaman Sea, Thailand, off Ko Phuket (Thai-Malaysian Border)].

Frequent Synonyms: *Octopus* sp. B. Nateewathana, 1997.

Misidentifications: *Octopus membranaceus* Quoy and Gaimard, 1832.

FAO Names: En — Neglected ocellate octopus; **Fr** — Poulpe négligé ocellé; **Sp** — Pulpo ocelado descuidado.

Diagnostic Features: Moderate-sized species with oval mantle and relatively slender arms. Arms of moderate length, 2 to 3 times mantle length. Lateral or ventral arms longest (typically 4=3>2>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20% of arm length. Web deepest on lateral or ventral arms; webs between dorsal arms considerably shallower. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 110 to 125 suckers on each normal arm. Enlarged suckers present in mature males, around 4 on arms 2 and 3, starting around the 6th proximal sucker. Gills with 7 to 8 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized; length 75 to 100% of opposite arm. Ligula slender and long, around 10% of arm length. Calamus short, 10 to 15% of ligula length. Hectocotylized arm with 50 to 70 suckers. Spermatophores of moderate size, around 20 mm, 35 to 40% of mantle length. Eggs small, around 7% of mantle length. **Colour:** Brownish-green colour dorsally and paler white ventrally. **Numerous small, rounded white spots distributed on dorsal mantle. A narrow, small, slightly U-shaped transverse bar present between eyes. False-eye spots (ocelli) present, containing a simple blue/ purple iridescent ring.** Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin texture of small, close-set tubercles over head, mantle and arms. One to 2 larger papillae over each eye. Skin ridge around lateral margin of mantle absent.



hectocotylus

ocellus

dorsal view

Fig. 79 ***Amphioctopus neglectus***

Size: Mantle length to 64 mm; total length to around 270 mm.

Geographical Distribution: Andaman Sea, Gulf of Thailand, Cambodia, Vietnam, and Taiwan Province of China, west to Kerala, India (Fig. 80).

Habitat and Biology: Depth range unknown. Nothing is known of the biology and behaviour of this species. Based on the small size of its eggs, the hatchlings are planktonic.

Interest to Fisheries: It is one of the major commercial species in Thailand, usually caught in large quantities by bottom trawls, in depths between 20 to 80 m. The species is normally mixed with other ocellate octopuses and is recorded as ***Octopus membranaceus*** Quoy and Gaimard, 1832. No statistics are available on the scale of its commercial harvest. It is commonly marketed with ***Amphioctopus aegina*** around the world under the name 'baby octopus'. Though common in fisheries catches along the south-west coast of India (often treated as ***O. membranaceus***), the scale of its commercial harvest in India is unknown.

Fig. 80 ***Amphioctopus neglectus***

🟥 Known distribution

Local Names: Unknown.

Literature: Nateewathana and Norman (1999), Sreeja *et al.* (2012).

Amphioctopus rex (Nateewathana and Norman, 1999) **Fig. 81**

Octopus rex Nateewathana and Norman, 1999, *Phuket Marine Biological Center Special Publication*, 19(2): 447. [Type locality: Gulf of Thailand, Trat Province, Ko Kood].

Frequent Synonyms: *Octopus* sp. 5 – Norman and Hochberg, 1994; *Octopus* sp. 1 – Norman and Sweeney, 1997; *Octopus ocellate* sp. A – Nateewathana, 1997; *Octopus* sp. A – Norman, 1998.

Misidentifications: *Octopus membranaceus* Quoy and Gaimard, 1832.

FAO Names: En — King ocellate octopus; **Fr** — Poulpe royal ocellé; **Sp** — Pulpo rey ocelado.

Diagnostic Features: Moderate-sized species. Arms of moderate length, 2 to 3 times mantle length. Lateral and ventral arms longest (typically 4>3>2>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20 to 30% of arm length. Web deepest on lateral and ventral arms; webs between dorsal arms obviously shallower. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 134 to 184 suckers on each normal arm. Enlarged suckers present in mature males, typically two pairs starting around the 5th proximal sucker. Gills with 8 to 9 lamellae per demibranch. Funnel organ W-shaped; limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 80% length of opposite arm. Ligula moderately elongate, 5 to 9% of arm length. Calamus small, around 15% of ligula length. Hectocotylized arm with 63 to 82 suckers. Spermatophores of moderate size, around 25 mm, length 45 to 60% of mantle length; produced in moderate numbers (~10 to 15). Spermatophores unarmed. Eggs small, around 2 to 3 mm; 4 to 6% of mantle length. **Colour:** Preserved animals reddish-brown on dorsal surfaces of head, arms and mantle, white and cream on ventral surfaces. **A short longitudinal brownish black bar present through eye. Narrow dark stripe along dorso-lateral surface of arms 1 to 3. False-eye spots (ocelli) present containing a small simple pink/purple iridescent ring.** Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture: Skin texture consists of a pattern of fine, rounded and closely set epidermal tubercles that cover dorsal and ventral surfaces of arms, head and mantle.** Single small papilla present over each eye. Skin ridge around lateral margin of mantle absent.

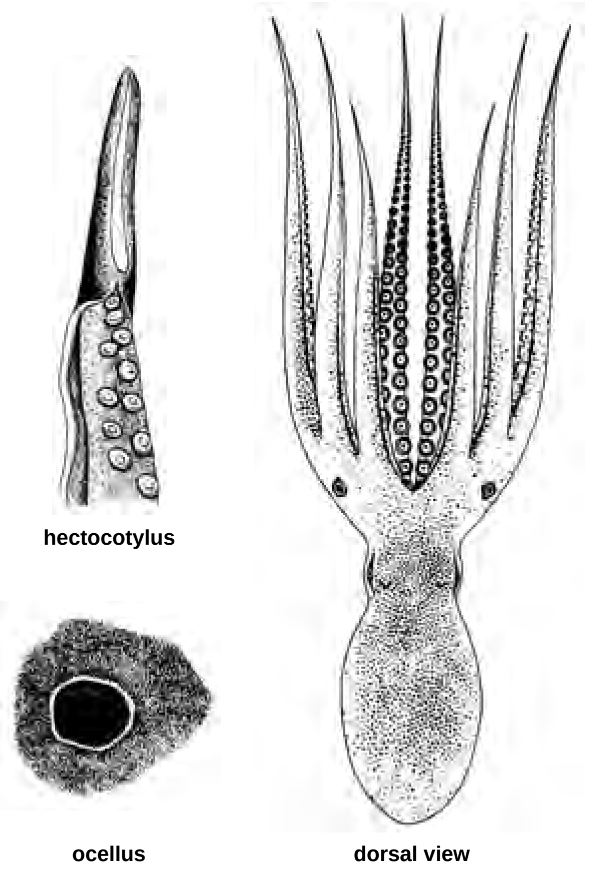


Fig. 81 ***Amphioctopus rex***

Size: Mantle length to 76 mm; total length to around 210 mm.

Geographical Distribution: Tropical continental waters of south and east Asia, from Kerala, India, to the Gulf of Thailand, through Indonesia to Northern Australia (Fig. 82).

Habitat and Biology: Depths to around 80 m. This species has been

Fig. 82 ***Amphioctopus rex***

🟥 Known distribution

collected in coastal waters on mud and sandy mud substrates in the intertidal to shallow subtidal zones. Females lay small eggs, up to 3 mm long, often in mollusc shells or discarded. Based on egg size, hatchlings are planktonic.

Interest to Fisheries: This octopus is one of the most important fisheries species in Thai waters. It is harvested in large quantities by trawlers, both in the Andaman Sea and the Gulf of Thailand. The species is always mixed with other octopuses during fishing operations. No information is available on fishery statistics in Thailand since the species is lumped with other ocellate octopus under the unresolved name ***Octopus membranaceus***. It is also mixed with other octopuses, particularly ***Amphioctopus aegina***, in exports to Europe, Australia, and the United States, where it is marketed as “baby octopus”. Present in fisheries catches off Kerala, India. Scale of harvest unknown.

Local Names: Unknown.

Literature: Nateewathana and Norman (1999), Sreeja *et al.* (2012).

Amphioctopus siamensis (Nateewathana and Norman, 1999)

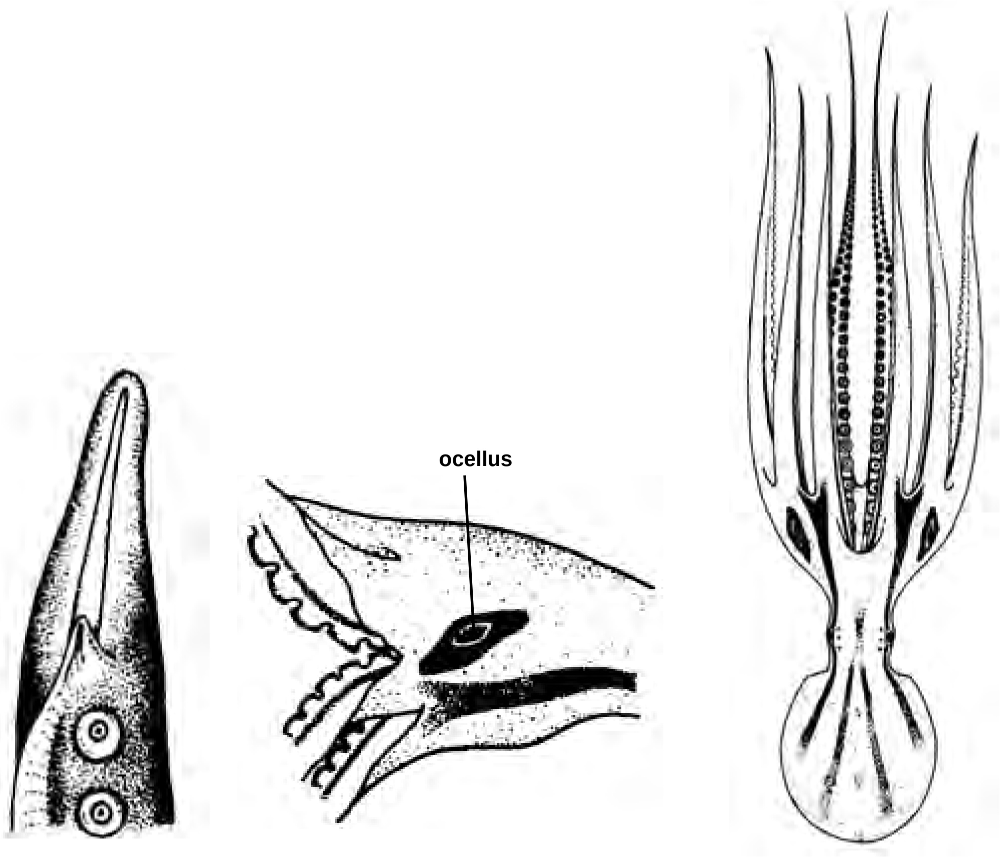
Fig. 83; Plate II, 13

Octopus siamensis Nateewathana and Norman, 1999, *Phuket Marine Biological Center Special Publication*, 19(2): 456. [Type locality: Thailand, Ranong Fish Landing].

Frequent Synonyms: *Octopus ocellate* sp. C – Nateewathana, 1997.

Misidentifications: *Octopus membranaceus* Quoy and Gaimard, 1832.

FAO Names: En — Siamese ocellate octopus; **Fr** — Poulpe siamois ocellé; **Sp** — Pulpo siamés ocelado.



hectocotylus

dorsal view

Fig. 83 ***Amphioctopus siamensis***

Diagnostic Features: Small to moderate-sized species. Arms of moderate length, 2 to 3 times mantle length. Lateral and ventral arms longest (typically 4=3>2>1). Arm autotomy at distinct plane absent. Webs moderate to deep, deepest up to 35% of arm length. Web deepest on lateral arms; webs between dorsal arms very shallow. Web margins extend to arm tips.

Interbrachial web pouches absent. Two rows of suckers on each arm. Larger animals have around 100 to 140 suckers on each normal arm. Enlarged suckers present in mature males, around 4 on arms 2 and 3, starting around the 5th proximal sucker. Gills with 7 to 8 lamellae per demibranch. Funnel organ W-shaped; limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length 75 to 80% of opposite arm. Ligula conical and of moderate length, 9 to 10% of arm length. Calamus small and sharply pointed. Hectocotylized arm with 56 to 61 suckers. Spermatophores not described. Eggs small, around 1.7 mm long, around 2.5% of mantle length. **Colour: Brown to pink base colour with four dark longitudinal stripes on the mantle and head, continuing as fine dark lines along the leading edge of arms 1 to 3. False-eye spots (ocelli) present as dark spot with silver white iridescent ring.** Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle (‘dorsal mantle white spots’ *sensu* Packard and Sanders, 1971). **Sculpture:** Skin texture of small and regular rounded patches. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 64 mm; total length to around 200 mm.

Geographical Distribution: Andaman Sea and Gulf of Thailand (Fig. 84).

Habitat and Biology: Depth range unknown. Little is known of the biology of this octopus. The small egg size indicates that hatchlings are planktonic.

Interest to Fisheries: This ocellate species is caught in low numbers in trawl catches compared with the large commercial catches of two other co-occurring ocellate species: ***Amphioctopus neglectus*** and ***A. rex***.

Local Names: Unknown.

Literature: Nateewathana and Norman (1999).

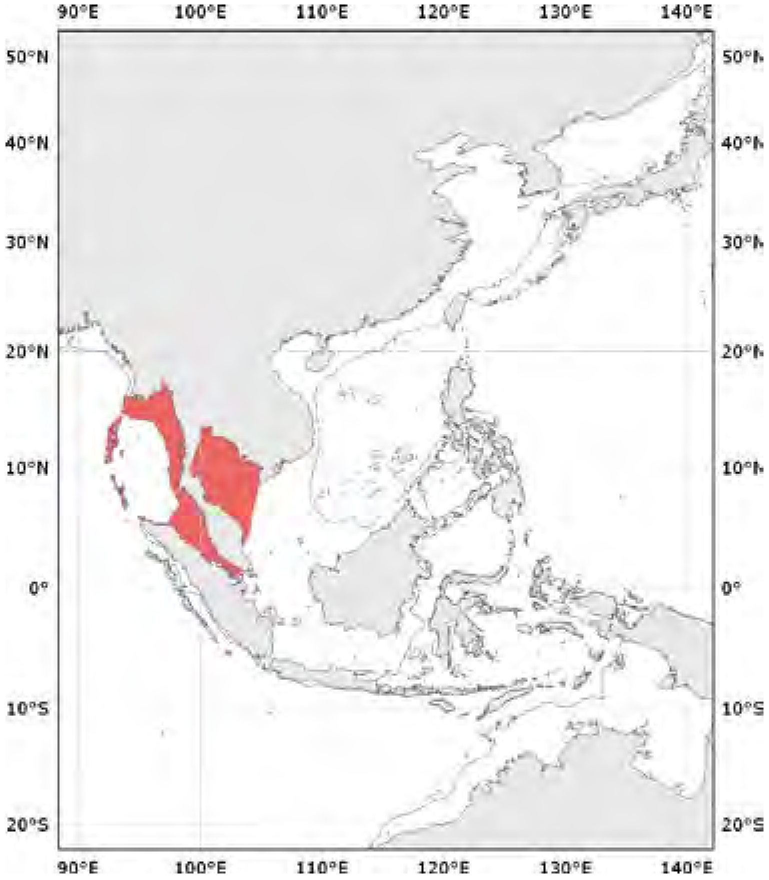


Fig. 84 ***Amphioctopus siamensis***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Amphioctopus arenicola Huffard and Hochberg, 2005

Plate I, 6

Amphioctopus arenicola Huffard and Hochberg, 2005, *Molluscan Research*, 25(3): 113-128. [Type locality: Northeastern Pacific Ocean, Hawaiian Islands Archipelago, O'ahu Island, Honolulu, between Black Point and Kahala Mandarin Oriental Hotel, 21°15.49'N, 157°46.34'W].

Size: Mantle length to 70 mm; total length to >400 mm; body weight to 245 g.

Geographical Distribution: Northeastern Pacific, Hawaiian Islands Archipelago.

Habitat and Biology: Depths range from 1 to >80 m.

Literature: Villanueva and Norman (2008).

Amphioctopus membranaceus (Quoy and Gaimard, 1832)

Octopus membranaceus Quoy and Gaimard, 1832. *Voyage de l'Astrolabe, pendant les anees 1826-1829*. Zoology, 2: 89. [Type locality: New Guinea (= West Papua), Port Dorey].

Size: Mantle length 19 mm; known only from single female type.

Geographical Distribution: Known only from type locality.

Habitat and Biology: Depth range unknown.

Remarks: This little-known taxon is the type species for the genus ***Amphioctopus*** (see discussion for genus above). As it is poorly diagnosed, other members of this genus are presented to characterise the genus. Additional material and full description of this taxon are required.

Literature: Norman (1993b).

Amphioctopus ovulum (Sasaki, 1917)

Polypus ovulum Sasaki, 1917. Notes on the Cephalopoda. *Annotationes Zoologicae Japonenses*, 9(3): 364. [Type locality: Japan, Tokyo Fish Market].

Size: Mantle length to 40 mm; total length to 150 mm.

Geographical Distribution: Known with certainty only from type specimen.

Habitat and Biology: Depth range unknown.

Remarks: Distinct from other Japanese ocellate ***Amphioctopus*** species on the basis of small eggs (versus large eggs in species such as ***A. fangsiao***). The ocellate octopuses of Asia require extensive revision.

Literature: Sasaki (1929).

Amphioctopus polyzenia (Gray, 1849)

Octopus polyzenia Gray, 1849, *Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Antepedia*: 13. [Type locality: Australia, Northern Territory, Port Essington (11°16'S, 132°09'E)].

Size: Up to 38 mm mantle length; total length to 130 mm; weight to 19 g.

Geographical Distribution: Northern Australia from Bowen, Queensland to Dampier Archipelago, Western Australia.

Habitat and Biology: Depths range from 1 to 20 m.

Literature: Norman (1993b).

Amphioctopus robsoni (Adam, 1941)

Octopus robsoni Adam, 1941, *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 17(52): 1. [Type locality: Red Sea, Gulf of Suez].

Size: Mantle length to 60 mm.

Geographical Distribution: Known only from type specimens.

Habitat and Biology: Depth range unknown.

Literature: Toll (1998).

Amphioctopus varunae (Oommen, 1971)

Octopus varunae Oommen, 1971, *Bulletin of the Department of Marine Biology and Oceanography, University of Kerala*, 5: 69. [Type locality: Arabian Sea, west coast of India].

Size: Mantle length to 62 mm.

Geographical Distribution: Known only from type specimens.

Habitat and Biology: Depths of types range from 125 to 135 m.

Literature: Toll (1998).

Bathypolypus Grimpe, 1921

Bathypolypus Grimpe, 1921, *Zoologischer Anzeiger*, 52(12/13): 300.

Type Species: *Bathypolypus arcticus* (Prosch 1847).

Diagnostic Features: Small to moderate-sized, deep-living, cold water species. Mantle muscular, rounded ovoid. Stylets present, non-mineralized. Arms short to long, 1.5 to 5 times mantle length. Arms of subequal length; dorsal arms longest in some species (1>2>3>4 in ***B. arcticus*** and ***B. bairdii***); ventral arm pairs longer in ***B. pugniger*** (3>4>2>1). Arm autotomy at distinct plane absent. Webs moderate to deep, deepest around 20 to 40% of longest arm. Webs subequal or deepest on lateral arms. Interbrachial web pouches absent. **Suckers in two rows.** Enlarged suckers absent. **Funnel organ V V-shaped. Gills with 6 to 8 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands small, significantly smaller than buccal mass. Distinct crop present as small side-branch off oesophagus in some species (e.g. ***B. arcticus***), absent in other species (e.g. ***B. bairdii*** and ***B. pugniger***). **Ink sac and anal flaps absent.** Third right arm of males hectocotylized. Copulatory organ clearly differentiated into ligula and calamus. **Ligula spoon- or fist-shaped, ligula groove well marked and very deep with 4 to 16 transverse ridges.** Diverticulum of terminal organ coiled. Spermatophores unarmed. Eggs large. Colour patterns violet to purple with or without spots. False eye-spots (ocelli) absent. Dorsal mantle and frontal white spots absent. **Skin typically sculptured with large distinct warts.** Single large papilla over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 100 mm; total length to 230 mm.

Geographical Distribution: Atlantic and Pacific Oceans at high latitudes.

Habitat and Biology: Benthic species at depths from 20 m to over 1 200 m.

Remarks: Seven species recognized. Muus (2002) reviewed existing museum material and found that the type species of the genus ***Benthoctopus*** is in fact ***Bathypolypus bairdii*** (Verrill, 1873). The genus ***Benthoctopus*** is in critical need of review.

Literature: Muus (2002).

Bathypolypus arcticus (Prosch, 1847)

Fig. 85

Octopus arcticus Prosch, 1847, *Kongelige Danske Videnskabernes Selskabs Skrifter*, 5(1): 59. [Type locality: SW Greenland].

Frequent Synonyms: *Bathypolypus groenlandicus* (Dewhurst *in* Steenstrup, 1856); *Benthoctopus piscatorum* (Verrill, 1879); *Octopus obesus* Verrill, 1880; *Bathypolypus faeroensis* (Russell, 1909); *Benthoctopus sasakii* Robson, 1927.

Misidentifications: *Bathypolypus piscatorum* (Verrill, 1879) (= junior synonym of *B. bairdii* Verrill, 1873).

FAO Names: En — North Atlantic octopus; **Fr** — Poulpe boreal; **Sp** — Pulpito violáceo.

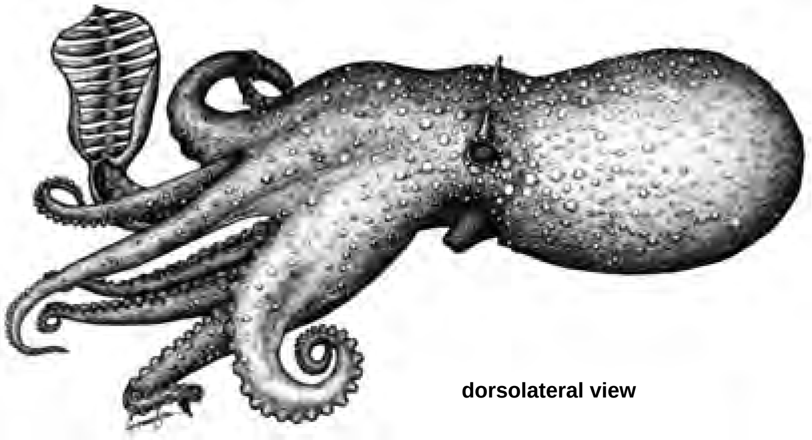


Fig. 85 ***Bathypolypus arcticus***

Diagnostic Features: Small to moderate-sized muscular species. Arms short, approximately 2 times mantle length, decreasing in length from dorsal pair to ventral pair (typically 1>2=3>4). Arm autotomy at distinct plane absent. Webs deep, deepest around 34 to 46% of arm length. Webs approximately equal in depth, ventral sector slightly shallower. Web margins extend as thick flanges to arm tips. Interbrachial web pouches absent. Suckers in two rows. In larger animals, around 60 to 90 suckers on each normal arm. Enlarged suckers absent. Gills with 6 to 7 (rarely 8) lamellae per demibranch. **Funnel organ V V-shaped.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. **Ink sac absent. Anal flaps absent.** Right third arm of males hectocotylized; length 75 to 100% of opposite arm. **Ligula spoon-shaped, pointed, with 11 to 17 deep, well-separated transverse laminae, up to 23% of arm length. Calamus short, pointed.** Hectocotylized arm with around 40 suckers.

Spermatophores large and robust, around 100% to 130% of mantle length; produced in low numbers (typically 3 to 6). Sperm reservoir short, thick, length approximately one third of spermatophore length. Spermatophores unarmed. Eggs large, around 16 to 18 mm; produced in low numbers (~60 to 80). **Colour: Violet to purple skin with lighter yellowish subcircular spots.** False-eye spots (ocelli) absent. **Sculpture: Skin texture of scattered large warts on dorsal surface, reduced or absent on ventral surfaces.** Large papilla over each eye often surrounded by smaller papillae. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 70 mm; total length to 230 mm.

Geographical Distribution: Far northern Atlantic Ocean. Depths range from 37 to 1 210 m, typically over 400 m. In the northernmost limits of distribution caught mainly in less than 100 m (Fig. 86).

Habitat and Biology: Little is known of the biology of this cold-water species (prior reports refer to a different species, ***Bathypolypus bairdii***; see **Remarks** below).

Interest to Fisheries: Unknown.

Local Names: Unknown.

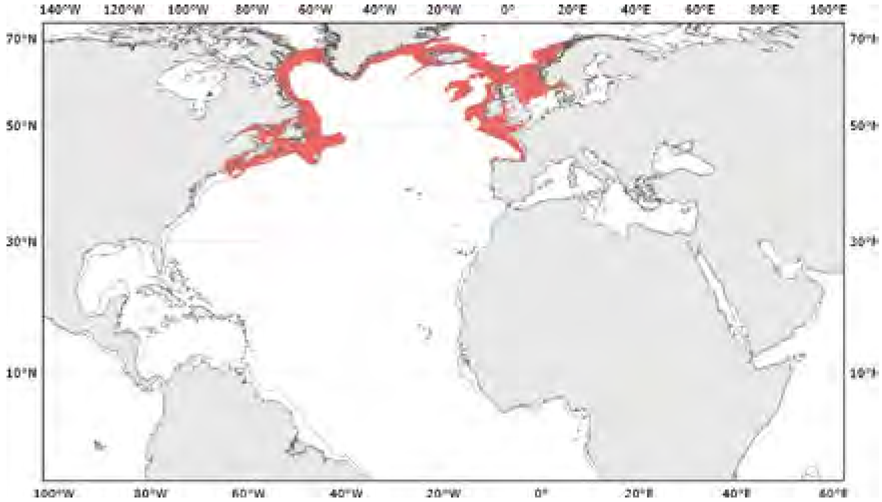


Fig. 86 ***Bathypolypus arcticus***

🟥 Known distribution

Remarks: Muus (2002) presented a thorough revision of the genus ***Bathypolypus*** resolving many of the prior taxonomic problems associated with this deep water genus. Many prior reports of this species name refer primarily to ***B. bairdii*** (e.g. O’Dor and Macalaster, 1983; Roper *et al.*, 1984; Wood *et al.*, 1998; Wood, 2000; see Muus, 2002).

Literature: Humes and Voight (1997), Nesis (2001), Furuya *et al.* (2002), Muus (2002), Zumholz and Frandsen (2006), Barratt *et al.* (2007), Gardiner and Dick (2010a, b).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Bathypolypus bairdii (Verrill, 1873)

Plate II, 14

Octopus bairdii Verrill, 1873, *American Journal of Science and Arts*, 5(25): 5. [Type locality: Northwest Atlantic Ocean, Canada, Nova Scotia, Bay of Fundy (~44ºN, 66ºW)].

Size: Mantle length to 70 mm; total length to 210 mm.

Geographical Distribution: North Atlantic Ocean.

Habitat and Biology: Depths range from 20 to 1 545 m.

Remarks: Muus (2002) determined that ***Benthoctopus piscatorum*** (Verrill, 1879) is a junior synonym. Often reported in the literature as ***Bathypolypus arcticus*** (see O’Dor and Macalaster, 1983), Wood *et al.* (1998), Wood (2000).

Literature: Nixon (1991; as ***Benthoctopus piscatorum***), Muus (2002), Allcock *et al.* (2006), Barratt *et al.* (2007), Gardiner and Dick (2010a), Roura *et al.* (2010b).

Bathypolypus ergasticus (Fischer and Fischer, 1892)

Octopus ergasticus Fischer and Fischer, 1892, *Journal de Conchyliologie*, 40(3): 298. [Type locality: Northeast Atlantic Ocean, West Africa, Sahara Banks (22º24'N, 19º46'E)].

Size: Mantle length to 100 mm.

Geographical Distribution: Northeast Atlantic, from Ireland to Cape Verde Islands and Senegal.

Habitat and Biology: Depths range from 450 to 1 400 m.

Remarks: ***Benthoctopus profundicola*** (Massy, 1907) and ***B. lothei*** (Chun, 1914) are junior synonyms.

Literature: Nesis (1987), Humes and Voight (1997; as ***Benthoctopus ergasticus***), Muus (2002), Barratt *et al.* (2007).

Bathypolypus pugniger Muus, 2002

Bathypolypus pugniger Muus, 2002, *Malacologia*, 44(2): 195. [Type locality: North Atlantic (64º58'N, 27º44'W)].

Size: Mantle length to 60 mm; total length to 200 mm.

Geographical Distribution: North Atlantic, Faroe Islands, Iceland and western Greenland.

Habitat and Biology: Depths range from 200 to 1 000 m.

Literature: Gardiner and Dick (2010a).

Bathypolypus rubrostictus Kaneko and Kubodera, 2008

Bathypolypus rubrostictus Kaneko and Kubodera, 2008, *Molluscan Research*, 28(3): 146. [Type locality: East China Sea, Japan (28º33.25'N, 126º58.11'E)].

Size: Mantle length 20 mm.

Geographical Distribution: Known only from type specimen. Northwestern Pacific, west of Amami Island, Japan.

Habitat and Biology: Depth 350 m.

Literature: No additional literature.

Bathypolypus sponsalis (Fischer and Fischer, 1892)

Octopus sponsalis Fischer and Fischer, 1892, *Journal de Conchyliologie*, Paris, 40(3): 297. [Type locality: Northeastern Atlantic Ocean, West Africa, Sahara coast].

Size: Mantle length to 100 mm.

Geographical Distribution: Northeast Atlantic, Mediterranean Sea to Senegal (Dakar) and Cape Verde Islands.

Habitat and Biology: Depths range from 930 to 1 250 m. Small individuals occur at greater depths than larger individuals, suggesting up-slope ontogenetic migration.

Literature: Nesis (1987), Villanueva (1992a), Quetglas *et al.* (2000, 2001), Salman *et al.* (2001), Muus (2002), Barratt *et al.* (2007), Barratt and Allcock (2010), Roura *et al.* (2010b), Cuccu *et al.* (2011).

Bathypolypus valdiviae (Thiele, *In* Chun, 1915)

Polypus valdiviae Thiele, in Chun, 1915, *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer Valdivia 1898-1899*, 18: 485. [Type locality: Southeastern Atlantic Ocean, South Africa, Aghulas Bank, 35º10.5'S, 23º02'E].

Size: Mantle length to 50 mm; total length to 130 mm.

Geographical Distribution: Southeast Atlantic, Namibia to SE South Africa.

Habitat and Biology: Depths range from 200 to 1 000 m.

Literature: Norman (2000), Muus (2002), Barratt *et al.* (2007).

Bathypurpurata Vecchione, Allcock and Piatkowski, 2005

Bathypurpurata Vecchione, Allcock and Piatkowski, 2005, *Phuket Marine Biological Center Special Publication*, 66: 110.

Type Species: *Bathypurpurata profunda* Vecchione, Allcock and Piatkowski, 2005.

Diagnostic Features: Mantle globose. Stylets unknown. **Arms short to moderate length, around 2.5 times mantle length. Arms of similar length, lateral arms slightly longer than other arms.** Arm autotomy at distinct plane absent. **Webs relatively shallow for a deep-water species, around 20% of arm length.** Interbrachial web pouches absent. **Suckers in single row.** Enlarged suckers absent in only known (female) specimen. Funnel organ W-shaped. **Gills with 4 to 5 lamellae per demibranch.** Radula not described. **Ink sac absent. Posterior salivary glands very large, ~45% of mantle length.** Digestive tract not dissected. Males unknown. Eggs large (4 mm, ~18% mantle length), produced in low numbers (~10 in gravid female). **Colour of live animal purple on dorsal, ventral and oral surfaces.** Skin with small papillae on at least dorsal mantle. Skin ridge around lateral margin of mantle absent.

Size: Small-sized octopod; mantle length 23 mm; total length 80 mm; known only from the type specimen.

Geographical Distribution: Polar southern Atlantic Ocean.

Habitat and Biology: Unknown.

Remarks: Single, poorly known species from polar Atlantic Ocean. Male characters are unknown, the single species in this genus is known only from a single mature female that was subsequently damaged during preservation.

Literature: Vecchione *et al.* (2005).

Bathypurpurata profunda Vecchione, Allcock and Piatkowski, 2005.

Fig. 87

Bathypurpurata profunda Vecchione, Allcock and Piatkowski, 2005, *Phuket Marine Biological Center Special Publication*, 66: 111. [Type locality: Southern Ocean, South Shetland Islands, off Elephant Island].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Purplish octopus; **Fr** — Poulpe pourpré; **Sp** — Pulpo morado.

Diagnostic Features: Small species; mantle length 23 mm in single known specimen; total length 80 mm. Arms of moderate length, ~2.5 times mantle length. Lateral arms slightly longer (2>3>1=4). Arm autotomy at distinct plane absent. **Webs relatively shallow for a deep-water species, around 20% of arm length.** Interbrachial web pouches absent. **One row of suckers on each arm.** 43 suckers on longest arm. Enlarged suckers absent in single known mature female. **Gills with 4 to 5 lamellae per demibranch.** Funnel organ W-shaped. Radula (tongue) unknown. Posterior salivary glands very large, **~45% of mantle length. Ink sac absent.** Males unknown. Eggs large, around 4 mm, ~18% of mantle length, produced in low numbers (8 to 10). **Colour: Purple on dorsal, ventral and oral surfaces. Colour quickly leached in preservative (formalin). Sculpture:** Skin damaged but small papillae on dorsal mantle. Skin ridge around lateral margin of mantle absent.

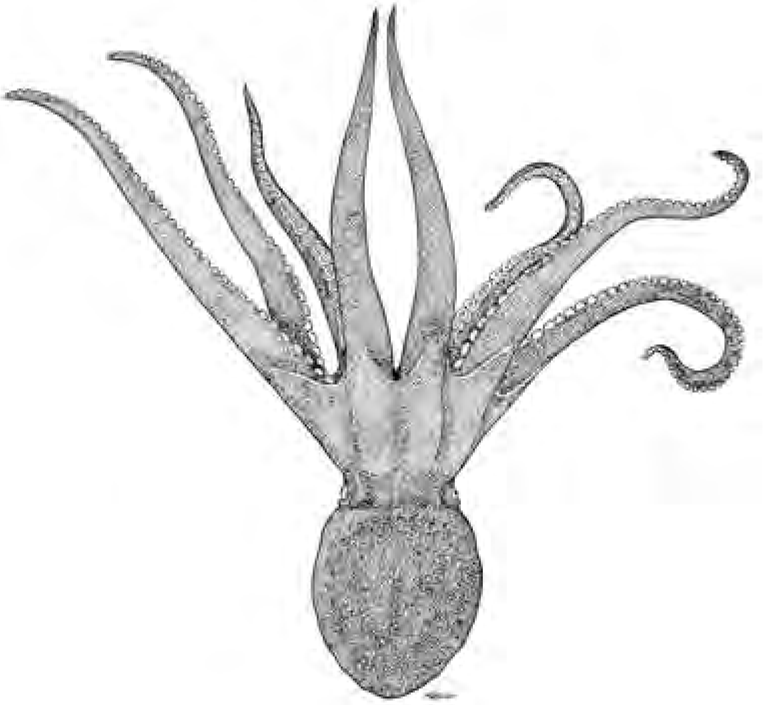


Fig. 87 *Bathypurpurata profunda*

Size: Mantle length 23 mm; total length 80 mm; known only from the type specimen.

Geographical Distribution: Known only from the South Shetland Islands, Southern Ocean (Fig. 88).

Habitat and Biology: Depth of capture of type specimen 509 to 565 m.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Remarks: Known from single mature female specimen.

Literature: Vecchione *et al.* (2005).

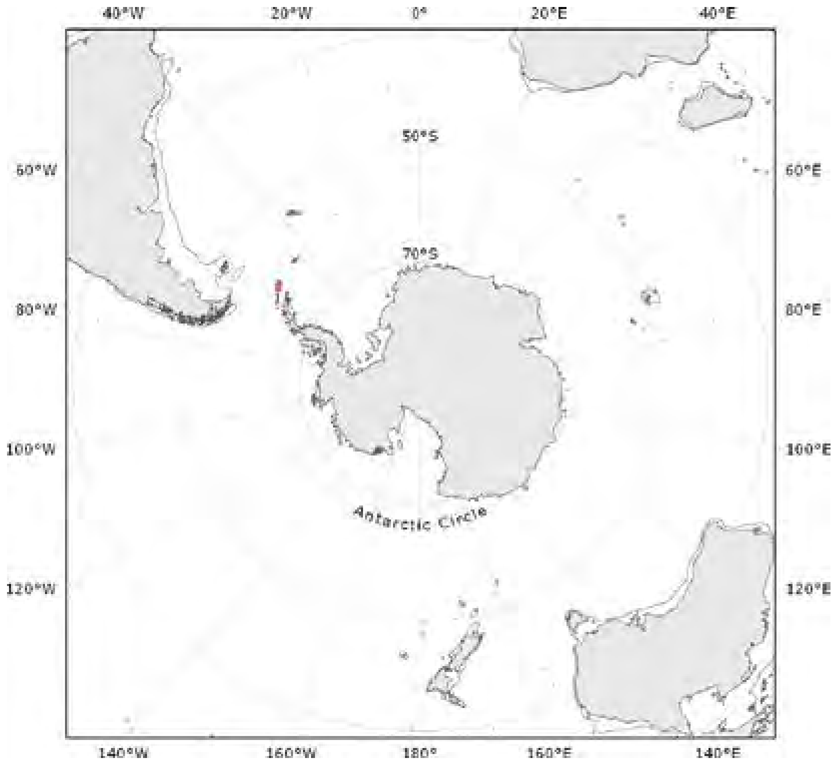


Fig. 88 ***Bathypurpurata profunda***

🟥 Known distribution

Bentheledone Robson, 1932

Bentheledone Robson, 1932, *A Monograph of the Recent Cephalopoda. Part II: The Octopoda, London, British Museum (Natural History)*: 317.

Type Species: *Eledone rotunda* Hoyle, 1885.

Diagnostic Features: Small, muscular, squat deep-water animals. Mantle spherical with narrow mantle opening. Stylets unknown. **Arms short and robust; length about 2 times mantle length. Arms subequal in length.** Arm autotomy at distinct plane absent. **Webs deep, deepest around 40% of longest arm. Webs subequal in depth.** Interbrachial web pouches absent. **Suckers in one row.** Enlarged suckers absent. **Funnel organ of single, fat V shape. Gills with 4 to 5 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands small, much smaller than buccal mass length. Crop diverticulum absent. **Ink sac absent. Anal flaps absent.** Third right arm of male hectocotylized. Ligula and calamus present. Spermatophores unarmed. Eggs very large, up to 30% of ML. **Distal oviducts greatly inflated.** Colour uniform or reverse counter-shaded. False eye-spots (ocelli) absent. **Skin smooth.** Patch and groove skin sculpture absent. Lateral mantle skin ridge absent.

Geographical Distribution: Known only from 1 to 2 described species in the Southern Ocean off Australia and one potential new species from the Pacific Ocean off the coast of Chile (F.G. Hochberg, unpubl. data).

Habitat and Biology: This genus is known only from very deep waters (> 2 000 m).

Remarks: This genus is poorly diagnosed and in urgent need of revision. Following O'Shea's (1999) broadened definition of the genus ***Thaumeledone***, Allcock *et al.* (2004) placed the type species of ***Bentheledone***, ***B. rotunda***, in the genus ***Thaumeledone*** (further amended) on the grounds of general size, arm shape, sucker count and gill count. These morphological characters show considerable overlap across many (distinct) deep-water octopodids that possess a single row of suckers. As the type specimen for ***B. rotunda*** is in poor condition, Allcock *et al.* (2004) justified this taxonomic decision primarily on additional octopus material collected off the Antarctic Peninsula that they attributed to ***B. rotunda***. A number of characters, particularly attributes of radula, posterior salivary glands and arm length relative to mantle length, distinguish ***B. rotunda*** from ***Thaumeledone*** (as diagnosed by Norman *et al.*, 2004b). At this stage we prefer to retain

Bentheledone as distinct, albeit in need of thorough revision. Allcock *et al.* (2004) considered ***B. albida*** Berry, 1917 as a *nomen dubium*, justifying the elimination of the genus ***Bentheledone***. We do not support this decision. Vecchione *et al.* (2005) reported a specimen tentatively under the name "***Bentheledone***" cf. ***albida*** due to superficial similarities with ***B. albida***. Both member species of this poorly diagnosed genus are in urgent need of revision.

Literature: Allcock *et al.* (2004), Norman *et al.* (2004b).

Bentheledone rotunda (Hoyle, 1885)

Fig. 89

Eledone rotunda Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 15: 230. [Type locality: Southern Ocean, SW of Australia (53°55'S, 108°35'E)].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Rounded octopus; **Fr** — Pulpe arrondi; **Sp** — Pulpo redondeado.

Diagnostic Features: Small, squat, muscular species. **Arms short, around 2 times mantle length,** subequal in length. Arm autotomy at distinct plane absent. Webs deep, deepest **around 40%** of arm length. Web approximately subequal with dorsal sector slightly deeper. Interbrachial web pouches absent. **One row of suckers on each arm.** Sucker counts on normal arms unknown. Enlarged suckers absent. Gills with 4 to 5 lamellae per demibranch. **Funnel organ consists of single broad V.** Radula (tongue) with 9 elements, 7 rows of teeth plus marginal plates. Rachidian tooth wide, lacks lateral cusps. **Posterior salivary glands small, much smaller than buccal mass length. Oesophagus with swelling only, no distinct crop. Ink sac absent. Anal flaps absent.** Males unknown. **Eggs very large, to 16 mm, ~33% of mantle length. Colour:** Dull purple. False-eye spots (ocelli) absent. **Sculpture:** Skin smooth. Skin ridge around lateral margin of mantle absent.

dorsal view

Fig. 89 ***Bentheledone rotunda***

Size: Mantle length 50 mm; total length approximately 150 mm.

Geographical Distribution: Known only with certainty from type locality (Fig. 90).

Habitat and Biology: Depth of type specimen 3 566 m.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Remarks: Allcock *et al.* (2004) placed this species in the genus ***Thaumeledone***. See comments on that taxon above.

Literature: Hoyle (1886), Robson (1932), Allcock *et al.* (2004).

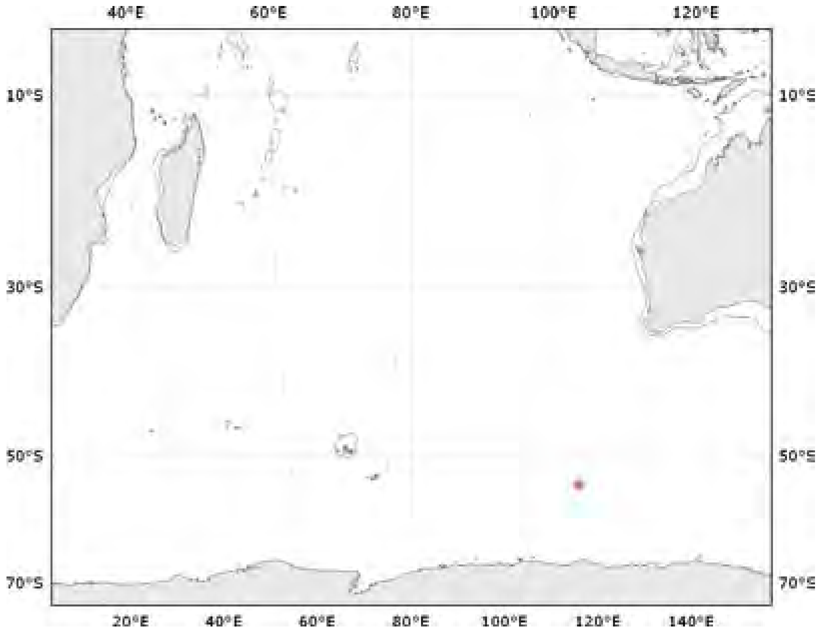


Fig. 90 ***Bentheledone rotunda***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Bentheledone albida (Berry, 1917)

Moschites albida Berry, 1917, *Scientific Reports of the Australasian Antarctic Expedition 1911-1914*, series C, 14(2): 15. [Type locality: Antarctica, off Wilkes Land].

Size: Mantle length to 35 mm; total length to 170 mm.

Geographical Distribution: Known only from type specimen.

Habitat and Biology: Depth of capture 3 100 m.

Remarks: Allcock *et al.* (2004) proposed that this species is a *nomen dubium*.

Literature: Allcock *et al.* (2004).

Benthoctopus Grimpe, 1921

Benthoctopus Grimpe, *1921, Zoologischer Anzeiger, 52(12/13): 300.*

Type Species: *Octopus piscatorum* Verrill, 1897.

Diagnostic Features: Small to moderate-sized deep-water species. Mantle muscular, globose to ovoid. Stylets present in at least some species. **Arms short to medium length, 2.5 to 4 times mantle length. Arms typically subequal in length or arm pairs 1 and 2 longest.** Arm autotomy at distinct plane absent. Webs moderate to deep. Interbrachial web pouches absent. **Suckers in two rows. Enlarged suckers present in some species.** Funnel organ UU- or W-shaped. Gills with 7 to 12 lamellae per outer demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus, but reduced in size. **Ink sac and anal flaps absent, intestine often pigmented.** Third right arm of male hectocotylized. **Ligula short to large, narrow, slightly to moderately excavated, never laminate. Calamus present. Colour typically uniform cream, grey or purple.** Reverse countershading occurs in some species. Oral web also is darkly pigmented in some species. Body entirely smooth or with low rounded papillae. Large mantle and ocular primary papillae absent. Skin ridge around lateral margin of mantle present or absent in different species.

Size: Mantle length to 140 mm; total length to 770 mm; body weight to at least 750 g.

Geographical Distribution: Deep-water habitats worldwide.

Habitat and Biology: Soft sediment substrates in deep water.

Remarks: The type species, ***Benthoctopus piscatorum***, was found by Muus (2002) to be a junior synonym of ***Bathypolypus bairdii*** (Verrill, 1873) and hence it belongs in a distinct genus. Norman *et al.* (1997) suggested that the genus ***Benthoctopus*** may represent a polyphyletic catchall genus. Molecular analyses by Strugnell *et al.* (2009c) of 9 ***Benthoctopus*** species found common ancestry in at least these taxa and proposed that ***Vulcanoctopus*** also might belong in the genus ***Benthoctopus***. As the generic name ***Benthoctopus*** is in common use for deep-water octopuses with two rows of suckers and no ink sac, Muus (2002) and Strugnell *et al.* (2009c) propose that the name should be preserved until a thorough revision of the genus is undertaken. ***Benthoctopus karubar*** is treated below as a better-diagnosed representative of the genus ***Benthoctopus*** (as it is understood currently). The relationship between this nominal genus and ***Muusoctopus*** requires further investigation

Literature: Mouche *et al.* (1999), Voight and Grehan (2000), Czaker (2002), Gleadall (2004), Kemp *et al.* (2006), Barry and Drazen (2007), Voight (2008), Strugnell *et al.* (2009b, 2011).

Benthoctopus karubar Norman, Hochberg and Lu, 1997

Fig. 91

Benthoctopus karubar Norman, Hochberg and Lu, 1997, *Bulletin de Museum National d'Histoire Naturelle, Paris*, 172: 360. [Type locality: Arafura Sea, off Tanimbar Islands (08°41'S, 131°47'E)].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Karubar octopus; **Fr** — Poulpe karubar; **Sp** — Pulpo karubar.

Diagnostic Features: Large, muscular species. Skin soft, semi-gelatinous. Stylets present, non-mineralized. **Funnel organ UU-shaped.** Arms of moderate length, around 2 to 3 times mantle length. Arm autotomy at distinct plane absent. Arms approximately equal in length; dorsal lateral arms slightly longer. Suckers form two rows and are small to moderate-sized, 7 to 10% of mantle length. Enlarged suckers absent in both sexes. Up to 100 suckers on intact normal arms of males; up to 150 in females. **Webs deep (deepest 33 to 38% of longest arm)**. Webs approximately equal in depth, ventral web shallower than other sectors. Third right arm of males hectocotylized. Modified arm around 80% length of opposite arm. **Ligula large (to 13% of arm length)** and sharply pointed with open groove. Calamus small and sharply pointed, around 25% of ligula length. 47 to 55 suckers on hectocotylized arm of males. **Gills with 8 to 9 lamellae per demibranch**. Posterior salivary glands moderate-sized, equal in length with buccal mass. Distinct crop present as side-branch off oesophagus. **Ink sac and anal flaps absent**. Radula with 7 teeth and two marginal plates in each transverse row. Rachidian tooth with 1 to 2 lateral cusps, typically 2, on each side of large medial cone. Lateral cusps in symmetrical to slightly asymmetrical seriation, migrating from lateral to medial position over approximately 6 to 7 transverse rows. Terminal organ ("penis") T-shaped with diverticulum distinctly longer than distal portion of organ. Spermatophores of moderate length (~70% of ML), produced in moderate numbers (26 in storage sac). Eggs large-type and produced in relatively low numbers (~150). **Colour:** Pink to dark purple base colour produced by tiny crimson to purple chromatophores. **Oral web dark purple in most specimens**. Multiple (~8) irregular rows of subdermal founder chromatophores on arms. **Sculpture:** Dorsal head and some of mantle scattered with small low rounded papillae. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 100 mm; total length to at least 400 mm; body weight to at least 750 g.

Geographical Distribution: Tanimbar and Kai Islands, Arafura Sea, Indonesia (Fig. 92).

Habitat and Biology: Depth range from 400 to 800 m.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Norman *et al.* (1997).

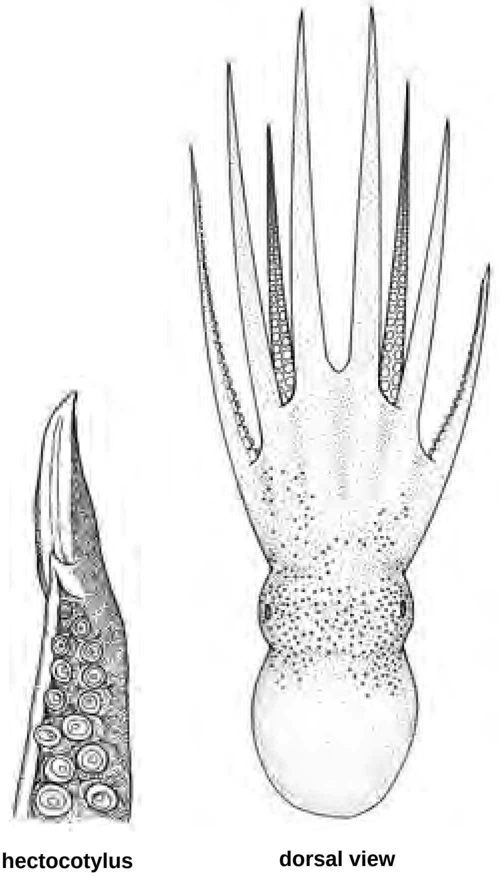


Fig. 91 ***Benthoctopus karubar***

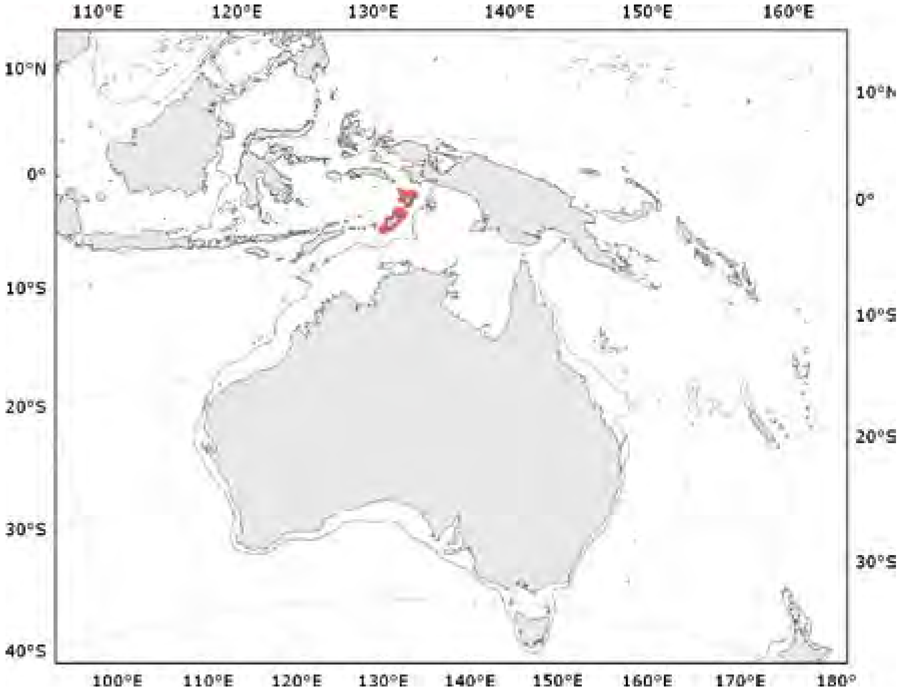


Fig. 92 ***Benthoctopus karubar***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Benthoctopus abruptus (Sasaki, 1920)

Polypus abruptus Sasaki, 1920, *Proceedings of the United States National Museum*, 57: 173. [Type locality: Japan, Honshu, off Kii Province, 33°23’40”N, 135°33’E].

Size: Mantle length 100 mm; total length 520 mm.

Geographical Distribution: Northwestern Pacific Ocean, Japan, off Honshu.

Habitat and Biology: Depth of type 1 074 m.

Literature: Nesis (1987).

Benthoctopus berryi Robson, 1924

Benthoctopus berryi Robson, 1924, *Proceedings of the Zoological Society of London*, 1924(2): 658. [Type locality: South Africa, southwest of Cape Town].

Size: Mantle length 47 mm.

Geographical Distribution: Known only from type locality.

Habitat and Biology: Depth of type 2 200 m.

Literature: Nesis (1987).

Benthoctopus canthylus Voss and Pearcy, 1990

Plate II, 15

Benthoctopus canthylus Voss and Pearcy, 1990, *Proceedings of the California Academy of Sciences*, 47(3): 69. [Type locality: Northeastern Pacific Ocean, United States, off Oregon, 44°58.1’N, 126°35.8’W].

Size: Mantle length to 83 mm; total length to 250 mm.

Geographical Distribution: Northeast Pacific.

Habitat and Biology: Depth range from 2 795 to 3 000 m.

Remarks: ***Benthoctopus macrophallus*** Voss and Pearcy, 1990 is a junior synonym.

Literature: Muus (2002).

Benthoctopus clyderoperi O’Shea, 1999

Benthoctopus clyderoperi O’Shea, 1999, *NIWA Biodiversity Memoir*, 112: 209. [Type locality: New Zealand, east of North Island, ~39°58.55’S, 178°14.80’E].

Size: Mantle length to 90 mm; total length to 380 mm.

Geographical Distribution: New Zealand and Chatham Rise.

Habitat and Biology: Depth range from 840 to 1 100 m.

Literature: No additional literature.

Benthoctopus fuscus Taki, 1964

Benthoctopus fuscus Taki, 1964, *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University*, 5(2): 316. [Type locality: Northwest Pacific Ocean, Japan, Kashima Nada].

Size: Mantle length 115 mm; total length 575 mm.

Geographical Distribution: Northwest Pacific Ocean, off Japan.

Habitat and Biology: Depth range unknown.

Remarks: The status of this species is at present unresolved.

Literature: Kubodera (2001).

Benthoctopus hokkaidensis (Berry, 1921)

Polypus hokkaidensis Berry, 1921, *Annals and Magazine of Natural History*, series 9, 8: 352. [Type locality: Northwestern Pacific Ocean, Japan, off Hokkaido (42°11'10"N, 142°12'E)].

Size: Mantle length to 58 mm; total length to 245 mm.

Geographical Distribution: North Pacific Ocean, Japan to Oregon, United States.

Habitat and Biology: Depth range from 130 to 1 000 m.

Remarks: Originaly described as ***Polypus glaber*** Sasaki, 1920 but it was a preoccupied name; ***Benthoctopus violaceus*** Taki, 1964 is a synonym.

Literature: Nesis (1987), Voss and Pearcy (1990).

Benthoctopus johnsoniana Allcock, Strugnell, Ruggiero and Collins, 2006

Benthoctopus johnsoniana Allcock, Strugnell, Ruggiero and Collins, 2006, *Marine Biology Research*, 2: 379. [Type locality: Northeast Atlantic Ocean, southern boundary of Porcupine Seabight, 49°27'N, 13°21'W].

Size: Mantle length to 113 mm; total length to 510 mm.

Geographical Distribution: Atlantic coast of Europe between 49° to 59°N; Porcupine Seabight to Rockall Trough.

Habitat and Biology: Depth range from 1 800 to 2 540 m.

Remarks: Specimens identified as ***Benthoctopus piscatorum*** in Collins *et al.* (2001b) were found by Allcock *et al.* (2006) to be this species.

Literature: Collins *et al.* (2001b).

Benthoctopus leioderma (Berry, 1911)

Polypus leioderma Berry, 1911, *Proceedings of the United States National Museum*, 40(1838): 590. [Type locality: Northeastern Pacific Ocean, Gulf of Georgia, United States, Alaska, Shelikof Strait].

Size: Mantle length to 70 mm; total length to 270 mm; body weight to 148 g.

Geographical Distribution: North Pacific from California, United States to Sea of Okhotsk, Russia.

Habitat and Biology: Depth range from 90 to 500 m.

Literature: Hochberg (1998), Jorgensen (2009).

Benthoctopus levis (Hoyle, 1885) **Plate II, 16**

Octopus levis Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 15: 229. [Type locality: Southern Indian Ocean, off Heard Island, 52°59'S, 73°33'E].

Size: Mantle length to 50 mm; total length to 180 mm.

Geographical Distribution: Known only from Heard Island.

Habitat and Biology: Depth range of type specimen 13 to 137 m.

Literature: Norman (2000), Barratt *et al.* (2007).

Benthoctopus normani (Massy, 1907)

Polypus normani Massy, 1907. *Annals and Magazine of Natural History*, 20(7): 379. [Type locality: Northeast Atlantic, northwestern boundary of the Celtic Sea, Ireland, off SW coast, 51°15'N, 11°47'W (type not extant); neotype locality: Northeast Atlantic, western boundary of Celtic Sea, 49°38'N 11°49'W].

Size: Mantle length to 107 mm; total length to 648 mm.

Geographical Distribution: Atlantic coasts of Europe between 38° to 60° N.

Habitat and Biology: Depth range from 537 to 1 835 m.

Remarks: Redescribed by Allcock *et al.* (2006). Specimens identified as ***Benthoctopus*** sp. A in Collins *et al.* (2001b) were found to be this species.

Literature: Collins *et al.* (2001b), Allcock *et al.* (2006), Barratt *et al.* (2007).

Benthoctopus oregonae Toll, 1981

Benthoctopus oregonae Toll, 1981, *Bulletin of Marine Science*, 31(1): 88. [Type locality: Southern Caribbean Sea, 10°56'N, 67°38'W].

Size: Mantle length to 58 mm; total length to 300 mm.

Geographical Distribution: Caribbean Sea.

Habitat and Biology: Depth range from 640 to 1 080 m.

Literature: Nesis (1987).

Benthoctopus oregonensis Voss and Pearcy, 1990

Benthoctopus oregonensis Voss and Pearcy, 1990, *Proceedings of the California Academy of Sciences*, 47(3): 73. [Type locality: United States, Oregon, Yaquina Bay, 44°37.0'N, 125°01.0'W].

Size: Mantle length to 93 mm.

Geographical Distribution: Northeastern Pacific Ocean, Oregon and Cascadia Abyssal Plain.

Habitat and Biology: Depth range from 1 000 to 1 260 m.

Literature: Jorgensen (2009).

Benthoctopus profundorum Robson, 1932

Benthoctopus profundorum Robson, 1932, *A Monograph of the Recent Cephalopoda. Part II. Octopoda.* London, British Museum (Natural History): 237. [Type locality: Northwestern Pacific Ocean, Japan, off Yokohama (34°37'N, 140°32'E)].

Size: Total length to 290 mm.

Geographical Distribution: North Pacific from Japan to Gulf of Alaska.

Habitat and Biology: Depth range from 150 to 3 400 m.

Literature: Nesis (1987).

Benthoctopus pseudonymus (Grimpe), 1922

Atlantoctopus pseudonymus Grimpe, 1922, *Sitzungsberichte der Naturforschenden Gesellschaft zu Leipzig*, 45: 41. [Type locality: Northeastern Atlantic Ocean (Azores Islands), south of Flores Island].

Size: Mantle length 40 mm (known only from type material).

Geographical Distribution: Known only from type locality, NE Atlantic Ocean, Azores Islands.

Habitat and Biology: Depth of type 1 600 m.

Remarks: The status of the genus ***Atlantoctopus***, which also lacks an ink sac, has not been critically evaluated.

Literature: Robson (1932).

Benthoctopus rigbyae Vecchione, Allcock, Piatkowski and Strugnell, 2009

Benthoctopus rigbyae Vecchione, Allcock, Piatkowski and Strugnell, 2009, *Malacologia*, 51(1): 13. [Type locality: Southern Ocean, Antarctica, South Shetland Islands, near Elephant Island, 61°17’S, 56°26’W].

Size: Mantle length to 105 mm; total length to 400 mm.

Geographical Distribution: Southern Ocean, Antarctica, South Shetland Islands.

Habitat and Biology: Depth range from 250 to 600 m.

Literature: Strugnell *et al.* (2009c).

Benthoctopus robustus Voss and Pearcy, 1990

Benthoctopus robustus Voss and Pearcy, 1990, *Proceedings of the California Academy of Sciences*, 47(3): 67. [Type locality: Northeast Pacific, United States, Oregon, 44°38.5’N, 126°03.8’W].

Size: Mantle length to 142 mm.

Geographical Distribution: Northeastern Pacific, Oregon, United States to Baja California, Mexico.

Habitat and Biology: Depth range from 1 200 to 3 850 m.

Literature: Hochberg (1998).

Benthoctopus sibiricus Loyning, 1930

Benthoctopus sibiricus Loyning, 1930, *Scientific Results, Norwegian North Polar Expeditions with the Maud 1918-1925*, 5(11): 1. [Type locality: Arctic Ocean, 76°N, 146°E].

Size: Not reported, type specimen damaged.

Geographical Distribution: Eastern Arctic Ocean.

Habitat and Biology: Depth range from 30 to 220 m.

Literature: Nesis (1987), Nesis (2001), Jorgensen (2009), Furuya (2010).

Benthoctopus tangaroa O’Shea, 1999

Benthoctopus tangaroa O’Shea, 1999, *NIWA Biodiversity Memoir*, 112: 202. [Type locality: New Zealand, off east coast].

Size: Mantle length to 122 mm; total length to 720 mm.

Geographical Distribution: New Zealand, Chatham Rise and subantarctic islands to the south.

Habitat and Biology: Depth range from 500 to 1 500 m.

Literature: No additional literature.

Benthoctopus tegginmathae O'Shea, 1999

Benthoctopus tegginmathae O'Shea, 1999, *NIWA Biodiversity Memoir*, 112: 200. [Type locality: New Zealand, east coast of North Island].

Size: Mantle length to 96 mm; total length to 330 mm.

Geographical Distribution: New Zealand and Chatham Rise.

Habitat and Biology: Depth range from 777 to 1 723 m.

Literature: No additional literature.

Benthoctopus thielei Robson, 1932

Benthoctopus thielei Robson, 1932, *A Monograph of the Recent Cephalopoda*. *Part II. Octopoda.* London, British Museum (Natural History): 233. [Type locality: Southern Indian Ocean, Kerguelen Island, Gazelle Harbour].

Size: Mantle length to 65 mm.

Geographical Distribution: Kerguelen Plateau.

Habitat and Biology: Depth range from 126 to 507 m.

Literature: Nesis (1987), Bustamante *et al.* (1998), Cherel *et al.* (2000, 2001).

Benthoctopus yaquinae Voss and Pearcy, 1990

Benthoctopus yaquinae Voss and Pearcy, 1990, *Proceedings of the California Academy of Sciences*, 47(3): 76. [Type locality: United States, Oregon, Cascadia Abyssal Plain, 44º48.8'N, 125º59.5'W].

Size: Mantle length to 83 mm.

Geographical Distribution: Northeastern Pacific Ocean, off Oregon and Cascadia Abyssal Plain.

Habitat and Biology: Depth range from 1 000 to 3 000 m.

Remarks: ***Benthoctopus macrophallus*** Voss and Pearcy, 1990 is a junior synonym (Strugnell *et al.,* 2009b).

Literature: Strugnell *et al.* (2009b).

Callistoctopus Taki, 1964

Callistoctopus Taki, 1964, *Journal of the Faculty of Fisheries and Animal Husbandry*, Hiroshima University, 5(2): 292.

Type Species: *Callistoctopus arakawai* Taki, 1964 [= *C. ornatus* (Gould, 1852)].

Diagnostic Features: Medium-sized to large species. Mantle ovoid to elongate cylindrical. Stylets reduced or absent. **Arms muscular and long, 5 to 8 times mantle length. Dorsal arms always longest (1>2>3>4).** Arm autotomy at distinct plane absent. Web depths shallow to moderate, about 5 to 20% of longest arm length. **Dorsal webs always deepest (typically A>B>C>D>E).** Interbrachial web pouches absent. **Suckers in two rows. Enlarged suckers absent in both sexes.** Funnel organ W- or UU-shaped, large. **Gills with 10 to 15 lamellae per outer demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. **Rachidian tooth with 2 to 3 lateral cusps and very tall mesocone.** Posterior salivary glands moderate to large, equal to or larger than buccal mass. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Third right arm of male hectocotylized, distinctly shorter than opposite arm. Ligula and calamus present; **ligula cylindrical with deep groove.** Spermatophores small, unarmed. Eggs small to large. **Colour typically red-brown to red with white spots or bars on mantle, head and arms.** False eye-spots (ocelli) absent. Skin smooth or with scattered low papillae, patch and groove system not evident. Conspicuous primary papillae present over each eye. Continuous skin ridge around lateral margin of mantle absent.

Size: Mantle length to 190 mm; total length to 1.3 m; body weight to at least 4.2 kg.

Geographical Distribution: Tropical and temperate waters of the world.

Habitat and Biology: Typically occur in shallow coastal waters on continental shelf to around 200 m. Occur on all habitats from reefs to seagrass beds and soft sediments.

Remarks: Members of this genus previously have been treated under the name "***Octopus macropus*** group" (e.g. Norman, 1993a, 2000). Many undescribed species from this genus occur throughout the Indo-Pacific region. Members of this group frequently are incorrectly identified as ***Octopus macropus*** (= ***Callistoctopus macropus***), a European member of this group restricted to the Mediterranean Sea and Atlantic Ocean.

Literature: Norman (1993a, 2000).

Callistoctopus ornatus (Gould, 1852)

Fig. 93; Plate III, 22

Octopus ornatus Gould, 1852, *United States Exploring Expedition during the Years 1838-1842*, 12: 476. [Type locality: Sandwich Islands (=Hawaii)].

Frequent Synonyms: *Callistoctopus arakawai* Taki, 1964.

Misidentifications: None.

FAO Names: En – White-striped octopus; **Fr –** Poulpe clouté; **Sp –** Pulpo listado.

Diagnostic Features: Large, muscular and elongate species. **Arms long, 6 to 8 times mantle length**. **Dorsal arms longest (1>2>3>4)**. Arm autotomy at distinct plane absent. **Webs shallow, deepest around 10% of arm length.** Web deepest on dorsal arm; webs between ventral arms shallowest. Web margins extend as narrow membranes for at least 70% of arm length. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 300 to 400 suckers on each normal arm. Enlarged suckers absent. Gills with 13 to 14 lamellae per demibranch. Funnel organ W-shaped, lateral limbs approximately 75 to 85% of length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, 50 to 70% length of opposite arm. Ligula robust and cylindrical, up to 6% of arm length. Calamus small, around 15% of ligula length. Hectocotylized arm with 150 to 170 suckers. Spermatophores small, around 40 mm, around 40 to 50% of mantle length, produced in low numbers (~8).


hectocotylus

dorsal view

Fig. 93 *Callistoctopus ornatus*

Spermatophores unarmed. Eggs small, around 3 to 4 mm, around 3% of mantle length. **Colour: Red brown in colour with a distinctive colour pattern of short white longitudinal stripes on the dorsal mantle. Paired white spots present along the entire length of the arms.** False-eye spots (ocelli) absent. **Sculpture:** Skin texture of small low papillae over dorsal surfaces. Two moderate-sized erectile papillae over each eye. Continuous skin ridge around lateral margin of mantle absent. **Short flaps of skin can be raised from within the longitudinal stripes on the lateral mantle.**

Size: Mantle length 130 mm; total length to 1.2 m; body weight to at least 1 kg.

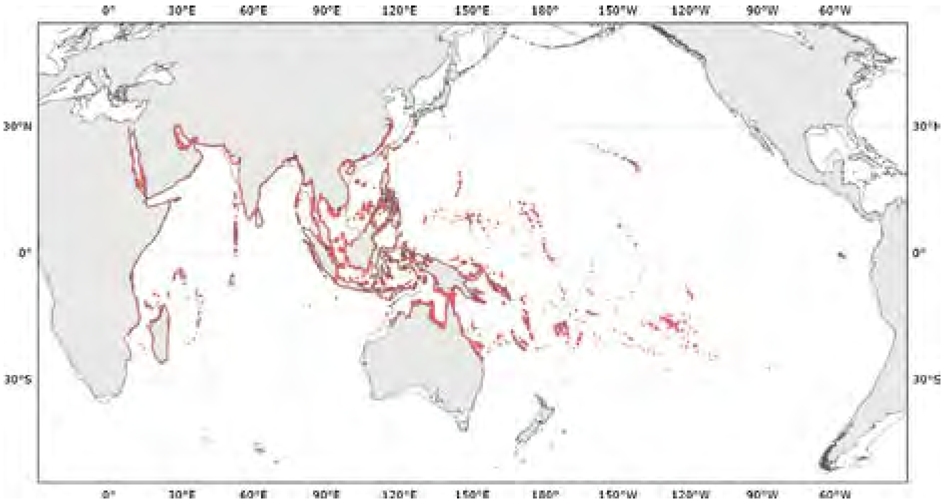


Fig. 94 ***Callistoctopus ornatus***

🟥 Known distribution

Geographical Distribution: Widely distributed in tropical waters of the Indian and western and central Pacific Oceans, from the Hawaiian Islands Archipelago and Easter Island in the east, through the Pacific Islands to Asia and Australia, and into the Indian Ocean to east Africa (Fig. 94).

Habitat and Biology: Depths range from 0 to ~10 m. This species occurs in shallow tropical waters, typically in association with coral reefs. It is a night active species, typically encountered on shallow reefs during night low tides. This species appears to occupy temporary lairs as deep vertical holes excavated in coral rubble. Foraging behaviour consists of moving over coral rubble at night, exploring burrows and holes with the dorsal arms. Diet includes fishes, shrimps, crabs, and other octopuses. The small egg size indicates that hatchlings are planktonic.

Interest to Fisheries: Harvested on a small scale throughout its range, primarily in local subsistence fisheries. It is sold in fish markets in the central and southern tropical Pacific, but less frequently than ***'Octopus' cyanea***. There are historical records of this species being harvested at night using torches and spears in Hawaii.

Local Names: Unknown.

Literature: Voss (1981), Norman (1993c), Yong and Armand (1997), Nagai *et al.* (2002; as ***Callistoctopus arakawai***).

Callistoctopus alpheus (Norman, 1993)

Fig. 95; Plate III, 17

Octopus alpheus Norman, 1993a, *Memoirs of the Museum of Victoria*, 53(2): 270. [Type locality: Australia, Great Barrier Reef, Tryon Island].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Capricorn octopus; **Fr** — Poulpe capricorne; **Sp** — Pulpo capricornio.

Diagnostic Features: Moderate-sized, muscular species. Arms of moderate length, 3 to 4.5 times mantle length. **Dorsal arms longest (1>2>3>4)**. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20% of arm length. Web deepest on dorsal arms; webs between ventral arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 200 suckers on each normal arm. Enlarged suckers absent. Gills with 10 to 12 lamellae per demibranch. Funnel organ UU-shaped, outer limbs slightly shorter than medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length around 70% of opposite arm. Ligula of moderate size, robust and cylindrical, 5 to 9% of arm length. Calamus of moderate size, 20 to 30% of ligula length. Hectocotylized arm with 82 to 97 suckers. Spermatophores large, similar in length to mantle length, produced in low numbers (~2). Spermatophores unarmed. Eggs large. **Colour: Orange to red with numerous large white spots over dorsal surfaces. White spots on arms in regular pairs**. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of scattered low papillae over smooth skin. Single slightly larger papilla over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 80 mm; total length to around 430 mm; body weight to at least 340 g.

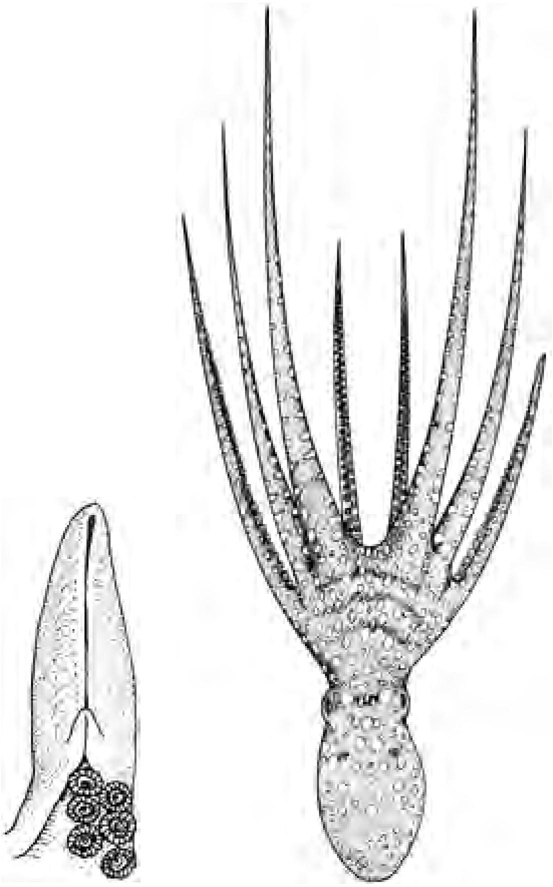
Geographical Distribution: Australia, southern Great Barrier Reef, Capricorn Bunker Islands (Fig. 96).

Habitat and Biology: Depths range from intertidal to shallow subtidal. This octopus occurs on intertidal coral reefs where it emerges at night to forage, primarily for crabs. Densities can be locally high with 34 octopuses encountered in an area of reef in one night. The eggs are large and hatchlings presumably are benthic.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: No additional literature.



hectocotylus **dorsal view**

Fig. 95 ***Callistoctopus alpheus***

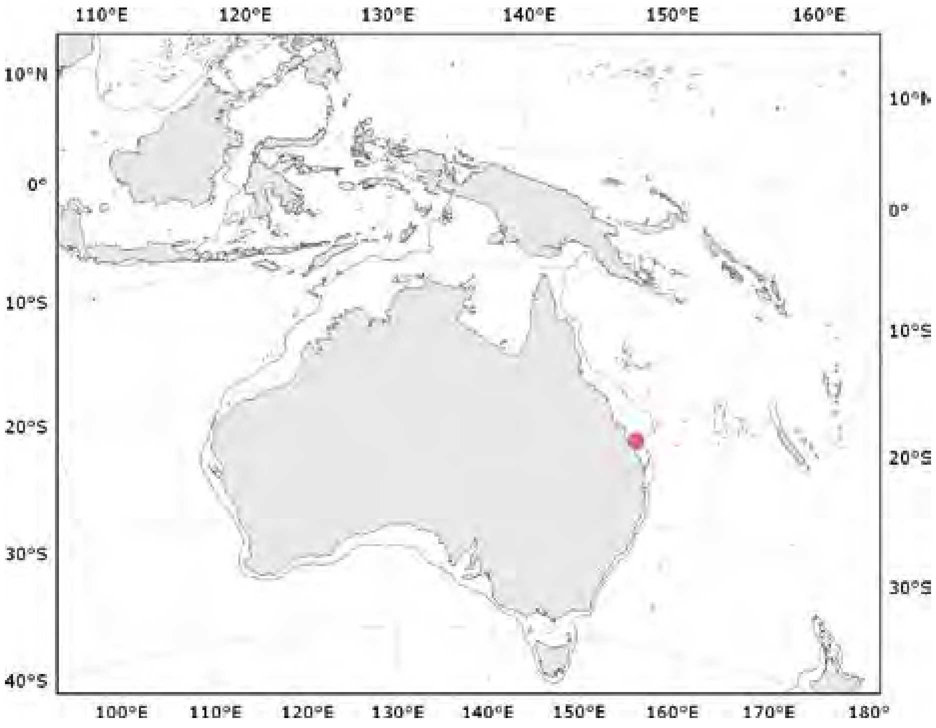


Fig. 96 ***Callistoctopus alpheus***

🟥 Known distribution

Callistoctopus aspilosomatis (Norman, 1993)

Fig. 97; Plate III, 18

Octopus aspilosomatis Norman, 1993a, *Memoirs of the Museum of Victoria*, 53(2): 279. [Type locality: Australia, Great Barrier Reef, Frankland Group, Russell Island].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Plain-body octopus; **Fr** — Poulpe aux taches blanches; **Sp** — Pulpo con manchas blancas.

Diagnostic Features: Moderate-sized, muscular and elongate species. Arms long and narrow, 4 to 6 times mantle length. **Dorsal arms longest (1>2>3>4)**. Arm autotomy at distinct plane absent. **Webs shallow, deepest around 10 to 15% of arm length.** Web deepest on dorsal arms; webs between ventral arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 230 suckers on each normal arm. Enlarged suckers absent. Gills with 10 to 11 lamellae per demibranch. Funnel organ W-shaped; outer limbs approximately 70% of the length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length around 60% of opposite arm. Ligula 6 to 9% of arm length. Calamus small, around 20% of ligula length. Hectocotylized arm with 78 to 95 suckers. Spermatophores of moderate size, around 28 to 40 mm, 50 to 80% of mantle length, produced in low numbers (~1 to 3). Spermatophores unarmed. Eggs small. **Colour:** Orange to red brown. **Paired white spots on arms and arm crown. White spots absent on mantle.** False-eye spots (ocelli) absent. **Sculpture:** Skin texture of scattered low papillae over smooth skin. Single, slightly larger papilla over each eye. Skin ridge around lateral margin of mantle absent.

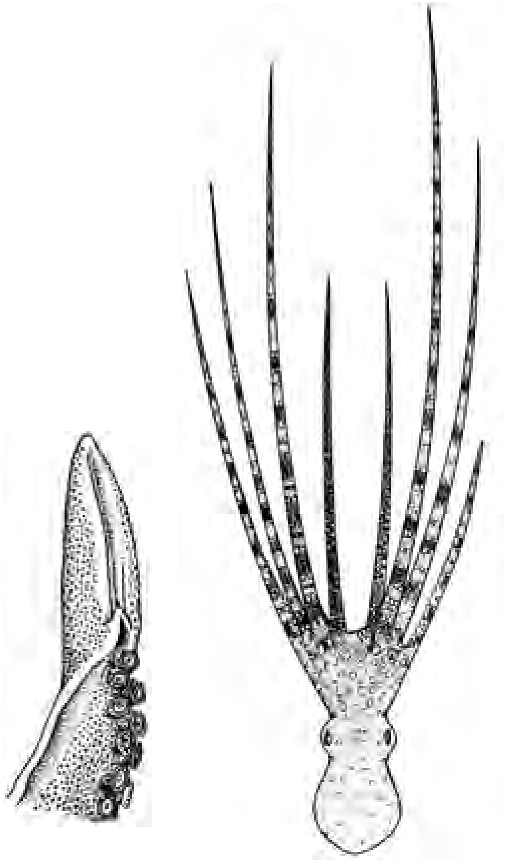

hectocotylus dorsal view

Fig. 97 *Callistoctopus aspilosomatis*

Size: Mantle length to 80 mm; total length to around 440 mm; body weight to at least 120 g.

Geographical Distribution: Australia, Great Barrier Reef. Potentially also from Okinawa (N. Kaneko, pers. comm.; Yasumuro and Ikeda, 2011) and Moorea in the Society Islands (C. Huffard, pers. comm.) (Fig. 98).

Fig. 98 *Callistoctopus aspilosomatis*

🟥 Known distribution

Habitat and Biology: Depths range from intertidal to shallow subtidal. This species forages on exposed intertidal coral reef flats and sand areas during night low tides; it occupies lairs within coral bedrock and under living coral, blocking the entrance during the day with pieces of dead coral. Diet is mainly small crabs and other crustaceans. Larger individuals readily attack smaller conspecifics. The eggs are small and hatchlings planktonic.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Norman (2000), Yasumuro and Ikeda (2011).

Callistoctopus dierythraeus (Norman, 1993)

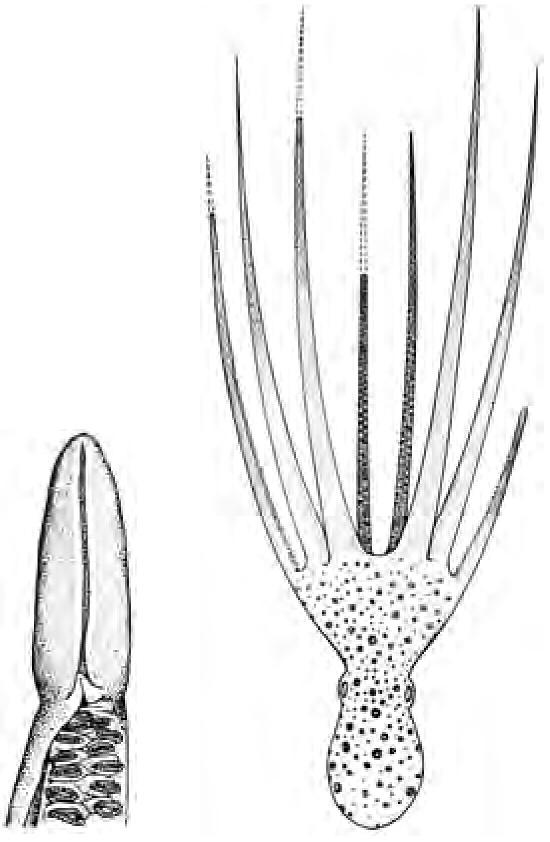
Fig. 99; Plate III, 19

Octopus dierythraeus Norman, 1993a, *Memoirs of the Museum of Victoria*, 53(2): 284. [Type locality: Australia, Queensland, Gulf of Carpentaria, western Cape York].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Red-spot octopus; **Fr** — Poulpe aux taches rouges; **Sp** — Pulpo con manchas rojas.


hectocotylus

dorsal view

Fig. 99 ***Callistoctopus dierythraeus***

Diagnostic Features: Large, muscular species. Arms moderate to long, 4 to 5 times mantle length. **Dorsal arms longest (1>2>3>4)**. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 18 to 28% of arm length. Web deepest on dorsal arms; webs between ventral arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 200 to 280 suckers on each normal arm. Enlarged suckers absent. Gills with 12 to 14 lamellae per demibranch. **Funnel organ UU-shaped**, outer limbs slightly shorter than medial limbs (75 to 90%). Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 75% length of opposite arm. Ligula cylindrical and muscular, around 6% of arm length. Calamus small, around 15% of ligula length. Hectocotylized arm with 103 to 125 suckers. Spermatophores large, around 100 mm, around 75% of mantle length, produced in low numbers (~4). Spermatophores unarmed. Eggs large, at least 14 mm long. **Colour: Resting colour pattern of red base colour with numerous white and dark spots scattered over all dorsal and lateral surfaces**. **Alarm colour pattern of white background with numerous large red spots on dorsal and lateral surfaces**. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of scattered rounded papillae over smooth skin. Papillae located in centres of spots. Single, slightly larger papilla over each eye, surrounded by low punctae. Skin ridge absent around lateral margin of mantle.

Size: Mantle length to 135 mm; total length to around 800 mm; body weight to at least 1.5 kg.

Geographical Distribution: Northern and north-east Australia from Great Barrier Reef to northwest Western Australia (Fig. 100).

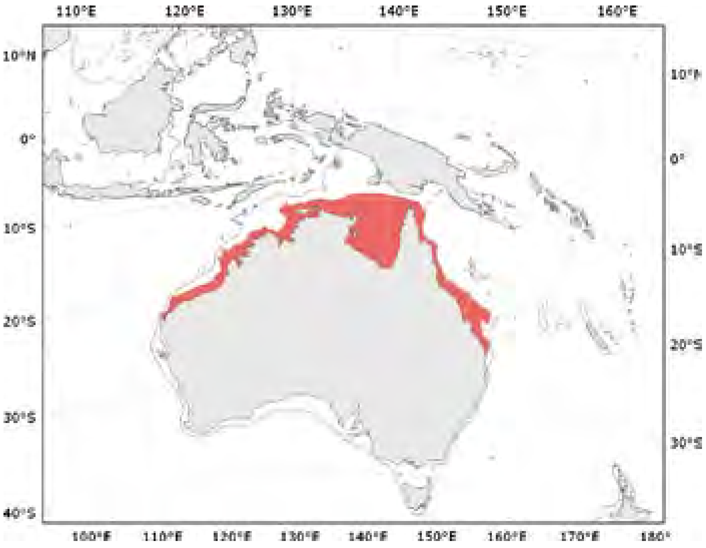


Fig. 100 ***Callistoctopus dierythraeus***

🟥 Known distribution

Habitat and Biology: Depths range from 0 to 78 m. This species is nocturnally-active and forages on intertidal rock and mud flats, and shallow subtidal habitats. The diverse diet includes bivalves, gastropods, crabs, polychaete worms and octopuses of indeterminate identity. Active lairs are surrounded by clean bivalve shells and crab carapaces. One specimen had accumulated over 100 bivalve shells. Based on the large egg size, hatchlings are benthic. This species uses drilling or pulling to open bivalves, depending on prey size.

Interest to Fisheries: Based on the prevalence of this species in shallow coastal and intertidal areas across northern Australia, there is likely to be a minor recreational/subsistence harvest of this octopus.

Local Names: Unknown.

Literature: Norman (2000), Steer and Semmens (2003).

Callistoctopus graptus (Norman, 1993)

Fig. 101

Octopus graptus Norman, 1993a, *Memoirs of the Museum of Victoria*, 53(2): 296. [Type locality: Australia, Queensland, Townsville, Cleveland Bay].

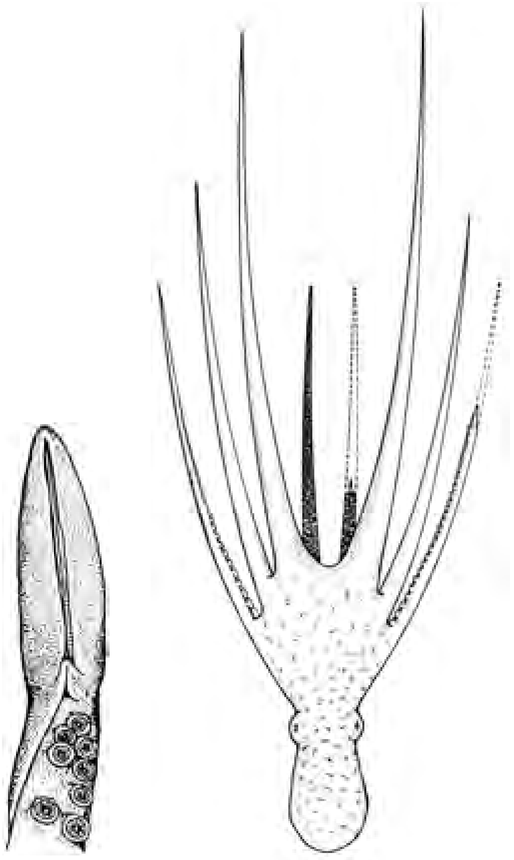
Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Scribbled octopus; **Fr** — Poulpe gribouillé; **Sp** — Pulpo pintarrajo.

Diagnostic Features: Large, robust and muscular species. Arms long, 4.5 to 7 times mantle length. **Dorsal arms longest and most robust (1>2>3>4)**. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20% of arm length. Web deepest between dorsal arms; webs between ventral arms shallowest. Web margins poorly developed. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 240 suckers on each normal arm. Enlarged suckers absent. Gills with 13 to 14 lamellae per demibranch. Funnel organ V V-shaped, outer limbs 60% of medial limb length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length 60 to 75% of opposite arm. Large cylindrical ligula with deep groove, around 6% of arm length. Calamus of moderate size, 20% of ligula length. Hectocotylized arm with around 90 suckers. Spermatophores large, around 130 mm long, around 90% of mantle length, produced in low numbers (~5). Spermatophores unarmed. Eggs large, around 28 mm, around 15% of mantle length. **Colour:** Background colour from uniform grey to uniform orange brown. **Short irregular dark brown lines and dots scattered over dorsal mantle and arm crown, forming a "scribbled" pattern**. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of scattered low papillae over smooth skin. Single moderate papilla present over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 190 mm; total length to 1.3 m; body weight to at least 4.2 kg.



hectocotylus **dorsal view**

Fig. 101 *Callistoctopus graptus*

Geographical Distribution: Northern Australian coastal waters from northern Queensland to northwest Western Australia (Fig. 102).

Habitat and Biology: Depths range from 11 to 36 m. This species is known only from trawled animals captured at night, which suggests nocturnal activities. It lives on soft substrates in the shallow subtidal zone. Stomach contents of trawl specimens contained mollusc remains suggesting a shellfish diet. Captive animals take all prey offered, including capturing live fish. A captive female attached the large eggs singly to hard surfaces. Based on the large egg size, young are benthic upon hatching.

Interest to Fisheries: Commercial prawn trawl operators report catches of this species when trawling at night over sandy substrates. Annual catch figures are not available, however it is likely that this large species makes up the bulk of the annual catch of octopuses in Queensland waters.

Local Names: Unknown.

Literature: Norman (2000).

Fig. 102 *Callistoctopus graptus*

🟥 Known distribution

Callistoctopus luteus (Sasaki, 1929)

Fig. 103; Plate III, 20

Polypus luteus Sasaki, 1929, *Journal of the Faculty of Agriculture, Hokkaido Imperial University,* Vol XX, supplement: 45. [Type locality: Taiwan, Pescadore Islands (Peng-hu)].

Frequent Synonyms: None.

Misidentifications: *Octopus macropus* Risso, 1826.

FAO Names: En — Small-spot octopus; **Fr** — Poulpe aux petites taches; **Sp** — Pulpo con pecas.

Diagnostic Features: Large, muscular species. Arms long, 4 to 6 times mantle length. **Dorsal arms longest and most robust (1>2>3>4)**. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 15 to 20% of arm length. Web deepest between dorsal arms; webs between ventral arms shallowest. Web margins extend along most of arm length. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 180 to 240 suckers on each normal arm. Enlarged suckers absent. Gills with 12 to 13 lamellae per demibranch. Funnel organ W-shaped, outer limbs approximately 80% of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 60% length of opposite arm. Ligula short and elongate, around 4% of arm length. Calamus small. Hectocotylized arm with 80 to 90 suckers. Spermatophores of moderate size, around 75 mm, around 70% of mantle length, produced in low numbers (~3). Spermatophores unarmed. Eggs small, around 1 mm, around 1% of mantle length. **Colour: Orange to red base colour with numerous small white spots scattered over all dorsal and lateral surfaces.** False-eye spots (ocelli) absent. **Sculpture:** Skin sculptured with large patches (which can be raised as large papillae), interspersed by small fine patches. Skin ridge around lateral margin of mantle absent.

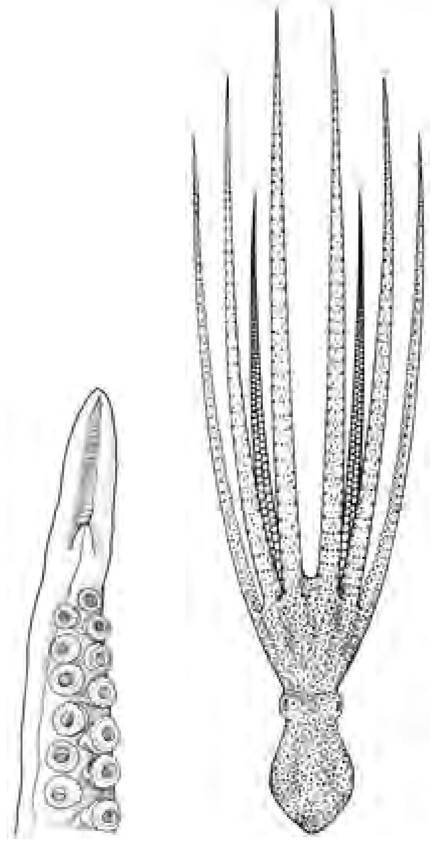

hectocotylus dorsal view

Fig. 103 ***Callistoctopus luteus***

Size: Mantle length to 125 mm; total length to 700 mm; body weight to at least 500 g.

Geographical Distribution: At present known only from Taiwan and Philippines, south to Sulawesi, Indonesia, and Thailand (Fig. 104).

Habitat and Biology: Depths recorded to 82 m. Little is known of the biology of this species. It occurs on sand, seaweed, and rubble areas where it forages at night.

Interest to Fisheries: Important fisheries species in at least the Philippines. Likely to be regular bycatch in trawl fisheries throughout its range.

Local Names: Unknown. Other common names: Starry night octopus.

Remarks: Awaits detailed description. May represent more than one species.

Literature: Nateewathana (1997), Norman and Sweeney (1997; as ***Octopus*** cf. ***luteus***), Norman (1998, 2000).

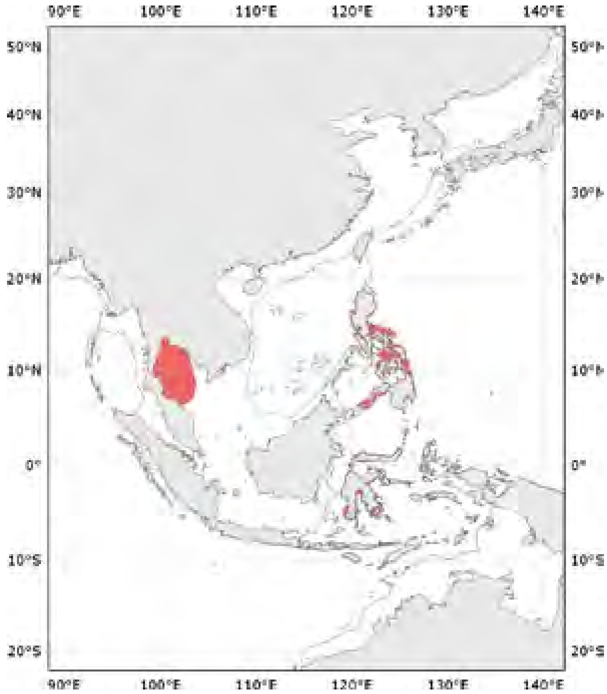


Fig. 104 ***Callistoctopus luteus***

🟥 Known distribution

Callistoctopus macropus (Risso, 1826)

Fig. 105; Plate III, 21

Octopus macropus Risso, 1826, *Histoire Naturelle… Europe méridionale...,* 4: 3. [Type locality: Not stated, presumed to be western Mediterranean Sea, near Nice (Mangold, 1998)].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — White-spotted octopus, **Fr** — Poulpe tacheté, **Sp** — Pulpo manchado.

Diagnostic Features: Medium-sized to large **muscular and elongate species. Mantle shape variable, usually elongate** or ovoid, widest in posterior half. Stylets present, non-mineralized, very small. Funnel organ W-shaped, lateral limbs shorter than median limbs. **Arms long, up to 7 times mantle length. Dorsal arms longest and most robust; arm formula 1>2>3>4**. Suckers medium-sized, dorsal arms with largest suckers up to 13.5% of mantle length, no noticeable difference between males and females, none dramatically enlarged. **Web shallow, deepest 7 to 17% of arm length, web formula A>B>C>D>E.** Ink sac present, well developed. Gills with 10 to 11 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Rachidian with large mesocone and up to 3 lateral cusps per side in asymmetrical seriation. Third right arm of male hectocotylized, significantly shorter than opposite arm (41 to 51%). Ligula small to medium-sized (4.5 to 8% of arm length), narrow, pointed rather than blunt, with swollen margins, deep groove with numerous delicate transverse laminae. Calamus short, 13 to 18% of ligula length. Terminal organ (“penis”) small (12 to 28% of mantle length), with large forward- or backward-directed diverticulum. Spermatophores medium-sized (around 50% of mantle length). Radula with 7 transverse rows of teeth plus marginal plates. Rachidian tooth with 2 to 3 lateral cusps. Mature eggs 2.5 mm long. **Colour: In life brick red or brownish with distinct pattern of numerous white spots on dorsal mantle, head, and arms.** Skin smooth, with large papilla over each eye. Lateral mantle skin ridge absent.

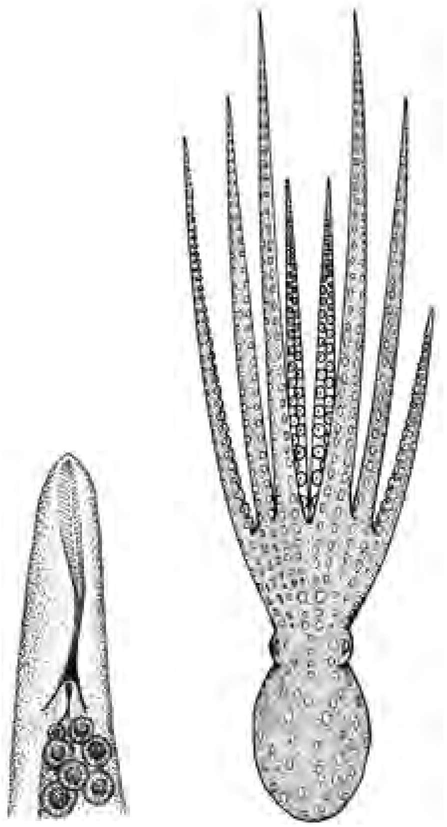

hectocotylus dorsal view

Fig. 105 *Callistoctopus macropus*

Size: Mantle length to 155 mm.

Geographical Distribution: Mediterranean Sea and eastern Atlantic Ocean to Dakar, Senegal (Fig. 106).

Habitat and Biology: Little known; most available data refer to other species historically treated under this name.

Interest to Fisheries: No catch statistics are available for this species. In the Mediterranean, it is likely to form a small proportion of the catch records for ***O. vulgaris***.

Local Names: ITALY: Polpessa.

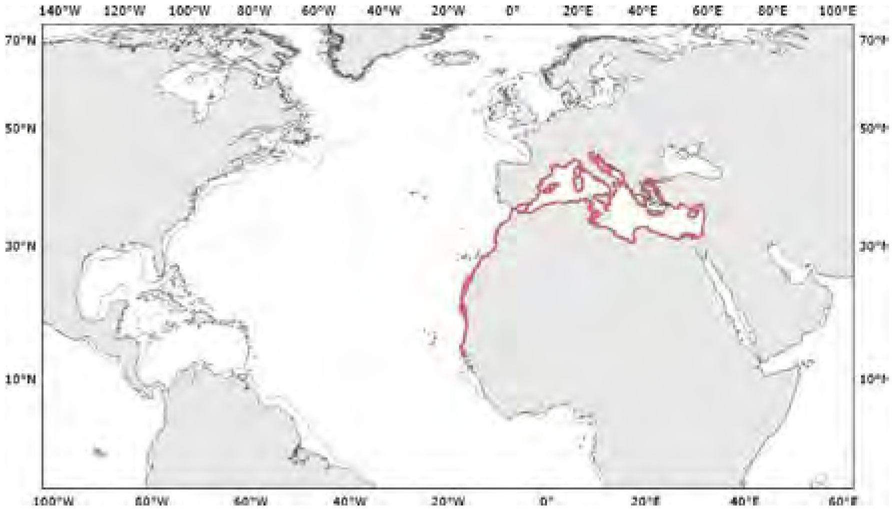


Fig. 106 *Callistoctopus macropus*

🟥 Known distribution

Remarks: The previous FAO treatment of this species (Roper *et al.*, 1984) included information and distributions of many cryptic member species of the genus ***Callistoctopus***. The taxonomic status of the western Atlantic form described by Voss (1957) is unresolved.

Literature: Mangold (1998), Boletzky *et al.* (2002).

Callistoctopus nocturnus (Norman and Sweeney, 1997)

Octopus nocturnus Norman and Sweeney, 1997, *Invertebrate Taxonomy*, 11: 117. [Type locality: Philippine Islands, Negros Oriental Province, Maloh].

Frequent Synonyms: None.

Misidentifications: *Octopus macropus* Risso, 1826.

FAO Names: En — Philippine octopus; **Fr** — Poulpe philippin; **Sp** — Pulpo de Filipinas.

Diagnostic Features: Moderate-sized, elongate species. Arms long, 4 to 7.5 times mantle length. **Dorsal arms longest (1>2>3>4).** Arm autotomy at distinct plane absent. **Webs short, deepest around 10 to 15% of arm length.** Web deepest on dorsal arms; webs between ventral arms shallowest. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 180 to 240 suckers on each normal arm. Enlarged suckers absent. **Gills with 10 to 11 lamellae per demibranch.** Funnel organ W-shaped, outer limbs 60 to 80% of length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 60% of length of opposite arm. Ligula conical with deep ligula groove, of moderate size, 4 to 5% of arm length. Calamus small, around 35% of ligula length. Hectocotylized arm with 80 to 90 suckers. Spermatophores of moderate size, around 28 mm, 60% of mantle length, produced in low numbers (1 in single mature male). Spermatophores unarmed. Eggs small. **Colour:** Colour in preserved material pink-brown with dorsal surfaces mottled with irregular dark red-brown blotches. **Paired white spots visible along aboral surfaces of arms. Larger specimens show white spots scattered over dorsal mantle.** False-eye spots (ocelli) absent. **Sculpture:** Skin texture of small low round papillae. Primary papillae not visible. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 60 mm; total length to 350 mm; body weight to at least 60 g.

Geographical Distribution: Known only from the Philippines (Fig. 108).

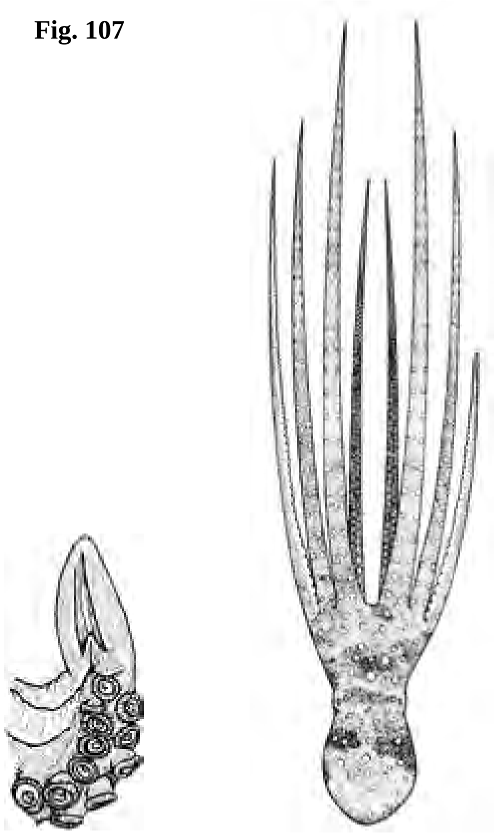
Habitat and Biology: Depths range from 0 to 5 m. Material examined was collected primarily from intertidal coral and rocky reefs.

Interest to Fisheries: Museum material dating back to 1908 was collected at night by local fishermen at Mansalay Bay on Mindoro Island, Philippines, who employed burning torches to locate these night-active intertidal animals. Scale of current fishery harvest is unknown.

Local Names: Unknown.

Literature: Norman and Sweeney (1997).

Fig. 107



hectocotylus dorsal view

Fig. 107 *Callistoctopus nocturnus*

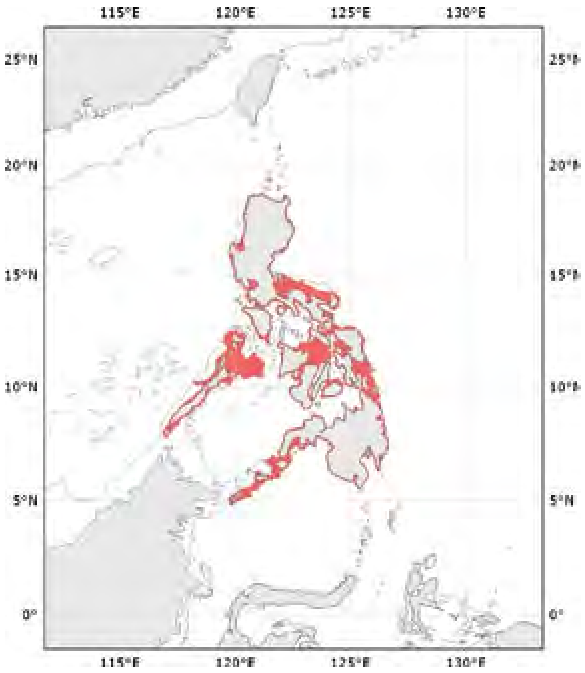


Fig. 108 *Callistoctopus nocturnus*

🟥 Known distribution

Callistoctopus rapanui (Voss, 1979)

Fig. 109

Octopus rapanui Voss, 1979, *Proceedings of the Biological Society of Washington*, 92(2): 360. [Type locality: Southeastern Pacific Ocean, Easter Island, Hanga Piko].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Rapanui octopus; **Fr** — Poulpe de Rapanui; **Sp** — Pulpo de Rapanui.

Diagnostic Features: Large, muscular species. Arms moderate to long, 3.5 to 4.5 times mantle length. **Dorsal arms longest (1>2>3>4)**. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20% of arm length. Web depths variable in limited material available. Web margins extend two thirds along arm length. Interbrachial web pouches absent. Two rows of suckers on each arm. Enlarged suckers absent. Gills with 11 to 12 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, 70 to 95% length of opposite arm. Ligula small, 1.5 to 4% of arm length. Calamus of moderate size, around 30% of ligula length. Hectocotylized arm with 101 to 106 suckers. Spermatophores long, around 66 to 75% of mantle length. Egg size unknown. **Colour:** Known only from preserved material. **Cream-grey with darker purple tinge to dorsal surfaces.** False-eye spots (ocelli) absent. **Sculpture: Skin texture of scattered large low papillae over dorsal and lateral surfaces.** Skin ridge around lateral margin of mantle absent.

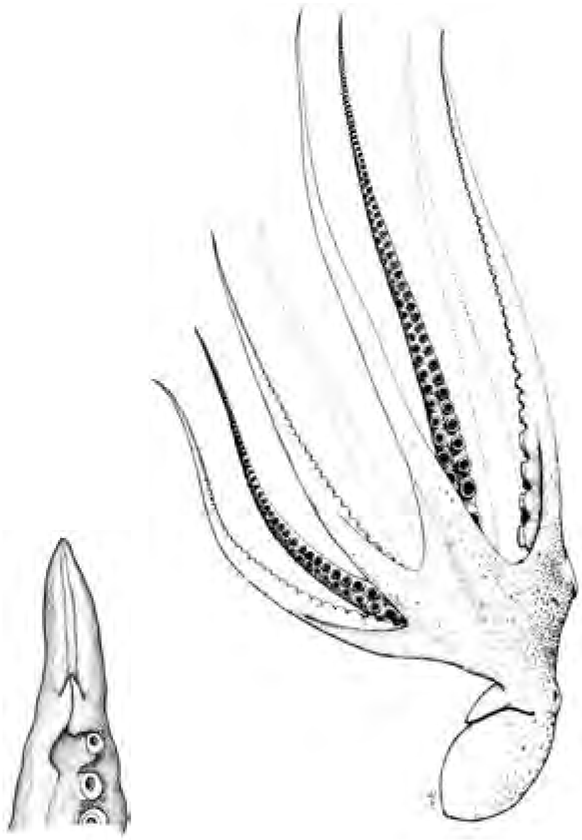

hectocotylus lateral view

Fig. 109 ***Callistoctopus rapanui***

Size: Mantle length to 115 mm; total length to at least 550 mm.

Geographical Distribution: Known only from Easter Island (Fig. 110).

Habitat and Biology: Depths range from 0 to 4 m. Nothing known of the biology of this species. Voss (1979) reported material collected from intertidal rock pools.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Toll and Voss (1998).

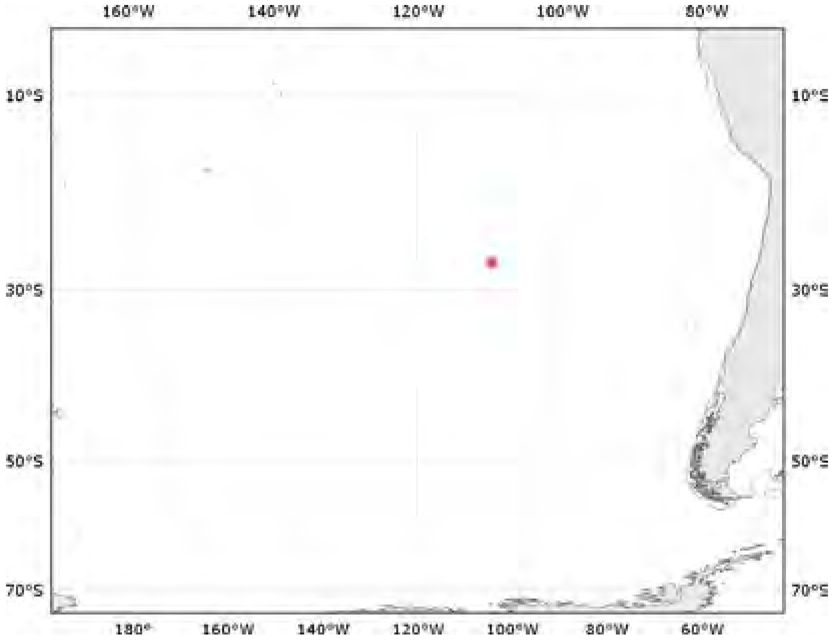


Fig. 110 ***Callistoctopus rapanui***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Callistoctopus lechenaultii (d'Orbigny, 1826)

Octopus lechenaultii d'Orbigny, 1826, *Annales des Sciences Naturelles, Paris,* series 1, 7: 18. [Type locality: India, Pondicherry].

Size: Mantle length to 62 mm.

Geographical Distribution: Known only from type material.

Habitat and Biology: Depth range unknown.

Remarks: ***Callistoctopus cuvieri*** (d'Orbigny, 1840) is a junior synonym. This species requires through description.

Literature: No additional literature.

Cistopus Gray, 1849

Cistopus Gray, 1849, *Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Antepedia*, 20.

Type Species: *Cistopus indicus* (Rapp, 1835).

Diagnostic Features: Moderate to large species. Mantle ovoid to elongate. Stylets long, non-mineralized. **Arms long, up to 6 times length of mantle, dorsal arms longer than ventral pair (arm formula 1>2>3>4).** Arm autotomy at distinct plane absent. **Webs of moderate depth ~15 to 20% of longest arm, dorsal web deeper than ventral web (WF typically A=B>C>D>E). Interbrachial web pouches present on oral surface of webs close to mouth; pores located at level of 3rd to 4th proximal sucker.** Suckers in two rows. **Enlarged suckers present on arms in mature males of at least two member species.** Funnel organ W-shaped. **Gills with 9 to 11 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands moderate to large, slightly larger than buccal mass. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Third right arm of male hectocotylized, around two thirds length of opposite arm. **Ligula a tiny blunt stump (~0.5% of arm length), calamus present or absent.** Spermatophores of moderate length, unarmed. Egg size small to large (species dependent). Colour uniform grey to pink, iridescent pink on lateral and ventral mantle in at least one species. Skin smooth with few, scattered, low papillae on dorsal mantle. Primary papillae absent. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 180 mm; total length to 1 m; body weight to around 2 kg.

Geographical Distribution: Coastal waters of Asia from Philippines and China, Hong Kong SAR west to India.

Habitat and Biology: Occurs on soft sediment substrates in shallow coastal waters.

Remarks: At least four shallow-water species occur from coastal waters of India, Indo-Malayan Archipelago and northern Australia. In addition to the named species treated below, an additional unresolved ***Cistopus*** species (misidentified as ***C. indicus***) also occurs on muddy substrates on the mainland coasts of Asia from at least Singapore, west to southern India. It also possesses water pouches, an arm formula of 1<2<3<4 and a tiny ligula that lacks a calamus. The taxonomy of this genus requires further research.

Literature: Norman and Sweeney (1997), Liao and Lu (2009), Yang *et al.* (2009), Zheng *et al.* (2012).

Cistopus indicus (Rapp, 1835)

Fig. 111

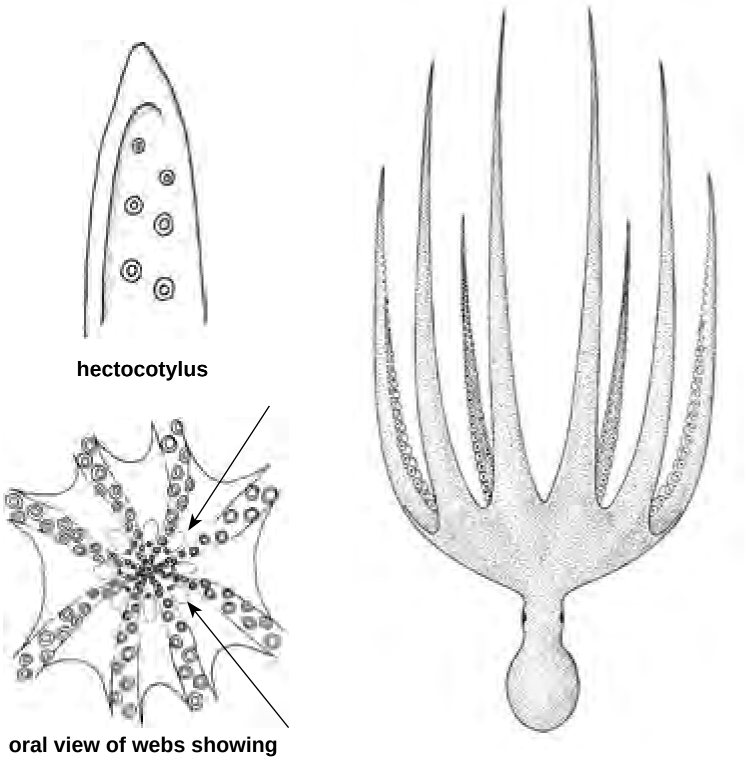
Octopus indicus Rapp, 1835, *In* Férussac and d'Orbigny, 1834-1848, *Histoire naturelle générale et particulière des Céphalopodes Acetabulferes vivants et fossiles*. J.B. Bailliere, Paris: 24. [Type locality: Celebes (Indonesia, Sulawesi)].

Frequent Synonyms: *Cistopus bursarius* Steenstrup *In* Hoyle, 1886.

Misidentifications: None.

FAO Names: En — Old woman octopus; **Fr** — Poulpe vieille femme; **Es** — Pulpo perforado.

Diagnostic Features: Moderate-sized species. Arms long, length around 6 times mantle length. **Dorsal arms longest (1>2>3>4)**. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 15 to 20% of arm length. Web deepest on dorsal arms; webs between ventral arms shallowest. **Water pouches present in oral surface of webs close to mouth; pores located adjacent to level of 3rd to 4th proximal sucker.** Two rows of suckers on each arm. In larger animals, around 180 to



hectocotylus

oral view of webs showing location of water pouches

dorsal view

Fig. 111 *Cistopus indicus*

200 suckers on each normal arm. Enlarged suckers absent. Gills with 9 to 10 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length around 75% of opposite arm. Ligula tiny and blunt, 0.5 to 0.7% of arm length. **Calamus absent. Hectocotylized arm with 116 to 123 suckers**. Spermatophores of moderate length, around 30 mm, 60% of mantle length, produced in moderate numbers (~12). Spermatophores unarmed. Egg size unknown. **Colour: Cream to grey on dorsal surfaces produced by low density of very small chromatophores.** Lateral and ventral mantle and arm crown almost iridescent pink-purple, possibly produced by iridophore layer in skin. False-eye spots (ocelli) absent. **Sculpture: Skin smooth with few, scattered, low papillae on dorsal mantle.** Primary papillae absent. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 180 mm; total length to 1 m; body weight to around 2 kg.

Geographical Distribution: At present known with certainty only from type locality (Celebes) and the Philippines. Many records of this species from coastal Asia to India refer to different species (see remarks above) (Fig. 112).

Habitat and Biology: Depths range to at least 50 m. A shallow subtidal species that occurs on soft sediment substrates. Norman (2000) suggests that the “water pouches” may be mucous glands, the resulting mucous being used to bind together soft sediments in forming a burrow in the mud or sand substrates in which this species lives.

Interest to Fisheries: Value of this specific taxon to fisheries is unknown. Distinct species (often treated under the name ***Cistopus indicus***) form the basis of major harvests across coastal mainland Asia (see species treatments below).

Local Names: Unknown.

Remarks: Primary reports of catches under this species name are from China, Hong Kong SAR (Voss and Williamson, 1971; Norman and Hochberg, 1994). It is not clear which ***Cistopus*** species are harvested in the different coastal countries from China to India.

Literature: Voss and Williamson (1971), Norman and Hochberg (1994), Norman and Sweeney (1997), Norman (2000).

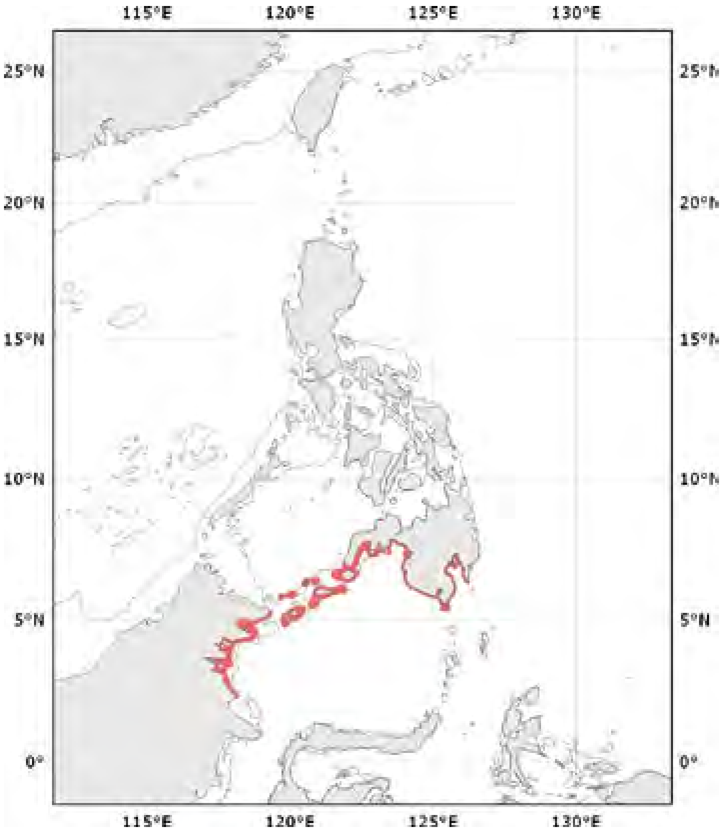


Fig. 112 *Cistopus indicus*

🟥 Known distribution

Cistopus chinensis Zheng, Lin, Lu and Ma, 2012

Fig. 113; Plate III, 23

Cistopus chinensis Zheng *et al.*, 2012. *Journal of Natural History*, 46(5–6): 358 [Type locality: Xiamen, 24°31’N, 118°03’E].

Frequent Synonyms: None.

Misidentifications: *Cistopus indicus* (Rapp, 1835).

FAO Names: En — White-spotted pouched octopus; **Fr** — Poulpe bouffant; **Sp** — Pulpo suave.

Diagnostic Features: Moderate-sized species. Arms long, around 3-4 times mantle length. **Dorsal arms longest (1>2>3>4)**. Arm autotomy at distinct plane absent. Webs shallow, deepest around 12% of arm length. Web deepest on dorsal arms; webs between ventral arms shallowest. **Water pouches present in oral surface of webs close to mouth, pores located adjacent to level of 2nd to 3rd proximal sucker**. Two rows of suckers on each arm. In larger animals, around 81 to 126 suckers on each normal arm. **Enlarged suckers present in mature males, 1 to 2 on arms 1, 2 and 4 (not 3), at level of 10th to 11th suckers.** Gills with 9 to 11 lamellae per demibranch. Funnel organ W-shaped, lateral limbs approximately 71-77% length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 60 to 90% length of opposite arm. **Ligula small with distinct calamus**, ligula around 2.4% of arm length. **Calamus present, one half to one third of ligula length. Hectocotylized arm with 57 to 67 suckers**. Spermatophores of moderate length, around 40 mm, around 45% of mantle length, produced in moderate numbers (~10 to 50). Spermatophores unarmed. Eggs moderate to large type, 11 to 15 mm long, produced in small numbers (up to 135 in reported material). **Colour: Live animals light brown with small iridescent spots scattered over dorsal surfaces of mantle and arms, two lines forming V shape with anterior opening on dorsal head and arm crown.** Preserved animals typically cream coloured. False-eye spots (ocelli) absent. **Sculpture: Skin scattered with low papillae on dorsal mantle and arm crown in location of iridescent spots.** Primary papillae absent. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 100 mm; body weight to around 1 kg.

Geographical Distribution: East China Sea and South China Sea, mainly coastal waters of Zhejiang and Fujian Provinces. Also found in Guangdong and Guangxi Provinces (Fig. 114).

Habitat and Biology: All reported material collected from intertidal mudflats. Broader depth range unknown. Occurs on soft sediment substrates.

Interest to Fisheries: This species has become the focus of an emerging fishery in China because of its fast growth rate and its nutritional and high economic value.

Local Names: CHINA: Bai Youshao (“White-spotted octopus”); CHINA, HONG KONG SAR: Laai Por (“Muddy old woman”).

Remarks: Voss and Williamson (1971) reported historical annual harvests of 50 tonnes of this taxon from China, Hong Kong SAR under the name ***Cistopus indicus***.

Literature: Zheng *et al.* (2012).


hectocotylus dorsal view

Fig. 113 *Cistopus chinensis*

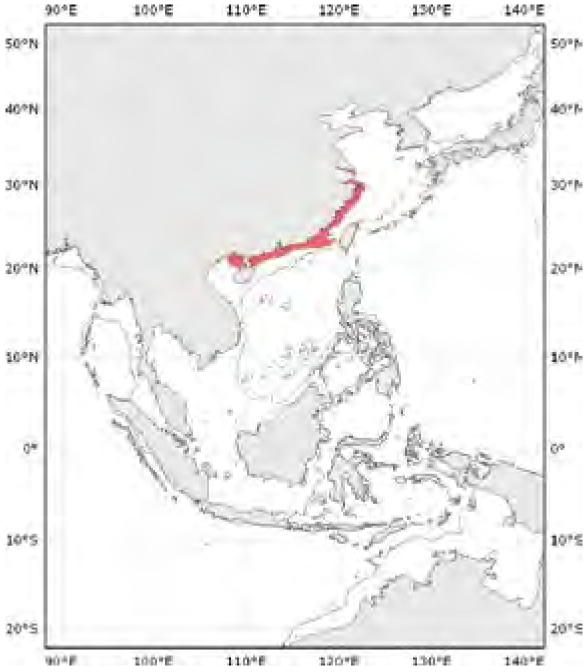


Fig. 114 *Cistopus chinensis*

🟥 Known distribution

Cistopus taiwanicus Liao and Lu, 2009

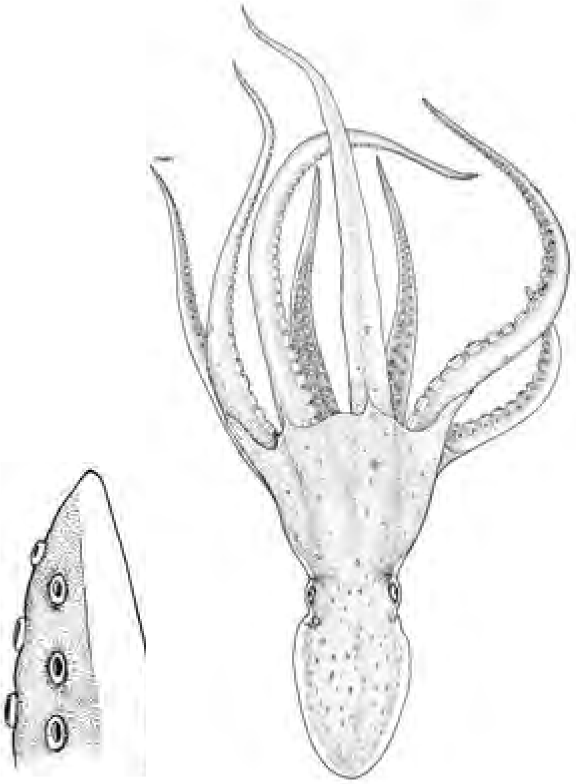
Fig. 115; Plate III, 24

Cistopus taiwanicus Liao and Lu, 2009. *Journal of Molluscan Studies*, 75: 269-278. [Type locality: Taiwan, Miaoli].

Frequent Synonyms: None.

Misidentifications: *Cistopus indicus* (Rapp, 1835).

FAO Names: En — Taiwan pouched octopus; **Fr** — Poulpe bouffant de Taiwan; **Sp** — Pulpo suave de Taiwan.



hectocotylus

dorsal view

Fig. 115 *Cistopus taiwanicus*

Diagnostic Features: Moderate-sized species. Arms long, around 5 times mantle length. **Dorsal arms longest (1>2>3>4)**. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20% of arm length. Web deepest on dorsal arms; webs between ventral arms shallowest. **Water pouches present in oral surface of webs close to mouth, pores located adjacent to level of 3rd to 4th proximal sucker**. Two rows of suckers on each arm. In larger animals, around 134 to 161 suckers on each normal arm. **Enlarged suckers present in mature males, 2 to 4 on arms 1 and 2, at level of 18th to 21st suckers**. Gills with 9 to 10 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 70 to 75% length of opposite arm. Ligula tiny and blunt, around 0.5% of arm length. **Calamus absent. Hectocotylized arm with 106 to 117 suckers**. Spermatophores of moderate length, around 24 to 33 mm, around 30% of mantle length, produced in high numbers (~200 to 250). Spermatophores unarmed. Eggs small type, 5 to 7 mm long, ~4 to 5% of mantle length, produced in large numbers (~7 000). **Colour: Live animals grey to dark maroon red on all dorsal surfaces produced by dense small chromatophores. Lateral and ventral mantle and arm crown iridescent green to pink, produced by iridophore layer in skin.** Scattered papillae on dorsal mantle dark in some colour patterns. Preserved animals uniform grey to cream. False-eye spots (ocelli) absent. Iridescent white/silver rings around water pore openings in mature males, function unknown. **Sculpture: Skin smooth with few scattered low papillae on dorsal mantle.** Primary papillae absent. Skin ridge around lateral margin of mantle absent.

Size: Mantle length 140 mm; body weight to around 1.2 kg.

Geographical Distribution: Taiwan, off the west coast from Hsinchu to Pingtung counties (Fig. 116).

Fig. 116 *Cistopus taiwanicus*

🟥 Known distribution

Habitat and Biology: Depths range from 10 to 75 m. A shallow subtidal species that occurs on soft sediment substrates. Captive animals readily bury in soft sediments

Interest to Fisheries: Collected in coastal trawl fisheries of western Taiwan and frequently sold live in local fish markets. Considered of high value, including live sales to restaurants. Scale of catch unknown but due to presence in fish markets year round, the scale is likely to be moderate (C.C. Lu, pers. comm.).

Local Names: Unknown.

Literature: Liao and Lu (2009).

Eledone Leach, 1817

Eledone Leach, 1817, *The Zoological Miscellany: Being Descriptions of New, or Interesting Animals*, 3(30): 137.

Synonym: *Moschites* Schneider, 1784; *Aphrodoctopus* Roper and Mangold (1992).

Type species: *Octopus moschata* Lamarck, 1798.

Diagnostic Features: Medium to large species. Mantle ovoid, broad. Stylets present, cartilaginous. **Arms short, stout, subequal, 2 to 3 times length of mantle.** Arm autotomy at distinct plane absent. **Webs moderate to deep, deepest around 30 to 40% of longest arm. Webs approximately subequal in depth; ventral and dorsal webs slightly shorter.** Interbrachial web pouches absent. **Suckers in one row. Enlarged suckers present in mature males of several species. Suckers near tips of arms of mature males modified into flattened plate-like ridges or elongate filaments (occupy < 2% of arm length).** Funnel organ variable between species, as W-, UU- or I∩I-shaped. **Gills with 8 to 13 lamellae per outer demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands moderate to large. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Third right arm hectocotylized, shorter than opposite arm. Copulatory organ small, 3 to 4% of arm length, in form of wrinkled rounded tip with convoluted brain-like texture, or as simple ligula (no calamus). Spermatophores medium-sized, armed or unarmed. Eggs small to large depending on the species, attached to substrate singly or in short festoons. Colour patterns variable. False eye-spots (ocelli) absent. Body covered with fine, closely set warts. Skin ridge around lateral margin of mantle present or absent (depending on species).

Size: Mantle length to 250 mm; total length to 550 mm.

Geographical Distribution: Restricted to the cooler waters of Atlantic Ocean and southern Africa. See comments below on ***'Eledone' palari*** from Australia (Fig. 124).

Habitat and Biology: Found at depths of 5 to 500 m with most species occurring at depths less than 300 m. Typically occurs on soft sediment substrates but also found on rubble and rocky reefs.

Remarks: At least 6 species occur in this genus, which is in critical need of revision. The Australian species ***'Eledone' palari*** Lu and Stranks, 1992 is morphologically distinct and its generic placement requires review. It is treated here under unplaced ***Eledone***, designated as ***'Eledone' palari***. The South African species ***Aphrodoctopus schultzei*** (Hoyle, 1910) was placed in its own genus by Roper and Mangold (1992), primarily on the grounds of 1 to 2 rows of suckers on each arm instead of the single row typical of ***Eledone***. This zigzag contraction of sucker rows also occurs in preserved and live specimens of other ***Eledone*** species. All other morphological attributes of ***A. schultzei*** justify its return to the genus ***Eledone***.

Literature: Lu and Stranks (1992), Roper and Mangold (1992).

Eledone moschata (Lamarck, 1798)

Fig. 117; Plate IV, 26

Octopus moschatus Lamarck, 1798, *Bulletin des Sciences, par la Société Philomatique de Paris*, 2(5): 130. [Type locality: not stated; presumed to be Mediterranean Sea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Musky octopus; **Fr** — Elédone musquée; **Sp** — Pulpo almizclado.

Diagnostic Features: Moderate-sized muscular species. Arms of moderate length, 2.5 to 3 times mantle length. Arms approximately equal in length, ventral pair slightly shorter (typically 1=2=3>4). Arm autotomy at distinct plane absent. Webs deep, deepest are over 30% of arm length. Web deepest on lateral arms; web sectors of dorsal and ventral arm pairs shallowest. Web margins thin and transparent, extend to arm tips. Interbrachial web pouches absent. **One row of suckers on each arm. Around 120 suckers on each normal arm in larger females. Mature males have modified suckers on arm tips in the form of paired transverse ridges, i.e. each non-hectocotylized arm has around 90 normal suckers followed distally by 30 pairs of low ridges.** Enlarged suckers present in larger mature males, up to 8 on arms 2 to 4, starting around the 4th proximal sucker. Gills with 11 to 12 lamellae per demibranch. **Funnel organ I∩I-shaped**, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Very large crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 85 to 90% the length of opposite third arm. **Ligula appears glandular with brain-like convolutions, around 2% of arm length. Calamus absent.** Hectocotylized arm with 63 to 66 suckers. Spermatophores short and squat, around 15 mm, around 20% of mantle length, produced in large numbers (~150). Spermatophores unarmed with a very short ejaculatory apparatus. Eggs large, around 8 to 10 mm, around 12% of mantle length. **Colour: Grey-brown with rows of large black spots on the dorsal mantle and arm crown.** False-eye spots (ocelli) absent. **Sculpture:** Skin texture of low rounded patches. Skin ridge absent around lateral margin of mantle. Iridescent green to gold lines along arm margins in live animals

Size: Mantle length to 190 mm; total length to 400 mm. Common at smaller size.

Geographical Distribution: Mediterranean Sea and Gulf of Cadiz (Atlantic Ocean), north to about 40°N. Recordrd from the Sea of Marmara (Fig. 118).

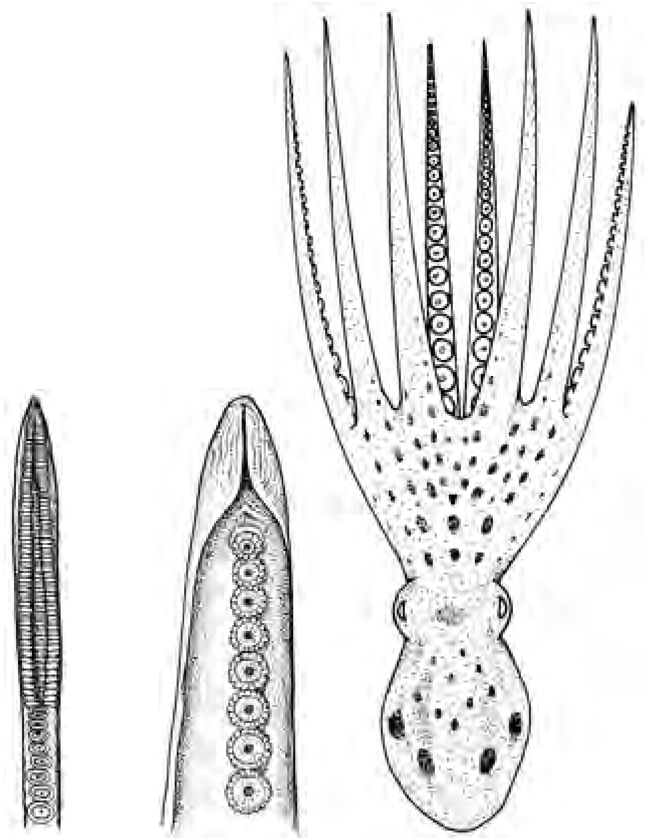

male - tip of normal arm **hectocotylus** **dorsal view**

Fig. 117 *Eledone moschata*

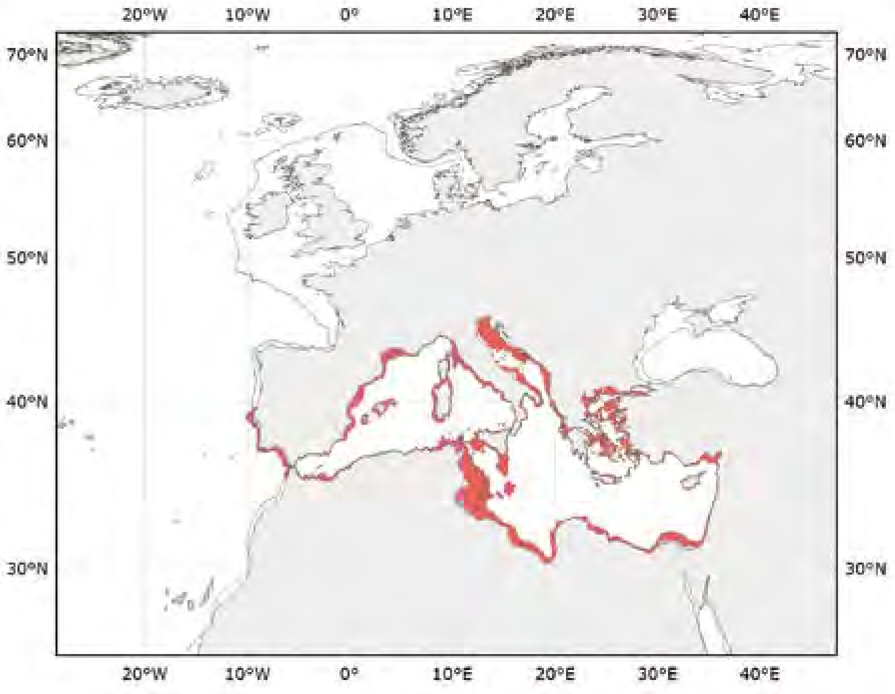


Fig. 118 *Eledone moschata*

🟥 Known distribution

Habitat and Biology: Depths range from 10 to 300 m. This coastal species occurs on muddy substrates. Observations of captive animals suggest night and crepuscular feeding activity. The diet consists primarily of crustaceans with captive animals generally rejecting mollusc prey. Females lay up to 500 eggs in small clusters joined at the base of the egg stalks, each containing 3 to 10 eggs. The large eggs hatch into benthic young. Two species of dicyemid parasites, *Dicyema moschatum* and *Dicyemennea eledones*, are present in the renal coelom. Species of three genera of cestodes, *Acanthobothrium*, *Scolex* and *Nybelinia*, are reported from the digestive tract. The copepod, *Pennella varians*, often is found on the gills and in the mantle cavity.

Interest to Fisheries: ***Eledone moschata*** is fished throughout the Mediterranean Sea, being particularly important in the Adriatic Sea. As this species is caught and marketed with the co-occurring ***E. cirrhosa***, there are no catch statistics specifically for ***E. moschata***.

Local Names: ITALY: Moscardino muschiato, Moscardino rosso; MALTA: Karnita tal misk; MONACO: Muscardin; TUNISIA: Bou msik; YUGOSLAVIA: Muzgavac.

Remarks: The common name of this species, musky octopus, comes from the pungent, musky odour given off by animals when they are removed from the water. The smell derives from secretions of glands in the skin. The function of this secretion is unknown. Mangold (1983b) reviewed the biology of this species. An update on the biology, ecology, fishery and distribution in European waters was recently carried out (Jereb *et al.*, 2015).

Literature: Dobell (1925), Boletzky (1975), Millard de Montrion (1981), Mangold (1983b), Mather (1984), Hochberg (1990), Salman and Katagan (1999), Quetglas *et al.* (2000), Salman *et al.* (2000, 2001), Belcari *et al.* (2002b), Akyol (2003), Rosa *et al.* (2004b), Silva *et al.* (2004), Storelli and Marcotrigiano (2004),Costa *et al*. (2005), Krustulović Šifner *et al.* (2005, 2011), Akyol *et al.* (2007a), Şen (2007),Ceriola *et al.* (2008), Duysak *et al.* (2008), Lougovois *et al.* (2008), Lourenço *et al.* (2008), Krustulović Šifner and Vrgoč (2009a, b), Şen and Tanrikul (2009), Şen and Akyol (2011), Jereb *et al.*, (2015).

Eledone cirrhosa (Lamarck, 1798)

Fig. 119; Plate IV, 25

Octopus cirrhosus Lamarck, 1798, *Bulletin des Sciences, par la Société Philomatique de Paris*, 2(5): 130. [Type locality: not specified; presumed to be Mediterranean Sea].

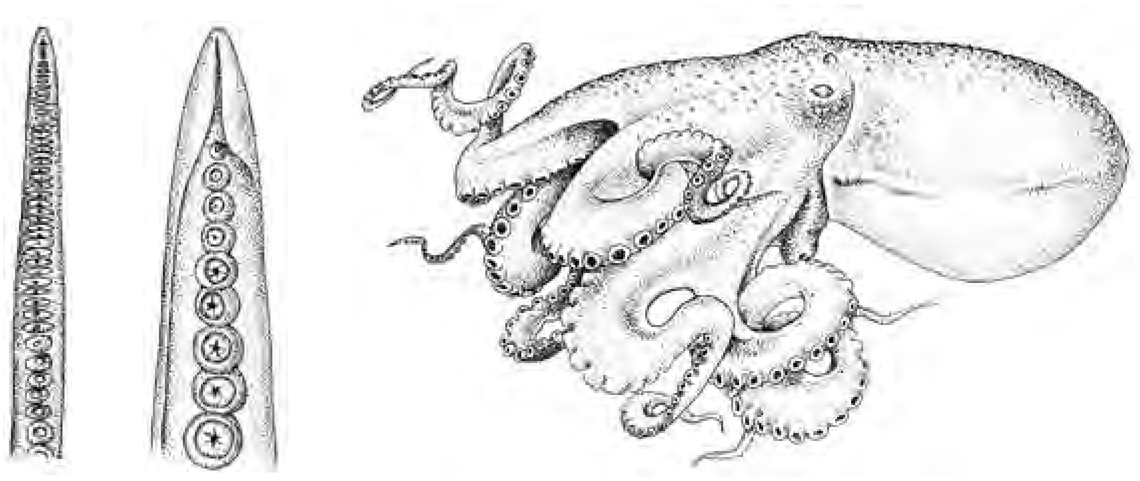
Frequent Synonyms: *Octopus aldrovandi* Montfort, 1802.

Misidentifications: None.

FAO Names: En — Horned octopus; **Fr** — Elédone commune; **Sp** — Pulpo blanco.

Diagnostic Features: Moderate-sized muscular species. Arms short, 2.5 to 3 times mantle length. Arms approximately equal in length, ventral pair slightly shorter (typically 3=2=1>4). Arm autotomy at distinct plane absent. Webs deep, deepest to 40% of arm length. Web approximately equal in length; web sectors of dorsal and ventral arms slightly shallower. Web margins extend to arm tips. Interbrachial web pouches absent. **One row of suckers on each arm. In larger females, around 120 to 140 suckers on each normal arm. Mature males have a series of modified suckers on non-hectocotylized arm tips in the form of transverse ridges, the free ends of which form free cirri.** Enlarged suckers present in mature males and females, 1 to 3 obviously enlarged on arms 1 to 3, starting around the 4th proximal sucker. Gills with 11 to 13 lamellae per demibranch. Funnel organ W-shaped, outer limbs slightly shorter than medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, length around 70 to 80% of opposite arm length. **Ligula short with simple groove, 2 to 4% of arm length. Calamus absent.** Hectocotylized arm with around 65 suckers. Spermatophores small, around 35 mm, length approximately 50% of mantle length, produced in moderate numbers (~15). **Spermatophores armed with inward pointing teeth, exposed on eversion**. Eggs of moderate size, length around 7 mm, approximately 8% of mantle length. **Colour:** Yellow to reddish brown with scattered small white markings. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of small round to elongate patches. Stellate fused patches scattered over dorsal surfaces. Single, large papilla over each eye. **Skin ridge present around lateral margin of mantle**.

Size: Mantle length to 190 mm; total length to 550 mm; body weight to 1.2 kg. Common at smaller size.



male - tip of normal arm

hectocotylus

lateral view

Fig. 119 ***Eledone cirrhosa***

Geographical Distribution: Iceland to Mediterranean Sea, south to about 33 °N. Recorded from the Sea of Marmara (Fig. 120).

Habitat and Biology: Depths range from 5 to 500 m. ***Eledone cirrhosa*** occurs most commonly at depths between 60 to 120 m on the continental shelf throughout its range. The species occurs on a wide range of habitats from sand and mud, to broken rock and rocky reefs. It captures a wide range of prey including shrimps, lobsters, crabs, brittlestars, polychaetes, gastropods, fishes and other cephalopods. In the western Mediterranean, spawning occurs between May and September with a peak in July. Females lay up to 1 500 large eggs that take around 100 days to hatch. Based on egg size, hatchlings are presumed to be benthic. In the western Mediterranean, lifespan appears to be 2 to 3 years and longer in colder waters further north in the eastern Atlantic. Two species of dicyemids, *Dicyemennea eledones* and *D. lameerei*, plus the ciliate, *Chromidina coronata*, inhabit the renal coelom of this species. An unidentified digene and three cestode genera, *Scolex*, *Phyllobothrium* and *Eutetrarhynchus* have been reported from the digestive tract. A fungus, *Cladosporium sphaerospermum*, and a fungus-like protozoan, *Labyrinthula*, have been reported from the skin of ***E. cirrhosa***. Although these organisms produce ulcers in the skin of laboratory animals, it is not known at present whether they should be considered to be pathogens or merely opportunistic saprophytes.

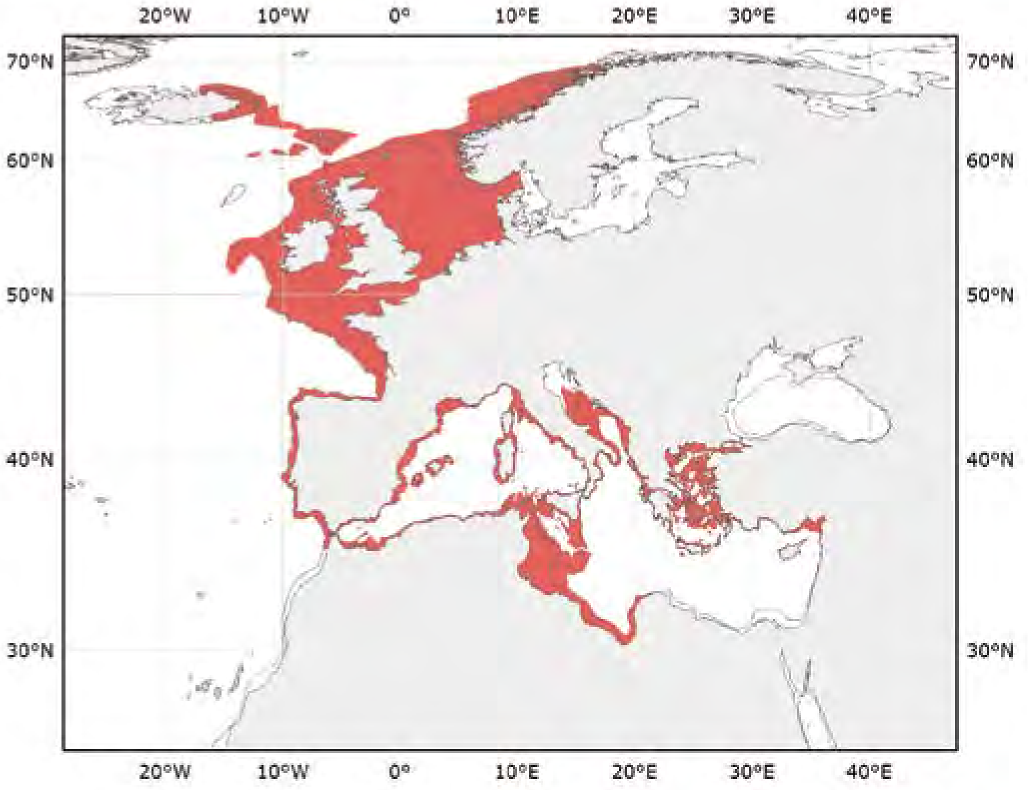


Fig. 120 ***Eledone cirrhosa***

🟥 Known distribution

Interest to Fisheries: ***Eledone cirrhosa*** is harvested on a large scale in the Mediterranean Sea where catch statistics report it combined with the smaller catch of ***E. moschata***. These species are caught primarily with bottom trawls and to a lesser extent with seines. The best catches occur between July and December.

Local Names: GREECE: Moscoctapoda; ITALY: Moscardino bianco; TUNISIA: Qarnit; UNITED KINGDOM: Curled octopus.

Remarks: Boyle (1997) and Relini *et al.* (2006) summarized fisheries information for this species. Distribution and abundance data for Mediterranean Sea are provided in Belcari *et al.* (2002b). An update on the biology, ecology, fishery and distribution in European waters was recently carried out (Jereb *et al.*, 2015).

Literature: Isgrove (1909), Adam (1934), Stevenson (1935), Morales (1958, as ***Eledone aldrovandi***), Rees (1956), Mangold *et al*. (1971), Bradbury (1974), Boyle (1981, 1983, 1986a,b, 1997), Boyle and Dubas (1981), Boyle and Knobloch (1981, 1982a,b, 1983, 1984a,b), Moriyasu (1981, 1983, 1988), Sánchez (1981), Nixon and Boyle (1982), Smith and Boyle (1983), Moriyasu and Benhalima (1983), Boyle and Thorpe (1984), Wurtz and Palumbo (1984), Dubas and Boyle (1985), Boyle *et al*. (1986, 1988), Baino *et al*. (1988), Belcari *et al*. (1990a, b, 1992), Hochberg (1990), Sánchez *et al*. (1990, 2004), Boyle and Chevis (1992), Gil-de-Sola Simarro (1992), Martin and Sánchez (1992), Miramand and Bentley (1992), Sola-Simarra (1992), Wurtz *et al*. (1992), Moriyasu and Benhalima (1993), Rossi *et al*. (1993), Cobb *et al*. (1995a,b), Tursi *et al*. (1995), Lefkaditou and Papaconstantinou (1995), Grisley *et al*. (1996, 1999), Tollit and Thompson (1996), Runham *et al*. (1997), Houlihan *et al*. (1998), Salman and Katagan (1999), Santos *et al*. (1999), Lefkaditou *et al*. (2000), Salman *et al*. (2000), Velasco *et al*. (2001), Belcari *et al*. (2002b), Collins *et al*. (2002), González and Sánchez (2002), Henderson *et al*. (2002), Lloret and Lleonart (2002), Cuccu *et al*. (2003), Costa *et al*. (2005), Krstulović Šifner *et al*. (2005, 2011), Ceriola *et al*. (2008), Duysak *et al*. (2008), Hastie *et al*. (2009), Giordano *et al*. (2010), Ligas *et al*. (2010), Quetglas *et al*. (2011), Jereb *et al*. (2015).

Eledone massyae Voss, 1964

Fig. 121

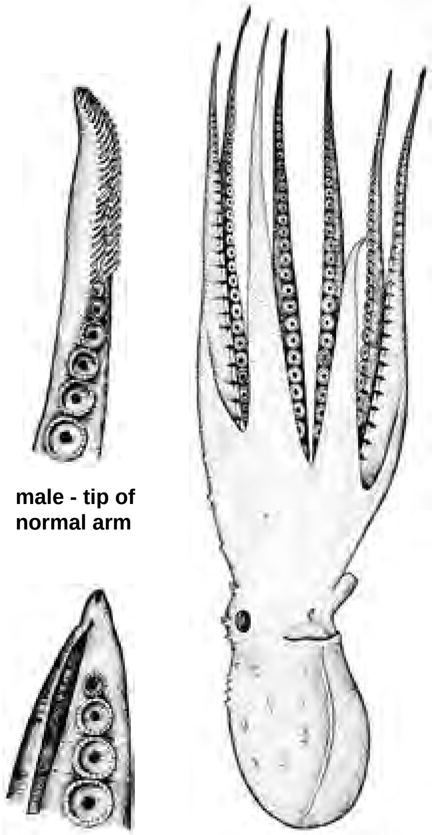
Eledone massyae Voss, 1964, *Bulletin of Marine Science of the Gulf and Caribbean*, 14(3): 511. [Type locality: Brazil, Rio de Janeiro State, Cabo Frio].

Frequent Synonyms: *Moschites brevis* Massy, 1916.

Misidentifications: None.

FAO Names: En — Combed octopus; **Fr** — Elédone peigne; **Sp** — Pulpo desflecado.

Diagnostic Features: Moderate-sized muscular species. Arms short, around 1.7 to 2.5 times mantle length. Arms approximately equal in length. Arm autotomy at distinct plane absent. Webs deep, deepest around 25 to 37% of arm length. Web deepest on lateral arms; webs between ventral arms slightly shallower. Interbrachial web pouches absent. **One row of suckers on each arm**. In larger females, around 57 suckers on each normal arm. **Mature males have a series of modified suckers on last 5 to 6 mm of non-hectocotylized arm tips in the form of two rows of thin cirri.** Enlarged suckers absent. Gills with 8 to 10 lamellae per demibranch. Funnel organ UU-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Ink sac present. Right third arm of males hectocotylized, length around 65 to 90% of opposite arm length. **Ligula appears glandular, with brain-like convolutions, around 6% of arm length. Calamus absent.** Hectocotylized arm with around 24 suckers. Spermatophores produced in low numbers, small, around 17 mm, length around 35% of mantle length. Spermatophores unarmed with a very short ejaculatory apparatus. Eggs large. **Colour:** Pale purple red in colour with scattered white spots and a pale bar across the head. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of fine round papillae interspersed by a few larger, simple warts over mantle and arm crown. 2 to 4 branching papillae over each eye. **Skin ridge present around lateral margin of mantle.**



male - tip of normal arm

hectocotylus

dorsolateral view

Fig. 121 *Eledone massyae*

Size: Mantle length to 75 mm; total length to at least 150 mm.

Geographical Distribution: Southeast coast of South America from Brazil to Argentina (20°S to 43°S) (Fig. 122).

Habitat and Biology: Depths of occurrence range from 30 to 300 m. Little is known of the biology of this species. Most specimens have come from trawl fisheries on sandy and muddy substrates. This species is likely to move to rocky substrates of the upper slope to spawn and breed. Off Cabo Frio, specimens move to shallow water only in spring and summer, with the upwelling of the South Atlantic Central Water. An undescribed species of the protozoan parasite, *Aggregata*, occurs in the digestive tract of this host species. *Scolex polymorphus*, a cestode parasite has been found in the wall of the caecum.

Interest to Fisheries: This octopus is taken as by-catch in trawl fisheries in Brazil and Argentina.

Local Names: Unknown.

Literature: Voss (1964), Ré and Taylor (1981), Levy *et al.* (1988), Perez (1990), Perez *et al.* (1990), Perez and Haimovici (1991, 1995), Haimovici and Perez (1991, 1992), Costa and Fernandes (1993), Sardella and Ré (1996).

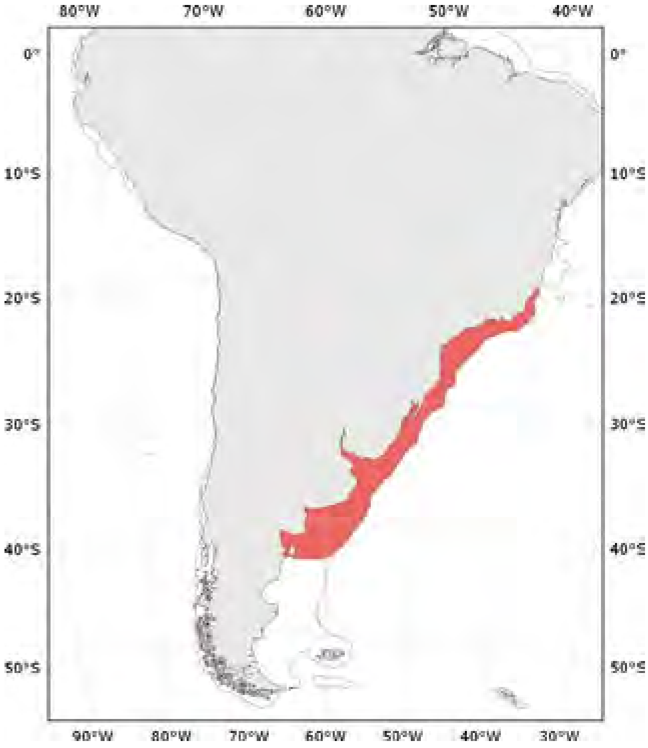


Fig. 122 *Eledone massyae*

🟥 Known distribution

'Eledone' palari Lu and Stranks, 1992

Fig. 123; Plate IV, 27

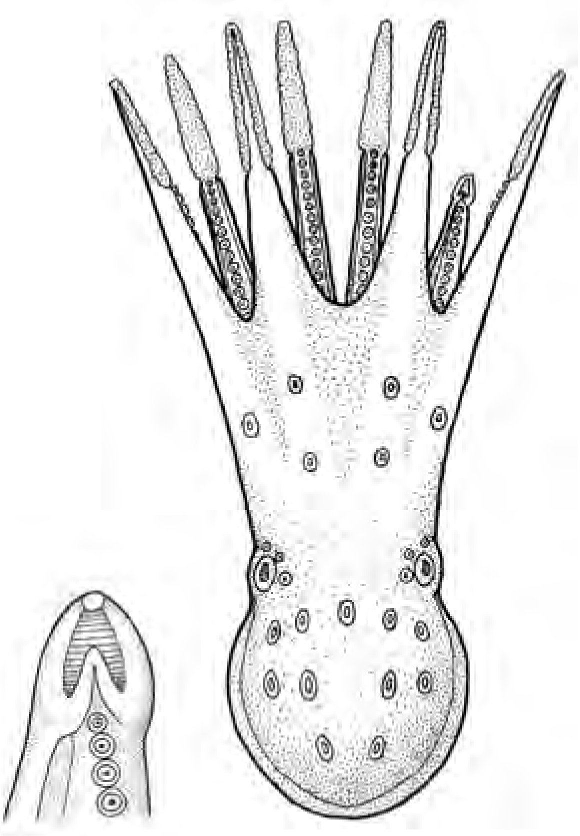
Eledone palari Lu and Stranks, 1992, *Bulletin of Marine Science*, 49(1-2): 73. [Type locality: Eastern Australia, Queensland, east of North Stradbroke Island, 27°35'S, 153°50'E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Spongetip octopus; **Fr** — Poulpe éponge; **Sp** — Pulpo esponja.

Diagnostic Features: Soft-bodied, squat species with short arms. Body flattened. Stylets large and very robust (length ~30% of mantle length). **Arms 1.5 to 2.5 times mantle length**, approximately equal in length. Arm autotomy at distinct plane absent. Webs deep, 38 to 67% of arm length. Interbrachial web pouches absent. **Suckers in single row**. No sucker enlargement in either sex. Gills with 5 lamellae per demibranch. **Funnel organ UU-shaped**. Radula with 7 rows of teeth plus marginal plates, rachidian tooth with 2 to 3 lateral cusps per side, in asymmetrical seriation. Distinct crop present as side-branch off oesophagus. **Ink sac present. Ink duct opens directly to exterior, anterior to anus**. Anal flaps absent. Right third arm hectocotylized, shorter than opposite arm (70 to 100%). **Ligula well developed**, 5 to 9% of hectocotylized arm length, groove open with weak transverse ridges. Calamus well developed, 50 to 75% of ligula length. Hectocotylized arm with 31 to 50 suckers. **All other arm tips of mature males bear pads of special spongy tissue of unknown function**. Spermatophores robust, about two thirds of length of mantle. Eggs large, to 16 mm long. **Colour:** Live animals yellow with iridescent green sheen. Cream to brown on upper surfaces, slightly lighter ventrally. **Sculpture:** Small, low, rounded papillae over upper surfaces. **Around four rows of larger dark red brown papillae on dorsal mantle and arm crown. Thick skin ridge present around lateral margin of mantle.**



hectocotylus dorsal view

Fig. 123 *'Eledone' palari*

Size: Mantle length to 76 mm; total length to 180 mm.

Geographical Distribution: Circum-Australia and southern Indonesia (Fig. 124).

Habitat and Biology: Depths range from 200 to 600 m. This species is known only from trawl specimens. The function of the male spongy arm tip modifications is unknown.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Remarks: The distinctive morphology of this species, particularly the male arm tip spongiform modifications and the distinct ligula and calamus, warrants review of its generic placement within ***Eledone***.

Literature: Lu and Stranks (1992), Norman *et al.* (1997).

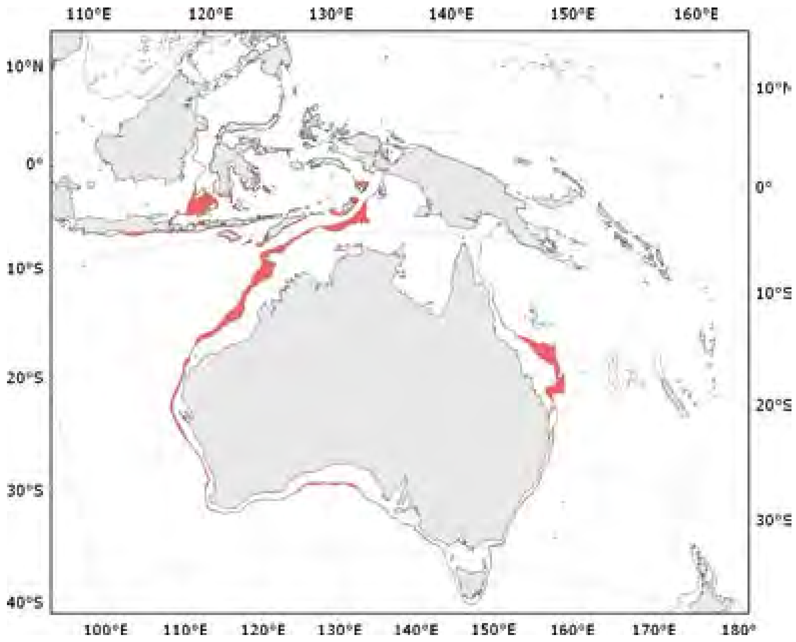


Fig. 124 *'Eledone' palari*

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Eledone caparti Adam, 1950

Eledone caparti Adam, 1950, *Bulletin du l'Institut Royal des Sciences Naturelles de Belgique*, 26(45): 7. [Type locality: West Africa, Congo, 5º52'S, 11º43'E].

Size: Mantle length to 47 mm.

Geographical Distribution: West Africa, Mauritania to Angola. Depths range from 64 to 146 m.

Literature: Nesis and Nigmatullin (1978), Nesis (1987).

Eledone gaucha Haimovici, 1988

Eledone gaucha Haimovici, 1988, *Nautilus*, 102(2): 82. [Type locality: Brazil, South of Rio Grande do Sul, 32º58'S, 51º19'W].

Size: Mantle length to 65 mm.

Geographical Distribution: Southern Brazil, off Rio Grande do Sul, between 30º to 34ºS. Depths range from 52 to 140 m.

Literature: Haimovici and Andriguitto Fo (1986), Levy *et al.* (1988), Perez (1990), Costa and Fernandes (1993), Perez and Haimovici (1995).

Eledone schultzei Hoyle, 1910

Plate IV, 28

Eledone schultzei Hoyle, 1910, *Zoologische und Anthropologise Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika ausgefuhrt in den Jahren 1903-1905*, 4(1): 261. [Type locality: German Southwest Africa (Namibia), Angra Pequeña (Lüderitz Bay)].

Size: Mantle length to 100 mm; total length to 500 mm; body weight to 350 g.

Geographical Distribution: Southeastern Atlantic, southwest Africa from Namibia to South Africa, 15º to 34ºS and 15º to 24ºE. Depths range from 0 to 18 m.

Remarks: Generic placement returned to ***Eledone*** (see comments under generic treatment above). Synonyms in the older literature include ***Moschites nigra*** Hoyle, 1910, ***Pareledone carlgreni*** Thore, 1945, and ***Eledone thysanophora*** Voss, 1962.

Literature: Roper and Mangold (1992; as ***Aphrodoctopus schultzei***), Villanueva and Sánchez (1993; as ***Eledone nigra***), Voight (1993; as ***Aphrodoctopus schultzei***), Smith (1999), Norman (2000; as ***Aphrodoctopus schultzei***).

Enteroctopus Rochebrune and Mabille, 1889

Enteroctopus Rochebrune and Mabille, 1889, *Mission Scientifique du Cap Horn*, 1882-1883, 6(2): H5.

Type Species: *Octopus megalocyathus* Gould, 1852, by subsequent designation of Hochberg (1998).

Diagnostic Features: Large to very large coastal to deep-water species. Mantle muscular and ovoid. Stylets present, non-mineralized. **Arms long and muscular, typically 3.5 to 5 times mantle length. Arms of similar length; dorsal arm pairs slightly longer in some species.** Arm autotomy at distinct plane absent. Webs moderate to deep, deepest around 20 to 30% of longest arm. **Webs deepest on lateral arms; webs between ventral arms shallowest (typically C>D>B>A>E).** Interbrachial web pouches absent. Suckers in two rows. Enlarged suckers present in some species, several pairs (typically 3 to 5 pairs) on all arms of mature males and females, larger in males. Funnel organ W-shaped, outer limbs about 1/2 the length of inner limbs. **Gills with 12 to 15 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands of moderate size. Distinct crop as side-branch off oesophagus absent or weakly developed. Ink sac present. Anal flaps present but tiny. Third right arm of male hectocotylized with large elongate copulatory organ; **ligula extremely long and narrow (typically >20% of arm length).** Calamus minute (typically <10% of ligula length). **Spermatophores extremely large, their length up to several times mantle length.** Eggs small, deposited in festoons. Colour patterns typically red-brown to orange, uniform to mottled. False eye-spots (ocelli) absent. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle (‘dorsal mantle white spots’ *sensu* Packard and Sanders, 1971). **Skin soft, semi-gelatinous, with distinct longitudinal wrinkles or folds dorsally and laterally, patch and groove system present.** Conspicuous primary papillae present on mantle and head, 4 elongate papillae in diamond pattern on mid-dorsal mantle. One to 2 large flap-like primary papillae over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 600 mm, total length to at least 3 m.

Geographical Distribution: Temperate and cooler waters of Indian and Pacific Oceans in both hemispheres, and southern Atlantic and Indian Ocean.

Habitat and Biology: This species occurs on reef and soft sediment substrates from intertidal habitats to at least 1 500 m deep.

Remarks: Three or more species occur in temperate waters in the Pacific, Indian and Atlantic Oceans. In 1889, Rochebrune and Mabille erected the genus ***Enteroctopus*** to include the new species ***E. membranaceus***. They also placed ***E. megalocyathus*** (Gould, 1852) in the same genus. Because ***E. membranaceus*** is the first-named species listed in the new genus, it has been regarded by some workers as the type species of the genus (by order of precedence). The name ***E. membranaceus*** has been considered as a *nomen dubium* by many authors because: 1) the original description is insufficient to identify individuals to species; 2) the holotype was an immature specimen; and 3) the type no longer exists. Robson (1929a) considered it a junior synonym of ***E. megalocyathus***. We agree with this decision and herein transfer the type species status for ***Enteroctopus*** to the second-named species in the genus, ***E. megalocyathus*** Gould, 1852.

Literature: Strugnell *et al.* (2005).

Enteroctopus megalocyathus (Gould, 1852)

Fig. 125; Plate IV, 31

Octopus megalocyathus Gould, 1852, *United States Exploring Expedition during the Years 1838-1842*, 12: 471. [Type locality: Chile, Tierra del Fuego Archipelago, Bahia Nassau].

Frequent Synonyms: *Octopus patagonicus* Lonnberg, 1899; *Enteroctopus zealandicus* Benham, 1944.

Misidentifications: None.

FAO Names: En — Patagonian giant octopus; **Fr** — Poulpe géant de Patagonie; **Sp** — Pulpo gigante de Patagonia.

Diagnostic Features: Large, muscular species. Arms long, 3.5 to 5 times mantle length. Lateral arms slightly longer (typically 2>3>1>4). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 18 to 23% of arm length. Webs equal in length for lateral and dorsal arm pairs; webs between ventral arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 180 to 210 suckers on each normal arm. Enlarged suckers present in mature males and females, 8 to 10 on all arms, starting around the 14th proximal sucker. Gills with 11 to 13 lamellae per demibranch. Funnel organ W-shaped, outer limbs distinctly shorter than medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as a side-branch off oesophagus. Ink sac present. Anal flaps present. Third right arm of males hectocotylized, its length 70 to 90% of opposite arm length. **Ligula very long and narrow, 11 to 22% of hectocotylized arm length**. Calamus tiny, 10 to 15% of ligula length. Hectocotylized arm with 78 suckers. Spermatophores very long, up to 3 times mantle length, produced in low numbers (~3). **Eggs large, around 17 mm**. **Colour:** Reddish purple dorsally, paler ventrally. Suckers whitish. False-eye spots (ocelli) absent. **Sculpture: Skin loose and folded in parallel longitudinal folds or flaps**. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 190 mm; total length to around 1 m.

Geographical Distribution: Southeastern Pacific to southwestern Atlantic; Chile to Argentina (Rio del Plata) (Fig. 126).

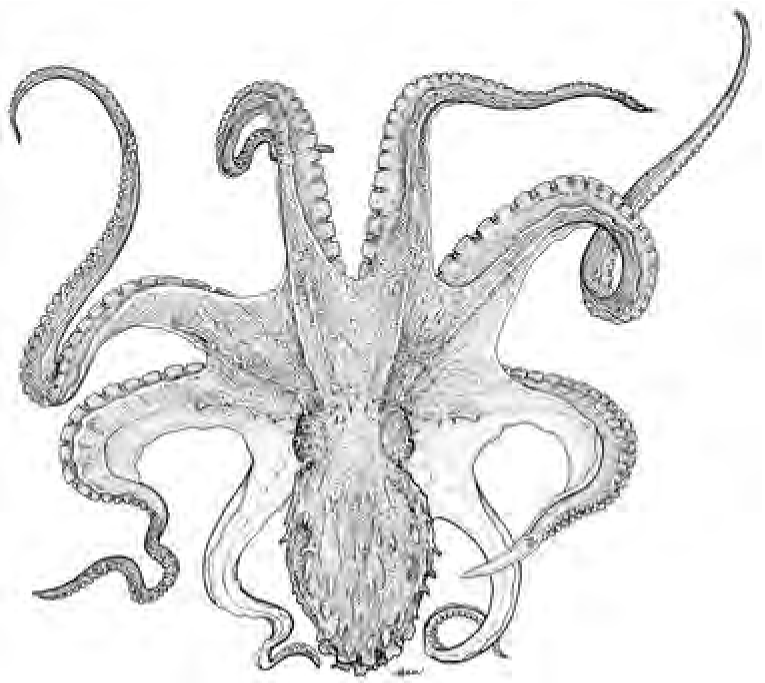
Habitat and Biology: Depths range from 5 to 25 m. Along the Patagonian coast the species lives in caves and large crevices in the shallow subtidal zone. Middens around dens consist principally of the shells of crabs. In some areas bivalve molluscs (*Chlamys*) are the primary prey. During the breeding season this species migrates offshore into deeper waters. The large eggs of this species presumably hatch into benthic young. ***Enteroctopus megalocyathus*** is preyed on by the South American sea lion, *Otaria flavescens*.

Interest to Fisheries: This species supports an extensive artisanal seasonal fishery off the coast of Argentina.

Local Names: Unknown.

Remarks: Molecular analysis (Hudelot, 2000) and morphological studies indicate that ***Enteroctopus magnificus*** and ***E. zealandicus*** Benham, 1944 may be conspecific.

Literature: Ré (1980, 1984), Ré and Taylor (1981), Alonso *et al.* (2000), Sardella *et al.* (2000), Rocha and Vega (2003), Ibáñez *et al.* (2005), Ortiz *et al.* (2006), Pérez *et al.* (2006), Ibáñez (2008), Ibáñez and Chong (2008), Farias *et al.* (2009, 2010, 2011), Marquez and Ré (2009).



dorsal view

Fig. 125 ***Enteroctopus megalocyathus***

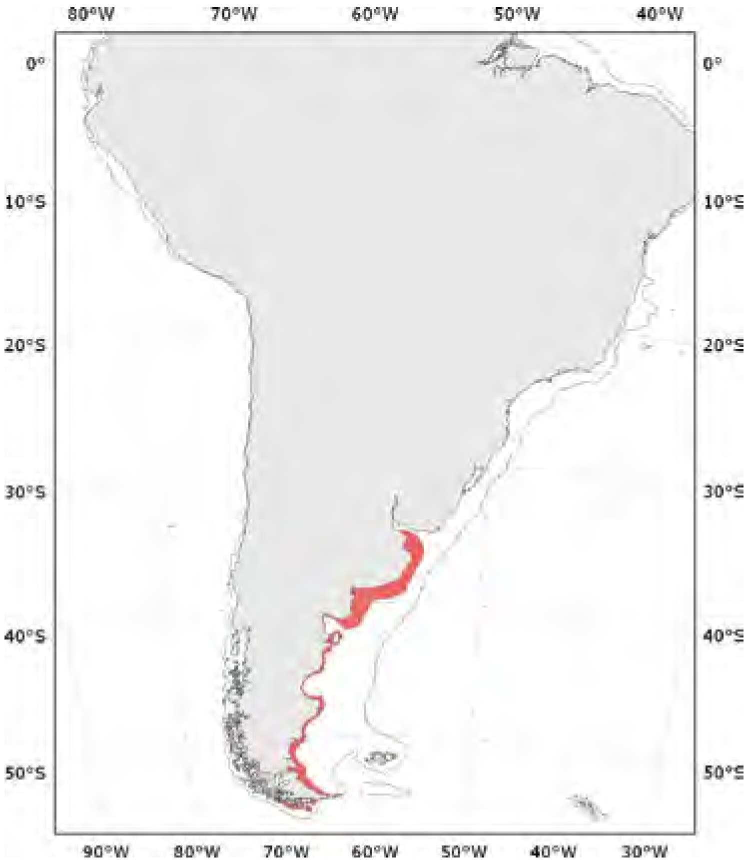


Fig. 126 ***Enteroctopus megalocyathus***

🟥 Known distribution

Enteroctopus dofleini (Wülker, 1910)

Fig. 127; Plate IV, 29

hectocotylus dorsal view

Fig. 127 ***Enteroctopus dofleini***

Polypus dofleini Wülker, 1910, *Abhandlungen der mathematische-physikalische Klasse der Koeniglich Bayerischen Akademie der Wissenschaften*, 3 (Suppl. 1): 7. [Type locality: Northwestern Pacific Ocean, Japan, Hokkaido Island].

Frequent Synonyms: *Octopus punctatus* Gabb, 1862; *Polypus apollyon* Berry, 1912; *Polypus gilbertianus* Berry, 1912, *Octopus dofleini martini* Pickford, 1964.

Misidentifications: None.

FAO Names: En — North Pacific giant octopus; **Fr** — Poulpe géant; **Sp** — Pulpo gigante.

Diagnostic Features: Massive, muscular species. Arms of moderate length, 3 to 5 times mantle length. **Arms almost equal in length, ventral pair shortest (typically 2=1>3>4)**. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 18 to 28% of arm length. Webs on lateral arms slightly deeper; web sectors of dorsal and ventral arm pairs shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, over 500 suckers on each normal arm. Suckers large but none conspicuously enlarged. Gills with 12 to 15 lamellae per demibranch. Funnel organ W-shaped, outer limbs approximately half the length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Ink sac present. Anal flaps present. Right third arm of males hectocotylized; length 80 to 100% of opposite arm length. **Ligula very long, slender and pointed, 20 to 24% of hectocotylized arm length**. Calamus short, 5 to 8% of ligula length. Hectocotylized arm with around 100 suckers. **Spermatophores extremely long, in excess of 1 m long, around 3.5 times mantle length**, produced in low numbers (~2 to 10). Spermatophores unarmed. Eggs small relative to body size, around 6 to 8 mm, laid in festoons. **Colour: Typically orange to red-brown base colour with fine irregular dark lines scattered over dorsal surfaces.** Animals in lairs sometimes show grey colour pattern with short dark red-brown bar through eye. False-eye spots (ocelli) absent. **Sculpture: Skin appears loose in live animals, typically wrinkled into parallel longitudinal ridges or folds.** Four large papillae in diamond arrangement on dorsal mantle. Two large flattened papillae above each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to at least 600 mm; total length to more than 3 m; body weight greater than 180 kg.

Geographical Distribution: North Pacific Ocean from Japan (including Okhotsk and Bering Seas) to Baja California, Mexico (Fig. 128).

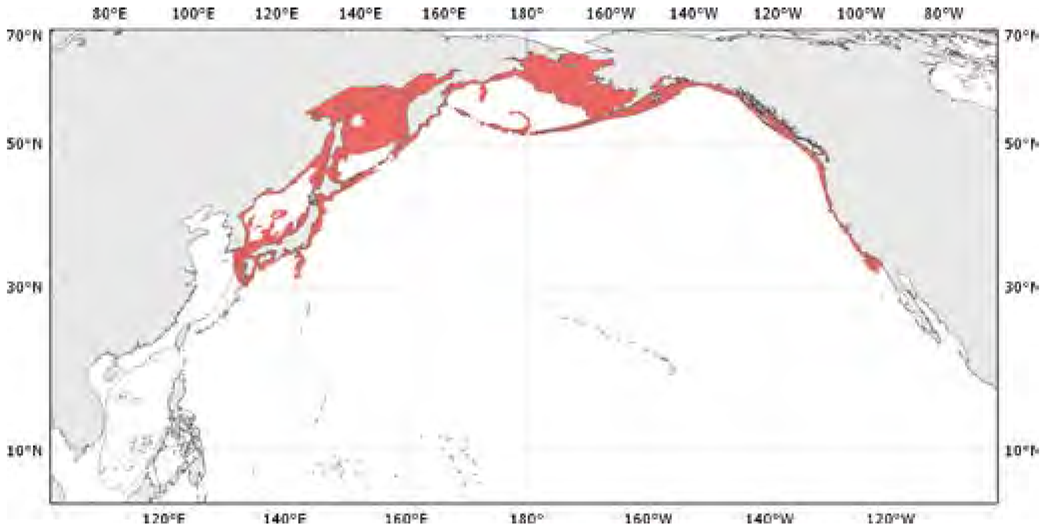


Fig. 128 ***Enteroctopus dofleini***

🟥 Known distribution

Habitat and Biology: Depths range from 0 to 1 500 m. ***Enteroctopus dofleini*** typically occurs in dens on rocky reefs or boulder areas with sand-shell substrate; the same den is utilized for up to several months. Individuals also have been observed in sand and mud habitats. At the northern end of its range, it occurs commonly on reefs in the intertidal zone. At the southern end of its range it has been recorded to depths over 1 500 m. It is primarily night active, emerging to hunt for a wide diversity of invertebrate and vertebrate prey. Diet consists mainly of bivalve and gastropod molluscs and decapod crustaceans. Shelled prey are drilled. Other prey includes echinoderms, brachiopods, assorted fishes, shark eggs, and even seabirds. Primary predators of this octopus are large fishes, sharks, seals, sea lions and even land mammals (mink). ***Enteroctopus dofleini*** migrates offshore into deeper water in summer in order to mate. In autumn and winter animals migrate back inshore where eggs are spawned. Females lay up to 100 000 small eggs in festoons in rock crevices, typically at depths of less than 50 m. Egg laying has been reported throughout the year. Egg development time averages 5 to 6 months, depending on water temperature. Hatchlings are planktonic and are thought to spend 1 to 2 months in the plankton. Acoustic radio tracking of this species off Japan found individuals remained around (and fed from) gill nets. This giant species typically is shy and retiring in the presence of humans, although on occasions individuals have been observed to be aggressive toward divers, in several cases resulting in non-lethal bites.

Interest to Fisheries: ***Enteroctopus dofleini*** is an important commercial resource for bait and food wherever it occurs in abundance. It is targeted in relatively large fisheries in the northeast Pacific and off Japan. It is typically harvested using pots or traps. Dive harvests off British Columbia account for most of the catch of this species. Larger animals are popular as display animals in public aquaria.

Local Names: JAPAN: Mizudako.

Remarks: The taxonomy of the giant octopuses of the north Pacific is in need of thorough review. It is thought that the populations currently being treated under the name ***Enteroctopus dofleini*** may represent a complex of species that are yet to be resolved (Hochberg, 1998).

Literature: Mottet (1975), Hartwick (1983), Kubodera (1992), Hartwick and Barriga (1997), Hochberg (1998), Scheel (2002), Cosgrove (2003), Rigby and Sakurai (2004, 2005), Anderson and Mather (2007), Anderson *et al.* (2007, 2010), Scheel *et al.* (2007), Furuya (2008), Landman *et al.* (2008), Villanueva and Norman (2008), Cosgrove and McDaniel (2009), Jorgensen (2009), Zalygalin (2009), Barry *et al.* (2010, 2011), Conners (2010), Hadjisolomou and Grasso (2010).

Enteroctopus magnificus (Villanueva, Sánchez and Compagno, 1992) **Fig. 129; Plate IV, 30**

Octopus magnificus Villanueva, Sánchez and Compagno, 1992, *Bulletin of Marine Science*, 49(1-2): 39. [Type locality: Southeastern Atlantic Ocean, off Namibia].

Frequent Synonyms: None.

Misidentifications: *Octopus dofleini* Wülker, 1910.

FAO Names: En — Southern giant octopus; **Fr** — Poulpe géant méridional; **Sp** — Pulpo gigante austral.

hectocotylus

dorsolateral view

Fig. 129 ***Enteroctopus magnificus***

Diagnostic Features: Large, muscular species. Arms of moderate length, 3.5 to 5 times mantle length. Arms almost equal in length, first two arm pairs slightly longer (typically 2=1>3=4). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20% of arm length. Web deepest on lateral arms; web sectors of dorsal and ventral arms shallowest. Web margins extend along majority of arm length. Interbrachial web pouches absent. Two rows of suckers on each arm. Up to 300 suckers on each normal arm in larger animals. Suckers large; conspicuously enlarged suckers absent. Gills with 12 to 15 lamellae per demibranch. Funnel organ W-shaped, lateral limbs conspicuously shorter than medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Oesophagus with swelling only, no distinct crop. Ink sac present. Anal flaps present but minute. Right third arm of males hectocotylized, length 80 to 95% of opposite arm length. **Ligula very long and pointed, 14 to 22% of hectocotylized arm length.** Calamus small, 5 to 19% of ligula length. Hectocotylized arm with 92 to 126 suckers. **Spermatophores very long, to 870 mm, 1.6 to 2.8 times mantle length**, produced in low numbers (to 8). Eggs small, around 6 to 8 mm. **Colour:** Dorsal surfaces of live animals variable from yellowish ochre to mottled cream and brown to uniform chocolate brown; paler ventrally. **Edges of longitudinal skin folds frequently white**. False-eye spots (ocelli) absent. **Sculpture: Skin soft and loose, erected as large longitudinal folds and smaller papillae**. Single large papilla present over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 360 mm; total length to 1.6 m; body weight to at least 11 kg.

Geographical Distribution: Southern Africa from Lüderitz, Namibia to Port Elizabeth, South Africa (Fig. 130).

Habitat and Biology: Depths range from 2 to 560 m. Limited biological information is available for this species. This large muscular octopus primarily has been collected by trawls on soft sediment habitats. This octopus appears to be a generalist feeder, preying on lobsters, crabs (including hermit crabs), amphipods, euphausid shrimps, gastropods, polychaetes, fishes (including hagfish) and octopuses. Females produce up to 20 000 small eggs that presumably hatch into planktonic young.

Interest to Fisheries: Harvests of this species are small, primarily as bycatch from finfish trawl fisheries. As it preys on spiny lobster, it is collected as bycatch in lobster fisheries in South Africa.

Local Names: Unknown.

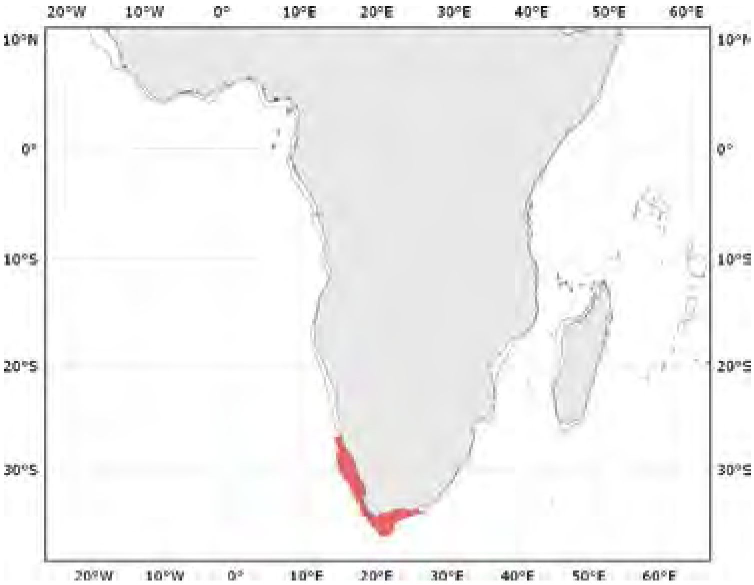


Fig. 130 ***Enteroctopus magnificus***

🟥 Known distribution

Literature: Villanueva *et al.* (1992), Villanueva (1993), Smith (1999), Groeneveld *et al.* (2006).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Enteroctopus zealandicus (Benham, 1944)

Plate IV, 32

Octopus zealandicus Benham, 1944, *Transactions and Proceedings of the Royal Society of New Zealand*, 73(4): 256. [Type locality: New Zealand, South Island, northeast of Moeraki].

Size: Mantle length to 270 mm; total length to around 1.4 m.

Geographical Distribution: New Zealand, South Island and associated plateaus and islands (Chatham, Antipodes, Stewart, Auckland, Campbell, Macquarie islands). Depth range from intertidal areas to at least 500 m.

Literature: O'Shea (1999), Childerhouse *et al.* (2001), Meynier *et al.* (2009).

Euaxoctopus Voss, 1971

Euaxoctopus Voss, 1971a, *Bulletin of Marine Science*, 21(1): 25.

Type Species: *Euaxoctopus panamensis* Voss, 1971; by monotypy.

Diagnostic Features: Small slender and elongate shallow-water species. **Mantle thin-walled and amphora-shaped.** Stylets present, non-mineralized. **Arms long and thin, length 5 to 11 times mantle length. Second arm pair always the longest, typically 2>3>1>4. Arms easily detached; arm autotomy probable. Webs very shallow, deepest <10% of longest arm.** Web sectors subequal in depth. Interbrachial web pouches absent. Suckers in two rows. **Enlarged suckers absent.** Funnel organ V V-shaped. Gills with 7 to 13 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands of moderate size, approximately equal to buccal mass length. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. **Third left or right arm of male hectocotylized (varies between species).** Ligula and calamus present. Spermatophores short and robust, unarmed. Eggs small. **Colour pattern of two conspicuous crescent-shaped markings on dorsal mantle. Skin with two primary papillae on mid-dorsal mantle (one in the centre of each crescent spot).** Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 32 mm; total length to around 200 mm.

Geographical Distribution: Endemic to both coasts of the Panamanian Isthmus, Central America.

Habitat and Biology: Unknown, shallow in two species. The only known specimen of ***E. scalenus*** was collected swimming over deep water (>2 km).

Remarks: Three small poorly known species.

Literature: Voss (1971a).

Euaxoctopus panamensis Voss, 1971 **Fig. 131**

Euaxoctopus panamensis Voss, 1971a, *Bulletin of Marine Science*, 21(1): 25. [Type locality: Pacific Ocean, Panama, near Punta Mala, north of Isla Iguana, 7°39.5'N, 80°00.7'W].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Crescent octopus ; **Fr** — Poulpe croissant ; **Sp** — Pulpo medialuna.

Diagnostic Features: Small, elongate species with long arms. Long, fine arms, taper to delicate tips, their length 7 to 8 times mantle length. Second arms longest (2>3>1>4). Arms frequently broken, likely to show autotomy at a distinct plane. Webs very shallow, deepest less than 10% of arm length. Web sectors approximately equal. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 100 to 140 suckers on each normal arm. Enlarged suckers absent. Gills with 11 to 13 lamellae per demibranch.

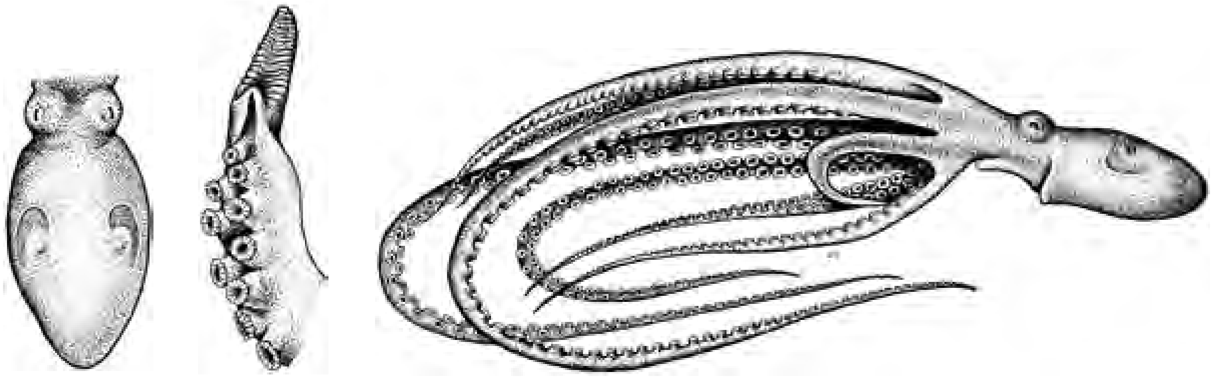


Fig. 131 *Euaxoctopus panamensis*

Funnel organ V V-shaped, slender limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Left third arm of males hectocotylized, length around 30 to 40% of opposite arm. Ligula small, 6 to 9% of hectocotylized arm length. Calamus large, 30 to 55% of ligula length. Hectocotylized arm with 51 suckers. Eggs small, around 1.5 mm. **Colour:** Live animal colours unknown. Preserved material grey-cream in colour with darker mottling on dorsal surfaces. **Two conspicuous crescent-shaped, dark spots on dorso-lateral mantle, each bordered by light bluish or pink line (iridescent in life?). Sculpture:** Skin in preserved material with faint patch and groove texture. One large papilla in middle of each crescent plus one papilla on mid-dorsal mantle between crescents. Single large papilla over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 32 mm; total length to around 200 mm.

Geographical Distribution: Pacific Ocean: Costa Rica, Gulf of Panama from Panama Canal to Ecuador (Fig. 132).

Habitat and Biology: Depths range from 30 to 40 m; broader depth range unknown. An offshore species restricted to soft mud substrates on the continental shelf. Small eggs hatch into planktonic young with long second arms. Paralarvae have been captured offshore from Costa Rica. Nothing else is known of biology or behaviour.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Nesis and Nikitina (1991), Salcedo-Vargas and Jaime-Rivera (1999).

Fig. 132 ***Euaxoctopus panamensis***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Euaxoctopus pillsburyae Voss, 1975

Euaxoctopus pillsburyae Voss, 1975, *Bulletin of Marine Science*, 25(3): 346. [Type locality: West Atlantic Ocean, Surinam, 6°49’N, 54°26 5’W].

Size: Mantle length to 30 mm; total length to 200 mm.

Geographical Distribution: Tropical western Atlantic Ocean.

Habitat and Biology: Depth range from 20 to 60 m.

Literature: Voss and Toll (1998).

Euaxoctopus scalenus (Hoyle, 1904)

Tremoctopus scalenus Hoyle, 1904, *Bulletin of the Museum of Comparative Zoology*, *Harvard*, 43(1): 13. [Type locality: Pacific Ocean, 7°N, 80°W].

Size: Mantle length to 17 mm; total length to 120 mm.

Geographical Distribution: Known only from type specimens.

Habitat and Biology: Type captured swimming in midwater over a bottom depth of 2 298 m.

Literature: No additional literature.

Galeoctopus Norman, Boucher and Hochberg, 2004

Galeoctopus Norman, Boucher and Hochberg, 2004a, *Journal of Molluscan Studies*, 70: 247.

Type Species: *Galeoctopus lateralis* Norman, Boucher-Rodoni and Hochberg, 2004.

Diagnostic Features: Small, muscular, deep-water octopus. Mantle round to squarish. Stylets present, long, chitinous (non-mineralized). **Arms of moderate length, 2.7 to 4.4 times mantle length. Arms approximately equal in length, dorsal pair slightly shorter.** Arm autotomy at distinct plane absent. **Webs deep, deepest around 30% of longest arm.** Webs approximately equal in depth; dorsal web slightly shorter. Interbrachial web pouches absent. Suckers in two rows. Enlarged suckers absent. Funnel organ W-shaped. Gills with 10 to 11 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands moderate to large. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Third right arm of male hectocotylized, significantly shorter than opposite arm (~40 to 60%). **Ligula large with unique barrel-shape (11 to 20% of hectocotylized arm length), with large calamus (>55% of ligula length). Ligula groove enclosed deep within tip of ligula, opening reduced to transverse crescent-shaped mouth, floor of groove with paired raised papillae.** Spermatophores large (~ equal to mantle length) and unarmed. Females with swollen distal oviducts. Egg size unknown. Colour pattern mottled orange to red-brown on dorsal surfaces of body and arms. False eye-spots (ocelli) absent. Skin texture of numerous raised rounded papillae on dorsal surfaces, larger ones being stellate. **Skin ridge around lateral margin of mantle present.**

Size: Mantle length to 37 mm; total length to 165 mm.

Geographical Distribution: Central and southwest Pacific Ocean.

Habitat and Biology: Deep-water species from tropical latitudes at depths between 200 and 400 m.

Remarks: Single deep-water species known from limited trawl material from the central and southwest Pacific Ocean.

Literature: Norman (2004a).

Galeoctopus lateralis Norman, Boucher and Hochberg, 2004a

Fig. 133

Galeoctopus lateralis Norman, Boucher and Hochberg, 2004a, *Journal of Molluscan Studies*, 70: 248. [Type locality: Pacific Ocean, Tonga].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Sharkclub octopus; **Fr** — Poulpe armé; **Sp** — Pulpo armado.

Diagnostic Features: Small, moderately-muscular species. Arms short, 2.7 to 4.4 times mantle length. Arms approximately equal in length, dorsal pair slightly shorter. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20 to 30% of arm length. Webs approximately equal in depth; dorsal sector slightly shorter. Web margins poorly developed. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 130 to 150 suckers on each normal arm. **Enlarged suckers absent**. Gills with 10 to 11 lamellae per demibranch. Funnel organ W-shaped. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Posterior salivary glands large, as large as buccal mass. Third right arm of males hectocotylized, length about 40 to 60% of opposite arm. **Distinctive fleshy ligula with deep transverse groove containing raised tooth-like lugs. Ligula large, 11 to 20% of arm length**. **Calamus over half ligula length**, 57 to 76% of ligula length. Hectocotylized arm with 35 to 43 suckers. Spermatophores large (~ equal to mantle length) and produced in low numbers. Egg size unknown. **Colour:** Mottled orange-brown with three irregular transverse bands across arm crown. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of numerous small, rounded

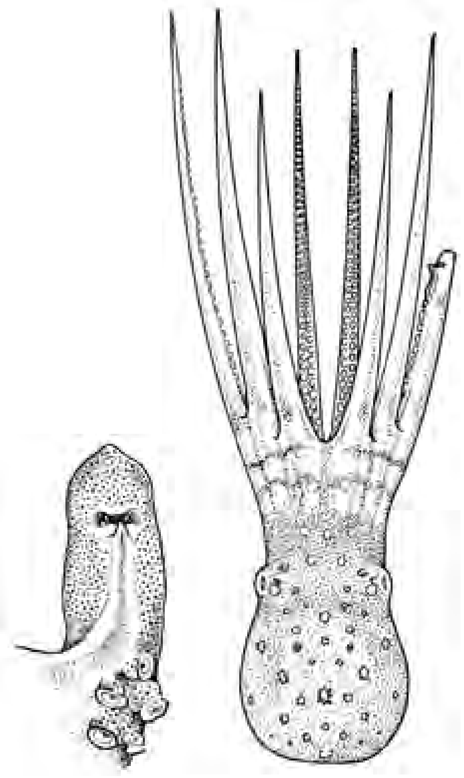

hectocotylus dorsal view

Fig. 133 *Galeoctopus lateralis*

papillae interspersed by larger papillae roughly stellate in shape. Single large and several smaller papillae over each eye. **Skin ridge around lateral margin of mantle present.**

Size: Mantle length to 37 mm; total length to 165 mm.

Geographical Distribution: Central and southwest Pacific Ocean (Fig. 134).

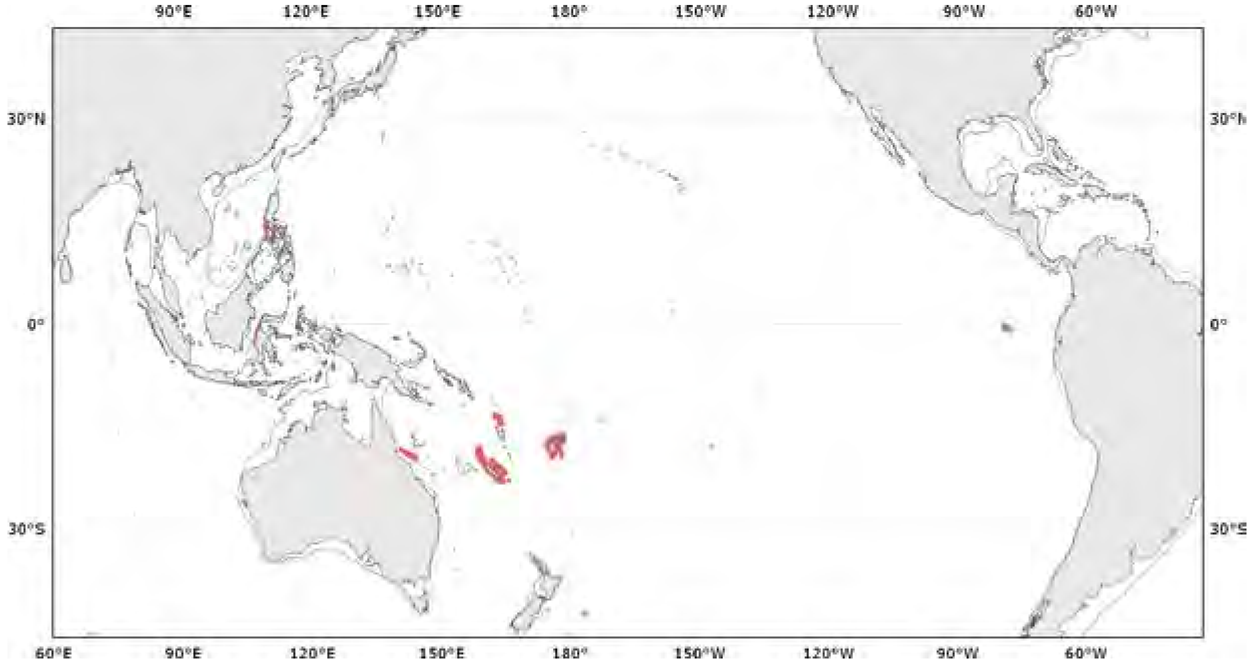


Fig. 134 ***Galeoctopus lateralis***

🟥 Known distribution

Habitat and Biology: Depths range from 200 to 400 m. The biology of this deep-water octopus is poorly known. The presence of a lateral ridge on the mantle is a character found in many octopuses that live on soft sediment substrates. Stomach contents contained remains of fishes and crustaceans.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Norman *et al.* (2004a).

Graneledone Joubin, 1918

Graneledone Joubin, 1918, *Bulletin de l'Institut Oceanographique*, Monaco, 340: 39.

Type Species: *Eledone verrucosa* Verrill, 1881.

Diagnostic Features: Robust, deep-water species. Mantle spherical to slightly ovoid. Stylets present, non-mineralized. **Arms moderate to long, length 2 to 4 times mantle length. Arms subequal in length.** Arm autotomy at distinct plane absent. Webs variable between species, deepest 15 to 40% of longest arm. **Webs approximately equal in depth.** Interbrachial web pouches absent. **Suckers in single row. Enlarged suckers absent.** Funnel organ V V-shaped. Gills with 5 to 8 lamellae per demibranch. Radula of most species with 9 elements, 7 rows of teeth plus marginal plates. Some specimens of ***Graneledone challengeri*** have been reported with an extra pair of lateral teeth elements. ***Graneledone antarctica*** can have 5 elements (no first laterals, no marginal plates) or 7 elements (no marginal plates). Posterior salivary glands small (35 to 40% of length of buccal mass). Oesophagus with swelling only; no distinct crop. **Ink sac absent. Anal flaps absent.** Third right arm of males hectocotylized with arm tip clearly differentiated into ligula and calamus. Ligula short to moderate

(3 to 8% of arm length) in most species but may be longer in ***G. yamana*** (LLI 5 to 14). Calamus long (30 to 60% of ligula length) in most species, very long in ***G. yamana*** (50 to 100%). Spermatophores long (1.2 to 1.8 times mantle length), unarmed. Eggs large, attached to a secreted solid mass in some species. **Colour pattern of relatively uniform grey to pink-purple, often darker around the eye rim and on the oral surface of the webs and arms. Skin of dorsal mantle, head, eyes and bases of arms 1 and 2 covered with permanent rosette-like clusters of raised rugose cartilaginous (wart-like) tubercles.** Tubercle expression variable, depending on preservation techniques. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 170 mm; total length to 683 mm.

Geographical Distribution: Deep waters of southern hemisphere and northern Pacific Ocean.

Habitat and Biology: Deep water species attaining depths of at least 3 000 m.

Remarks: At least 10 deep-water species from all oceans. Freezing specimens of this genus can mask the cartilaginous skin inclusions, giving the impression of smooth skin. This preservation artifact has lead to some confusion and resulted in placement of some members of this genus into other genera. Strugnell *et al.* (2008a) used molecular evidence to demonstrate that members of this genus arose from shallow-water Antarctic ancestors and moved into deeper habitats along an isothermic gradient from southern polar waters.

Literature: Voss (1976), Villanueva and Sanchéz (1993), Bustamante *et al.* (1998), O'Shea (1999), Kommritz (2000), Voight (2000a,b, 2001b, 2008), Voight and Grehan (2000), Allcock *et al.* (2003a), Drazen *et al.* (2003), Collins *et al.* (2004), Strugnell *et al.* (2008a), Voight (2008).

Graneledone verrucosa (Verrill, 1881)

Fig. 135

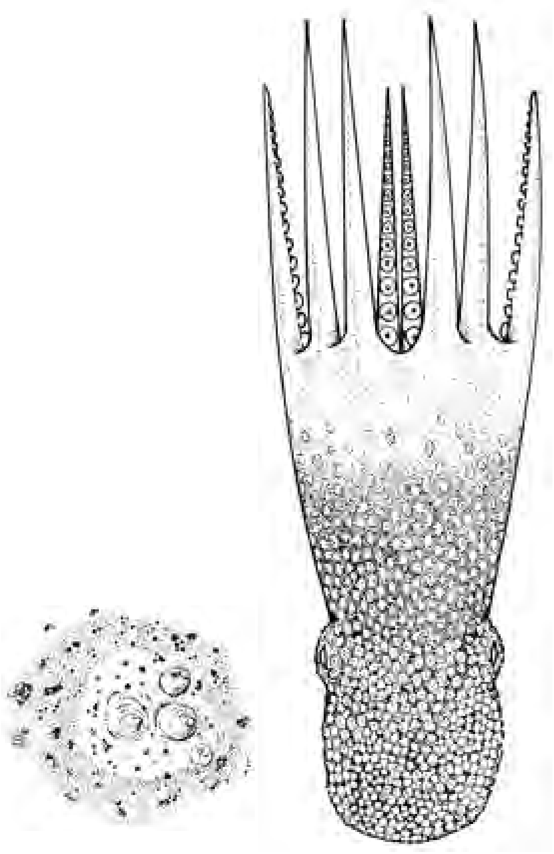
Eledone verrucosa Verrill, 1881, *Bulletin of the Museum of Comparative Zoology*, Harvard, 8(5): 105. [Type locality: Northwest Atlantic Ocean, United States, off New England, 39°50'45"N, 70°11'00"W and 41°33'15"N, 65°51'25"W].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Warty octopus; **Fr** — Poulpe verruqueux; **Sp** — Pulpo verrugoso.

Diagnostic Features: Moderate-sized, robust species covered with raised cartilage-like warts. Arms short, 2.3 to 3.5 times mantle length. Arms approximately equal in length. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 30% of arm length. Webs approximately equal in depth. Web margins extend to arm tips. Interbrachial web pouches absent. **One row of suckers on each arm**. In larger animals, around 70 to 90 suckers on each normal arm. Enlarged suckers absent. Gills with 6 to 8 lamellae per demibranch. **Funnel organ V V-shaped**. Radula with 9 elements, 7 rows of teeth plus marginal plates. Oesophagus with swelling only, no distinct crop. Ink sac absent. Right third arm of males hectocotylized, length around 85% length of opposite arm length. Ligula of moderate size, around 5% of arm length. Calamus large, around 50% of ligula length. Hectocotylized arm with 42 to 45 suckers. Spermatophores large (~1.5 x ML) and produced in low numbers. Eggs large, to 17 mm. **Colour: Dark purplish-brown with darker undersides**. False-eye spots (ocelli) absent. **Sculpture**: **Skin texture of large raised patches scattered over dorsal and lateral surfaces**. **Each patch contains clusters of 3 to 7 cartilage-like white knobs**. Four to 5 larger patches present over each eye. Skin ridge around lateral margin of mantle absent.



warty papillae in skin patch dorsal view

Fig. 135 *Graneledone verrucosa*

Size: Mantle length to at least 110 mm; total length to 500 mm.

Geographical Distribution: North Atlantic Ocean (Fig. 136).

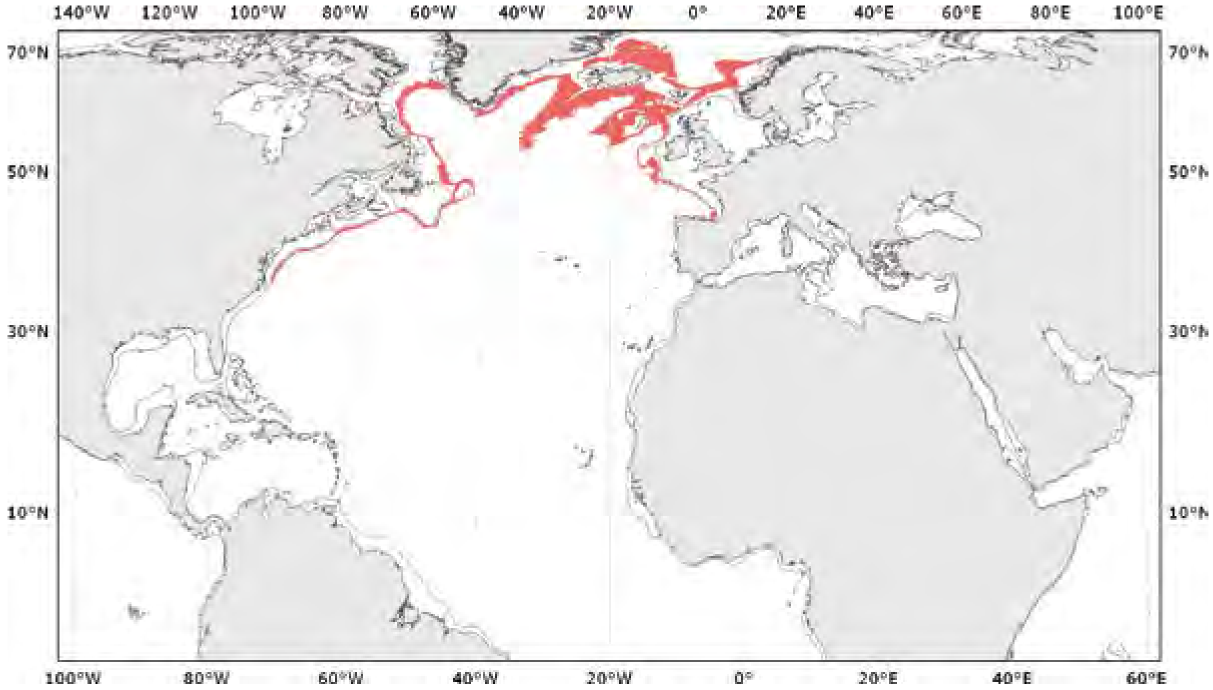


Fig. 136 ***Graneledone verrucosa***

🟥 Known distribution

Habitat and Biology: Depth range from 850 to 2 300 m. Little is known of the biology of this deep-water octopus. Barratt *et al.* (2007) investigated fecundity and reproductive strategy of this species.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Collins *et al.* (2001b), Allcock *et al.* (2003a), Barratt *et al.* (2007).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY A FEW RECORDS EXIST

Graneledone antarctica Voss, 1976

Graneledone antarctica Voss, 1976, *Proceedings of the Biological Society of Washington*, 88(42): 448. [Type locality: Southern Ocean, 74°S, 175°W].

Size: Mantle length to 45 mm.

Geographical Distribution: Southern Ocean, Antarctica, Ross Sea.

Habitat and Biology: Known depth 2 341 m.

Literature: Furuya and Hochberg (2002).

Graneledone boreopacifica Nesis, 1982

Plate V, 33

Graneledone boreopacifica Nesis, 1982, *Abridged Key to the Cephalopod Molluscs of the World's Oceans: 322*. [Type locality: Northwest Pacific Ocean, 50°N, 151°E].

Size: Mantle length to 145 mm.

Geographical Distribution: A widely distributed boreal species known to occur in the North Pacific off Japan, in the Sea of Okhotsk off Russia, and off the west coast of the United States from Alaska to southern California.

Habitat and Biology: Depth range 1 000 to 3 000 m.

Remarks: ***Graneledone pacifica*** Voss and Pearcy, 1990 is a synonym (Hochberg, 1998).

Literature: Nesis (1987), Voss and Pearcy (1990), Hochberg (1998), Voight (2000a; as ***Graneledone*** cf. ***boreopacifica***), Voight and Drazen (2004), Bello (2006; as ***G. pacifica***), Jorgensen (2009), Voight and Feldheim (2009).

Graneledone challengeri (Berry, 1916)

Moschites challengeri Berry, 1916, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 68: 49. [Type locality: South Pacific Ocean, Kermadec Islands, 29°45'S, 178°11'W].

Size: Mantle length to 145 mm; total length to 600 mm.

Geographical Distribution: Kermadec Islands, eastern New Zealand and Chatham Rise.

Habitat and Biology: Depth range 766 to 1 500 m.

Literature: O'Shea (1999).

Graneledone gonzalezi Guerra, González and Cherel, 2000

Graneledone gonzalezi Guerra, González and Cherel, 2000, *Antarctic Science*, 12(1): 33. [Type locality: Southern Indian Ocean, off Kerguelen Island (47°15'S, 69°14'E)].

Size: Mantle length to 84 mm; total length to 335 mm; body weight to 344 g.

Geographical Distribution: Off Kerguelen Island.

Habitat and Biology: Depth range 500 to 540 m.

Literature: Roura *et al.* (2009).

Graneledone macrotyla Voss, 1976

Graneledone macrotyla Voss, 1976, *Proceedings of the Biological Society of Washington, 88*(42): 454. [Type locality: Southwestern Atlantic Ocean, off the Falkland Islands, 45°43'S, 55°50'W].

Size: Mantle length to 35 mm.

Geographical Distribution: Known only from type locality; Atlantic Ocean off Falkland Islands.

Habitat and Biology: Depth range 1 647 to 2 044 m.

Literature: Kubodera and Okutani (1994).

Graneledone taniwha taniwha O'Shea 1999

Graneledone taniwha taniwha O'Shea 1999, *NIWA Biodiversity Memoir*, 112: 222. [Type locality: Pacific Ocean, New Zealand, Chatham Rise].

Size: Mantle length to 170 mm; total length to 660 mm.

Geographical Distribution: New Zealand and Chatham Rise to Auckland and Campbell Islands.

Habitat and Biology: Depth range 447 to 1 157 m.

Literature: O'Shea and Kubodera (1996; as ***Graneledone*** sp.).

Graneledone taniwha kubodera O'Shea 1999

Graneledone taniwha kubodera O'Shea 1999, *NIWA Biodiversity Memoir*, 112. [Type locality: Bounty Plateau, off New Zealand].

Size: Mantle length to 147 mm; total length to 683 mm.

Geographical Distribution: Bounty Plateau, Campbell Rise, off New Zealand.

Habitat and Biology: Depth range 500 to 840 m.

Literature: O'Shea and Kubodera (1996; as ***Graneledone*** sp.).

Graneledone yamana Guerrero-Kommritz, 2000

Graneledone yamana Guerrero-Kommritz, 2000, *Journal of Molluscan Studies*, 66: 544. [Type locality: Southwestern Atlantic Ocean, off southern Argentina, 54°56'S, 58°05'E].

Size: Mantle length to 80 mm.

Geographical Distribution: Southwest Atlantic from 26° to 55°S.

Habitat and Biology: Depth range 90 to 1 000 m.

Literature: No additional literature.

Grimpella Robson, 1928

Grimpella Robson, 1928, *Annals and Magazine of Natural History*, series 10, 2: 110.

Type Species: *Grimpella thaumastocheir* Robson, 1928.

Diagnostic Features: Moderate-sized muscular species. Mantle round to ovoid. Stylets absent. Arms of moderate length, ~4 times mantle length. **Arms subequal in length.** Arm autotomy at distinct plane absent. **Webs of moderate depth, deepest up to 32% of arm length. Web sectors approximately equal in depth.** Interbrachial web pouches absent. Suckers in two rows. **Enlarged suckers present in mature males, 2 to 3 on all arms.** Funnel organ UU-shaped, limbs of approximately equal length. Gills with 7 to 9 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands moderate to large, ~1.5 times buccal mass length. Distinct crop present as side-branch off oesophagus. **Ink sac absent. Anal flaps absent.** Third right arm of males hectocotylized, around 70% length of opposite arm. Ligula large and robust, length 5 to 7% of arm length. **Calamus very large and pointed, length around 80% of ligula length.** Spermatophores of moderate length, unarmed with swollen sperm reservoir containing few coils. **Eggs large, attached singly. Colour uniform grey purple to deep velvet red with iridescent green sheen.** Skin with regularly spaced low rounded papillae. Larger papillae absent over eyes. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 50 mm; total length to around 250 mm.

Geographical Distribution: Restricted to southern Australia.

Habitat and Biology: Occurs on rocky substrates 0 to 420 m.

Remarks: Single shallow-water to mid depth species from southern Australia. The relationship between this genus and the deep-water genus ***Benthoctopus*** is yet to be resolved. Both genera possess two rows of suckers, lack an ink sac and require taxonomic revision.

Literature: Norman (2000).

Grimpella thaumastocheir Robson, 1928

Fig. 137; Plate V, 34

Grimpella thaumastocheir Robson, 1928, *Annals and Magazine of Natural History*, series 10, 2: 110. [Type locality: South Australia, Port Lincoln].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Velvet octopus; **Fr** — Poulpe velouté; **Sp** — Pulpo aterciopelado.

Diagnostic Features: Moderate-sized muscular species. Arms of moderate length, 4 to 4.5 times mantle length. Arms of similar length. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest up to 32% of arm length. Web sectors approximately equal in depth. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 130 suckers on each normal arm. **Enlarged suckers present in mature males, 2 to 3 on each arm, starting around the 8th proximal sucker**. Gills with 7 to 9 lamellae per demibranch. Funnel organ UU-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac absent. Anal flaps absent. Right third arm of males hectocotylized, length around 70% of

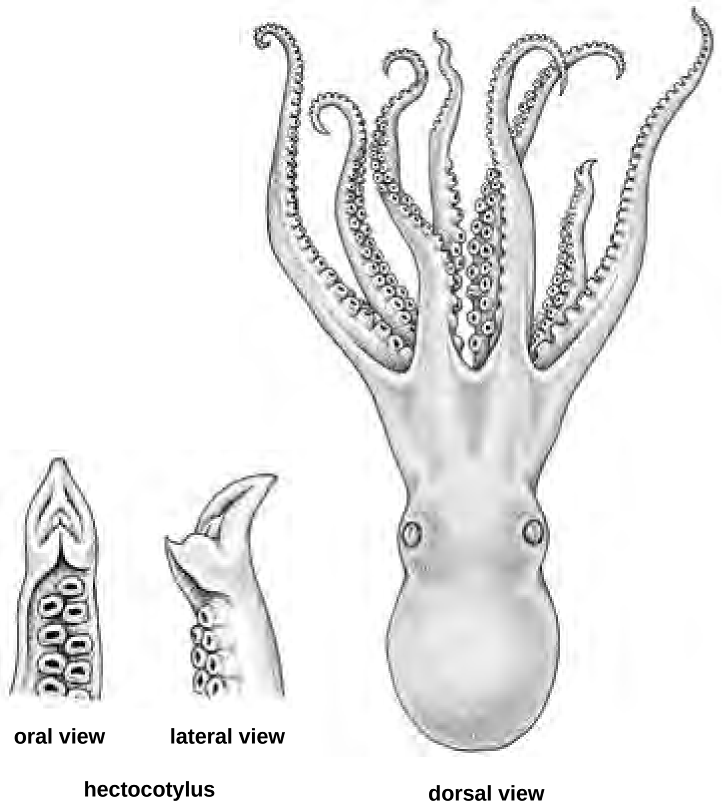


Fig. 137 *Grimpella thaumastocheir*

opposite arm. **Ligula large and robust, 5 to 7% of arm length. Calamus very large and pointed, length around 80% of ligula length**. Hectocotylized arm with 52 suckers in examined male. Spermatophores of moderate length, 25 to 30 mm, around 80% of mantle length, produced in moderate numbers (~15). Eggs large, around 15 mm, 45 to 60% of mantle length. **Colour: Uniform grey purple to maroon red with iridescent green sheen on lateral surfaces**. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of scattered low rounded papillae. No large papillae over eyes. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 50 mm; total length to around 250 mm.

Geographical Distribution: Southern Australia (Fig. 138).

Habitat and Biology: Depth range 0 to 420 m. Night active in rocky reef and rubble areas near shore, adjacent to deep water. The large eggs hatch into benthic young.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Robson (1932), Stranks (1988a), Norman (2000).

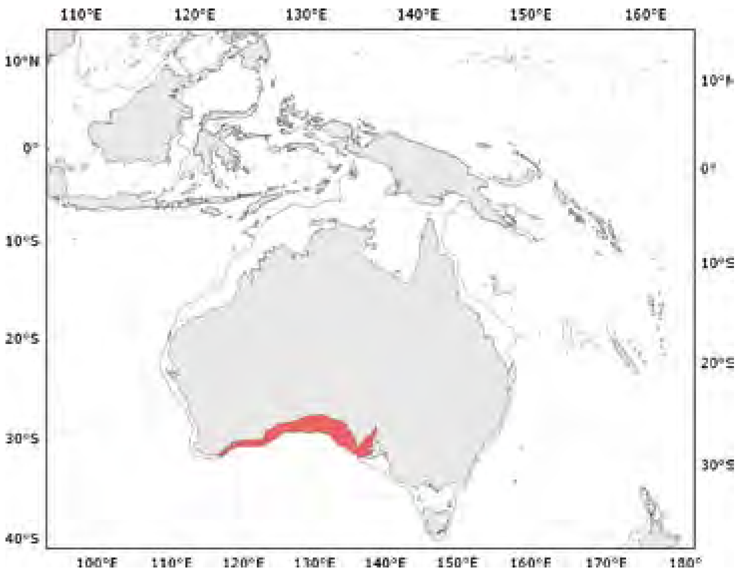


Fig. 138 ***Grimpella thaumastocheir***

🟥 Known distribution

Hapalochlaena Robson, 1929

Hapalochlaena Robson, 1929a, *A Monograph of the Recent Cephalopoda, I: Octopodinae:* 207.

Type Species: *Hapalochlaena lunulata* (Quoy and Gaimard, 1832).

Diagnostic Features: Small to moderate-sized, muscular species. Mantle squat to ovoid, posterior tip pronounced in some postures. Stylets absent. **Arms short to moderate, 1.5 to 2.5 times mantle length. Lateral arms longest, dorsal arms always shortest (typically 2=3>4>1 or 4=3=2>1).** Arm autotomy at distinct plane absent. **Webs moderate to deep, deepest around 20 to 35% point on longest arm. Webs on lateral arms deepest; dorsal web always shortest.** Interbrachial web pouches absent. Suckers in two rows. Enlarged suckers absent. Funnel organ W-shaped. **Gills with 5 to 7 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands large to very large, much larger than buccal mass. Distinct crop present as side-branch off oesophagus. Ink sac present, reduced and non-functional in adults of some species. Anal flaps present. Third right arm of male hectocotylized, slightly shorter than opposite arm. Ligula and calamus present. Spermatophores short, narrow, unarmed. Eggs small to large, laid in strings and brooded unattached in web by females. **Colour patterns of distinctive rings and/or lines of iridocytes producing brilliant iridescent blue in live individuals. Ring size varies between species.** Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ("dorsal mantle white spots" *sensu* Packard and Sanders, 1971). Skin with sculpture of small, low papillae. **Longitudinal flap-like papillae in diamond arrangement on mid dorsal mantle.** Large papilla on posterior tip of mantle. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 57 mm; total length to 220 mm.

Geographical Distribution: Central Indo-West Pacific Ocean north to Japan and south to southern Australia.

Habitat and Biology: Shallow coastal waters on rocky and coral reefs, seagrass and algal beds. Collected from 0 to 50 m.

Remarks: At least 10 species from tropical to temperate waters of eastern Indian Ocean, western Pacific Ocean and Australia. Only three species adequately described to date.

Public health risk: Members of this genus possess powerful neurotoxins including tetrodotoxin. Bites by these small octopuses have resulted in human fatalities. Live animals should never be directly handled.

Hapalochlaena lunulata (Quoy and Gaimard, 1832)

Fig. 139; Plate V, 36

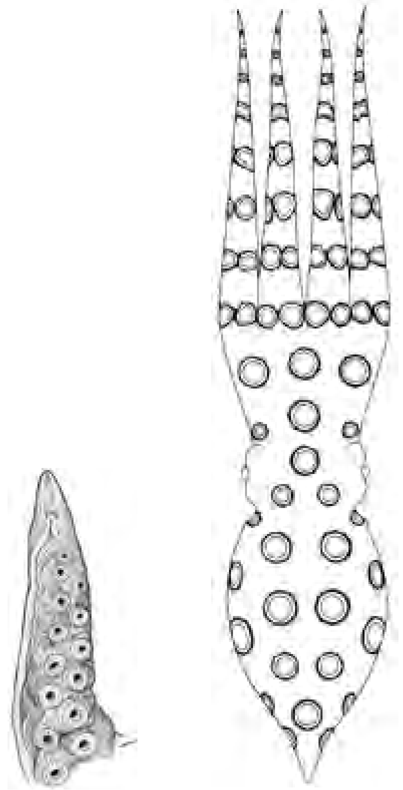
Octopus lunulatus Quoy and Gaimard, 1832, *Voyage de Découvertes de l'Astrolabe pendant les Annees* 1826-1829, Zoologie, 2(1): 86. [Type locality: Papua New Guinea, New Ireland (Bismarck Archipelago), Havre Carteret].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Greater blue-ringed octopus; **Fr** — Poulpe annelé majeur; **Sp** — Pulpo anillado mayor.

Diagnostic Features: Small, brilliantly coloured, muscular species. Arms short, around 2 times mantle length. Lateral and ventral arms longest (typically 3=4>2>1). Arm autotomy at distinct plane absent. Webs deep, deepest around 35% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 60 suckers on each normal arm. Enlarged suckers absent. Gills with 7 lamellae per demibranch. Funnel organ W-shaped, outer limbs approximately 60% length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. **Ink sac present**. Anal flaps present. Right third arm of males hectocotylized. Ligula conical, moderately elongate, 10% of arm length. Calamus of moderate size, around 30% of ligula length. Hectocotylized arm with 43 suckers on examined male. Spermatophores undescribed. Egg size undescribed. **Colour: Base colour of cream to yellow with pattern of large iridescent blue rings covering dorsal surfaces, largest on posterior dorsal mantle (up to 3.2 mm, 18% of ML)**. Each iridescent ring set in a broader ring of dark chromatophores. Short horizontal iridescent line through eye. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin sculpture of low relief patch and groove system, patches small and circular. Skin ridge around lateral margin of mantle absent.



hectocotylus **dorsal view**

Fig. 139 ***Hapalochlaena lunulata***

Size: Mantle length to 50 mm; total length to around 120 mm.

Geographical Distribution: Indonesia, Philippines, Papua New Guinea, Vanuatu and Solomon Islands (Fig. 140).

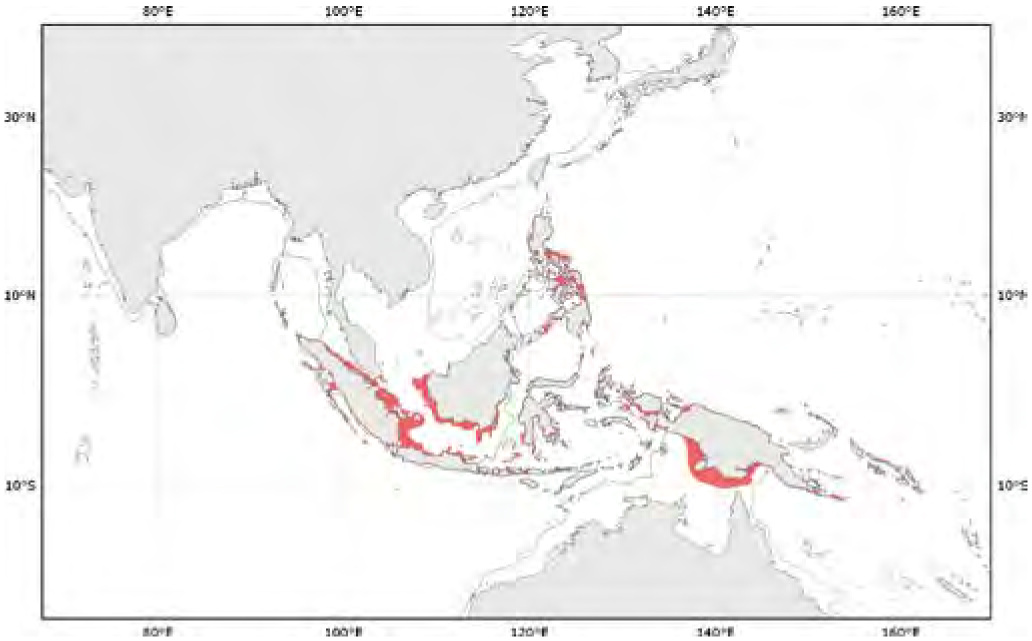


Fig. 140 ***Hapalochlaena lunulata***

🟥 Known distribution

Habitat and Biology: Depths range 0 to 20 m. A resident of coral reefs and rubble areas in shallow waters. The colour pattern potentially advertises strong toxicity. Hatchlings are planktonic. Tetrodotoxin is distributed throughout the body organs and skin of this species.

Interest to Fisheries: ***Hapalochlaena lunulata*** is collected at least in the Philippines for export in the aquarium trade.

Local Names: Unknown.

Remarks: Numerous undescribed species of blue-ringed octopus have been treated under this species name. No human fatalities have been linked specifically to this species but direct handling should be avoided.

Literature: Roper and Hochberg (1988), Cheng (1996), Norman and Sweeney (1997), Cheng and Caldwell (2000), Norman (2000), Williams and Caldwell (2009), Williams *et al.* (2011).

Hapalochlaena fasciata (Hoyle, 1886) **Fig. 141; Plate V, 35**

Octopus pictus var. *fasciata* Hoyle, 1886, *Report on the Scientific Results of the Voyage of the H.M.S. Challenger during the years 1873-76, Zoology,* 16(44): 94. [Type locality: Australia, New South Wales, Port Jackson, (33°50'S, 151°17'E)].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Blue-lined octopus; **Fr** — Poulpe aux lanières bleues; **Sp** — Pulpo rayas-azules.

Diagnostic Features: Small, muscular species. Arms short, 2 to 3 times mantle length. Lateral and ventral arms longest (typically 4=3=2>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 30% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 100 suckers on each normal arm. Enlarged suckers absent. Gills with 5 to 7 lamellae per demibranch. Funnel organ W-shaped. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, shorter than opposite arm. Ligula of moderate size, 7 to 12% of hectocotylized arm length. Calamus large. Hectocotylized arm with 32 to 43 suckers. Spermatophores undescribed. Eggs large, around 6 to 9 mm, around 12% of mantle length. **Colour: Cream to orange base colour with iridescent blue lines (not rings) on dorsal mantle and single or linked blue rings on arm crown and arms**. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin texture consists of small low papillae. Diamond of four short longitudinal ridges on dorsal mantle. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 45 mm; total length to around 150 mm.

Geographical Distribution: Subtropical waters of eastern Australia from southern Queensland to southern New South Wales (Fig. 142).

Habitat and Biology: Depth range from 0 to at least 20 m. Occurs on intertidal and shallow rocky reefs. Primarily active at night, feeding on small crustaceans. Females carry the eggs within the web. Hatchlings are benthic. Tetrodotoxin is distributed throughout the body organs and skin of this species.

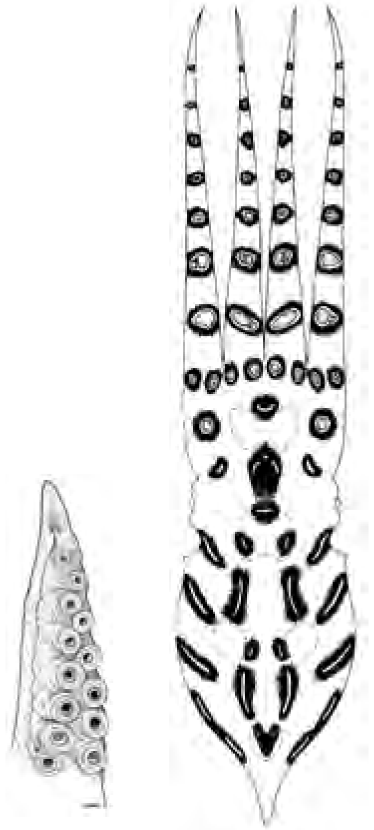

hectocotylus dorsal view

Fig. 141 *Hapalochlaena fasciata*

Interest to Fisheries: No fisheries value but extremely venomous, tetrodotoxin venom produced in the salivary glands. Responsible for at least one human death.

Local Names: Unknown.

Remarks: A related undescribed species with blue lines is also present in Japan.

Literature: Tranter and Augustin (1973), Stranks (1998), Williams and Caldwell (2009).

Fig. 142 *Hapalochlaena fasciata*

🟥 Known distribution

Hapalochlaena maculosa (Hoyle, 1883)

Fig. 143; Plate V, 37

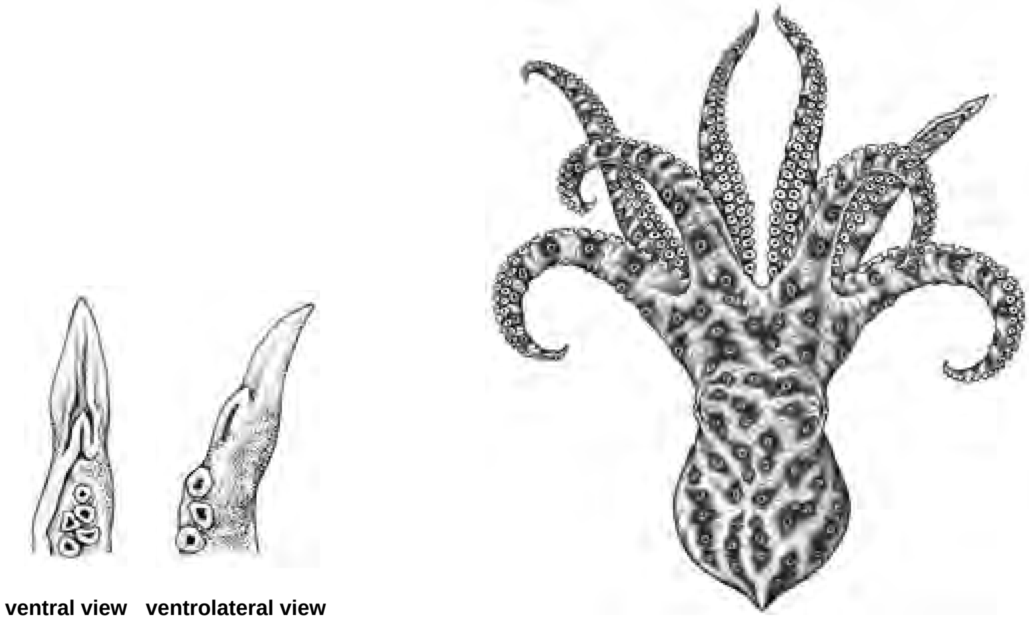
Octopus maculosus Hoyle, 1883, *Proceedings of the Royal Physical Society of Edinburgh*, 7: 319. [Type locality: "Australia"].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Southern blue-ringed octopus; **Fr** — Poulpe annelé méridional; **Sp** — Pulpo anillado austral.

Diagnostic Features: Small, muscular species. Arms short, length to 3 times mantle length. Lateral and ventral arms longest (typically 4=3=2>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20 to 30% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Web margins extend to arm tips.



ventral view **ventrolateral view**

hectocotylus

dorsal view

Fig. 143 *Hapalochlaena maculosa*

Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 90 suckers on each normal arm. Enlarged suckers absent. Gills with 6 to 7 lamellae per demibranch. Funnel organ W-shaped, outer limbs approximately 75% length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present in juveniles, reduced or absent in sub-adults and adults. Anal flaps present. Right third arm of males hectocotylized, length 75 to 85% of opposite arm length. Ligula of moderate size, 7 to 13% of arm length. Calamus large, 33 to 62% of ligula length. Hectocotylized arm with 45 to 56 suckers. Spermatophores of moderate size, around 43 to 118% of mantle length. Eggs large, around 7 to 9 mm, 25 to 30% of mantle length. **Colour: Dorsal and lateral surfaces with grey-green to cream base colour covered with approximately 50 to 60 small dark spots containing small iridescent blue rings (0.5 to 2.0 mm in diameter)**. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin has wrinkled texture containing small, closely-set, low papillae. Diamond of four short longitudinal ridges on dorsal mantle. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 57 mm; total length to around 220 mm.

Geographical Distribution: Southern Australia from eastern Victoria to southern Western Australia (Fig. 144).

Habitat and Biology: Depths range from 0 to over 50 m. This small octopus lives on intertidal and shallow subtidal reefs, seagrass meadows, and rubble areas. It emerges mainly at night to forage for small crustaceans and fishes. Females carry the eggs within the web. Hatchlings are benthic. Tetrodotoxin has been detected in the eggs, arms, abdomen and 'cephalothorax' of this species.

Interest to Fisheries: No fisheries value but extremely venomous; tetrodotoxin venom produced in the salivary glands has potential to cause human deaths.

Local Names: Unknown.

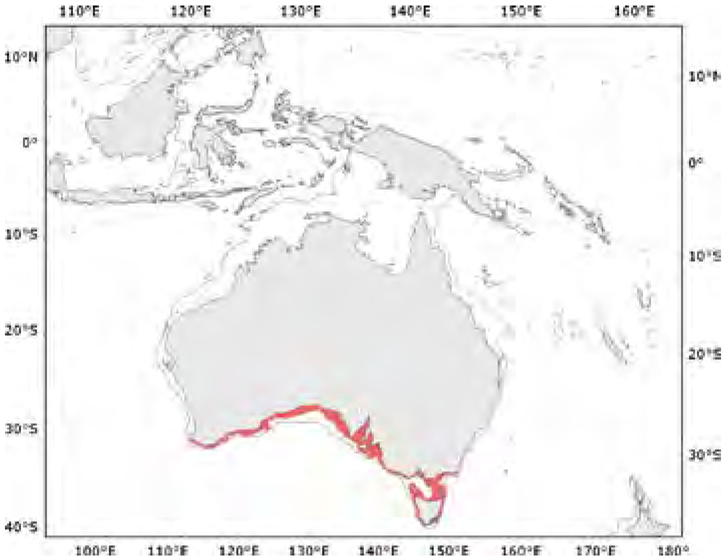


Fig. 144 ***Hapalochlaena maculosa***

🟥 Known distribution

Literature: Sheumack *et al.* (1984), Stranks (1998), Norman and Reid (2000), Yotsu-Yamashita (2007).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Hapalochlaena nierstraszi (Adam, 1938)

Octopus nierstraszi Adam, 1938, *Bulletin du Musee Royal d'Histoire Naturelle de Belqique*, 14(7), 14. [Type locality: Indian Ocean, North Andaman Islands, Aves Island].

Size: Mantle length 16 mm (female holotype).

Geographical Distribution: Known only from the type locality, Andaman Islands.

Habitat and Biology: Nothing known.

Literature: No additional literature.

Histoctopus Norman, Boucher-Rodoni and Hochberg, 2009

Histoctopus Norman, Boucher-Rodoni and Hochberg, 2009, *Journal of Molluscan Studies*, 75: 325.

Type Species: *Histoctopus zipkasae* Norman, Boucher-Rodoni and Hochberg, 2009.

Diagnostic Features: Small to moderate-sized deep-water species. Mantle muscular, globose to rounded ovoid. Stylets present, long, chitinous (mineralized). Arms muscular, medium length, 2.5 to 3.8 times mantle length. Arms approximately equal in length, lateral arms slightly longer (typically 2>3>4>1 or 3>2>4>1). Arm autotomy at distinct plane absent. **Webs moderate to deep, deepest around 20 to 30% of longest arm. Web sectors approximately equal in depth, slightly deeper on lateral arms (typically B=C=D>E>A). Web margins along ventral faces of all arms very wide, forming loose semi-transparent membranes in preserved material.** Interbrachial web pouches absent. Suckers in two rows. **Enlarged suckers present on all arms in mature males.** Funnel organ W-shaped. **Gills with 8 to 9 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Rachidian tooth with 2 to 3 lateral cusps in asymmetrical seriation. Posterior salivary glands moderate to large, approximately equal in length with buccal mass. Distinct crop present as side-branch off oesophagus. Ink sac and anal flaps present. Third right arm of male hectocotylized, length 75 to 85% of opposite arm length. Ligula of moderate size, 4.5 to 8% of hectocotylized arm length. Calamus large and pronounced, approximately 40 to 60% of ligula length. Terminal organ (penis) large and T-shaped with diverticulum longer than distal portion. Spermatophores large (equal to or longer than mantle length), bulbous with swollen short sperm reservoir containing few coils (<10) of sperm cord coiled in a double strand. Eggs (where known) of moderate size (6.5 to 8 mm, 7 to 9% of mantle length). Colour patterns orange brown dorsally, cream ventrally. **Transverse rows of small white papillae/leucophores visible in live animal and in some preserved material.** False eye-spots (ocelli) absent. Skin sculptured with evenly spaced small rounded papillae. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 107 mm; total length to 380 mm.

Geographical Distribution: Southwest Pacific Ocean (New Caledonia) and southeastern Indian Ocean (Western Australia).

Habitat and Biology: Collected from 350 to 550 m.

Remarks: Members of the genus ***Histoctopus*** share extreme web margin development with three other octopodid genera, ***Velodona*** Chun, 1915, ***Pteroctopus*** Fischer, 1882 and ***Graneledone*** Joubin, 1918.

Histoctopus zipkasae Norman, Boucher-Rodoni and Hochberg, 2009 **Fig. 145**

Histoctopus zipkasae Norman, Boucher-Rodoni and Hochberg, 2009, *Journal of Molluscan Studies*, 75: 329. [Type locality: Australia, Western Australia, North West Shelf, 18° 44’S 117° 00’E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Zippy’s octopus; **Fr** — Poulpe de Zippy; **Sp** — Pulpo de Zippy.

Diagnostic Features: Moderate-sized species. Arm length approximately 3 times mantle length (longest 2.4 to 3.7 x ML). Arms approximately equal in length, dorsal arms slightly shorter. Web sectors very thin and membranous, deep, up to 30% of longest arm length. Webs approximately equal in depth; lateral webs slightly deeper. **Webs extend as membranous flared margins along entire length of arms, very well developed towards arm tips**. Suckers in two rows. Sucker counts to around 168 on normal arms. Large W-shaped funnel organ. Gill count 9 lamellae per demibranch. Ink sac and anal flaps present. Third right arm hectocotylized. Ligula small to moderate size (length 4.5 to 6.2% of arm length), spoon-shaped with robust rims and wide, open groove; floor with around 10 to 12 simple transverse creases. Calamus large and robust, 34.7 to 59.7% of ligula length. Hectocotylized arm with 66 to 68 suckers; **2 to 3 slightly to moderately enlarged and flattened suckers present on all arms of mature males, diameter up to 15% of ML at level of seventh to thirteenth proximal sucker**. Spermatophores large (0.9 to 1.1% ML) and produced in low numbers (3 to 8). Distal oviducts thickened along length. Eggs of moderate size (6.5 to 7.8 mm, 7.2 to 9.1% ML). **Colour**: Pink orange dorsally, cream ventrally. Orange brown basal colour on first three arm pairs. **Two transverse rows of small white spots on dorsal mantle. Regularly spaced white spots present along aboral midline of first three arm pairs**. **Sculpture:** Skin scattered with regular, small, round papillae over all dorsal surfaces. Larger supraocular papillae absent. Lateral mantle ridge absent.

Size: Mantle length to 107 mm; total length to 380 mm.

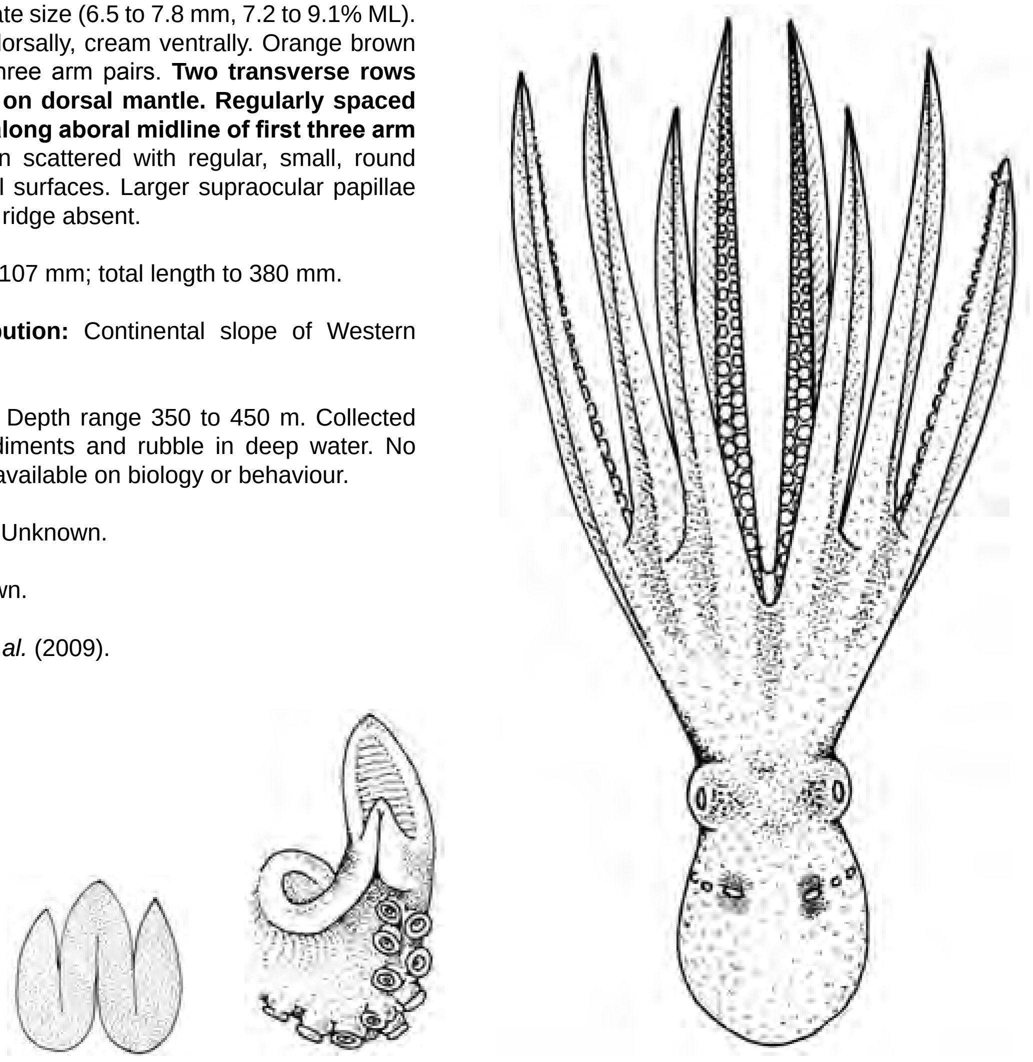
Geographical Distribution: Continental slope of Western Australia (Fig. 146).

Habitat and Biology: Depth range 350 to 450 m. Collected by trawl from soft sediments and rubble in deep water. No additional information available on biology or behaviour.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Norman *et al.* (2009).



funnel organ **hectocotylus** **dorsal view**

Fig. 145 ***Histoctopus zipkasae***

Fig. 146 ***Histoctopus zipkasae***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Histoctopus discus Norman, Boucher-Rodoni and Hochberg, 2009

Histoctopus discus Norman, Boucher-Rodoni and Hochberg, 2009, *Journal of Molluscan Studies*, 75: 326. [Type locality: South of New Caledonia, Norfolk Ridge, Sponge Bank].

Size: Mantle length to 51 mm; total length to 238 mm.

Geographical Distribution: Known only from the type locality.

Habitat and Biology: Available material captured from 500-545 m.

Literature: No additional literature.

Macrochlaena Robson, 1929

Macrochlaena Robson, 1929a, *A Monograph of the Recent Cephalopoda, Part I. Octopodinae,* London, British Museum (Natural History): 193.

Type Species: *Octopus winckworthi* Robson, 1926.

Diagnostic Features: Small, squat, fleshy species. Eyes small; head relatively flush with spherical mantle. Stylets unknown. **Arms short, around 1.5 to 2.5 times mantle length. Arms subequal in length, lateral arms slightly longer.** Arm autotomy at distinct plane absent. Webs deep, approximately one third of arm length. Webs subequal in length; lateral webs slightly deeper. Interbrachial web pouches absent. Suckers in two rows. Enlarged suckers absent. **Funnel organ UU-shaped. Gills with 8 to 10 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Details of digestive tract unknown. Ink sac present, small. Third right arm of males hectocotylized, shorter than opposite arm (~80%). Simple, short, conical ligula (~6% of arm length) with open groove and ~8 weak transverse ridges, calamus poorly developed. Spermatophores small, length approximately 30% of mantle length. Eggs large. Colour pattern red-brown to purple with darker mottling giving marbled effect. Skin relatively smooth. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 33 mm; total length to at least 93 mm.

Geographical Distribution: From off India and into eastern Indian Ocean.

Habitat and Biology: Unknown. One record from relatively shallow oyster beds.

Remarks: Single, poorly known species. Characters that clearly distinguish this genus from ***Octopus*** *sensu stricto* include the short, subequal arms, small eyes but broad head, small suckers without enlargement in either sex, UU funnel organ with short outer limbs, reduced ink sac and smooth skin. This genus (and species) is in need of revision.

Macrochlaena winckworthi (Robson, 1926)

Fig. 147

Octopus winckworthi Robson, 1926, *Annals and Magazine of Natural History*, series 9, 17: 161. [Type locality: South India, Tuticorin].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Winckworth's octopus; **Fr** — Poulpe de Winckworth; **Sp** — Pulpo de Winckworth.

Diagnostic Features: Small, squat, fleshy species. **Eyes small, head relatively flush with mantle. Arms short, around 1.5 to 2.5 times mantle length. Subequal in length**, lateral arms slightly longer. Arm autotomy at distinct plane absent. **Webs deep, approximately one third of arm length**. Webs subequal in length; lateral webs slightly deeper. Interbrachial web pouches absent. **Suckers in two rows, small: 3.6 to 6.9% of mantle length. None enlarged in either sex**. Around 65 suckers on normal arms. **UU funnel organ**. Gills with 8 to 10 lamellae per demibranch. Radula with 9 elements, 7 teeth rows and marginal plates. Rachidian tooth with single lateral cusp in symmetrical seriation. Ink sac present, small. Third right arm of males hectocotylized, shorter than opposite arm (~80%). Simple, short, conical ligula (~6% of arm length) with open groove and ~8 weak transverse ridges, calamus poorly developed. Hectocotylized arm with 36 to 40 suckers. Terminal organ linear with simple, slightly swollen diverticulum. Spermatophores small, 8 to 10 mm, approximately 30% of mantle length. **Colour:** Red-brown to purple with darker mottling giving marbled effect. **Sculpture:** Skin relatively smooth,

Size: Mantle length to 33 mm; total length to at least 93 mm.

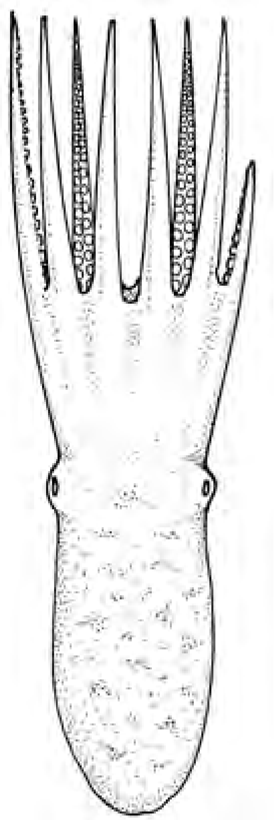


Fig. 147 ***Macrochlaena winckworthi***

Geographical Distribution: Off Thoothukudi, southern India, potentially east to Java, Indonesia (Fig. 148).

Fig. 148 ***Macrochlaena winckworthi***

🟥 Known distribution

Habitat and Biology: Depth range unknown; type specimen presumed to be from shallow oyster beds (~20 m). Biology and behaviour unknown.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Robson (1929a), Toll (1998).

Macrotritopus Grimpe, 1922

Macrotritopus Grimpe, 1922, *Sitzungsberichte der Naturforschenden Gesellschaft zu Leipzig*, 45: 41.

Type Species: *Octopus gracilis* Vérany, 1851 [= *M. equivocus* (Robson, 1929a)].

Diagnostic Features: Small to medium-sized, elongate, shallow-water species. Mantle elongate-ovoid in shape. Stylets present, non-mineralized. **Arms long and slender, length around 4 to 7 times mantle length. Third arms distinctly longer than other arms, dorsal arms always shortest (3.4.2.1).** Arm autotomy at distinct plane present. **Webs shallow and thin, deepest around 7 to 11% of longest arm.** Webs deepest on lateral arms; webs between dorsal arms shallowest (typically C>D>B>E>A). Interbrachial water pore system absent. Suckers in two rows. Enlarged suckers absent. Funnel organ W-shaped. **Gills with around 11 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands moderate, slightly larger than buccal mass length. Crop diverticulum present as side-branch off oesophagus. Ink sac present. Anal flaps present. Third right arm of male hectocotylized. Ligula and calamus present. Spermatophores unarmed. Eggs small, laid in festoons. Base colour of animal cream-brown with a loose net-like pattern of darker brown narrow lines on dorsal mantle and regular narrow dark brown bands along arms. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). False eye-spots (ocelli) absent. **Skin with low rugose sculpture with scattered, moderate-size papillae.** Patch and groove skin sculpture absent. Small papillae over eyes. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 55 mm.

Geographical Distribution: Unclear, at least Mediterranean Sea and Atlantic Ocean. Potential members of this genus also are present in the tropical Indo-West Pacific Ocean.

Habitat and Biology: Poorly known with some species occurring on soft sediment substrates. Reported from 0 to 200 m.

Remarks: This genus is in need of revision. Currently, it contains one described species, ***Macrotritopus defilippi***, two poorly described unresolved species known only from planktonic hatchlings (***M. equivocus*** and ***M. scorpio***), and potentially three undescribed Indo-Pacific species (Norman and Hochberg unpubl. data), including **'*Octopus*** sp. 17' of Norman (2000) from Australia. ***Macrotritopus*** was originally described from a single juvenile specimen (***M. equivocus***) with elongate third arms. This form of paralarva gained the name "***Macrotritopus*** larva" and was identified incorrectly as the hatchlings of ***Scaeurgus unicirrhus*** (see Hochberg *et al.,* 1992). Captive rearing of ***M. defilippi*** eggs hatched into this distinctive larval type (see Hanlon *et al.,* 1985), thus connecting the juveniles with adult forms. As the type species is juvenile, ***M. defillipi*** is presented here as representative of this genus. "***Macrotritopus*** larvae" also have been identified off South Africa and the Indo-West Pacific from Hawaii to Australia (Hochberg *et al.,* 1992), suggesting that there may be a suite of undescribed species within this poorly known genus.

Literature: Hanlon *et al.* (1985), Hochberg *et al.* (1992).

Macrotritopus defilippi (Verany, 1851)

Fig. 149

Octopus defilippi Verany, 1851, *Mollusques Méditeranéens Observés, Décrits Figurés et Chromolithographiés d'après le Vivant Ouvrage Dedie à SM le Roi Charles Albert*, 1: 30. [Type locality: Western Mediterranean Sea, Italy].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Lilliput longarm octopus; **Fr** — Poulpe à longs bras; **Sp** — Pulpito patilargo.

Diagnostic Features: Small to medium-sized species. Mantle small in relation to total length, elongate or pear-shaped, widest in posterior third and ending in a small point. Head narrower than mantle. **Eyes prominent, projecting. Arms long, slender, with delicate tips, tending to autotomize at level of 10 to 11th proximal sucker. Third arms distinctly longer than other arms, typically 3>2>4>1 or 3>4>2>1**. Webs shallow, depth 7 to 11% of length of longest arm, extend as narrow web margin to middle of arms along ventral edge, especially on lateral arms. Lateral webs deepest, typically C>D>B>E>A. Interbrachial web pouches absent. Suckers in two rows, widely set, of medium size. Enlarged suckers absent in both sexes. Funnel organ W-shaped, slender, posterior angles rounded, lateral limbs shorter than medial limbs. Gills with 11 to 12 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands moderate, slightly larger than buccal mass length. Crop diverticulum present as side-branch off oesophagus. Ink sac present. Anal flaps present. Third right arm of male hectocotylized, **significantly shorter than opposite arm** (35 to 67%), bearing 60 to 100 suckers. Ligula minute (0.5 to 3% of hectocotylized

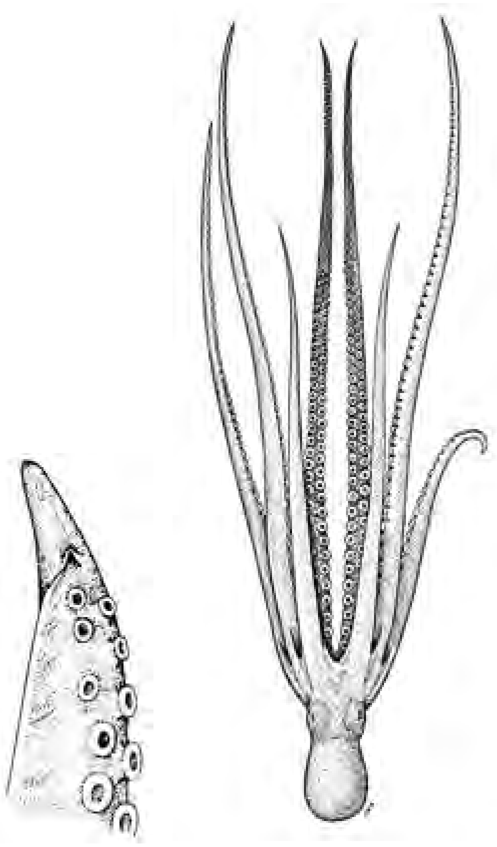

hectocotylus dorsal view

Fig. 149 *Macrotritopus defilippi*

arm length), well differentiated with blunt tip and fine cross striations. Calamus small to moderate size, around 15 to 40% of ligula length. Hectocotylized arm with 60 to 100 suckers. Spermatophores small, around 30 to 50% of mantle length. Mature eggs small, around 2 mm long. **Colour:** In life brown yellow, grey brown, or red brown with dark transverse arm bars and heart-shaped pattern on dorsal mantle, often with greenish iridescence, especially around eyes. Darker markings form an irregular netlike pattern on the dorsal mantle. False eye-spots (ocelli) absent. **Sculpture:** Skin soft, relatively smooth and loose. Papillae transient except over eyes. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 55 mm.

Geographical Distribution: Mediterranean Sea and northeastern Atlantic Ocean (Fig. 150).

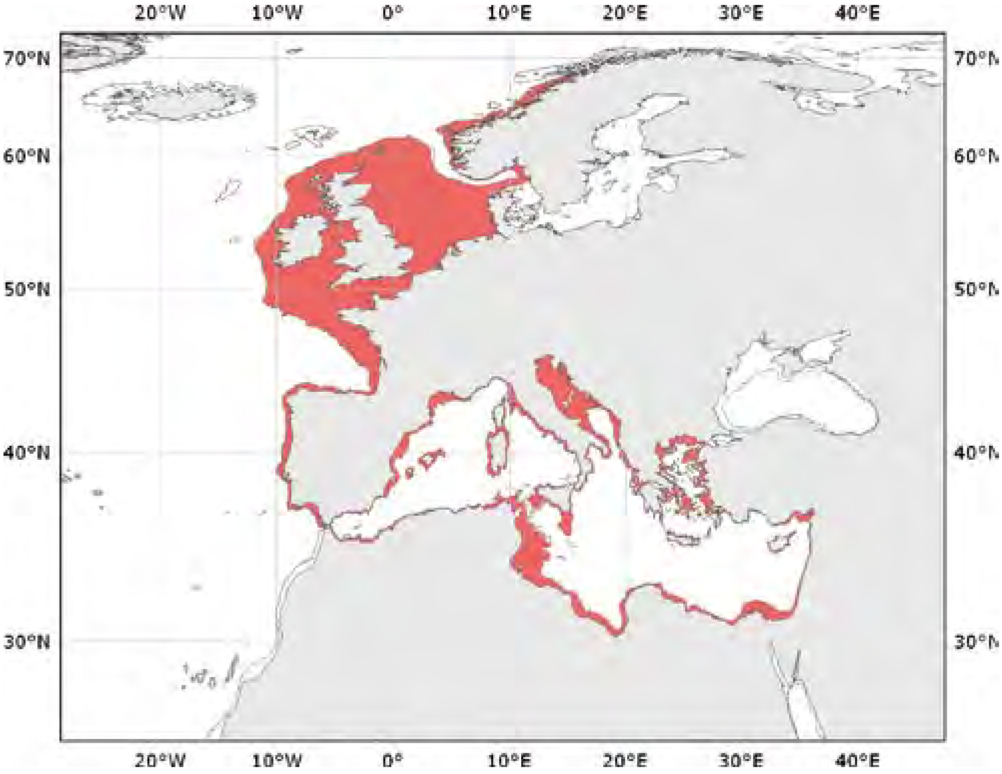


Fig. 150 ***Macrotritopus defilippi***

🟥 Known distribution

Habitat and Biology: Depth range to 200 m. A shallow-water species that occurs on sandy and muddy substrates of the continental shelf. Little is known of the biology and behaviour.

Interest to Fisheries: Unknown.

Local Names: ITALY: Polpetto braccialunghe.

Remarks: Unresolved species are treated under the same name in the western Atlantic (Voss, 1964; Hanlon *et al.* 2010).

Literature: Naef (1923), Voss (1964, western Atlantic form), Mangold (1998), Norman (2000), Rosa *et al.* (2004), Hanlon *et al.* (2010; western Atlantic form), Krustulović Šifner *et al.* (2011, as ***O. defilippi***).

Megaleledone Taki, 1961

Megaleledone Taki, 1961, *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University*, 3(2): 297.

Type Species: *Megaleledone senoi* Taki, 1961 [=*M. setebos* (Robson, 1932)].

Diagnostic Features: Large, semi-gelatinous species. Mantle ovoid to slightly flattened dorso-ventrally. Stylets present, non-mineralized. **Arms robust and of moderate length (2 to 3 times mantle length).** Arm autotomy at set level absent. **Web deep, well developed (40 to 60% length of longest arm).** Web deepest on lateral arms; web sectors of dorsal and ventral arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. **Suckers in single row,** small to medium in size (6 to 12% of mantle length). Enlarged suckers absent. Funnel organ V V-shaped. **Gills with 10 to 13 lamellae per demibranch.** Radula composed of 7 elements, 7 teeth per transverse row but marginal plates absent. Rachidian tooth without lateral cusps. Posterior salivary glands medium sized (70 to 80% length of buccal mass). Oesophagus with swelling only, no distinct crop. **Ink sac present.** Ink duct opens to exterior anterior to anus. Anal flaps absent. Third right arm of males hectocotylized, slightly shorter than opposite arm. Ligula and calamus present. Ligula small to medium (3 to 6% of arm length). Calamus large, 30 to 50% of ligula length. Arm tips not otherwise modified. Spermatophores short to moderate length (40 to 60% of mantle length), slender. Eggs large. Colour uniform cream-pink to grey-pink, sometimes mottled with red-pink patches. **Skin soft, loose and semi-gelatinous. Skin ridge around lateral margin of mantle present.**

Size: Mantle length to 280 mm; total length to around 900 mm.

Geographical Distribution: Circumpolar Antarctica, but does not extend to sub-Antarctic islands.

Habitat and Biology: Poorly known. Collected from 32 to 850 m.

Remarks: Single Antarctic species. Allcock *et al.* (2003b) synonymised ***Megaleledone senoi*** with ***M. setebos*** and redescribed the genus.

Literature: Allcock *et al.* (2003b).

Megaleledone setebos (Robson, 1932)

Fig. 151; Plate V, 38

Graneledone setebos Robson, 1932, *A Monograph of the Recent Cephalopoda. Part II. Octopoda.* London, British Museum (Natural History): 313. [Type locality: Antarctica, Maud Land, off Dronning].

Frequent Synonyms: *Megaleledone senoi* (Taki, 1961).

Misidentifications: None.

FAO Names: En — Giant Antarctic octopus; **Fr** — Poulpe géant antarctique; **Sp** — Pulpo gigante antártico.

Diagnostic Features: Large, muscular species with loose skin. Arms short, 2 to 3 times mantle length. Arms of similar length; dorsal pair slightly shorter (typically 4=3=2>1). Arm autotomy at distinct plane absent. **Webs deep, deepest over 40% of arm length**. Web deepest on lateral arms; web sectors of dorsal and ventral arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. **One row of suckers on each arm**. In larger animals, around 40 to 69 suckers on each normal arm. Enlarged suckers absent. Gills with 10 to 13 lamellae per demibranch. Funnel organ V V-shaped, thick limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. **Oesophagus with swelling only, no distinct crop. Ink sac present. Ink duct opens to exterior anterior to anus. Anal flaps absent**.
Right third arm of males hectocotylized, length 90 to 95% of opposite arm. Ligula small, 3 to 4% of arm length. Calamus of moderate size, around 40% of ligula length. Hectocotylized arm with 35 to 40 suckers. Spermatophores

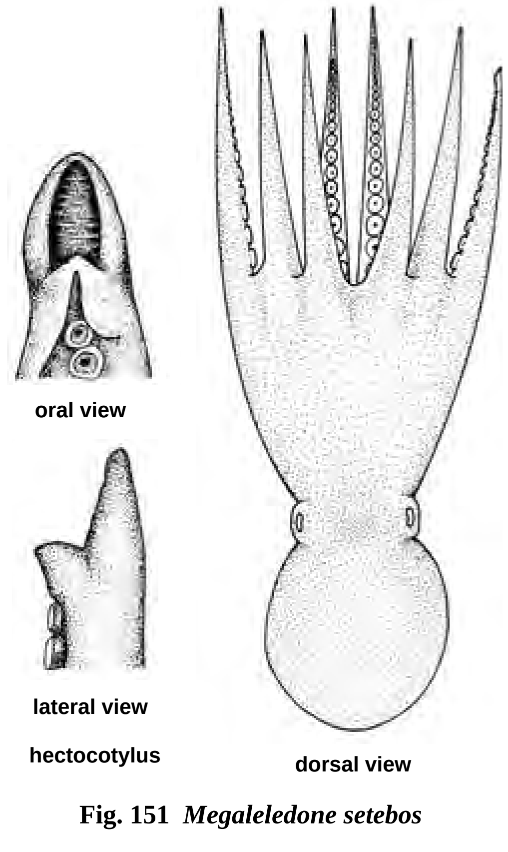


Fig. 151 ***Megaleledone setebos***

large, 150 to 235 mm, around 80 to 95% of mantle length. Eggs large, up to 42 mm, 15 to 22% of mantle length. **Colour: Upper surfaces cream-pink to grey-pink mottled with red-pink patches.** Ventral surfaces cream. False-eye spots (ocelli) absent. **Sculpture:** Skin loose with fine, rounded and widely spaced papillae on dorsal surfaces. **No large papillae over eyes. Skin ridge present around lateral margin of mantle**.

Size: Mantle length to 280 mm; total length to around 900 mm.

Geographical Distribution: Circumpolar Antarctica; does not extend to sub-Antarctic islands (Fig. 152).

Habitat and Biology: Depth range from 32 to 850 m. Collected from continental shelf at temperatures of -1.4° to -1.9°C. Found on mud and sand substrates with pebbles and rocks, and among sponges and bryozoans.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Bresciani and Lützen (1994; as *Megaleledone senoi*), Kubodera and Okutani (1986, 1994; as *M. senoi*), Lu and Stranks (1994), Zielinski and Sartoris (2001), Allcock *et al.* (2003b), Barratt and Allcock (2010), Undheim *et al.* (2010a).

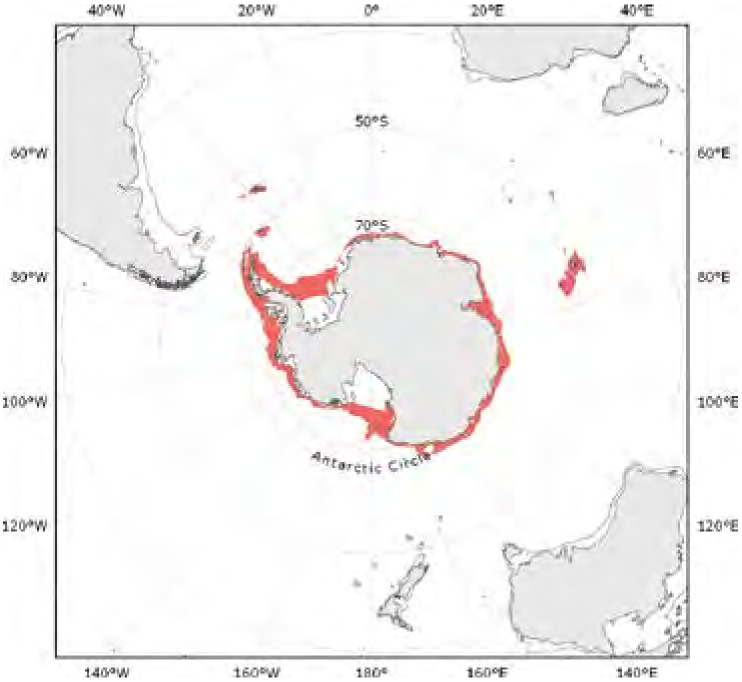


Fig. 152 ***Megaleledone setebos***

🟥 Known distribution

Microeledone Norman, Hochberg and Boucher-Rodoni, 2004

Microeledone Norman, Hochberg and Boucher-Rodoni, 2004b, *Molluscan Research*, 24: 194.

Type Species: *Microeledone mangoldae* Norman, Hochberg and Boucher-Rodoni, 2004.

Diagnostic Features: Small, robust, deep-water species. Mantle muscular, roughly spherical. **Eyes large.** Stylets long, chitinous (non-mineralized). **Arms robust, very short, longest 1.3 times mantle length.** Arms subequal in length. Arm autotomy at distinct plane absent. Webs deep, deepest >40% length of longest arm. Interbrachial web pouches absent. Suckers in single row. Suckers normal, functional to tips of all arms. Enlarged suckers absent. Funnel organ UU-shaped, limbs of equal length with sharp tips. **Gills with 4-5 (typically 5) lamellae per demibranch.** Radula with 7 elements, 7 rows of teeth, marginal plates absent. **Rachidian teeth broad-based with elongate anteriorly curved and sickle-shaped mesocone with grooved anterior face. Other teeth flattened and blade-like, without obvious sharp cusps.** Posterior salivary glands large, length similar to buccal mass. Oesophagus with swelling only, no distinct crop. Ink sac and anal flaps absent. Right third arm hectocotylized, slightly shorter than opposite arm. Copulatory organ with distinct ligula and large calamus. Spermatophores unknown. Females unknown. **Colour uniform pink-cream. Proximal third of oral surface of arms and webs dark maroon.** Functional chromatophores absent. **Skin smooth; papillae absent.** Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 18 mm; total length to around 46 mm.

Geographical Distribution: Southwest Pacific Ocean, Coral Sea.

Habitat and Biology: Unknown.

Remarks: Known only from a single well-preserved male.

Literature: Norman *et al.* (2004b).

_**Microeledone mangoldae**_* Norman, Hochberg and Boucher-Rodoni, 2004

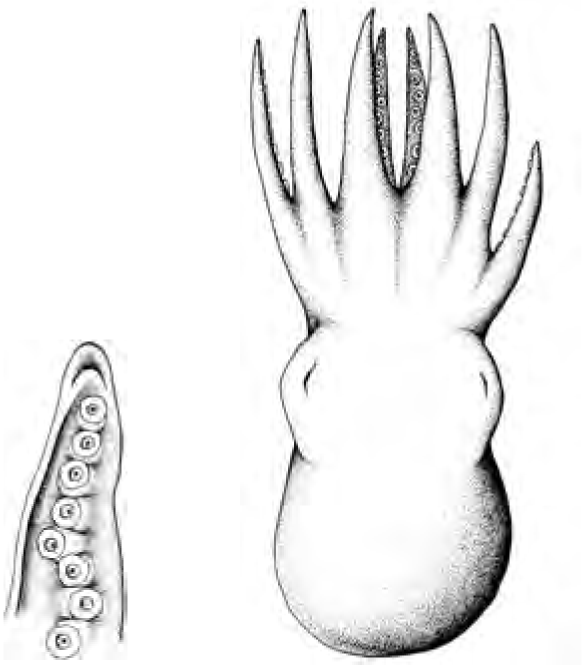
Fig. 153

Microeledone mangoldi Norman, Hochberg and Boucher-Rodoni, 2004b, *Molluscan Research*, 24: 194. [Type locality: Southwestern Pacific Ocean, Coral Sea, Norfolk Ridge (23°23'S, 167°52'E)].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Sickletooth pygmy octopus; **Fr** — Poulpe pygmée de Mangold; **Sp** — Pulpo pigmeo de Mangold.



hectocotylus dorsal view

Fig. 153 *Microeledone mangoldae*

Diagnostic Features: Small muscular species with loose skin. Arms short, ~1.3 times mantle length. Arms of similar length. Arm autotomy at distinct plane absent. **Webs deep, deepest over 40% of arm length**. Webs approximately equal in depth, ventral sector slightly shallower. Web margins absent. Interbrachial web pouches absent. **One row of suckers on each arm**. In single known animal (male), 31 to 32 suckers on normal arms. Enlarged suckers absent. Gills with 4 to 5 lamellae per demibranch. **Funnel organ UU-shaped, limbs of approximately equal length**. Radula with 7 elements, 7 rows of teeth, marginal plates absent. **Central rachidian tooth wide with elongate, flattened and curved central cone, lateral cusps absent. Other teeth flattened and blade-like. Oesophagus with swelling only, no distinct crop. Ink sac and anal flaps absent.** Right third arm of males hectocotylized, length ~95% of opposite arm length. Ligula of moderate size, 7.6% of arm length in single male. Calamus large, around 45% of ligula length. Hectocotylized arm with 22 suckers. Spermatophores and eggs unknown. **Colour: Surfaces of mantle, arm crown and aboral surfaces of arms pink cream**. Chromatophores absent. Oral surface of web dark maroon for proximal third of arms. False-eye spots (ocelli) absent. **Sculpture:** Skin loose and smooth. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 18 mm; total length to around 46 mm.

Geographical Distribution: Known only from type locality (Fig. 154).

Habitat and Biology: Depth of type specimen 980 to 1 000 m. Collected from bathyal plain. Stomach contained remains of polychaete worm. Presence of *Aggregata* parasites suggest crustaceans also are included in diet. Pigmented intestine suggests consumption of luminescent prey.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Remarks: *The original description coined the Latin ending of the species name incorrectly for the gender. As the species was named in honour of Dr. Katharina Mangold, the epithet should be 'ae' not 'i' and is corrected here.

Literature: Norman *et al.* (2004b as *Microeledone mangoldi*).

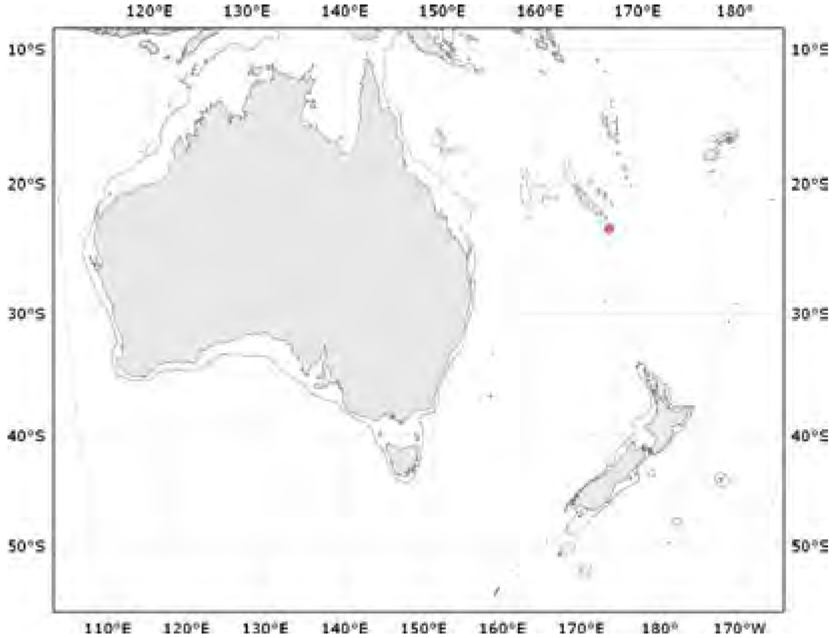


Fig. 154 *Microeledone mangoldae*

🟥 Known distribution

Muusoctopus Gleadall, 2004

Muusoctopus Gleadall, 2004, *Interdisciplinary Information Sciences*, 10(2): 105.

Type Species: *Octopus januarii* Hoyle, 1885

Diagnostic Features: Medium-sized to large species. Mantle globose to ovoid; head broad; eyes relatively large. Stylets present, non-mineralized. **Arms moderately long, slender, cylindrical, (3 to 4 times mantle length); arms subequal or 1 and 2 longer than arms 3 and 4.** Arm autotomy absent. Suckers in 2, moderately spaced rows. **Enlarged suckers absent.** Web of moderate, subequal depth, slightly shallower between arms 3 and 4. Interbrachial web pouches absent. Third right arm hectocotylized; **ligula slender, conical shape; calamus of modest size or reduced; sculpting of oral surface of ligula weak or absent.** Terminal organ relatively large; with 2 chambers. Funnel moderately large, free for half its length. Funnel organ typically W-shaped. Ink sac and anal flaps absent or present. **Gills with 7 to 10 lamellae per demibranch.** Radula with well defined pentacuspid rachidian. Posterior salivary glands of modest size, smaller than buccal mass; flattened, triangular, to discoid. Crop diverticulum present. Skin without well defined patch and groove system.

Size: Mantle length of females to 170 mm; males to 140 mm; total length to 770 mm.

Geographical Distribution: West and southwest Atlantic Ocean and southeast Pacific Ocean.

Habitat and Biology: Typically soft sediment substrates at depths from 30 to 1 000 m.

Remarks: Gleadall (2004) coined the genus ***Muusoctopus*** to contain the species ***januarii***. Subsequently Gleadall *et al.* (2010) described several additional species that were placed in this genus, as well as ***eureka*** and ***longibrachus***, which had originally been treated under the genus name ***Benthoctopus*** (see Toll, 1981; Ibáñez *et al.,* 2006). In the absence of comparative material and tissue samples for molecular analyses, Strugnell *et al.* (2009c, 2011) treated the genus ***Muusoctopus*** as unresolved. A number of complex internal characters are used to diagnose this genus; they require dissection and critical examination to identify specimens to species (see Gleadall, 2004 and Gleadall *et al.,* 2010). A broad-scale morphological and molecular revision of all taxa currently or historically treated under the genus ***Benthoctopus*** is urgently required. For this volume, we treat the genus ***Muusoctopus*** as valid and as containing four species.

Literature: Strugnell *et al.* (2009c, 2011), Gleadall *et al.* (2010).

Muusoctopus januarii (Hoyle, 1885)

Fig. 155

Octopus januarii Hoyle, 1885, *Annals and Magazine of Natural History,* series 5, 15: 229 (in part). [Type locality: Southwestern Atlantic Ocean, Brazil, off Barra (09°05’S, 34°50’W)].

Frequent Synonyms: *Benthoctopus januarii.*

Misidentifications: None.

FAO Names: En — January octopus; **Fr** — Poulpe filamenteux; **Sp** — Pulpo filamentoso.

Diagnostic Features: Medium-sized species. Mantle globose, aperture wide. Eyes large. Funnel robust, tapered, free for half its length; funnel organ not described. Gills with 7 to 8 lamellae per demibranch. Arms long and slender, cylindrical in cross-section; arm length 3-4 times mantle length, in the order **1=2>3=4; arms 1 and 2 markedly longer than 3 and 4**. Webs subequal, slightly shorter in sectors D and E. Suckers small, with small infundibulum, in two moderately spaced rows directly from mouth. **Enlarged suckers absent**. Hectocotylized third right arm two-thirds the length of third left arm, bearing approximately 80 suckers. Longest unmodified arms with sucker count of approximately 180. **Ligula modest in size (approx. 8% length of third right arm)**, with distinct margin surrounding wide, flat, shallow inner surface, tapering evenly to an acute point; approximately 20 weakly developed transverse ridges within ligula groove; calamus well defined, sharply pointed. Spermatophoric groove well developed. Terminal organ large, spermatophoric duct joining close to anterior, turning in posterior direction as it joins. Spermatophores in spermatophore sac 10 to 15, slim, approximately 85 mm in length. **Eggs large, capsule length to 14 mm**. **Colour:** In ethanol uniform pinkish grey, slightly paler beneath. Some specimens show evidence of approximately 9 rows of short, thin, straight dark lines arranged longitudinally on the dorsal mantle.

Size: Mantle length to 65 mm; total length to 465 mm.

Geographical Distribution: West Atlantic, from Gulf of Mexico to mid-coast of Brazil (Fig. 156).

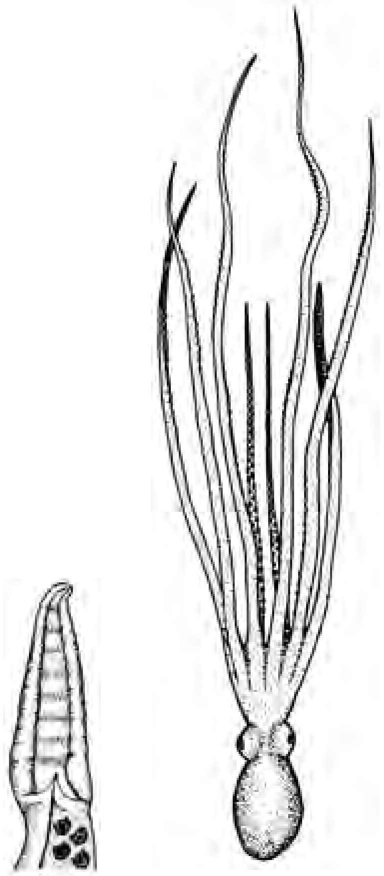

hectocotylus dorsal view

Fig. 155 ***Muusoctopus januarii***

Fig. 156 ***Muusoctopus januarii***

🟥 Known distribution

Habitat and Biology: Depth range from 350 to 750 m.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Toll (1981), Nesis (1987), Gleadall (2004), Strugnell *et al.* (2011).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Muusoctopus bizikovi Gleadall, Guerro-Kommritz, Hochberg and Laptikhovsky, 2010

Muusoctopus bizikovi Gleadall, Guerro-Kommritz, Hochberg and Laptikhovsky, 2010, *Zoological Science*, 27: 543. [Type locality: Southwestern Atlantic Ocean, approx. 240 km directly north of West Falkland Island (48°43.6'S, 59°48'W)].

Size: Mantle length to about 60 mm.

Geographical Distribution: Southwest Atlantic, restricted to the southeastern continental shelf of South America that extends around the Falkland Islands.

Habitat and Biology: Depths range from 467 to 796 m.

Remarks: An ink sac is reported to be present unlike other members of the genus (Gleadall *et al.,* 2010).

Literature: No additional literature.

Muusoctopus eureka (Robson, 1929)

Enteroctopus eureka Robson, 1929a, *A Monograph of the Recent Cephalopoda. Part I: Octopodinae:* 179. [Lectotype locality: Southwestern Atlantic Ocean, Falkland Islands, shore, 51°49'S, 57°51'W].

Size: Mantle length of females to 110 mm, males to 80 mm; total length to 300 mm.

Geographical Distribution: Southwest Atlantic, northern Argentina to Falkland Islands.

Habitat and Biology: Depth range from 30 to 500 m.

Remarks: *Octopus hyadesi* Rochebrune and Mabille, 1889 and ***Benthoctopus magellanicus*** Robson, 1930 are treated as synonyms by Gleadall *et al.* (2010), see also Robson (1930).

Literature: Robson (1932), Nesis (1987), Laptikhovsky (2001), Gleadall *et al.* (2010), Guerra *et al.* (2011).

Muusoctopus longibrachus akambei Gleadall, Guerro-Kommritz, Hochberg and Laptikhovsky, 2010

Muusoctopus longibrachus akambei Gleadall, Guerro-Kommritz, Hochberg and Laptikhovsky, 2010, *Zoological Science*, 27: 538. [Type locality: Southwestern Atlantic Ocean, off Argentina, Bahia San Julian (49°22'S, 66°07'W)].

Size: Mantle length of females to 170 mm; males to 100 mm.

Geographical Distribution: Southwest Atlantic, Argentina.

Habitat and Biology: Depth range from 147 to 377 m.

Literature: No additional literature.

Muusoctopus longibrachus longibrachus (Ibáñez, Sepúlveda and Chong, 2006)

Benthoctopus longibrachus Ibáñez, Sepúlveda and Chong, 2006, *Proceedings of the Biological Society of Washington,* 119(3): 356. [Type locality: Southeastern Pacific Ocean, Chile, off coast of Constitucion, 35°20'S 73°00'W].

Size: Mantle length of females to 170 mm; males to 140 mm; total length to 770 mm.

Geographical Distribution: Southeast Pacific, coast of Chile and Juan Fernández Archipelago.

Habitat and Biology: Depth range from 436 to 1 000 m.

Literature: Gleadall *et al.* (2010).

Pareledone Robson, 1932

Pareledone Robson, 1932, *A Monograph of the Recent Cephalopoda, II: The Octopoda:* 270.

Type Species: *Eledone charcoti* Joubin 1905.

Diagnostic Features: Small to moderate-sized, muscular Antarctic octopuses. Mantle round to ovoid. Stylets present, non-mineralized. **Arms short to moderate length, 1.3 to 3 times mantle length. Arms of similar length, ventral arms slightly shorter in some species.** Arm autotomy at distinct plane absent. **Webs well developed, up to 50% of arm length in some species. Webs subequal in depth.** Interbrachial web pouches absent. **Suckers in single row.** Enlarged suckers absent. Funnel organ V V- or W-shaped (depending on species). Gills with 6 to 11 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands of moderate size, approximately equal to length of buccal mass. Distinct crop present as side-branch off oesophagus. Ink sac present or absent (absent in ***Pareledone panchroma***). Anal flaps present or absent (absent in ***P. panchroma***). Third right arm of males hectocotylized with copulatory organ clearly differentiated into ligula and calamus. Ligula groove shallow and without marked transverse ridges. Spermatophores long (1 to 2 times mantle length), unarmed. Eggs large. Colour pattern variable between species, base colour typically cream, pink or orange-brown. White leucophore markings present in many species. Skin smooth to papillate. Papillate species with even covering of regular small papillae patches. **Skin ridge around lateral margin of mantle present.**

Size: Mantle length to 100 mm; total length to 350 mm.

Geographical Distribution: Antarctic and Southern Ocean waters.

Habitat and Biology: At depths between 0 and 4 000 m.

Remarks: This genus contains 20 or more Antarctic species. Allcock *et al.* (2003b) and Allcock (2005) reviewed this genus, describing many new species.

Literature: Allcock and Piertney (2002), Allcock *et al.* (2001, 2003b, 2011), Allcock (2005), Galarza-Munoz *et al.* (2011).

Pareledone charcoti (Joubin, 1905)

Fig. 157; Plate VIII, 64

Eledone charcoti Joubin, 1905, *Mémoires de la Société Zoologique de France*, 18: 22. [Type locality: Antarctica, 65°S, 64°W].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Charcot's octopus; **Fr** — Poulpe de Charcot; **Sp** — Pulpo de Charcot.

Diagnostic Features: Moderate-sized, robust species. **Arms short, 1.5 to 2.3 times mantle length**. Arms of similar length, dorsal arms shortest (typically 4>3>2>1). Arm autotomy at distinct plane absent. **Webs deep, deepest to 45% of arm length.** Web deepest on lateral arms; web sectors of dorsal and ventral arms shallowest. Interbrachial web pouches absent. **One row of suckers on each arm.** In larger animals, around 37 to 54 suckers on each normal arm. Enlarged suckers absent. Gills with 7 to 8 lamellae per demibranch. Funnel organ V V-shaped, with thick limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Ink sac present. Right third arm of males hectocotylized, 88 to 92% length of opposite arm. **Ligula robust and spoon like**, 5 to 9% of arm length. Calamus large, 35 to 67% of ligula length. Hectocotylized arm with 31 to 38 suckers. Spermatophores long, to 1.6 times mantle length. Eggs large, around 11 to 14 mm, 18 to 24% of mantle length. **Colour:** Resting animals uniform pink-brown. Alarmed animals are dark purple-brown dorsally and cream white ventrally. False-eye spots (ocelli) absent. **Single white**

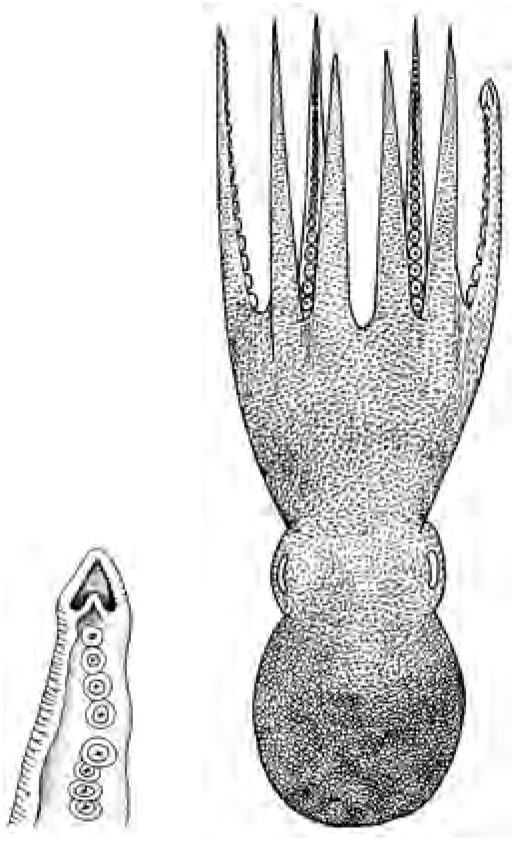


Fig. 157 *Pareledone charcoti*

spots on medial upper arm crown and mid-dorsal posterior mantle. White transverse head bar present. Sculpture: Skin texture a patchwork of regular fine, rounded and closely-set papillae. Ventral surface of mantle smooth. Single slightly larger papilla over each eye. **Skin ridge present around lateral margin of mantle.**

Size: Mantle length to 65 mm; total length to around 210 mm.

Geographical Distribution: Circumpolar Antarctic (Fig. 158).

Habitat and Biology: Depths range from 100 to 700 m. Species occurs on the Antarctic continental shelf at temperature ranges of -1.6 to -2.1°C. Lives on mud and sand substrates with pebbles and rocks amongst sponges, gorgonaceans, and bryozoans.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Janssen (1993), Kubodera and Okutani (1994), Lu and Stranks (1994), Casaux *et al.* (1997), Daly and Peck (2000), Daneri *et al.* (2000), Strugnell *et al.* (2009b).

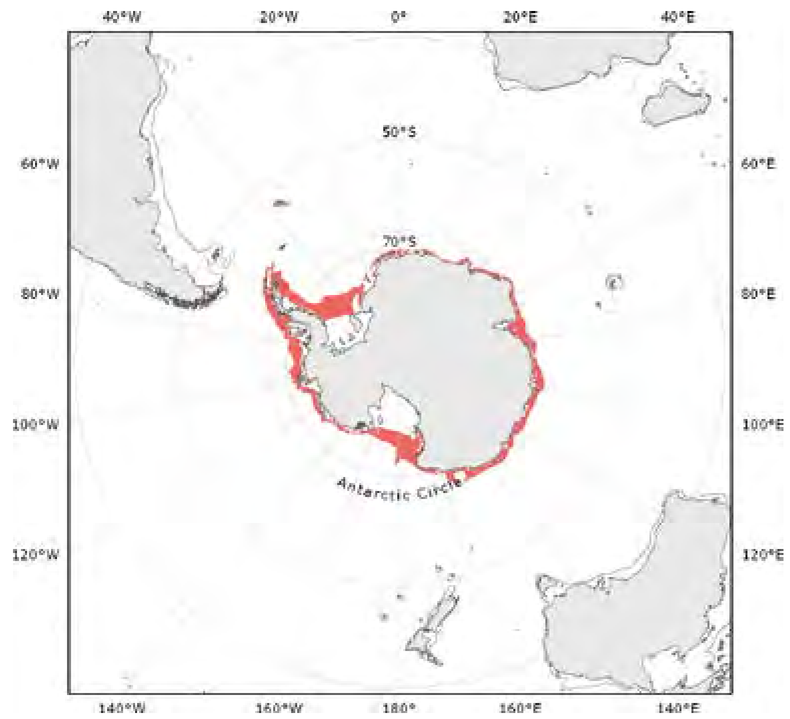


Fig. 158 ***Pareledone charcoti***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Pareledone aequipapillae Allcock, 2005

Pareledone aequipapillae Allcock, 2005, *Zoological Journal of the Linnean Society*, 143: 81. [Type locality: South Shetland Islands, 61°10'S, 54°34'W].

Size: Mantle length to 63 mm; total length to 190 mm.

Geographical Distribution: South Shetland Islands.

Habitat and Biology: Depths range from 110 to 465 m.

Literature: Undheim *et al.* (2010a).

Pareledone albimaculata Allcock, 2005

Pareledone albimaculata Allcock, 2005, *Zoological Journal of the Linnean Society*, 143: 84. [Type locality: South Shetland Islands, 61°19'S, 56°33'W].

Size: Mantle length to 38 mm; total length to 133 mm.

Geographical Distribution: South Shetland Islands.

Habitat and Biology: Depth range from 190 to 465 m.

Literature: No additional literature.

Pareledone aurata Allcock, 2005

Pareledone aurata Allcock, 2005, *Zoological Journal of the Linnean Society*, 143: 87. [Type locality: South Shetland Islands, 61°21'S, 55°14'W].

Size: Mantle length to 49 mm; total length to 136 mm.

Geographical Distribution: South Shetland Islands.

Habitat and Biology: Depth range from 89 to 465 m.

Literature: No additional literature.

Pareledone aurorae (Berry, 1917)

Moschites aurorae Berry, 1917. *Cephalopoda. Scientific Reports, Australian Antarctic Expedition, series C, Zoology and Botany,* 4(2): 20. [Type locality: Southern Ocean, Antarctica, Queen Mary Land, 66°08'S, 94°17'E].

Size: Holotype mantle length 24 mm; total length 88 mm.

Geographical Distribution: Known only from type material.

Habitat and Biology: Depth of type specimen: 219 m.

Remarks: Removed from synonymy of ***Pareledone charcoti*** by Allcock (2005).

Literature: Allcock (2005).

Pareledone cornuta Allcock, 2005

Pareledone cornuta Allcock, 2005, *Zoological Journal of the Linnean Society*, 143: 90. [Type locality: South Shetland Islands, 61°10'S, 56°04'W].

Size: Mantle length to 60 mm; total length to 162 mm.

Geographical Distribution: South Shetland Islands.

Habitat and Biology: Depth range from 130 to 454 m.

Literature: No additional literature.

Pareledone felix Allcock, Strugnell, Prodohl, Piatkowski and Vecchione, 2007

Pareledone felix Allcock, Strugnell, Prodohl, Piatkowski and Vecchione, 2007, *Polar Biology*, 30: 885.

[Type locality: Antarctic Ocean, Elephant Island, (61°10'S, 54°41'W)].

Size: Mantle length to 60 mm; total length to 150 mm.

Geographical Distribution: South Shetland Islands.

Habitat and Biology: Depth range from 200 to 800 m.

Literature: No additional literature.

Pareledone framensis Lu and Stranks, 1994

Pareledone framensis Lu and Stranks, 1994, *Memoirs of the Museum of Victoria*, 54: 227. [Type locality: East Antarctica, off MacRobertson Land, Fram Bank, 67°S, 68°E].

Size: Mantle length to 70 mm; total length to 270 mm.

Geographical Distribution: Eastern Antarctica.

Habitat and Biology: Depth range from 150 to 300 m.

Literature: Allcock *et al.* (2003b).

Pareledone harrissoni (Berry, 1917)

Moschites harrissoni (Berry, 1917), *Scientific Reports of the Australasian Antarctic Expedition* 1911-1914, series C, 14(2): 24. [Type locality: Southern Ocean, Antarctica, 65°06'S, 96°13'E].

Synonym: *Pareledone antarctica* (Thiele, 1920).

Size: Mantle length to 100 mm; total length to 350 mm.

Geographical Distribution: Southern Ocean, East Antarctica.

Habitat and Biology: Depth range from 25 to 743 m.

Literature: Kubodera and Okutani (1994), Lu and Stranks (1994).

Pareledone panchroma Allcock, 2005

Pareledone panchroma Allcock, 2005, *Zoological Journal of the Linnean Society*, 143: 93. [Type locality: South Shetland Islands, 61°59'S, 60°19'W].

Size: Mantle length to 43 mm; total length to 105 mm.

Geographical Distribution: South Shetland Islands.

Habitat and Biology: Depth range from 427 to 804 m.

Literature: No additional literature.

Pareledone prydzensis Lu and Stranks, 1994

Pareledone prydzensis Lu and Stranks, 1994, *Memoirs of the Museum of Victoria*, 54: 232. [Type locality: Antarctica, Prydz Bay].

Size: Mantle length to 30 mm; total length to 95 mm.

Geographical Distribution: Antarctica, Prydz Bay.

Habitat and Biology: Depth range from 526 to 676 m.

Literature: No additional literature.

Pareledone serperastrata Allcock, 2005

Pareledone serperastrata Allcock, 2005, *Zoological Journal of the Linnean Society*, 143: 94. [Type locality: South Shetland Islands, 61°01'S, 55°46'W].

Size: Mantle length to 36 mm; total length to 104 mm.

Geographical Distribution: South Shetland Islands.

Habitat and Biology: Depth range from 130 to 454 m.

Literature: No additional literature.

Pareledone subtilis Allcock, 2005

Pareledone subtilis Allcock, 2005, *Zoological Journal of the Linnean Society*, 143: 98. [Type locality: South Shetland Islands, 61°04'S, 54°36'W].

Size: Mantle length to 44 mm; total length to 109 mm.

Geographical Distribution: South Shetland Islands.

Habitat and Biology: Depth range from 190 to 427 m.

Literature: No additional literature.

Pareledone turqueti (Joubin, 1905)

Eledone turqueti Joubin, 1905, *Mémoires de la Société Zoologique de France*, 18: 29. [Type locality: Southern Ocean, Antarctica, Wandel Island (=Booth Island), 65°05'S, 64°00'W].

Size: Mantle length to 60 mm; total length to 180 mm.

Geographical Distribution: Southern Ocean, western Antarctica.

Habitat and Biology: Depth range from 0 to 4 000 m.

Literature: Daly and Rodhouse (1994), Lu and Stranks (1994), Allcock *et al.* (1997), Yau *et al.* (2002), Xavier *et al.* (2002), Allcock *et al.* (2003b), Collins *et al.* (2004), Barratt *et al.* (2008), Strugnell *et al.* (2009b), Undheim *et al.* (2010a).

Paroctopus Naef, 1923

Paroctopus Naef, 1923, *Fauna e Flora de Golfo di Napoli*, Monograph 35, 1(1): 692.

Frequent Synonyms: *Pseudoctopus* Grimpe, 1925.

Type Species: *Octopus digueti* Perrier and Rochebrune, 1894.

Diagnostic Features: Small-bodied; mantle short, bursiform. Stylets present, non-mineralized. **Arms short, stocky, 2 to 3 times mantle length. One to 3 enlarged suckers on all arms of males only.** Right third arm hectocotylized, shorter than opposite arm. Copulatory organ (ligula) medium size; calamus short. **Gills with 6-8 lamellae per outer demibranch.** Oviducal glands without obvious braiding chambers. Spawned eggs small to medium size, stalks very short, attached singly in small clusters in empty gastropod and bivalve shells. Body (in life) uniformly coloured with little pattern variability; patch and groove system absent; dorsal mantle and large arm base white spots absent, frontal white spot complex present but faint. Skin without large primary papillae.

Size: Mantle length to 60 mm.

Geographical Distribution: Northeastern Pacific Ocean off Mexico and in the Gulf of California; southern limits of distribution unknown. Western Atlantic Ocean, Caribbean Sea and Gulf of Mexico.

Habitat and Biology: Depths typically range from intertidal to 30 m.

Remarks: The genus ***Paroctopus*** was proposed by Naef (1923) based on the relatively large size of the eggs of ***P. digueti*** (capsule length 10 mm) that was unlike anything Naef was familiar with in the Mediterranean. Two years later Grimpe (1925) erected the genus ***Pseudoctopus*** based on the same type species citing the single attachment of eggs as well as egg size. Naef abandoned the genus name ***Paroctopus*** in 1928 apparently because he felt it was not valid, although he did not discuss the reasons for his decision. Robson (1929a) resurrected the name but had reservations about erecting a new genus based solely on egg size. In an attempt to validate Naef's genus he amplified the diagnosis with several additional characters, namely: 1) possession of relatively long copulatory organ (LLI 7-20); 2) short arms; and 3) squat, bursiform body. Pickford (1945, 1946) initially accepted the validity of the genus in her treatment of the octopodine fauna of the western Atlantic. However, she later rejected the name when discussing the generic placement of the large-egg species ***Octopus bimaculoides*** (Pickford and McConnaughey, 1949). As currently understood, the genus is represented by a trans-isthmian geminate species complex endemic to tropical and subtropical waters in the Americas (see Berry, 1953, Nesis, 1975, 1978 and Voight, 1988a). In the western Atlantic ***O. joubini*** Robson, 1929 and ***O. mercatoris*** Adam, 1937 have been reported as possible congeners. We consider ***mercatoris*** and a large-egg species being incorrectly treated under the name ***joubini*** as belonging in this genus. The existence of at least three distinct species in a well-defined clade strongly supports the validity of the genus ***Paroctopus*** with ***digueti*** as the type species. Whether the genus is restricted to the Americas or has broader geographic ties has not been determined. In Australia ***O. superciliosus*** Quoy and Gaimard, 1832 and ***O. warringa*** Stranks, 1990 appear closely related and need to be compared in detail (see Stranks, 1988b, 1990). Robson (1929a), Pickford (1945, 1946), and workers in Japan (see especially Okutani *et al.* 1987), have variously placed a number of species endemic to the North Pacific Ocean in the genus ***Paroctopus***, namely: ***apollyon, briareus, conispadiceus, dofleini, hongkongensis, joubini, megalops, mercatoris, tenuicirrus*** and ***yendoi***. Of these only the large-egg "***joubini***" and ***mercatoris*** are correctly placed.

Literature: Perrier and Rochebrune (1894), Rochebrune (1885), Naef (1923), Grimpe (1925), Robson (1929a), Pickford (1945, 1946), Berry (1953), Nesis (1975, 1978), Okutani *et al.* (1987), Voight (1988a), Stranks (1988b, 1990).

Paroctopus digueti (Perrier and Rochebrune, 1894) **Fig. 159**

Octopus digueti Perrier and Rochebrune, 1894, *Compte Rendu des Séances de l'Academie des Sciences*, 118: 770. [Type locality: Mexico, Gulf of California].

Frequent Synonyms: *Octopus digueti*.

Misidentifications: None.

FAO Names: En — Diguet's pygmy octopus; **Fr** — Pouple pygmée de Diguet; **Sp** — Pulpo pigmeo de Diguet.

Diagnostic Features: Pygmy species. Eyes large, protrude from head. Web relatively shallow (~25% of arm length), formula typically C.D.B.E.A. **Arms short, about 2 to 3 times mantle length**; formula typically 4>3>2>1 or 3>4>2>1. Suckers medium-sized (8 to 14% of mantle length), **1 to 3 conspicuously enlarged suckers (up to 23% of mantle length) on all arms of mature males near web insertion**, occasionally slightly enlarged in females. Sucker counts on normal arms to 138. Funnel organ W-shaped, limbs subequal in length. Gills with 6 to 8 lamellae per outer demibranch. Third right arm hectocotylized; approximately equal in length with opposite arm (85 to 105%), with 70 to 90 suckers. Ligula medium size (5 to 8% of arm length), spatulate, copulatory groove deep, smooth or with distinct mid-rib and several faint grooves. Calamus small, 35% of ligula length. Spawned eggs medium size (capsule length 7 to 10 mm), stalk short (length 3 to 5 mm); attached singularly, in small clusters or sets of 2 to 5 eggs, deposited inside empty bivalve or gastropod shells. Hatchlings large (4.5 to 6.0 mm mantle length), benthic. **Colour:** In life uniform dull cream to bright red, often with dark reticulations or mottled with red and white; occasionally with irregular rows of white spots dorsally and white transverse bands on arms. Dorsal mantle white spots absent; **frontal mantle white spot complex** (*sensu* Packard and Sanders, 1971) **present but very faint**. Large arm base white spots absent. False eye spots (ocelli) absent. **Sculpture:** Patch and groove system absent. Skin smooth or wrinkled in shallow longitudinal folds, often entirely covered with minute to small transient papillae (granular) situated on anastomosing lines or reticulations; large primary papillae absent; 1 prominent papilla above and 1 to 2 papillae below each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 74 mm; total length to 220 mm; body weight to 85 g.

Geographical Distribution: Mexico, Gulf of California and Pacific coast of southern half of Baja California Peninsula; southern limits of distribution unknown (Fig. 160).

Habitat and Biology: Depths range from intertidal to 30 m. The species lives in sandy and muddy intertidal areas. It is typically found in areas of permanent standing water such as small tidal pools and sand channels where empty shells accumulate. Like its presumed congeners in the western Atlantic, adults of this species live in the

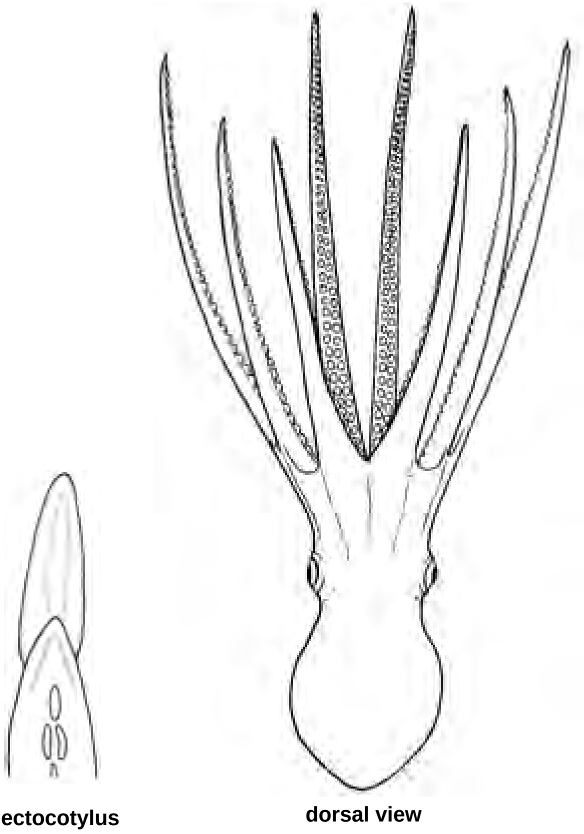


Fig. 159 ***Paroctopus digueti***

Fig. 160 ***Paroctopus digueti***

🟥 Known distribution

shelter of a wide diversity of empty gastropod and bivalve shells. The octopus often plugs the apertures of large gastropod shells with small bivalves or gastropod shells. Anatomical features of the species have been described and extensive field and laboratory studies have been conducted on the biology and behaviour. Growth, reproduction and life span have been studied in the laboratory because of the ease of rearing this small, large egg species. Males develop the copulatory organ (hectocotylus) and begin to mate 3 months after hatching. Females spawn 50 to 250 eggs gradually over a 2 to 3 week period. Eggs are attached singly inside empty shells. Females spawn year round but eggs are most commonly encountered in March to April. Development takes 36 to 50 days during which time the female broods and guards the eggs. The entire life cycle is completed in 125 to 240 days (average 7 months) indicating that there may be 1 to 2 generations per year. Based on egg size the young are benthic on hatching. Diet consists of a diversity of shrimps, crabs, especially hermit crabs and brachyurans, small molluscs and fishes. The species will bite handlers if agitated. They are active during periods of high tides, especially during new moon periods. An undescribed species of dicyemid parasite inhabits the renal coelom of this octopus.

Interest to Fisheries: May be collected for food by coastal inhabitants in Mexico. Extensively utilized in laboratory studies on biology, behaviour, anatomy and physiology.

Local Names: Unknown.

Literature: Rochebrune (1885, 1886, 1895), Perrier and Rochebrune (1894), Boone (1928), Robson (1929a), Voight (1984, 1988a, 1988b, 1988c, 1990, 1991a, 1991b, 1992), Hanlon and Forsythe (1985), Kobayashi (1986), De Rusha *et al.* (1987), Michels *et al.* (1987), Warr (1987), Toll and Strain (1988), Roper *et al.* (1995), Stoskopf and Oppenheim (1996), Sánchez (2003), Sellheim (2006), Kier and Stella (2007).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Paroctopus mercatoris (Adam, 1937)

Octopus mercatoris Adam, 1937, *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, series 2(9): 76. [Type locality: Gulf of Mexico, United States, Florida, off Dry Tortugas and Tampa].

Size: Mantle length to 20 mm.

Geographical Distribution: Known only from type material.

Habitat and Biology: Depth range unknown.

Remarks: The generic placement of this species requires review. Sometimes appears in aquarium trade (C. Huffard, pers. comm.).

Literature: Forsythe and Toll (1991), Voss and Toll (1998).

Praealtus Allcock, Collins, Piatkowski and Vecchione, 2004

Praealtus Allcock, Collins, Piatkowski and Vecchione, 2004, *Deep-Sea Research*, 51: 1893.

Type Species: *Praealtus paralbida* Allcock, Collins, Piatkowski and Vecchione, 2004.

Diagnostic Features: Moderate-sized species. Mantle roughly spherical. Stylets absent. **Arms of moderate length, approximately 3 times mantle length. Arms subequal in length, ventral pair slightly shorter (1=2=3>4).** Arm autotomy at distinct plane absent. **Webs deep, deepest approximately 30% length of longest arm.** Relative web depths unknown due to damaged material. Interbrachial web pouches absent. **Suckers in single row.** Enlarged suckers absent. Funnel organ V V-shaped. **Gills with 7 to 8 lamellae per demibranch.** Radula with 7 elements, 7 rows of teeth all unicuspid, marginal plates absent. **Posterior salivary glands tiny, much smaller than buccal mass.** Oesophagus with swelling only; no distinct crop. **Ink sac absent.** Anal flaps absent. Third right arm of males hectocotylized, slightly shorter than opposite arm. Distinct ligula and calamus present. Ligula small to medium (4 to 5% of arm length). Ligula groove round and shallow without transverse ridges. **Calamus very large, 50 to 70% of ligula length.** Spermatophores long, almost twice mantle length. Mature females unknown. Colour pattern of uniform pale slaty grey to very pale violet. Skin texture of small rounded papillae scattered over dorsal surfaces. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 82 mm; total length to 380 mm.

Geographical Distribution: Known only from off Antarctic Peninsula.

Habitat and Biology: Unknown habitat. Known only from 2 896 to 3 222 m.

Remarks: Single deep water species. The relationship between this genus and the poorly diagnosed genus ***Bentheledone*** (which also possesses tiny posterior salivary glands) requires revision.

Literature: No additional literature.

Praealtus paralbida Allcock, Collins, Piatkowski and Vecchione, 2004

Fig. 161

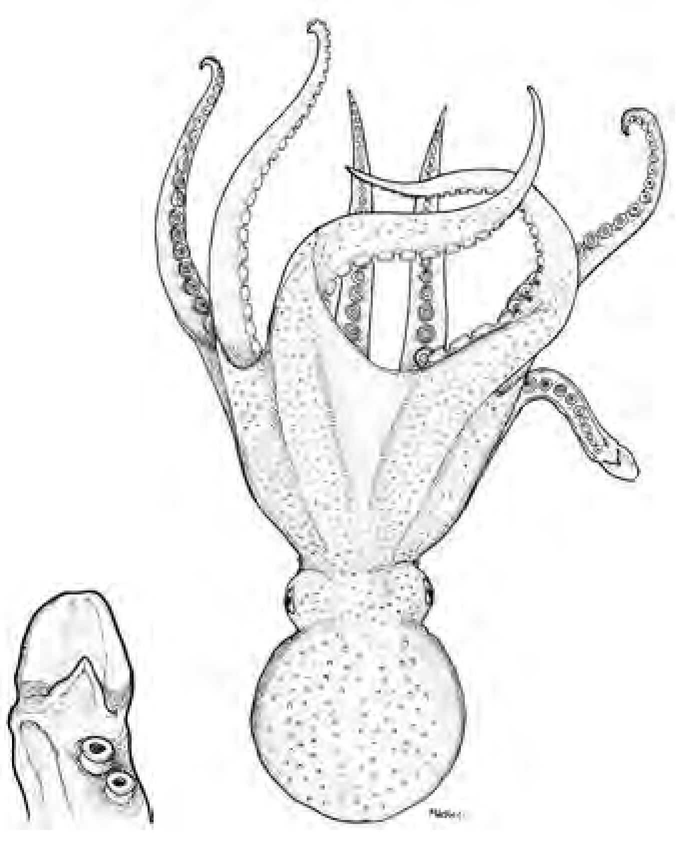
Praealtus paralbida Allcock, Collins, Piatkowski and Vecchione, 2004, *Deep-Sea Research*, 51: 1894. [Type locality: Southern Ocean, off the Antarctic Peninsula, 60°39'S, 53°58'W].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — White octopus; **Fr** — Poulpe blanc; **Sp** — Pulpito blanco.

Diagnostic Features: Animals medium-sized. Mantle approximately round, head narrower than mantle. Stylets absent. Arms medium length, 2.5 to 3.4 times mantle length, subequal; arm order usually 1=2=3>4. Arm autotomy at distinct plane absent. Webs deep (~30% of arm length), damage prevents estimation of relative web depths. Interbrachial web pouches absent. **Suckers uniserial, small** (~6% of mantle length), **without sucker enlargement.** Normal sucker count to 66 suckers. Funnel organ V V-shaped. Gills with 7 to 8 lamellae per demibranch. Radula with 7 elements, rachidian unicuspid, 3 slightly smaller unicuspid elements on each side of rachidian. **Posterior salivary glands tiny**. **Oesophagus with swelling only, no distinct crop**. Ink sac absent. Anal flaps absent. Marginal plates absent. Third right arm of males hectocotylized, usually slightly shorter than opposite number (~93%).


hectocotylus

dorsal view

Fig. 161 *Praealtus paralbida*

Ligula small to medium (~5% of arm length); ligula groove round and shallow, without transverse ridges. **Calamus distinct and large to very large** (typically >50% of ligula length). Hectocotylized arm with 38-42 suckers. **Spermatophores long, almost twice mantle length**. Mature females unknown. **Colour:** Newly captured specimens are uniformly pale slaty grey to very pale violet (almost white). **Sculpture:** Numerous small, simple, papillae scattered over the dorsal surface. Supraocular papillae not apparent. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 82 mm; total length to 380 mm.

Geographical Distribution: Known only from off the Antarctic Peninsula (Fig. 162).

Habitat and Biology: Depths range from 2 896 to 3 222 m. Biology and behaviour unknown.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: No additional literature.

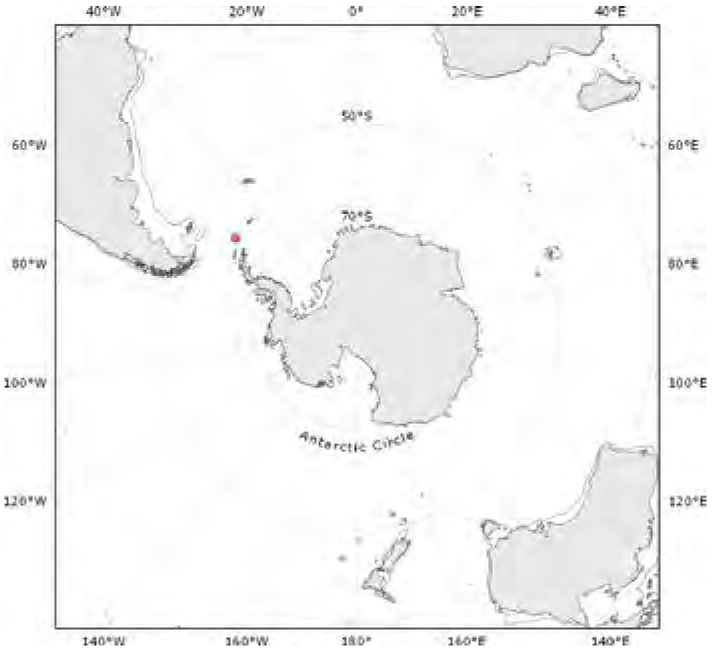


Fig. 162 ***Praealtus paralbida***

🟥 Known distribution

Pteroctopus Fischer, 1882

Pteroctopus Fischer, 1882, *Manuel de Conchyliologie et de Paléntologie Conchyliologique ou Histoire Naturelle des Mollusques Vivante et Fossiles. Deuxième partie, Synopsis des Genres. F. Savy: Paris, France (1880-1887)*: 334.

Frequent Synonyms: *Berrya*, Adam, 1939.

Type Species: *Octopus tetracirrhus* Delle Chiaje, 1830.

Diagnostic Features: Small to moderate-sized muscular species. **Mantle roughly square to spherical. Mantle aperture distinctly narrow, <40% of mantle circumference at level of aperture.** Stylets present, non-mineralized. Arms approximately 3 to 4.5 times mantle length. **Arms approximately equal in length.** Arm autotomy at distinct plane absent. Webs deep, deepest >40% length of longest arm. **Web margins extend and widen toward arm tips to form net-like flanges off distal portions of arms.** Interbrachial web pouches absent. Suckers in two rows. Enlarged suckers absent. **Funnel organ V V-shaped, with narrow limbs.** Gills with 9 to 10 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands of moderate size, around size of buccal mass. Oesophagus with swelling only or slight diverticulum, enlarged crop absent. Ink sac present. Anal flaps present. **Third left or right arm of male hectocotylized (depending on species),** distinctly shorter than opposite arm (60 to 80%). Ligula broad and conical, 5 to 11% of arm length with obvious calamus. Colour pattern of uniform cream to red-brown. **Skin loose and semi-gelatinous, sculptured in small and regular low patches. Two elongate papillae over each eye.** Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 130 mm; total length to around 280 mm.

Geographical Distribution: Indo-West Pacific Ocean and Atlantic Ocean.

Habitat and Biology: Soft substrates, typically at depths of 200 to 800 m.

Remarks: Two or more species from deep waters of all oceans. The right-handed species, ***Pteroctopus hoylei***, previously has been treated under the generic synonym ***Berrya***. This genus requires revision.

Literature: Norman *et al.* (1997).

Pteroctopus tetracirrhus (Delle Chiaje, 1830)

Fig. 163; Plate IX, 65

Octopus tetracirrhus Delle Chiaje, 1830, *Memorie Sulla Storia e Notomia Degli Animali Senza Vertebre del Regno di Napoli*, pl.72. [Type locality: Mediterranean Sea, Italy, Naples].

Frequent Synonyms: None.

Misidentifications: None.

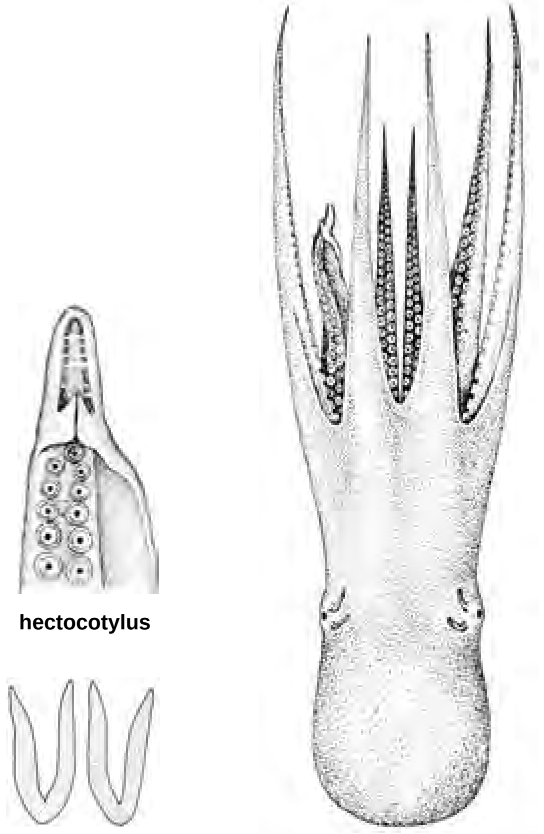
FAO Names: En — Fourhorn octopus; **Fr** — Poulpe à quatre cornes; **Sp** — Pulpo cuatro cuernos.

Diagnostic Features: Moderate-sized, muscular species with loose skin. Opening to mantle cavity very narrow, <40% of body circumference at level of opening. Stylets present, non-mineralized. Arms of moderate length, around 3.5 to 4 times mantle length. Arms approximately equal in length. Arm autotomy at distinct plane absent. **Webs deep, deepest >40% of arm length**. Web sectors approximately equal in depth. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 130 to 150 suckers on each normal arm. Enlarged suckers absent. **Funnel organ V V-shaped, limbs very slender and of approximately equal length**. Gills with 9 to 10 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Oesophagus with swelling only, no distinct crop. Ink sac present. Anal flaps present. **Left third arm of males hectocotylized**, length around 60 to 80% of length of opposite arm. Ligula broad and conical, 5 to 11% of arm length. Calamus large. Hectocotylized arm with around 80 suckers. Spermatophores large, around 50 mm, approximately equal to mantle length, produced in low numbers (1 in material examined). Eggs moderate to large, to 8 mm. **Colour: Live animal uniform red-orange**. False-eye spots (ocelli) absent. **Sculpture: Skin soft and loose, sculptured in small regular raised patches. Two large digit-like papillae over each eye**. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 130 mm; total length to around 280 mm.

Geographical Distribution: Mediterranean Sea and eastern Atlantic Ocean on west coast of Africa to the equator, including the Cape Verde and Azores Islands (Fig. 164). Related form(s) of unresolved taxonomic status present in Caribbean Sea, eastern Americas from Uruguay to North Carolina and off Australia and Indonesia.

Habitat and Biology: Depths range from 25 to 720 m. Typically found in deeper part of range. Occurs primarily on muddy substrates. Males and females mature consecutively by May/June and June/July respectively. Young immature animals appear in catches from November and December. Lifespan considered to be 2 or 3 years.



hectocotylus

funnel organ

dorsal view

Fig. 163 *Pteroctopus tetracirrhus*

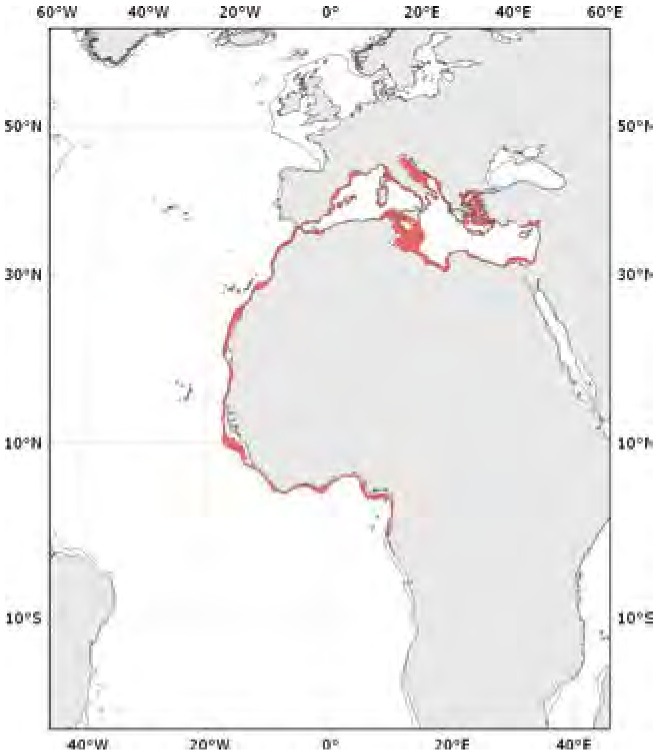


Fig. 164 *Pteroctopus tetracirrhus*

🟥 Known distribution

Interest to Fisheries: Taken on a minor scale as bycatch in shrimp or finfish trawl fisheries in the western Mediterranean and western Atlantic. Separate catch statistics for this species are not reported.

Local Names: ITALY: Polpo incamiciato.

Literature: Mangold-Wirz (1963), Bonichon-Laubier (1971), Toll and Binger (1991), Quetglas *et al.* (2000, 2009), Krstulović Šifner *et al.* (2005).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Pteroctopus hoylei (Berry, 1909)

Polypus hoylei Berry, 1909, *Proceedings of the United States National Museum*, 37(1713): 407. [Type locality: Hawaiian Islands, exact locality unknown].

Size: Mantle length to 60 mm; total length to 230 mm.

Geographical Distribution: Hawaiian Islands Archipelago.

Habitat and Biology: Depth range from 200 to 800 m.

Literature: Norman (2000).

Robsonella Adam, 1938

Robsonella Adam, 1938, *Zoologischer Anzeiger*, 121(7/8): 223.

Type Species: *Octopus fontanianus* d'Orbigny, 1834: 28.

Frequent Synonyms: *Joubinia* Robson, 1929.

Diagnostic Features: Moderate-sized species. Mantle muscular, ovoid. Stylets present, non-mineralized. **Arms moderate to long, length 3.5 to 5 times mantle length. Arms subequal in length or lateral and ventral pairs slightly longer.** Arm autotomy at distinct plane absent. Webs moderately deep, deepest around 16 to 32% longest arms. Interbrachial web pouches absent. **Suckers in two rows, medium-sized (7 to 12% ML); distinctly enlarged in mature males on arms 2 and 3.** Funnel organ W-shaped. **Gills with 8 to 10 lamellae per outer demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Rachidian with two cusps on either side, in asymmetrical seriation. First lateral tooth with crescent to bicuspid form. Posterior salivary glands of moderate size, approximately same size as buccal mass. Distinct crop as side branch off oesophagus absent. Ink sac present. Anal flaps present. Right third arm hectocotylized, slightly shorter than opposite arm (~75%). Ligula of moderate size, 5 to 9% of arm length, stout margins fleshy and inrolled, copulatory groove deep with shallow transverse furrows. **Calamus large and prominent (50 to 60% ligula length).** Terminal organ T-shaped with diverticulum longer than distal portion. Spermatophores of medium to large length (83 to 174% ML), slender with singly coiled sperm cord in 15 to 17 coils, produced in low numbers (<10). Eggs small. Colour in life bluish to violet to dark brown. Preserved material pale purple to dark brown dorsally, light pink ventrally. Frontal white spot and dorsal mantle white spots present. **Skin texture of patch and groove system of regular circular patches. Single large papilla over each eye.** Posterior mid to dorsal mantle papilla present; others not visible. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 70 mm; total length to around 270 mm.

Geographical Distribution: Pacific coast of South America from Peru and Chile.

Habitat and Biology: On rocky reefs and soft sediments from 0 to 200 m.

Remarks: Since the syntype is a female it is difficult to justify using ***fontanianus*** as the type species for the genus ***Robsonella***, which is based primarily on male characters. At present, there are not enough characters to consistently and confidently separate it at the generic level as distinct from ***Octopus*** *sensu stricto*. In addition, the status of this genus and its relation to Australian and New Zealand species (***O. australis, O. berrima, O. campbelli*** and ***O. huttoni***) require critical revision. This species currently is represented by a single species from the coast of South America (Peru, Chile, and potentially Argentina). See Pickford (1955), Thore (1959), and Ibáñez *et al.* (2008) for reviews and redescriptions.

Robsonella fontanianus (d'Orbigny, 1834)

Fig. 165; Plate IX, 66

Octopus fontanianus d'Orbigny, 1834 [*In* 1834 to 1847], *Voyage dans l'Amerique Meridionale*, 5(3): 28. [Type locality: Southeastern Pacific Ocean, Chile, Valparaiso].

Frequent Synonyms: None.

Misidentifications: *Octopus mimus* Gould, 1852.

FAO Names: En — Fontaine's octopus ; **Fr** — Poulpe de Fontaine; **Sp** — Pulpo de Fontaine.

Diagnostic Features: Moderate-sized muscular species. Arms moderate to long, around 3.5 to 5 times mantle length. Arms of similar length, ventral arm pair longest. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 16 to 32% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, up to 150 suckers on each normal arm. **Enlarged suckers present in mature males, 1 to 4 (typically 3) on arms 2 and 3, diameter 13 to 17% ML**. Gills with 8 to 10 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. **First lateral tooth crescent-shaped to bicuspid**. Distinct crop as side branch off oesophagus absent. Ink sac and anal flaps present. Right third arm of males hectocotylized, length ~75% length of opposite arm. **Ligula stout and conical, 5 to 9% of arm length, copulatory groove deep with around 7 transverse shallow furrows. Calamus large and robust, around half ligula length**. Hectocotylized arm with

47 to 60 suckers. Spermatophores of moderate size, around 80 to 170% of mantle length. Eggs small, around 3.5 mm. **Colour:** Bluish to violet to dark brown. **Large white frontal white spot present on dorsal arm crown**, as well as pair of small dorsal mantle white spots. False eye spots (ocelli) absent. **Sculpture: Skin texture of regular patch and groove sculpture with circular patches**. Single large papilla over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 70 mm; total length to around 270 mm.

Geographical Distribution: Common along rocky coasts in South America. Occurs in the southeastern Pacific from north of Peru to Chile (56°S) and in the southwestern Atlantic off Tierra del Fuego (Fig. 166).

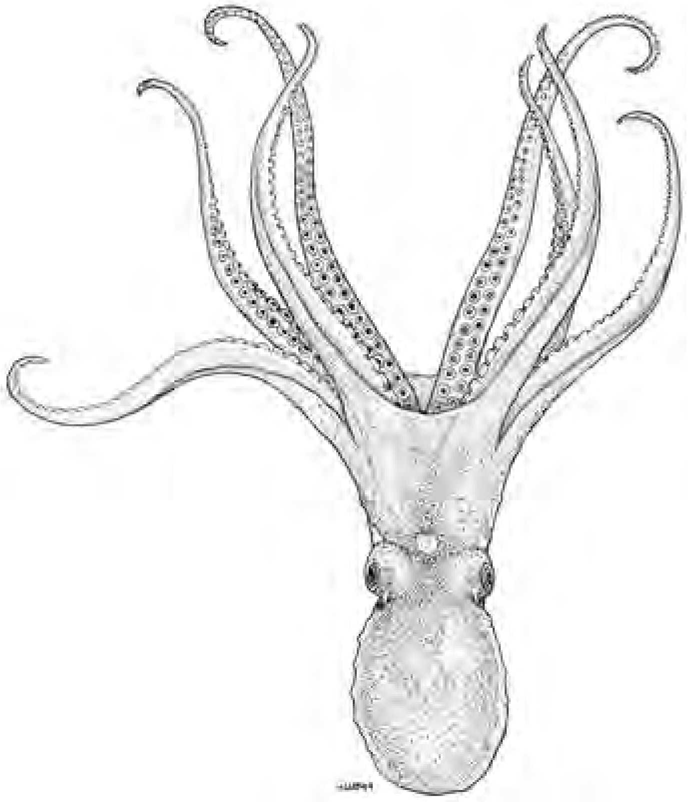
Habitat and Biology: Depth range from 0 to 200 m. Found in the intertidal and subtidal zones in association with both rocky reefs and soft substrates. Small crustaceans and fishes are the main prey. Eggs are small and hatchlings planktonic.

Interest to Fisheries: A small artisanal fishery has been reported that targets this species in Chile (Osorio *et al.,* 1979). Currently being investigated for potential aquaculture (Pereda *et al.,* 2009).

Local Names: Unknown.

Remarks: The species name often is presented incorrectly as ***Robsonella fontaniana***.

Literature: Pickford (1955), Ibáñez *et al.* (2008, 2009; as ***Robsonella fontaniana***), González *et al.* (2008b, 2011), Pereda *et al.* (2009; as ***R. fontaniana***), Uriarte *et al.* (2009, 2010, 2011; as ***R. fontaniana***), Ortiz and Ré (2011; as ***R. fontaniana***).



dorsal view

Fig. 165 ***Robsonella fontanianus***

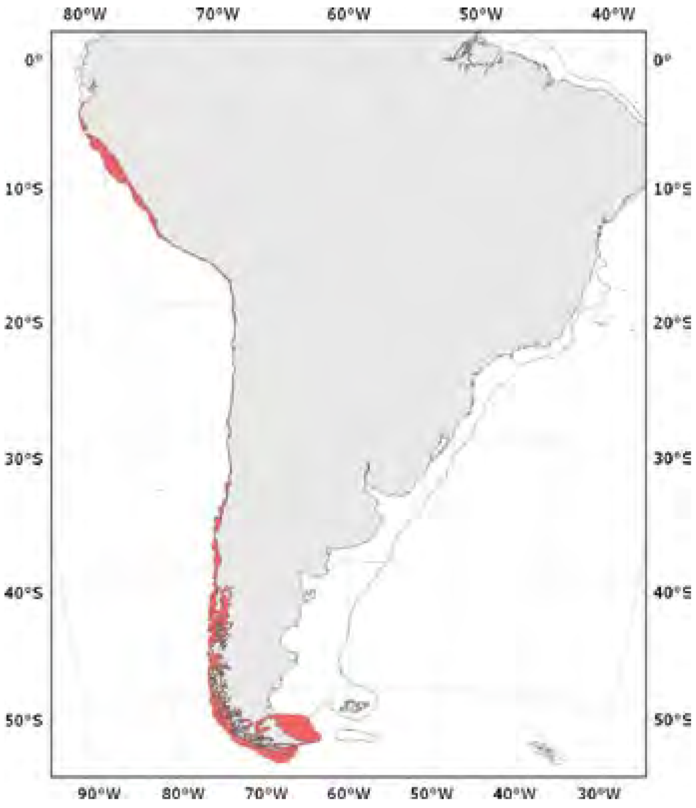


Fig. 166 ***Robsonella fontanianus***

🟥 Known distribution

Sasakiopus Jorgensen, 2009

Sasakiopus Jorgensen, 2009, *Field Guide to Squids and Octopods of the Eastern North Pacific and Bering Sea*: 82.

Type Species: *Polypus salebrosus* Sasaki, 1920.

Diagnostic Features: Moderate-sized species. Mantle muscular and roughly spherical. Stylets present. **Arms short, approximately twice mantle length. Arms subequal in length (typically 3>4>2>1).** Arm autotomy at distinct plane absent. **Webs deep, deepest around 35% of longest arms.** Interbrachial web pouches absent. **Suckers in two rows, none enlarged in either sex.** Funnel organ W-shaped, lateral limbs half length of medial limbs. **Gills with 7 to 10 lamellae per outer demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands of moderate size, approximately same size as buccal mass. Distinct crop present as side-branch off oesophagus. **Ink sac present, greatly reduced;** anal flaps absent. Right third arm hectocotylized, slightly shorter than opposite arm (~75%). **Ligula large, ~15% of arm length, elongate with shallow open groove, lacking transverse ridges or laminae.** Calamus moderate, ~30% of ligula length. Spermatophores approximately 70% of mantle length, produced in moderate to high numbers (~70). Eggs large (>20% of mantle length). Colour in life uniform red to purple, brown in preserved material. Dorsal mantle white spots (*sensu* Packard and Sanders, 1971) absent. Ocelli absent. **Skin sculpture of extensive, closely-set, irregularly-shaped, flat-topped papillae that form pavement over entire dorsal and ventral surfaces.** Supraocular or other enlarged papillae absent. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 65 mm; total length to 200 mm.

Geographical Distribution: Northern Pacific Ocean.

Habitat and Biology: From 200 to 1 100 m.

Remarks: Represented by a single species. Removed from the genus ***Bathypolypus*** by Muus (2002) and placed in ***Benthoctopus***. Recently placed in its own genus by Jorgensen (2009). See also Jorgensen *et al.* (2010).

Literature: Muus (2002), Jorgensen (2009), Jorgensen *et al.* (2010).

Sasakiopus salebrosus (Sasaki, 1920)

Fig. 167

Polypus salebrosus Sasaki, 1920, *Proceedings of the United States Museum*, 57: 182. [Type locality: Northwestern Pacific Ocean, Japan, Honshu Island, Rikuzen Prefecture, off Kinka-san, 38°11.30’N, 142°08’E].

Frequent Synonyms: *Bathypolypus salebrosus* (Sasaki, 1920).

FAO Names: En — Rough octopus; **Fr** — Poulpe rugueux; **Sp** — Pulpo àspero.

Misidentifications: *Enteroctopus dofleini* (Wülker, 1910) (juveniles).

Diagnostic Features: Moderate-sized muscular species. Arms of moderate length, around 2 times mantle length. **Arms of similar length; lateral pairs slightly longer** (typically 3>4>2>1). Arm autotomy at distinct plane absent. Webs deep, deepest around 35% of arm length. Webs approximately equal in depth, deepest on lateral arms (typically C>D>B>A>E). Interbrachial web pouches absent. Arms with two rows of small suckers, around 8% of mantle length. In larger animals, up to 87 suckers on each normal arm. Enlarged suckers absent. Gills with 7 to 10 lamellae per demibranch, typically 8 to 9. **Funnel organ W-shaped; outer limbs approximately 50% length of medial limbs**. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. **Ink sac present, greatly reduced. Anal flaps absent**. Right third arm of males

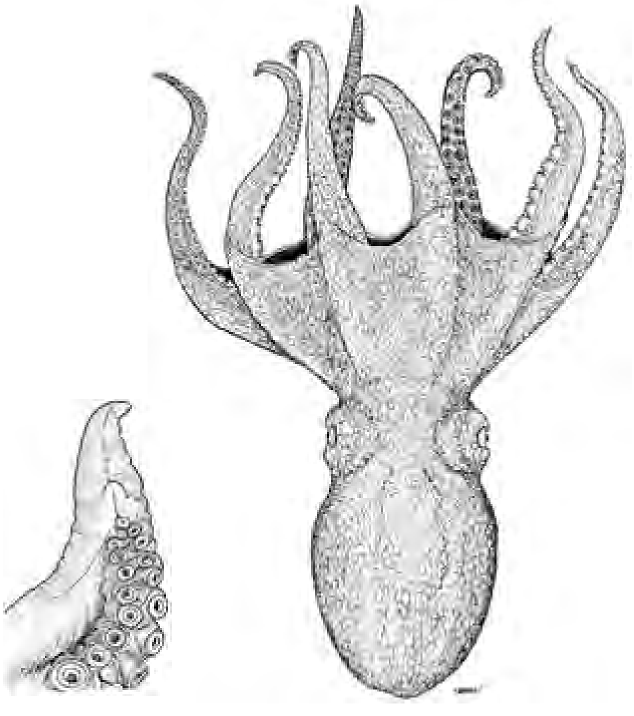


Fig. 167 *Sasakiopus salebrosus*

hectocotylized, ~75% length of opposite arm. **Ligula large (~15% of arm length), stout and conical, evenly tapered to a sharp tip**. Ligula groove shallow without transverse ridges or laminae. Calamus of moderate size, around 30% of ligula length. Hectocotylized arm with around 38 to 43 suckers. Spermatophores of moderate size, around 30 mm, around 70% of mantle length, produced in large numbers (~70). Eggs large, capsule length to 15 mm. **Colour:** Live animals uniform deep red to purple, preserved animals cream. False-eye spots (ocelli) absent. **Sculpture: Skin texture as dense complete cover of small compound papillae over entire dorsal and ventral surfaces**. Enlarged papillae absent. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 65 mm; total length to 200 mm.

Geographical Distribution: Northwestern Pacific from Sea of Japan to the Okhotsk and Bering seas (Fig. 168).

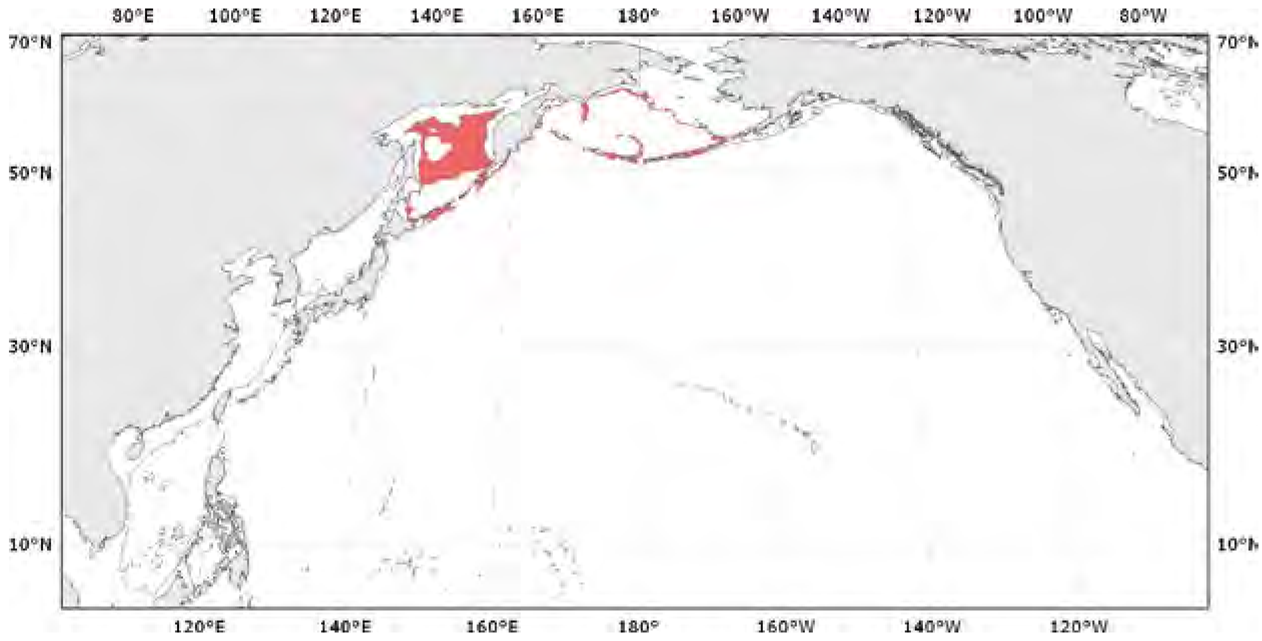


Fig. 168 ***Sasakiopus salebrosus***

🟥 Known distribution

Habitat and Biology: Depth range from 212 to 1 160 m. This species primarily is known from trawl material collected at depths. Habitat associations are not known. The large eggs of this species indicate that young are benthic upon hatching.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Remarks: This species recently was transferred to the genus ***Sasakiopus*** by Jorgensen (2009). The relationship of this species to Sasaki's (1920) ***Polypus validus*** from deep water off Japan requires further resolution, as does its relationship to ***Bathypolypus arcticus*** found in the North Atlantic and Arctic regions.

Literature: Laptikovsky (1999), Muus (2002), Jorgensen (2009), Jorgensen *et al.* (2010).

Scaeurgus Troschel, 1857

Scaeurgus Troschel, 1857, *Archiv fur Naturgeschichte*, 23(1): 51.

Type Species: *Octopus cocco* Verany, 1846 [= *Scaeurgus unicirrhus* (Delle Chiaje, 1839-1841)].

Diagnostic Features: Small to moderate-sized species. Mantle muscular ovoid. Stylets present, large, often mineralized. **Arms short, 2 to 3 times mantle length. Arms of similar length, lateral pairs longest (typically 3=2>4>1).** Arm autotomy at distinct plane absent. Webs moderately deep, deepest around 25-30% longest arms. Interbrachial web pouches absent. **Suckers in two rows, medium-sized and slightly to distinctly enlarged in males of different species.** Funnel organ W-shaped. Gills with 8 to 14 lamellae per outer demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Rachidian with one to two cusps on each side (typically two), in asymmetrical seriation. Posterior salivary glands of moderate size, approximately same size as buccal mass. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. **Left third arm hectocotylized,** slightly shorter than opposite arm (~80%). **Ligula of moderate size, elongate with fleshy thick rims, often peanut-shaped.** Calamus small to very large (up to 70% ligula length). **Spermatophores with double-strand coiled sperm cord, forming a braided pattern.** Spermatophores produced in low numbers (<10). Distal oviducts fleshy and swollen. Eggs small to moderate-sized (3 to 10% of mantle length in different species). **Colour pattern of cream to orange-brown with four paired black spots on mantle, anterior pair on lateral mantle adjacent to mantle aperture and dorsal to lateral skin ridge. Posterior pair on posterior tip of mantle dorsal to lateral ridge, faint in some species.** Dorsal mantle white spots (*sensu* Packard and Sanders, 1971) visible in live animals and some preserved material. Skin texture of regular numerous rounded papillae, dense on dorsal surfaces, present but less dense on ventral mantle, absent from aboral surface of fourth arm pair and ventral half of third arms from midline. Diamond of primary papillae present on dorsal mantle. Single large papilla present over each eye and large papilla present on posterior tip of mantle. **Skin ridge around lateral margin of mantle present (interrupted dashed line in pygmy species, *Scaergus tuber*).**

Size: Mantle length to 90 mm.

Geographical Distribution: Pacific, Indian and Atlantic Oceans, and Mediterranean Sea.

Habitat and Biology: Deep-water species; typically on continental slopes and associated with seamounts at depths usually between 100 and 500 m.

Remarks: At least seven species found on seamounts and continental slopes in all oceans.

Literature: Norman *et al.* (2005).

Scaeurgus unicirrhus (Delle Chiaje, 1839-1841)

Fig. 169; Plate IX, 67

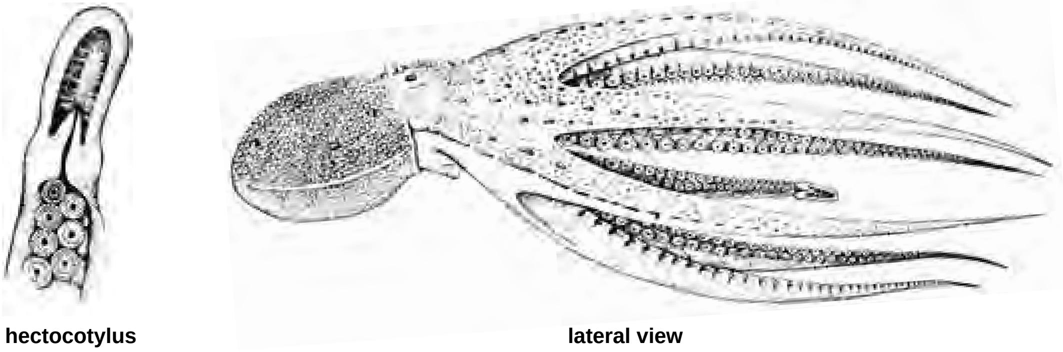
Octopus unicirrhus Delle Chiaje, 1839-1841, *Memorie Sulla Storia e Notomia Degli Animali Senze Vertebre del Regno di Napoli*: 70. [Type locality: None designated but presumed to be western Mediterranean Sea (Mangold, 1998); neotype locality: Mediterranean Sea, France, off Banyuls sur Mer].

Frequent Synonyms: *Octopus cocco* Verany, 1846.

Misidentifications: None.

FAO Names: En — Unihorn octopus; **Fr** — Poulpe licorne; **Sp** — Pulpo unicornio.

Diagnostic Features: Moderate-sized muscular species. Arms of moderate length, around 3 to 4.5 times mantle length. Arms of similar length, lateral pairs longest (typically 3=2>4>1). Arm autotomy at distinct plane absent. Webs of moderate



hectocotylus lateral view

Fig. 169 ***Scaeurgus unicirrhus***

depth, deepest around 15 to 23% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Web margins extend halfway along arm length. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, up to 200 suckers on each normal arm. Enlarged suckers absent. Gills with 12 to 14 lamellae per demibranch. Funnel organ W-shaped (sometimes V V), outer limbs approximately 80% length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. **Left third arm of males hectocotylized**, 60 to 75% length of opposite arm. **Ligula large and peanut-shaped with deep groove, 7 to 11% of arm length**. **Calamus long and sharp, over half ligula length**. Hectocotylized arm with around 85 suckers. Spermatophores of moderate size, around 45 mm, around 70 to 100% of mantle length, produced in low numbers (~8). Eggs small, around 2.5 mm. **Colour:** Red-brown to orange with irregular darker brown markings. **Two pairs of black spots often visible on the dorsal mantle**. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of regular blunt rounded papillae fused in places on the dorsal arm crown to form short longitudinal ridges. Single large papilla over each eye. **Skin ridge around lateral margin of mantle present**.

Size: Mantle length to 90 mm.

Geographical Distribution: Mediterranean Sea and northeastern Atlantic (Portugal). Voss (1951a) reported this species from the western Atlantic Ocean (see **Remarks** below) (Fig. 170).

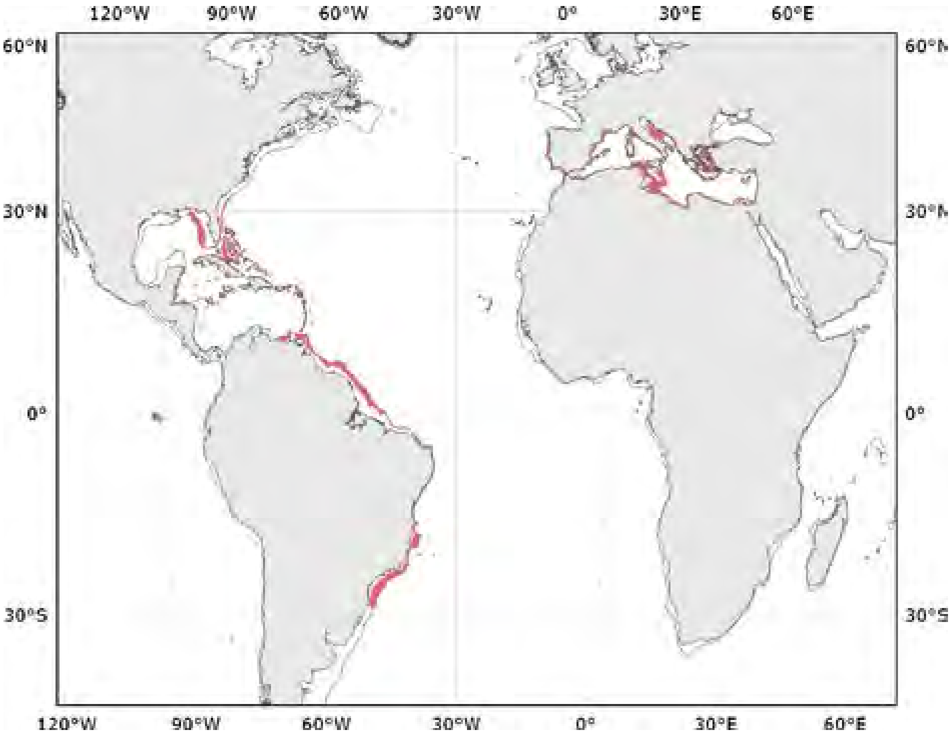


Fig. 170 ***Scaeurgus unicirrhus***

🟥 Known distribution

Habitat and Biology: Depth range from 50 to 500 m (typically >100 m). This species lives on the continental shelf and slope, on sandy, coralline, or muddy substrates. It feeds on molluscs, crustaceans, and small fishes. The spawning period in the Mediterranean Sea is from May to August. Females attach festoons of eggs to the substrate. Hatchlings are planktonic.

Interest to Fisheries: Unknown.

Local Names: ITALY: Polpo riccio; UNITED STATES OF AMERICA: Atlantic warty octopus.

Remarks: Norman *et al.* (2005) reviewed the genus ***Scaeurgus*** and described a neotype. There is still very little voucher material available for this species. The status of the western Atlantic form is yet to be resolved from the Mediterranean form.

Literature: Voss (1951a), Mangold (1988), Haimovici and Perez (1992), Sanchéz and Alvarez (1998), Quetglas *et al.* (2000), Bello (2004), Norman *et al.* (2005), Giordano *et al.* (2010).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Scaeurgus jumeau Norman, Hochberg and Boucher-Rodoni, 2005

Scaeurgus jumeau Norman, Hochberg and Boucher-Rodoni, 2005, *Journal of Molluscan Studies*, 71: 325. [Type locality: Southwest Pacific Ocean, South New Caledonia, Norfolk Ridge, East Jumeau Bank, 23°48'S, 168°17'E].

Size: Mantle length to 44 mm.

Geographical Distribution: Known only from East Jumeau Bank seamount, South New Caledonia.

Habitat and Biology: Depth range from 378 to 530 m.

Literature: No additional literature.

Scaeurgus nesisi Norman, Hochberg and Boucher-Rodoni, 2005

Scaeurgus nesisi Norman, Hochberg and Boucher-Rodoni, 2005, *Journal of Molluscan Studies*, 71: 329. [Type locality: Southwest Pacific Ocean, Coral Sea, Nova Bank, 22°24'S, 159°17'E].

Size: Mantle length to 56 mm.

Geographical Distribution: Known only from Nova Bank seamount, Coral Sea.

Habitat and Biology: Depth range from 295 to 340 m.

Literature: No additional literature.

Scaeurgus patagiatus Berry, 1913

Scaeurgus patagiatus Berry, 1913, *Proceedings of the United States National Museum*, 45: 564. [Type locality: Hawaiian Islands, off Maui Island].

Size: Mantle length to 63 mm.

Geographical Distribution: Hawaii and Japan.

Habitat and Biology: Depth range to 325 m.

Literature: Toll and Voss (1998), Norman *et al.* (2005).

Scaeurgus tuber Norman, Hochberg and Boucher-Rodoni, 2005

Scaeurgus tuber Norman, Hochberg and Boucher-Rodoni, 2005, *Journal of Molluscan Studies*, 71: 321. [Type locality: Southwest Pacific Ocean, south of New Caledonia, Norfolk Ridge, Jumeau Ouest, 23°41'S, 168°01'E].

Size: Mantle length to 24 mm.

Geographical Distribution: New Caledonia and Norfolk Ridge.

Habitat and Biology: Depth range from 230 to 391 m.

Literature: No additional literature.

Teretoctopus Robson, 1929

Teretoctopus Robson, 1929b, *Annals of the Magazine of Natural History*, (10), III: 608.

Type Species: *Teretoctopus indicus* Robson, 1929.

Diagnostic Features: Small to moderate-sized species. **Arms short, ~2 to 3 times mantle length. Arms subequal in length.** Arm autotomy at distinct plane absent. Webs deep, deepest >30% length of longest arm. **Dorsal and lateral webs subequal; ventral web slightly shorter.** Interbrachial web pouches absent. Suckers in two rows. **Enlarged suckers absent. Funnel organ consists of an arched transverse row of four short, rounded, longitudinal pads. Gills with 10 to 11 lamellae per demibranch.** Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary gland size not reported. Distinct crop present as side-branch off oesophagus. Ink sac absent. Radula with 9 elements, 7 rows of teeth and marginal plates. **Third right arm hectocotylized, distinctly shorter than opposite arm (60%).** Ligula elongate and moderate to large in size, 6 to 16% of arm length. Calamus present. Spermatophores unknown. Egg size unknown. **Colour pattern of preserved material pale buff with minute yellow-brown chromatophores, interspersed with a few larger ones.** Skin smooth. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 60 mm.

Geographical Distribution: Northern Indian Ocean.

Habitat and Biology: Poorly known; from depths of 300 to 1 200 m.

Remarks: The genus ***Teretoctopus*** remains poorly diagnosed, based on two poorly known species from deep waters off India.

Teretoctopus indicus Robson, 1929

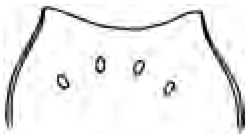
Teretoctopus indicus Robson, 1929b, *Annals of the Magazine of Natural History*, (10), III: 608. [Type locality: Arabian Sea, 24°45’N, 63°50’15”E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Fourpad octopus; **Fr** — Poulpe quatre-tampons; **Sp** — Pulpo con almohadillas.

Diagnostic Features: Small to moderate-sized species. Arms short, around 2 times mantle length. Arms approximately equal in length. Arm autotomy at distinct plane absent. Webs deep, 30 to 40% of arm length. Dorsal and lateral webs subequal; ventral web slightly shorter. Interbrachial web pouches absent. Suckers biserial and small, around 3% of mantle length. Sucker counts unknown. Enlarged suckers absent. Gills with 10 to 11 lamellae per demibranch. **Funnel organ of 4 short longitudinal pads**. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. **Ink sac absent**. Right third arm of males hectocotylized, around 60% length of opposite arm. Ligula elongate (~6% of arm length), narrow with small calamus. Hectocotylized arm sucker count unknown. Spermatophores unknown. Egg size unknown. **Colour:** Preserved material pale buff with minute yellow-brown chromatophores, interspersed with a few larger ones. **Two alternating longitudinal rows of large, subdermal, light-coloured chromatophores (founder chromatophores) on outer surface of each arm**. False-eye spots (ocelli) absent. **Sculpture: Skin smooth**. Skin ridge around lateral margin of mantle absent.



funnel organ

Size: Mantle length 34 mm; Known only from type specimen.

Geographical Distribution: Known only from the type material (Fig. 171).

Habitat and Biology: Depth range to 1 000 m. Biology and behaviour unknown.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Remarks: This poorly known deep-water species requires thorough revision.

Literature: Robson (1932), Voss (1988a).

Fig. 171 ***Teretoctopus indicus***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Teretoctopus alcocki Robson, 1932

Teretoctopus alcocki Robson, 1932, *A Monograph of the Recent Cephalopoda. Part II. Octopoda*. London, British Museum (Natural History): 251. [Type locality: Northern Indian Ocean, Bay of Bengal].

Size: Mantle length to 60 mm.

Geographical Distribution: Andaman Sea to Gulf of Oman.

Habitat and Biology: Depth range from 360 to 1 200 m.

Literature: No additional literature.

Tetracheledone Voss, 1955

Tetracheledone Voss, 1955, *Bulletin of Marine Sciences of the Gulf and Caribbean*, 5(2): 107.

Type Species: *Tetracheledone spinicirrus* Voss, 1955.

Diagnostic Features: Small, muscular species. Mantle spherical to ovoid, broad. Stylets present, large and mineralized. **Arms short, stout, 1.5 to 2 times length of mantle. Arms subequal in length.** Arm autotomy at distinct plane absent. **Webs deep, up to 45% of arm length.** Web deepest on lateral arms; web sectors of dorsal and ventral arms slightly shallower. Interbrachial web pouches absent. **Suckers in single row,** small and deeply set, 5 to 9% of mantle length. Enlarged suckers absent. **Funnel organ of 4 short longitudinal bars (IIII).** Gills with 7 to 9 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Rachidian tooth with long central cusp. Posterior salivary glands of moderate size, approximately equal in length with buccal mass. Oesophagus with swelling only, no distinct crop. **Ink sac present, free from digestive tract, unpigmented. Anal flaps absent.** Third right arm of males hectocotylized, shorter than opposite arm (~85%). Ligula large, approximately 4 to 7% of arm length, triangular with open groove. Calamus present, of moderate size, around 40% of ligula length. Spermatophores of moderate size, approximately 60% of mantle length, unarmed. Mature females and eggs unknown. Colour of preserved material pale pink. **Skin texture of body, arms and webs closely set with large, stellate papillae, giving spinous appearance. Two large stellate papillae over each eye. Skin ridge around lateral margin of mantle present.**

Size: Mantle length to 100 mm; total length to 260 mm.

Geographical Distribution: Off Florida, Cuba and Gulf of Mexico.

Habitat and Biology: Deep-water species from 200 to 400 m.

Remarks: Known only from a single species.

Tetracheledone spinicirrus Voss, 1955

Fig. 172

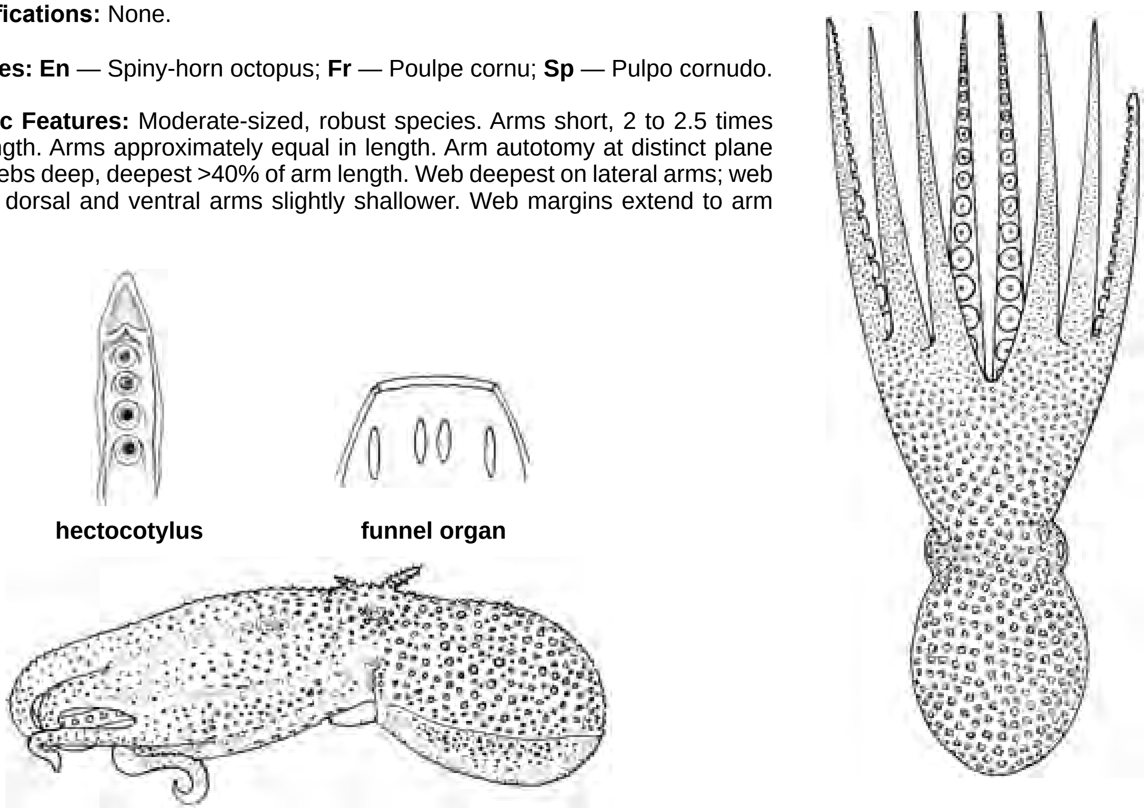
Tetracheledone spinicirrus Voss, 1955, *Bulletin of Marine Sciences of the Gulf and Caribbean*, 5(2): 107. [Type locality: Gulf of Mexico, Cuba, off Matanzas].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Spiny-horn octopus; **Fr** — Poulpe cornu; **Sp** — Pulpo cornudo.

Diagnostic Features: Moderate-sized, robust species. Arms short, 2 to 2.5 times mantle length. Arms approximately equal in length. Arm autotomy at distinct plane absent. Webs deep, deepest >40% of arm length. Web deepest on lateral arms; web sectors of dorsal and ventral arms slightly shallower. Web margins extend to arm


hectocotylus

funnel organ

lateral view

dorsal view

Fig. 172 *Tetracheledone spinicirrus*

tips. Interbrachial web pouches absent. **One row of suckers on each arm**. In larger animals, around 65 suckers on each normal arm. Enlarged suckers absent. Gills with 6 to 9 lamellae per demibranch. **Funnel organ of 4 short longitudinal pads**. Radula with 9 elements, 7 rows of teeth plus marginal plates. Oesophagus with swelling only, no distinct crop. Ink sac present. Right third arm of males hectocotylized, around 85% length of opposite arm. Ligula leaf-shaped, 4 to 10% of arm length. Calamus of moderate size, around 40% of ligula length. Hectocotylized arm with 34 suckers in examined material. Spermatophores of moderate size, around 45 mm, around 60% of mantle length, produced in moderate numbers (~25). Egg size unknown. **Colour:** Preserved material with pale pink base colour and crimson papillae. False-eye spots (ocelli) absent. **Sculpture: Pavement-like skin texture of numerous regular stellate papillae. Two large branched papillae over each eye. Skin ridge around lateral margin of mantle present.**

Size: Mantle length to 100 mm; total length to 260 mm.

Geographical Distribution: Gulf of Mexico, Straits of Florida, and Caribbean Sea; limits unknown (Fig. 173).

Habitat and Biology: Depth range from 200 to 400 m. Occurs on mud substrates. Nothing known of biology or behaviour.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Voss (1956), Humes and Voight (1997).

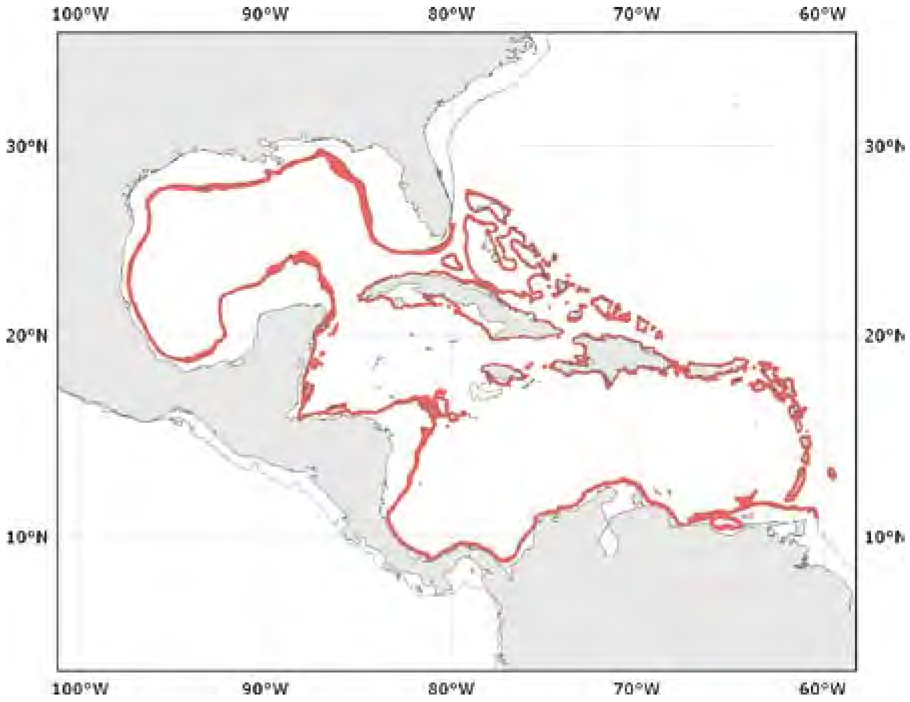


Fig. 173 ***Tetracheledone spinicirrus***

🟥 Known distribution

Thaumeledone Robson, 1930

Thaumeledone Robson, 1930, *Discovery Reports*, 2: 392.

Type Species: *Eledone brevis* Hoyle 1885. By original designation.

Diagnostic Features: Small to moderate-sized deep-water species. Mantle shape round to slightly ovoid. Stylets present, non-mineralized. **Arms short, around 1.5 to 2 times mantle length. Arms subequal in length.** Arm autotomy at distinct plane absent. **Web depth moderate to very deep, deepest 30 to 65% length of longest arm. Webs subequal in depth.** Interbrachial web pouches absent. **Suckers in single row,** small (3 to 8% of mantle length). Enlarged suckers absent. Funnel organ V V-shaped or 4 separate linear components (IIII). **Gills with 4 to 6 lamellae per demibranch. Radula degenerate with 1 to 5 rows of teeth, marginal plates absent.** Posterior salivary glands of moderate size (70 to 80% length of buccal mass). Oesophagus with swelling only, no distinct crop. **Ink sac absent. Anal flaps absent.** Third right arm of males hectocotylized with end of arm clearly differentiated into ligula and calamus, ligula large (9 to 17% of arm length), club-shaped with deep ligula groove without transverse ridges. **Calamus very long, 60 to 85% of ligula length.** Spermatophores long (1.2 to 1.4 times mantle length) and slender. Colour pattern variable among species. **A deep purple base is a common component of colour patterns,** either in base colour, on oral web and/or in skin papillae. **Skin texture papillose, typically with irregular and slightly stellate papillae, densely packed and intertwined to form fine-scale leopard-skin appearance.** Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 50 mm; total length to 170 mm.

Geographical Distribution: Southern Atlantic Ocean, perhaps broader.

Habitat and Biology: Deep waters between 350 and at least 1 500 m.

Remarks: O'Shea (1999) expanded the definition of the genus ***Thaumeledone*** to include two difficult-to-place taxa,

T. marshalli and ***T. zeiss***. Norman *et al.* (2004b) challenged this decision and proposed condensation of the generic diagnosis for ***Thaumeledone*** back to the original member taxa, ***T. brevis*** and ***T. gunteri*** only. Allcock *et al.* (2004) described a new species for this genus, ***T. peninsulae***. This work also placed the type species for the genus ***Bentheledone***, ***B. rotunda*** (Hoyle, 1885) in the genus ***Thaumeledone***, a decision not supported herein (see discussion for the genus ***Bentheledone***). Strugnell *et al.* (2008) reviewed relationships of the genus based on molecular sequences. As the type species for the genus ***Thaumeledone***, ***T. brevis***, is poorly diagnosed, ***T. gunteri*** is presented here as an example of this genus. O'Shea's (1999) two taxa, ***marshalli*** and ***zeiss***, are listed below under the generic form ***'Thaumeledone'***, awaiting further review.

Literature: O'Shea (1999), Allcock *et al.* (2004), Norman *et al.* (2004b), Strugnell *et al.* (2008).

Thaumeledone gunteri Robson, 1930

Fig. 174; Plate IX, 68

Thaumeledone gunteri Robson, 1930, *Discovery Reports*, 2: 392. [Type locality: South Atlantic Ocean (off South Georgia Island), 53°48'S, 35°57'W].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Gunter's octopus; **Fr** — Poulpe de Gunter; **Sp** — Pulpo de Gunter.

Diagnostic Features: Small to moderate-sized deep-water species. Eyes large and slightly pronounced. Stylets present, non-mineralized. **Arms short (1.5 to 2 times mantle length)**, subequal; dorsal pair slightly shorter (arm formula typically 4>3=2>1). Arm autotomy at distinct plane absent. Webs deep, around 40% length of longest arm. Webs subequal; ventral web slightly shorter (A=B=C=D>E). Interbrachial web pouches absent. One row of suckers on each arm. Sucker counts on normal arms to 36. Enlarged suckers absent. Funnel organ V V-shaped. **Gills with 5 lamellae per demibranch. Radula with 5 elements**: unicuspid rachidian, 1st lateral tooth low and conical, 2nd lateral tooth broad and nearly acuspid. Marginal plates absent. Posterior salivary glands of moderate size, approximately 80% length of buccal mass. Oesophagus with swelling only; no distinct crop. Ink sac absent. Anal flaps absent. Third right arm of males hectocotylized, ~85% length of opposite arm. Ligula large, around 17% length of hectocotylized arm, club-like with well-developed, deep groove lacking transverse ridges. **Calamus very large, around 80% length of ligula**. Hectocotylized arm with 19 to 22 suckers. Spermatophores large (around 110% of mantle length), unarmed. Eggs large (>10 mm). **Colour: Dorsal surfaces of live animals with densely packed irregular and roughly stellate dark purple papillae over white base colour. Ventral surfaces deep purple**. **Sculpture:** Skin relatively smooth with low rugose sculpture formed by stellate papillae. Larger papillae over eyes. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 50 mm; total length to 107 mm.

Geographical Distribution: South Atlantic Ocean, off South Georgia (Fig. 175).

dorsal view

Fig. 174 ***Thaumeledone gunteri***

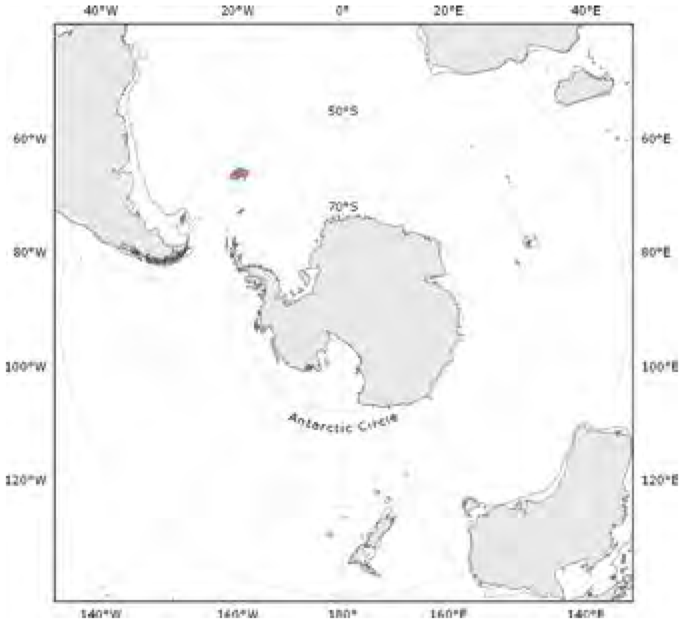


Fig. 175 ***Thaumeledone gunteri***

🟥 Known distribution

Habitat and Biology: Depth range from 365 to 965 m. Nothing known of the biology or behaviour of this deep-water species. Large eggs indicate hatchlings are benthic.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Yau *et al.* (2002), Allcock *et al.* (2004), Collins *et al.* (2004), Strugnell *et al.* (2008).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Thaumeledone brevis (Hoyle, 1885)

Eledone brevis Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 15: 230. [Type locality: Southwestern Atlantic Ocean, Uruguay, off Montevideo, 37°17’S, 53°52’W].

Size: Mantle length to 20 mm.

Geographical Distribution: Known only from the type locality in southwestern Atlantic Ocean.

Habitat and Biology: Depth range to 1 000 m.

Literature: Robson (1932).

Thaumeledone peninsulae Allcock, Collins, Piatkowski and Vecchione, 2004

Thaumeledone peninsulae Allcock, Collins, Piatkowski and Vecchione, 2004, *Deep-Sea Research II*, 51: 1891. [Type locality: Southern Ocean, Antarctic Peninsula, 61°59’S, 60°19’W].

Size: Mantle length to 48 mm; total length to 120 mm.

Geographical Distribution: Southern Ocean, Antarctic Peninsula.

Habitat and Biology: Depth range from 377 to 1 512 m.

Literature: Strugnell *et al.* (2008).

‘Thaumeledone’ marshalli O’Shea, 1999

Thaumeledone marshalli O’Shea, 1999, *NIWA Biodiversity Memoir*, 112: 249. [Type locality: New Zealand, off east coast of North Island].

Size: Mantle length to 44 mm; total length to 100 mm.

Geographical Distribution: New Zealand and Chatham Rise.

Habitat and Biology: Depth range from 2 000 to 2 500 m.

Remarks: Generic placement questioned in Norman *et al.* (2004b).

Literature: Norman, *et al.* (2004b).

‘Thaumeledone’ zeiss O’Shea, 1999

Thaumeledone zeiss O’Shea, 1999, *NIWA Biodiversity Memoir*, 112: 246. [Type locality: East of New Zealand].

Size: Mantle length to 55 mm; total length to 120 mm.

Geographical Distribution: New Zealand and Chatham Rise.

Habitat and Biology: Depth range from 1 000 to 1 400 m.

Remarks: Generic placement questioned in Norman *et al.* (2004b).

Literature: Norman *et al.* (2004b).

Thaumoctopus Norman and Hochberg, 2005

Thaumoctopus Norman and Hochberg, 2005b, *Molluscan Research*, 25(2): 58.

Type Species: *Thaumoctopus mimicus* Norman and Hochberg, 2005.

Diagnostic Features: Moderate-sized shallow-water species. Mantle elongate ovoid. Stylets present, short, non-mineralized. **Arms long and thin, 7 to 10 times mantle length. Dorsal arms shortest, (typically 4>3>2>1). Arm autotomy present at the level of the 12th to 13th proximal sucker. Webs shallow when retracted (deepest <10% length of longest arm), thin and retractile** with well-developed margin along ventral edges of all arms. Interbrachial web pouches absent. Suckers in two rows. **Enlarged suckers absent.** Funnel organ small, W-shaped with short lateral limbs. Gills with 9 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands large, twice the length of buccal mass. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Third right arm of males hectocotylized, significantly shorter than opposite arm (~50%). Ligula small (<2% of arm length) with distinct groove. **Calamus absent.** Spermatophores unarmed and short (around 40% mantle length), produced in moderate numbers (~25). Eggs small-type (but mature females unknown). Colour patterns variable in single known species, from uniform pale or dark, to mottled, to dramatically banded. False eye-spots (ocelli) absent. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). Skin largely smooth with secondary papillae scattered around lateral and posterior margins of mantle. **Paired, elongate, sharply pointed papillae present over each eye.** Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 58 mm; total length to over 480 mm.

Geographical Distribution: Tropical Indo-West Pacific from north-east Australia and New Caledonia to the Philippines and west to the Red Sea.

Habitat and Biology: Shallow coastal waters on soft sediment substrates to at least 37 m.

Remarks: Single, shallow-water species found in Indo-Malayan Archipelago, western Pacific and tropical Indian Ocean.

Thaumoctopus mimicus Norman and Hochberg, 2005

Fig. 176; Plate IX, 69

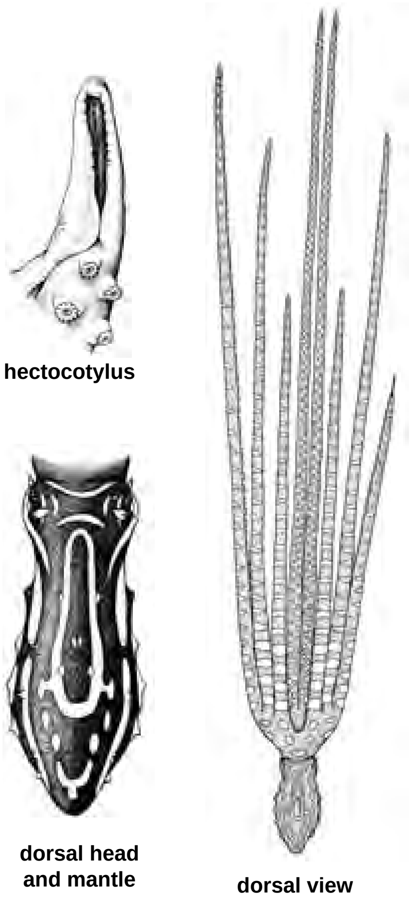
Thaumoctopus mimicus Norman and Hochberg, 2005b, *Molluscan Research*, 25(2): 58. [Type locality: New Caledonia, lagoon off north tip of island, 19°49'S, 163°48'E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Mimic octopus; **Fr** — Poulpe mimétique; **Sp** — Pulpo mímico.

Diagnostic Features: Moderate-sized, elongate, muscular species. Eyes of moderate size and slightly pronounced. Stylets present, short and non-mineralized. **Arms long (7-10 times mantle length)**, ventral arms longest (arm formula 4>3>2>1). **Arm autotomy present at level of 12th to 13th proximal sucker**. Webs thin and retractile, extending as well-developed margins along ventral edges of all arms, lateral webs deepest with sector A typically most shallow. Interbrachial web pouches absent. Two rows of suckers on each arm. Sucker counts on normal arms to 283. Enlarged suckers absent. Funnel organ W-shaped with short outer limbs. **Gills with 9 lamellae per demibranch**. Third right arm of males hectocotylized, ~50% length of opposite arm. **Ligula small**, length 1.7 to 1.9% of hectocotylized arm length, elongate with well developed groove. **Calamus absent, replaced by slight thickening of rim of proximal ligula groove**. Hectocotylized arm with 130 and 146 suckers in the two available males. Spermatophores unarmed and short (around 40% mantle length), produced in moderate numbers (~25). Eggs small-type (mature females unknown). **Colour:** patterns variable, dorsal mantle typically with irregular longitudinal white markings against dark brown background. Two mantle pattern components are consistently present: 1) teardrop ring in mid to anterior dorsal mantle, and 2) white "U" on posterio-dorsal mantle. Arms with regular white bands against dark brown base colour. Arm white spots present in dark arm bands. **Sculpture:** Skin relatively smooth with a rim of secondary papillae around lateral and


hectocotylus

dorsal head and mantle

dorsal view

Fig. 176 ***Thaumoctopus mimicus***

posterior mantle forming spiked appearance; patch and groove system absent. Paired, sharply pointed, elongate papillae present over each eye: larger above eye, smaller on anterior face of eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 58 mm; total length to over 480 mm.

Geographical Distribution: New Caledonia and north-east Australia (Lizard Island) and Papua New Guinea, through Indonesia and north to the Philippines. Also recorded from the Red Sea (Fig. 177).

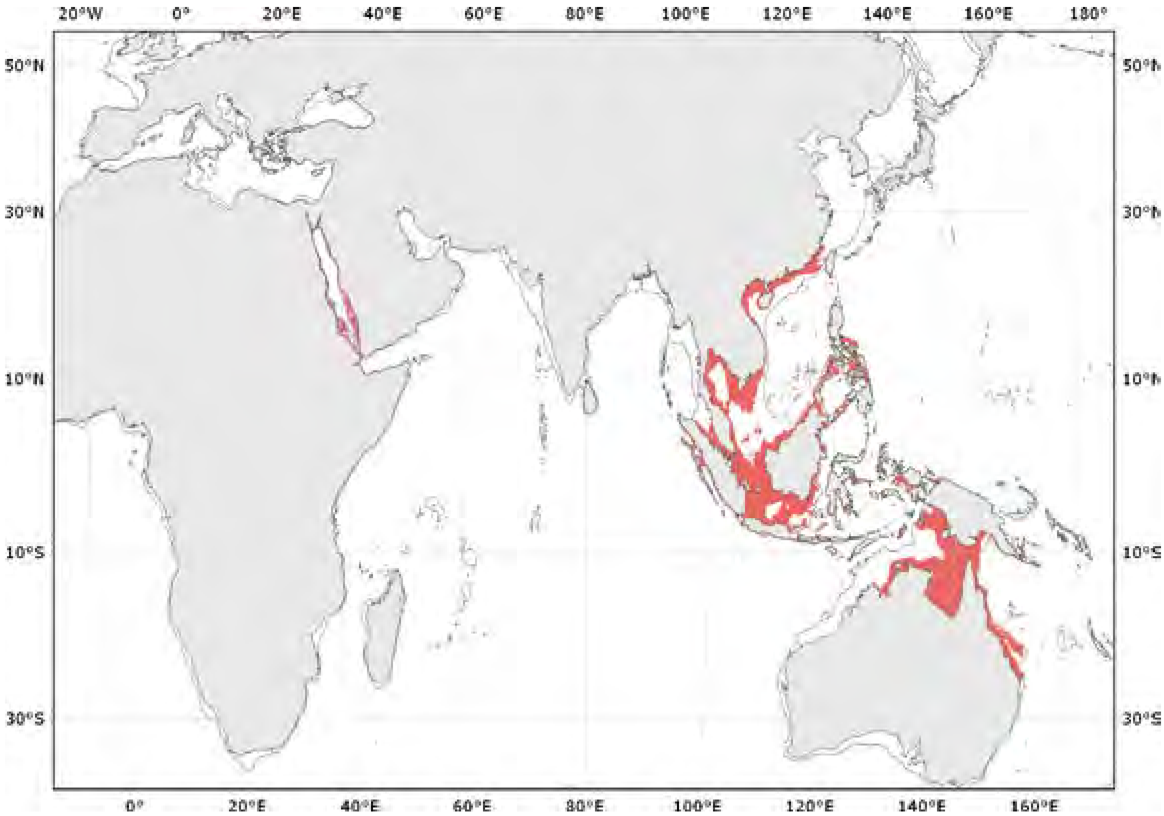


Fig. 177 ***Thaumoctopus mimicus***

🟥 Known distribution

Habitat and Biology: Depth range from 0.5 to at least 37 m. Inhabits open plains of sand and/or mud. Often found in areas adjacent to silt-laden river outflows. The species is active during the day, making foraging bouts from the safety of a lair throughout daylight hours. This octopus often occupies the vacated burrows of other animals. These lairs appear temporary or may form a network of regular lairs within a home range. Individuals were observed to occupy a particular hole for periods of between one and four days. Some individuals were observed to leave one hole at first light, forage throughout the day (including entering and exiting from various animal burrows throughout the day) and remaining overnight within the last hole encountered during foraging bouts. These animals were observed to emerge from the same hole at first light the next day.

This species is best known for its mimicry of toxic models that co-occur in the same habitat, namely banded soles, sea snakes, and lionfish, with other distinct postures and behaviours currently being open to interpretation.

Interest to Fisheries: Some aquarium trade occurs for this species. High fatality rates would make such harvest a potential conservation issue. The high tourism, photography and documentary profile of this species means that it is of significant commercial value alive and in its natural habitat, particularly in places such as Bali and northern Sulawesi, Indonesia.

Local Names: Unknown.

Literature: Norman *et al.* (2001, 2005b), Hanlon *et al.* (2008), Huffard *et al.* (2010b).

Velodona Chun, 1915

Velodona Chun, 1915, *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer Valdivia 1898-1899*, 18: 479.

Type Species: *Velodona togata* Chun, 1915.

Diagnostic Features: Large, muscular, deep-water species. Mantle spherical to ovoid. Stylets present, showing some calcification. **Arms muscular, moderate to long, 3 to 4.5 times mantle length. Dorsal arms longest, arm formula 1>2>3>4.** Arm autotomy at distinct plane absent. Webs of moderate depth, 18 to 26% of arm length. **Web margins extend to arm tips, flaring to form veil-like extensions in distal portions.** Interbrachial web pouches absent. **Suckers in single row.** Enlarged suckers absent. Funnel organ V V-shaped. Gills with 9 to 11 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands of moderate size, approximately size of buccal mass. Oesophagus with swelling only, no distinct crop. Ink sac poorly developed. Anal flaps absent. Third right arm of males hectocotylized, shorter than opposite arm. Ligula and distinct calamus present. Spermatophores large, around 110% of mantle length. Eggs large, around 19 mm. Colour pattern of live animals unknown. Preserved material shows uniform orange-brown. **Skin texture of regular scattering of rounded warts on all dorsal surfaces.** Single large papilla on each base of the dorsal arm pair. Larger patch of papillae present over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 150 mm; total length to around 680 mm.

Geographical Distribution: Genus restricted to southwest Indian Ocean.

Habitat and Biology: Known depth range 290 to 749 m.

Remarks: Single, deep-water species from off the south-east coast of Africa.

Velodona togata Chun, 1915

Fig. 178

Velodona togata Chun, 1915, *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer Valdivia 1898-1899*, 18: 479. [Type locality: off coast of east Africa (Tanzania), north of Zanzibar].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Angel octopus; **Fr** — Poulpe ange; **Sp** — Pulpo angel.

Diagnostic Features: Large, muscular species with veil-like webs on arm tips. Arms moderate to long, 3 to 4.5 times mantle length. **Dorsal arms longest (typically 1>2>3>4)**. Arm autotomy at distinct plane absent. Webs of moderate length, deepest around 18 to 26% of arm length. Web deepest on lateral arms; web sectors of dorsal and ventral arms shallowest. **Web margins expand towards arm tips to form wide veil-like extensions on the arm tips, particularly obvious on larger dorsal arm pair**. Interbrachial web pouches absent. One row of suckers on each arm. In larger animals, up to 102 suckers on each normal arm. Enlarged suckers absent. Gills with 9 to 11 lamellae per demibranch. Funnel organ V V-shaped, outer limbs much shorter than medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Oesophagus with swelling only, no distinct crop. **Ink sac poorly developed**. Third right arm of males hectocotylized, 72 to 85% length of opposite arm. Ligula of moderate size with thick margins, 6 to 9% of arm length. Calamus of moderate size and sharp, 30 to 34% of ligula length. Hectocotylized arm with 38 to 47 suckers. Spermatophores large, around 120 mm, around 110% of mantle length, produced in low numbers (<10). Eggs large, around 19 mm. **Colour:** Live animal colour patterns unknown. Preserved material uniform orange-brown. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of numerous, raised, rounded papillae of various sizes scattered over dorsal and lateral surfaces. Single, large papilla on base of each dorsal arm. Larger patch of papillae present over each eye. Skin ridge around lateral margin of mantle absent.

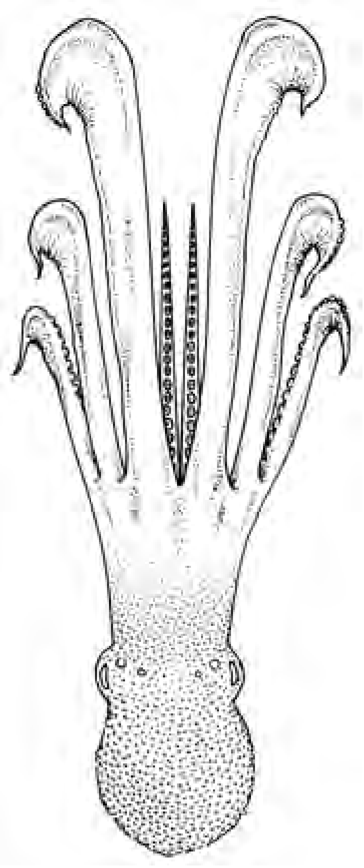


Fig. 178 ***Velodona togata***

Size: Mantle length to 150 mm; total length to around 680 mm.

Geographical Distribution: Western Indian Ocean: south-east coast of Africa from Durban, South Africa to Mozambique (Fig. 179).

Habitat and Biology: Depth range from 290 to 749 m. Biology and behaviour poorly known. Large eggs hatch into benthic young.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Glaubrecht and Salcedo-Vargas (2000).

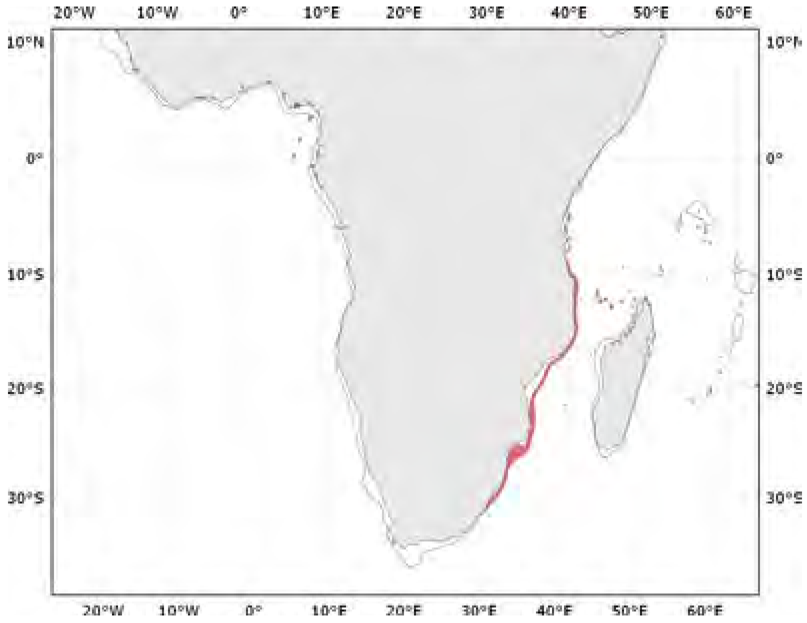


Fig. 179 ***Velodona togata***

🟥 Known distribution

Vosseledone Palacio, 1978

Vosseledone Palacio, 1978, *Bulletin of Marine Science*, 28(2): 282.

Type Species: *Vosseledone charrua* Palacio, 1978.

Diagnostic Features: Moderate-sized, robust, deep-water species. Mantle spherical, broad. Stylets not reported. **Arms short, approximately 2 times mantle length. Arms subequal in length.** Arm autotomy at distinct plane absent. **Webs deep, deepest around 40% length of longest arm.** Web deepest on lateral arms; web sectors of dorsal and ventral arms shallowest. Interbrachial web pouches absent. **Suckers in single row.** Enlarged suckers absent. Funnel organ V V-shaped, limbs of approximately equal length. **Gills with 6 to 7 lamellae per demibranch. Radula highly modified with only 3 elements, 3 rows of teeth, a central rachidian tooth with wide paddle-like flanges between two rows of wide flattened teeth.** Posterior salivary glands not described. Distinct crop present as side-branch off oesophagus. Ink sac present. Third right arm of males hectocotylized, shorter than opposite arm. Ligula large and wide with open groove. Calamus large. Spermatophores large, approximately equal to mantle length. Eggs large. Colour patterns unknown. Preserved material a uniform cream-brown. **Skin texture of numerous well-spaced, small, papillose warts on dorsal and lateral surfaces. Ventral surfaces smooth.** Two papillae over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 76 mm; total length to around 200 mm.

Geographical Distribution: Known only from western Atlantic Ocean off Brazil and Uruguay.

Habitat and Biology: Collected from 10 to 200 m.

Remarks: Single, poorly known species from shallow waters off southern Brazil and Uruguay, Atlantic Ocean.

Vosseledone charrua Palacio, 1978

Fig. 180

Vosseledone charrua Palacio, 1978, *Bulletin of Marine Science*, 28(2): 282. [Type locality: Western Atlantic Ocean, Uruguay, east of Punta del Este, 35°14’S, 52°28’W].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Charrua octopus; **Fr** — Poulpe charrua; **Sp** — Pulpo charrúa.

Diagnostic Features: Small, muscular species. Arms short, around 2 times mantle length. Arms approximately equal in length. Arm autotomy at distinct plane absent. **Webs deep, deepest around 40% of arm length**. Web deepest on lateral arms; web sectors of dorsal and ventral arms shallowest. Interbrachial web pouches absent. **One row of suckers on each arm**. Sucker counts unknown. Enlarged suckers absent. Gills with 6 to 7 lamellae per demibranch. **Funnel organ V V-shaped, limbs of approximately equal length. Radula highly modified with three rows of teeth, a central rachidian tooth with wide paddle-like flanges between two rows of wide flattened teeth**. Distinct crop present as side-branch off oesophagus. Ink sac present. Right third arm of males hectocotylized, 73 to 86% length of opposite arm. Ligula large and wide with open groove, 8 to 11% of arm length. Calamus large, 43 to 59% of ligula length. Hectocotylized arm sucker count unknown. Spermatophores large, around 50 mm, approximately equal to mantle length, produced in low numbers (~3). **Eggs large, around 13 mm. Colour:** Live colour patterns unknown. Preserved material is uniform cream-brown in colour. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of numerous, well-spaced, small, papillose warts on dorsal and lateral surfaces. Ventral surfaces smooth. Two papillae over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 76 mm; total length to around 200 mm.

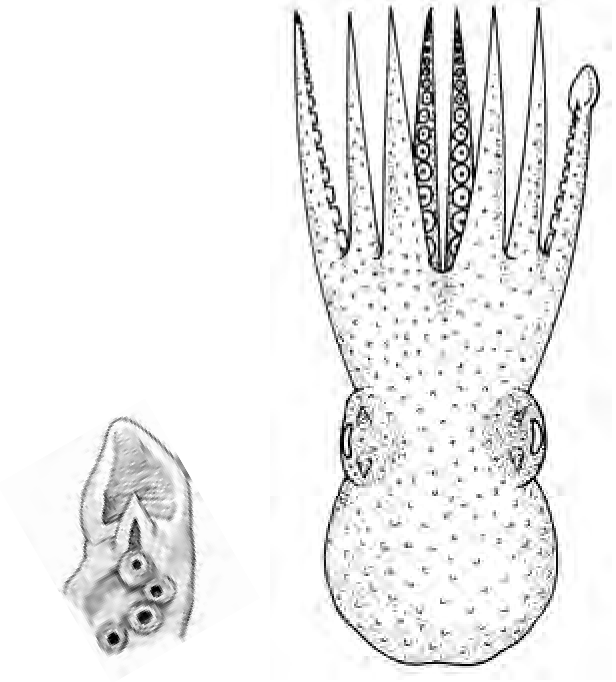
Geographical Distribution: Known only from western Atlantic, off southern Brazil and Uruguay (Fig. 181).

Habitat and Biology: Depth range from 10 to 200 m. Nothing known of the biology or behaviour of this species.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Palacio (1978).



hectocotylus

dorsal view

Fig. 180 *Vosseledone charrua*

Fig. 181 *Vosseledone charrua*

🟥 Known distribution

Vulcanoctopus González and Guerra, 1998

Vulcanoctopus González and Guerra *in* González, Guerra, Pascual and Briand, 1998, *Cahiers de Biologie Marine*, 39: 171.

Type Species: *Vulcanoctopus hydrothermalis* González and Guerra, 1998.

Diagnostic Features: Small, deep-water, vent species. **Mantle amphora-shaped. Eyes small.** Stylets absent. **Arms of moderate length, 3 to 4 times mantle length, thin and finely attenuate. Dorsal arms longest, typically 1>2>3>4.** Arm autotomy at distinct plane absent. **Webs shallow, deepest 10 to 15% of arm length. Webs deepest between dorsal arms, shortest between ventral arms.** Interbrachial web pouches absent. **Suckers in two rows, very small,** ~6% of mantle length. Enlarged suckers absent. Funnel organ W-shaped with wide and short outer limbs. Gills with 8 to 10 lamellae per demibranch. Radula with 9 elements, 7 transverse rows of teeth plus marginal plates. Rachidian with long central cusp and 1 to 2 lateral cusps. Posterior salivary glands large, larger than buccal mass. Distinct crop present as side branch off oesophagus. **Ink sac absent. Anal flaps absent.** Third right arm of males hectocotylized, distinctly shorter than opposite arm (60 to 70%). Ligula as sharply pointed cone with open groove. Calamus present. Spermatophores moderate to large, as long or longer than mantle length, produced in high numbers (up to 50). Eggs of intermediate size, approximately 10% of mantle length. **Colour white, chromatophores absent. Skin smooth in life without apparent papillae.** Preserved specimens with convoluted contractions forming uniform finely wrinkled or rugose texture. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 55 mm; total length to around 180 mm; body weight to 45 g.

Geographical Distribution: Hydrothermal vents of the East Pacific Rise, Pacific Ocean.

Habitat and Biology: Associated with hydrothermal vent systems and associated biota. Collected from depths between 2 600 and 2 832 m.

Remarks: Strugnell *et al.* (2009c) found close phylogenetic affinities between this octopus and the deep-sea genus ***Benthoctopus***, proposing that they belong in the same family.

Literature: Voight (2008), Strugnell *et al.* (2009c).

Vulcanoctopus hydrothermalis González and Guerra, 1998

Fig. 182; Plate IX, 70

Vulcanoctopus hydrothermalis González and Guerra in González, Guerra, Pascual and Briand, 1998, *Cahiers de Biologie Marine*, 39: 172. [Type locality: Northeastern Pacific Ocean, eastern Pacific Ocean, north of Genesis 12° 48' 43"S, 103°56.41'W].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Vent octopus; **Fr** — Poulpe thermal; **Sp** — Pulpo de fumarola.

Diagnostic Features: Small, deep-sea, benthic octopus. Mantle amphora-shaped. **Eyes small. Stylets absent**. Arms thin, finely attenuate, of moderate length, 3 to 4 times mantle length. Dorsal arms longest (typically 1>2>3>4). Arm autotomy at distinct plane absent. Webs shallow, deepest between dorsal arms, shallowest between ventral arms. Interbrachial web pouches absent. Two rows of suckers on each arm, small, ~6% of mantle length. In larger animals, around 130 to 150 suckers on each normal arm. Enlarged suckers absent. **Funnel organ W-shaped, wide with short lateral limbs**. Gills with 8 to 10 lamellae per outer demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Posterior salivary glands large, larger than buccal mass. Distinct crop present as side-branch off oesophagus. **Ink sac and anal flaps absent**. Third right arm of males hectocotylized, about 60 to 70% length of opposite arm. Ligula of moderate-size, 7 to 10% of arm length. Calamus of moderate size, 25 to 40%. Hectocotylized arm with 65 to 75 suckers. Spermatophores long, around 25 to 60 mm, 75 to 110% of mantle length; produced in moderate numbers (~15 to 50). Spermatophores unarmed. Eggs relatively small, around 10% of mantle length. **Colour: Uniformly white, chromatophores absent**. False-eye spots (ocelli) absent. **Sculpture:** Skin smooth; lateral mantle ridge, supraocular and dorsal mantle papillae absent.

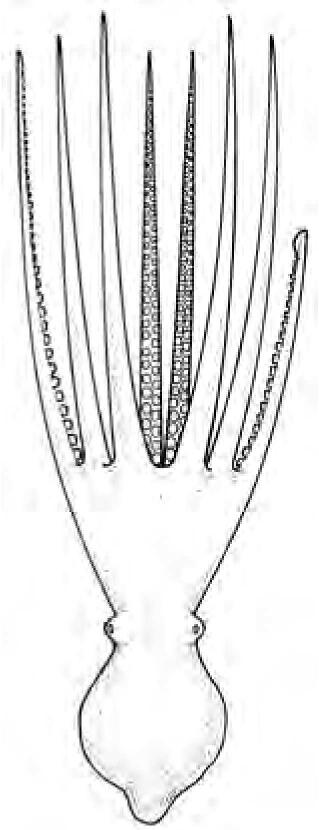

dorsal view

Fig. 182 ***Vulcanoctopus hydrothermalis***

Size: Mantle length to 55 mm; total length to around 180 mm; body weight to 45 g.

Geographical Distribution: Pacific Ocean, hydrothermal vents of the East Pacific Rise (Fig. 183).

Habitat and Biology: Depth range from around 2 600 to 2 832 m. Known to live in association with hydrothermal vents. Found in very high densities with highly male-biased sex ratios. Feeds on amphipods.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: López-González *et al.* (2000), González *et al.* (2002, 2008a), Rocha *et al.* (2002), Voight (2005, 2008), Strugnell *et al.* (2009b), Gestal *et al.* (2010), Roura *et al.* (2010c).

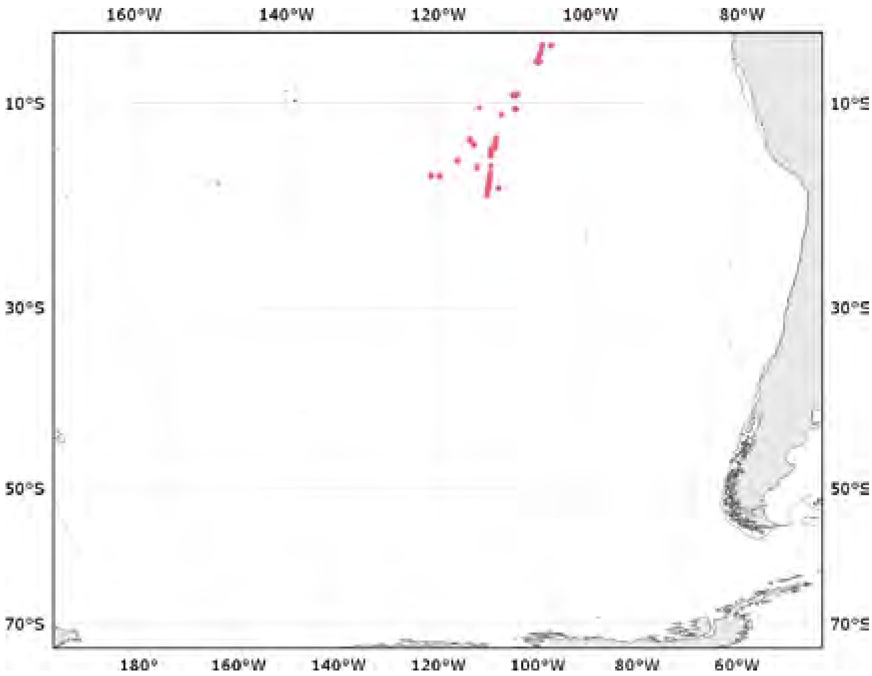


Fig. 183 ***Vulcanoctopus hydrothermalis***

🟥 Known distribution

Wunderpus Hochberg, Norman and Finn, 2006

Wunderpus Hochberg, Norman and Finn, 2006, *Molluscan Research*, 26(3): 129.

Type Species: *Wunderpus photogenicus* Hochberg, Norman and Finn, 2006.

Diagnostic Features: Small, shallow-water species. **Mantle thin-walled, elongate ovoid to amphora-shaped. Eyes small on elongate stalks.** Stylets present, short, chitinous (non-mineralized). **Arms long, thin and muscular, >5 times mantle length. Dorsal arms shortest; arm formula typically 4=3=2>1. Arm autotomy present at the level of the 8th to 12th proximal sucker. Webs shallow in preserved material (deepest 7 to 10% length of longest arm), thin and elastic in life, extend for length of arms as well-developed margins.** Interbrachial web pouches absent. Suckers in two rows, small and widely spaced. Enlarged suckers absent. Funnel organ small, W-shaped with very short lateral limbs. Gills with 6 to 7 (rarely 5) lamellae per demibranch plus terminal lamella. Radula with 9 elements, 7 transverse rows of teeth plus marginal plates. Posterior salivary glands larger than buccal mass. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. **Third right arm hectocotylized, very short, less than one third of opposite arm.** Copulatory organ with ligula and calamus; ligula size small to moderate (<6% of arm length) with distinct groove. Spermatophores short, around 50% of mantle length, unarmed. Eggs small (chorion capsule 2.9 to 3.6 mm long). **Diagnostic colour pattern of distinct white bands along arms and white spots and bars or stripes on mantle, head and eye stalks.** Ocelli absent. Skin largely smooth between erectile primary and secondary papillae. **Single long conical papilla present above each eye, tip bluntly rounded.** Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 36 mm; total length to over 230 mm.

Geographical Distribution: Indo-Malayan Archipelago, Pacific Ocean.

Habitat and Biology: Occurs on soft sediment substrates and rubble at depths between 0.5 and 20 m.

Remarks: Single Indo-Malayan species.

Wunderpus photogenicus Hochberg, Norman and Finn, 2006

Fig. 184; Plate IX, 71

Wunderpus photogenicus Hochberg, Norman and Finn, 2006, *Molluscan Research*, 26(3): 129. [Type locality: Indonesia, Bali].

Frequent Synonyms: None.

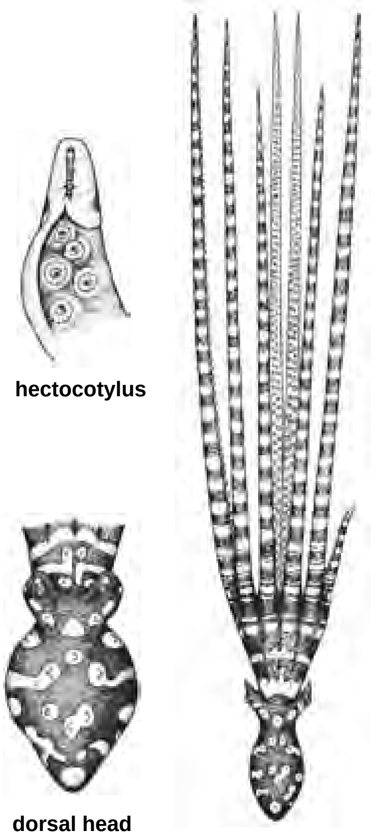
Misidentifications: None.

FAO Names: En — Wunderpus; **Fr** — Poulpe photogénique; **Sp** — Pulpo fotogénico.

Diagnostic Features: Small, elongate muscular species. **Eyes small and stalked, often raised in live animals so head appears Y-shaped**. Stylets present, short and chitinised. **Arms long** (**5 to 7 times mantle length**), ventral or lateral arms typically longest, dorsal arms slightly shorter. **Arm autotomy appears present at level of 8th to 12th proximal sucker**. Webs thin and retractile, extend as well-developed margins along ventral edges of all arms; short relative to arm length in preserved (retracted specimens), depth around 7 to 10% length of longest arm. Dorsal web typically most shallow. Interbrachial web pouches absent. Suckers in two rows. Sucker counts on normal arms to 230. Enlarged suckers absent. Funnel organ W-shaped with very short outer limbs. **Gills with 6 to 7 lamellae per demibranch** (**rarely 5**). Third right arm of males hectocotylized, very short, less than one third length of opposite arm. **Ligula small**, length 3.4 to 5.3% of hectocotylized arm length, squat with well developed groove. **Calamus low, around 30 to 50% of ligula length**. Hectocotylized arm with 64 suckers in two available males. Spermatophores unarmed and short (around 50% mantle length), produced in moderate numbers (~25). Eggs small. **Colour: Base colour of pale orange to red. Distinct white bands along arms and distinctive contrasting pattern of white spots and bars or stripes on mantle, head and eye stalks**. **Sculpture:** Skin smooth, patch and groove system absent. **Single elongate and blunt-tipped papilla present over each eye**. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 36 mm; total length to over 230 mm.

Geographical Distribution: Tropical Indo-Malayan Archipelago from Philippines to Vanuatu (Fig. 185).



hectocotylus

dorsal head and mantle

dorsal view

Fig. 184 ***Wunderpus photogenicus***

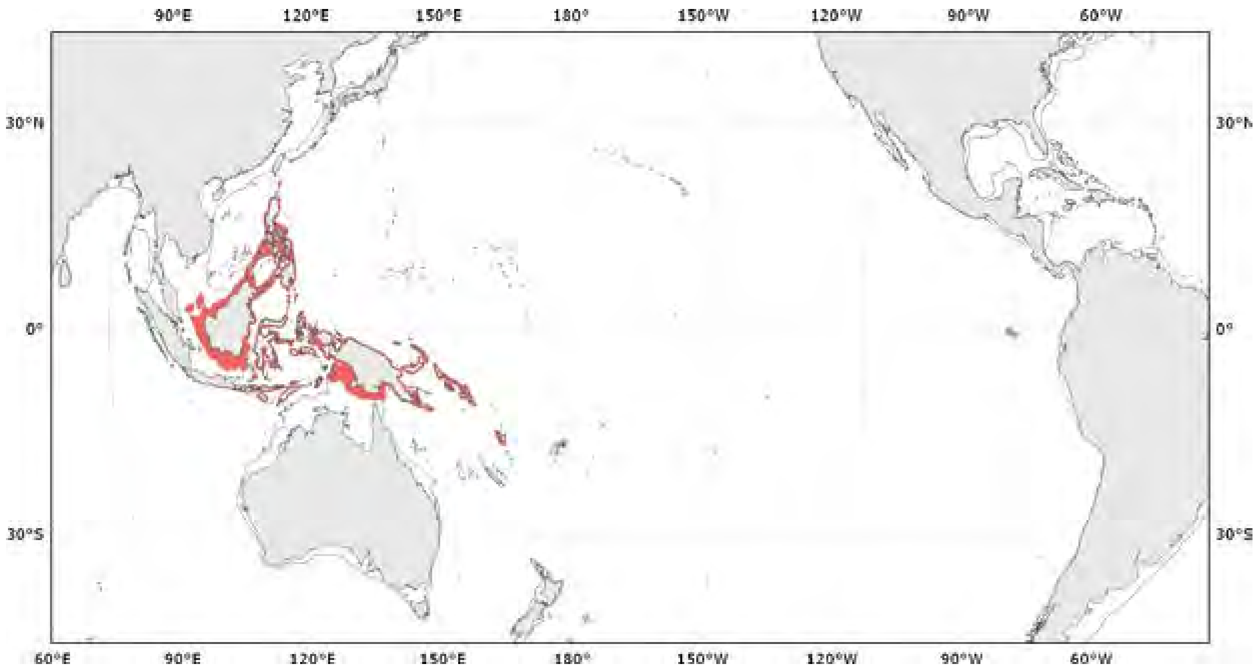


Fig. 185 ***Wunderpus photogenicus***

🟥 Known distribution

Habitat and Biology: Depths range from 0.5 to 20 m. This species has been encountered primarily on soft sediment substrates where it occupies burrows in deep sand. Individuals were found to occupy the same burrow for periods of at least three weeks. This species appears to have a crepuscular activity pattern, emerging to forage during half-light periods at dusk and dawn. Reports of day activity from photographers and film crews were determined to be observations of another long-armed species, ***Thaumoctopus mimicus***.

Interest to Fisheries: Some aquarium trade occurs for this species. High fatality rates would make such harvest a potential conservation issue. The high tourism, photography and documentary profile of this species means that it is of significant commercial value alive and in its natural habitat, particularly in places such as Bali and northern Sulawesi, Indonesia.

Local Names: Unknown.

Remarks: This species frequently is confused with the mimic octopus (***Thaumoctopus mimicus***) which co-occurs in similar tropical habitats.

Literature: Norman (2000), Miske and Kirchhauser (2006), Huffard *et al.* (2008b, 2009).

SPECIES PROVISIONALLY PLACED IN THE GENUS ‘*Octopus*’

As outlined above, recent molecular studies (Guzik *et al.,* 2005, Strugnell *et al.,* 2005) indicate that numerous distinct genera are represented within the genus ***Octopus*** as it currently is defined. Many of the 100+ species previously placed within this genus are likely to belong in distinct genera (both existing or currently undescribed). As this major taxonomic revision of the family Octopodidae has only recently commenced, many of the species historically treated under the genus name ***Octopus*** are yet to be reviewed. Until these revisions are undertaken, these species are provisionally retained under the generic name ***‘Octopus’***, with quotation marks indicating their unknown position. The following species fall into this category and it is likely that the majority will be transferred to genera distinct from ***Octopus*** *sensu stricto* over the coming decade.

These disparate species share the following morphological attributes:

- two rows of suckers on arms
- ink sac and anal flaps present
- third right arm of males hectocotylized

‘Octopus’ alecto Berry, 1953

Fig. 186

Octopus alecto Berry, 1953, ***Leaflets in Malacology***, 1(10): 56. [Type locality: Mexico, Sonora, south of Estero Doldado].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Snakearm octopus; **Fr** — Poulpe serpent; **Sp** — Pulpo serpiente.

Diagnostic Features: Moderate-sized, elongate species with squat body. **Arms long and snake-like**, 4 to 6 times mantle length. Lateral arms longest (typically 2=3>1>4). **Arm autotomy present**; many animals have one or more arms missing. Webs of moderate depth, deepest 14 to 22% of arm length. **Web thin and translucent**, deepest on lateral arms; webs between dorsal and ventral arm pairs shallowest. Web margins extend to arm tips when webs are inflated. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 130 suckers on each normal arm. Enlarged suckers present in mature males on arms 2 and 3. Gills with 6 to 7 lamellae per demibranch. Funnel organ W-shaped. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, approximately equal in length with opposite arm. Ligula narrow and recurved with a deep groove. Ligula length around 10% of arm length. Calamus minute, weakly developed.

Hectocotylized arm with around 130 suckers. Spermatophores ~18 mm long, produced in moderate numbers (32 in storage sac of one individual). Eggs small, around 2 to 2.5 mm. **Colour: Reddish brown with small, conspicuous white spots on dorsal mantle, head, web and arms. Green iridophores scattered over dorsal surfaces**. Ventral mantle pale cream with few large dark chromatophores. False-eye spots (ocelli) absent. **Sculpture:** Skin soft and puffy, generally smooth but can appear wrinkled. Dorsal mantle and area around eyes densely covered with minute papillae. One large and three smaller papillae over each eye. One large primary flap on posterior dorsal mantle. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 65 mm; total length to at least 300 mm.

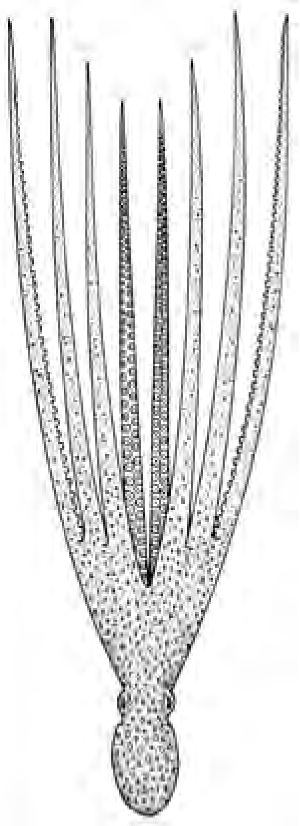
Geographical Distribution: Gulf of California, Mexico to Ecuador (Fig. 187).

Habitat and Biology: Depths range from 0 to 4 m. Little is known about the biology of this rarely seen intertidal to shallow subtidal species. '***Octopus***' ***alecto*** lives amongst rocks in tide pools and in rocky and coral reef areas. It appears to be nocturnally active and often is found at night foraging during low tide in rocky intertidal areas. The species is presumed to feed on small crabs and hermit crabs. Festoons of small eggs are laid in June and July. Hatchlings are planktonic.

Interest to Fisheries: *'Octopus alecto'* supports a small subsistence fishery in Mexico.

Local Names: Unknown.

Literature: Hochberg *et al.* (1992), Roper *et al.* (1995).



dorsal view

Fig. 186 *'Octopus' alecto*

Fig. 187 *'Octopus' alecto*

🟥 Known distribution

'Octopus' australis Hoyle, 1885

Fig. 188; Plate VII, 50

Octopus australis Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 15: 224. [Type locality: Australia, New South Wales, Port Jackson 3°50'S, 151°17'E].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Hammer octopus; **Fr** — Poulpe tambour; **Sp** — Pulpo martillo.

Diagnostic Features: Moderate-sized, robust species. Arms of moderate length, 2.5 to 4 times mantle length. Lateral arms longest (typically 3>2>4>1). Arm autotomy at distinct plane absent. Webs deep, deepest to 30% of arm length. Web deepest on lateral arms; shallowest between dorsal arms. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, up to 220 suckers on each normal arm. Slightly enlarged suckers present in mature males, up to five on arms 2 and 3, starting around the 16th proximal sucker. Gills with 7 to 9 lamellae per demibranch. Funnel organ V V-shaped; limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, 70 to 90% length of opposite arm. **Ligula large, swollen and club-like, 8 to 17% of arm length**. Calamus of moderate size, 15 to 30% of ligula length. Hectocotylized arm with 60 to 80 suckers. Spermatophores large, 30 to 40 mm long, 70 to 90% of mantle length. Eggs large, to 12 mm, 10 to 20% of mantle length. **Colour:** Cream to purple-brown dorsally, cream on ventral surfaces. White dumbbell marking often visible between eyes. False-eye spots (ocelli) absent. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin texture of regular and small, rounded patches. Scattered, small papillae over dorsal surfaces, single small supraocular papilla over each eye. **Skin ridge present around lateral margin of mantle**.

Size: Mantle length 70 mm; total length to around 300 mm.

Geographical Distribution: Australia, southern Queensland to southern New South Wales (Fig. 189).

Habitat and Biology: Depth range to at least 134 m. Lives on sand and mud substrates. Emerges at night to forage. Hides during the day in shells, human refuse, or buries directly the sand.

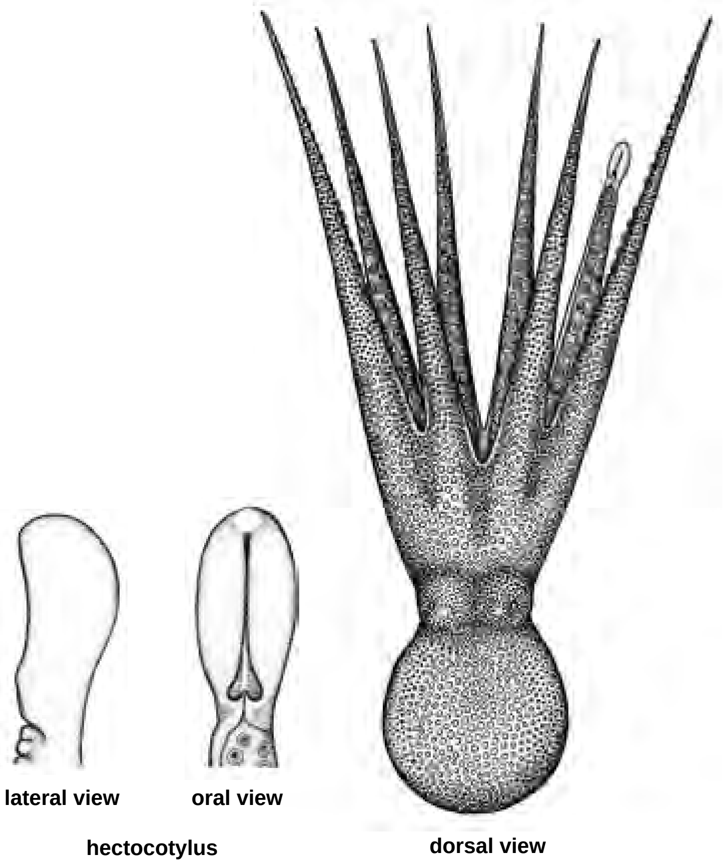


Fig. 188 'Octopus' australis

Fig. 189 'Octopus' australis

i n

Known distribution

Interest to Fisheries: Small-scale trawl harvest for human consumption and as bait. Nottage (2007) reported presence of this species in multispecies benthic trawl catches in New South Wales, Australia.

Local Names: Unknown.

Remarks: Reports of ***'Octopus' australis*** from Victoria, Tasmania and South Australia refer to the sister species, ***'Octopus' berrima***.

Literature: Stranks and Norman (1993), Norman (2000), Nottage (2007).

'Octopus' berrima Stranks and Norman, 1993

Fig. 190; Plate VII, 51

Octopus berrima Stranks and Norman, 1993, *Memoirs of the Museum of Victoria*, 53(2): 355. [Type locality: Australia, Victoria, Port Phillip Bay].

Frequent Synonyms: None.

Misidentifications: *Octopus australis* Hoyle, 1885.

FAO Names: En — Southern keeled octopus; **Fr** — Poulpe membraneux méridional; **Sp** — Pulpo membranoso austral.

Diagnostic Features: Moderate-sized species. Arms of moderate length, 2 to 4 times mantle length. Lateral arms longest (typically 3=2>4>1). Arm autotomy at distinct plane absent. Webs deep, deepest to 30% of arm length. Web deepest on lateral arms, shallowest between dorsal arms. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 220 suckers on each normal arm. Enlarged suckers absent. Gills with 7 to 8 lamellae per demibranch. Funnel organ V V-shaped; limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, 70 to 100% length of opposite arm. **Large, tapering ligula, 11 to 16% of arm length**. Calamus of moderate size, 15 to 20% of ligula length. Hectocotylized arm with 66 to 78 suckers. Spermatophores of moderate size, around 35 to 50 mm, 60 to 130% of mantle length. Eggs large, 10 to 14 mm, 11 to 23% of mantle length. **Colour:** Cream to dark brown in colour. False-eye spots (ocelli) absent. Transverse pair of large white spots present on dorsal mantle. **Sculpture:** Skin texture of regular and small rounded patches. Scattered, small papillae over dorsal surfaces, single small supraocular papilla over each eye. **Skin ridge ("lateral ridge") present around lateral margin of mantle**.

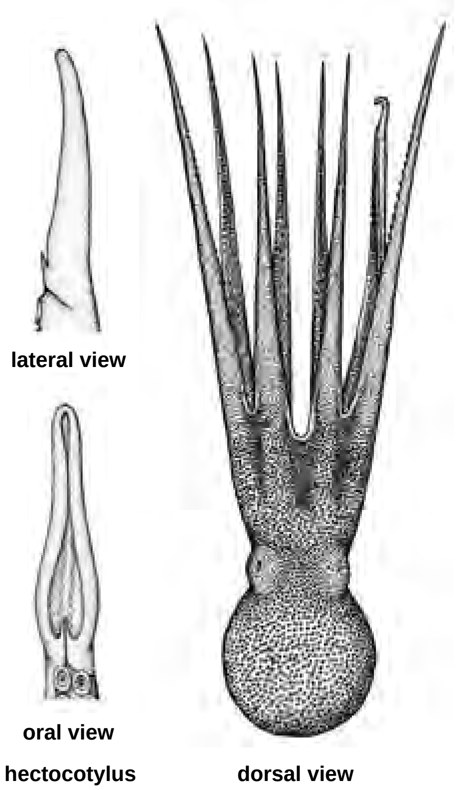


Fig. 190 *'Octopus' berrima*

Size: Mantle length to 105 mm; total length to around 360 mm.

Geographical Distribution: Australia: Victoria, Tasmania and South Australia to the Great Australian Bight (Fig. 191).

Habitat and Biology: Depth range to over 250 m. Sand and mud habitats. Active at night feeding on crustaceans and shellfish. Hides during the day by burying in the sand, in dead tunicate (sea squirt) tests or human refuse. Buried animals often raise a single eye above the sand, presumably to scan for predators. They also temporarily extend the funnel out of the sand to access clean water. In the presence of females, males raise themselves on their arm tips, fully extend their webs and display a colour pattern of violet purple arm tips and a cream-coloured mantle prior to mating attempts. Females attach eggs individually to hard surfaces including the insides of bivalve shells, rock surfaces, or bottles.

Interest to Fisheries: There are intermittent small-scale fisheries for this species in Victoria, Tasmania and South Australia. Most fishers use PVC plastic pots attached to set lines in shallow coastal waters. Catch rates vary with some winter catches synchronised with mating activity and resulting in catch rates of up to 110%. Most of the catch is used as bait in recreational and commercial line fisheries, although several operators directly service the restaurant trade.

Local Names: Unknown.

Literature: Stranks and Norman (1993), Norman (2000).

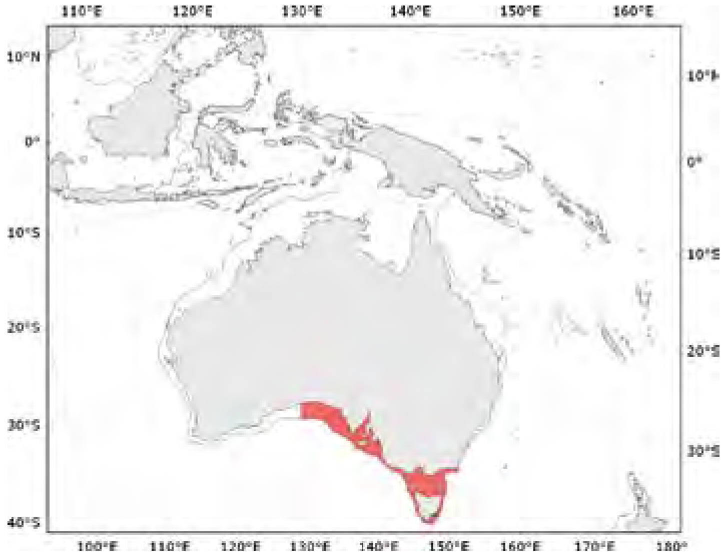


Fig. 191 *‘Octopus’ berrima*

🟥 Known distribution

‘Octopus’ briareus Robson, 1929

Fig. 192; Plate VII, 52

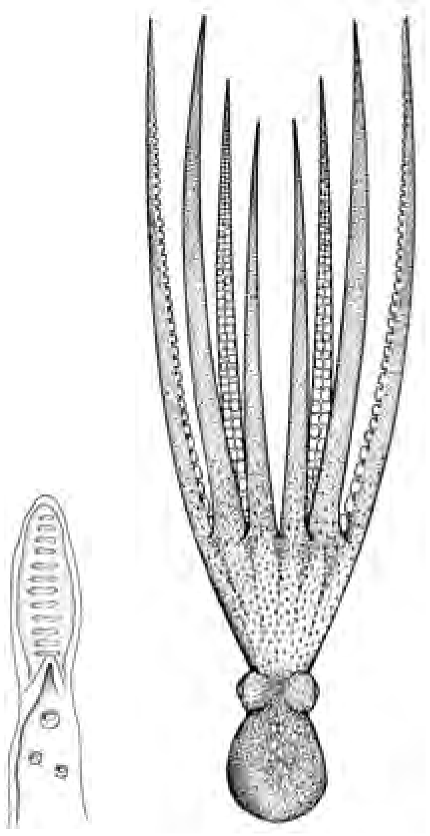
Octopus briareus Robson, 1929b, *Annals of the Magazine of Natural History*, (10)3: 612. [Type locality: Western tropical Atlantic Ocean, Netherlands West Indies, off Curaçao].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Caribbean reef octopus; **Fr** — Poulpe ris; **Sp** — Pulpo de arrecife.

Diagnostic Features: Moderate-sized, elongate species. **Eyes large, prominent.** Arms long (~4 to 6 times mantle length), arms 2 and 3 longer, thicker, somewhat swollen in midregion; arm order 2=3>4>1. Arm autotomy at distinct plane absent. **Webs loose, deep and thin in live animals (almost billowing)**, used to envelope coral heads and rubble when hunting. Web moderate in depth in preserved material (deepest to 20% of longest arm length), web formula A=B=C=D>E. Interbrachial web pouches absent. Two rows of suckers on each arm, large (13 to 22% of mantle length), largest on arms 2 and 3; none especially enlarged in either sex. Normal sucker count unknown. Funnel organ W-shaped. Ink sac and anal flaps present. Gills with 6 to 8 lamellae per demibranch. Radula with 9 elements, 7 rows of teeth plus marginal plates. Third right arm of males hectocotylized; ligula small but well developed (3 to 4% of arm length), broad, rounded distally, with lateral fringing membranes and with central ridge and about 12 to 16 transverse laminae. Calamus moderate in size (28 to 32% of ligula length). Number of suckers on hectocotylized arm unknown. Terminal organ (penis) small (PLI 31-34% of mantle length), with well-developed diverticulum; entire penile apparatus boomerang-shaped. Spermatophores long (126% of mantle length). **Mature eggs large, capsule 10 to 14 mm long** and 4 to 5 mm wide, stalk 5 to 10 mm long; egg masses with 200 to 500 (rarely to 1 000) eggs arranged in clusters of 7 to 34 (mean= 25). Hatchlings benthic, mean mantle length 5.5 mm. **Colour in life iridescent blue-green with irregular red-brown marbled effect**. Eye often dark red-brown. Regular red-brown transverse bands shown along arms in some colour patterns. Skin sculptured in numerous small rounded papillae. Skin ridge around lateral margin of mantle absent.



hectocotylus **dorsal view**

Fig. 192 *‘Octopus’ briareus*

Size: Mantle length to 120 mm; body weight to around 1 kg.

Geographical Distribution: United States from South Florida, southeastern Gulf of Mexico, Bahamas, Caribbean Sea to northern South America (to 40°W) (Fig. 193).

Habitat and Biology: Depth range from 3 to 20 m. Typically found associated with coral reefs. Feeds at night amongst live coral and coral rubble, often enveloping small coral heads within ballooning webs.

Interest to Fisheries: Minor. Fished locally throughout its range using spears, hooks and clay pots (Voss, 1985). May be reported under the species name ***Octopus vulgaris*** in western central Atlantic catch. A popular species in the aquarium trade in the United States (C. Huffard, pers. comm.).

Local Names: Unknown.

Literature: Above description based on Toll (1998); see also Messenger (1963), Boletzky (1969, 1973), Borer (1971), Wolterding (1971), Opresko (1974), Hanlon (1983a, 1988), Aronson (1989), Hanlon and Wolterding (1989), Toll and Binger (1991), Butler and Lear (2009).

Fig. 193 *'Octopus' briareus*

🟥 Known distribution

'Octopus' bunurong Stranks, 1990

Fig. 194; Plate VII, 53

Octopus bunurong Stranks, 1990, *Memoirs of the Museum of Victoria*, 50(2): 462. [Type locality: Australia, Victoria, Wilsons Promontory].

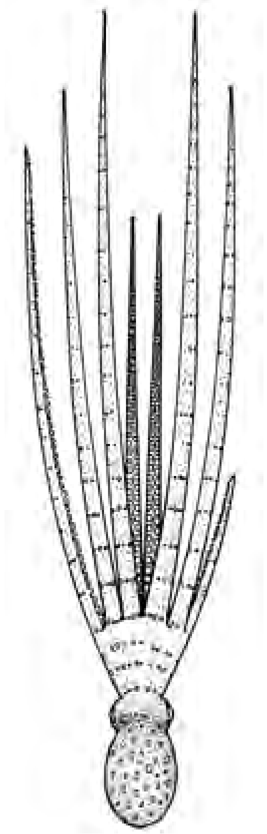
Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Southern white-spot octopus; **Fr** — Poulpe bunurong; **Sp** — Pulpo bunurong.

Diagnostic Features: Moderate-sized, elongate species. Arms long, to 7 times mantle length. **Dorsal arms longest (1>2>3>4)**. Arm autotomy at distinct plane absent. **Webs shallow, deepest around 10 to 15% of arm length**. Web deepest on dorsal arm; webs between ventral arms shallowest. Interbrachial web pouches absent. Two rows of suckers on each arm. Enlarged suckers absent. Gills with 9 to 10 lamellae per demibranch. Funnel organ V V-shaped, outer limbs approximately 75% length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 60% length of opposite arm. Ligula robust, 9 to 12% of arm length. Calamus small, 13 to 22% of ligula length. Hectocotylized arm with 70 to 96 suckers. Spermatophores of moderate size, around 65% of mantle length. Eggs large, around 8 to 10 mm. **Colour: Typically orange-red with numerous small white spots on dorsal mantle. Regular narrow transverse rows of small white spots along arms. Capable of pale colour displays of pink-grey base colour with iridescent green sheen**. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of scattered low papillae over smooth skin. **Broken ridge of skin present around lateral margin of mantle**.

Size: Mantle length to 95 mm; total length to around 475 mm.



dorsal view

Fig. 194 *'Octopus' bunurong*

Geographical Distribution: Southeast Australia from southern New South Wales and northern Tasmania to the Great Australian Bight (Fig. 195).

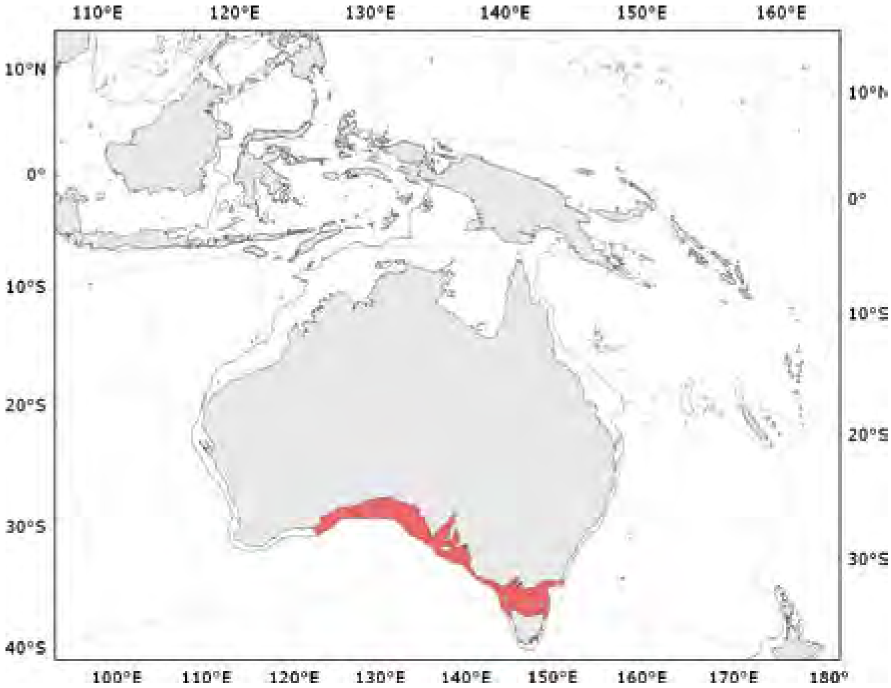


Fig. 195 ***‘Octopus’ bunurong***

🟥 Known distribution

Habitat and Biology: Depth range from 1 to 130 m. This octopus typically occurs in sand and seagrass habitats where it emerges at night to forage. It remains buried in the sand during the day. Little is known of the biology or behaviour of this species. Large eggs indicate hatchlings are benthic.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Norman (2000).

‘Octopus’ californicus Berry, 1911

Fig. 196; Plate VII, 54

Octopus californicus Berry, 1911, *Proceedings of the United States National Museum*, 40(1838): 590. [Type locality: Northeastern Pacific Ocean, United States, California, off San Diego].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — North Pacific big-eye octopus; **Fr** — Poulpe du Pacifique Nord; **Sp** — Pulpo del Pacifico norte.

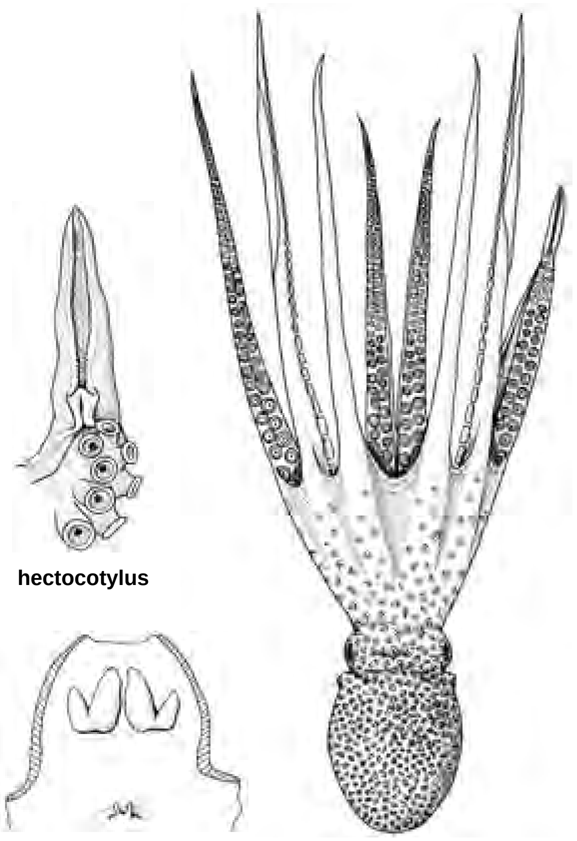
Diagnostic Features: Moderate-sized, **robust, muscular species with large eyes**. Arms short, 2.5 to 3.5 times mantle length. Arms 2 slightly longer (typically 2>1>3>4). Arm autotomy at distinct plane absent. Webs deep, deepest to 30% of arm length. Web deepest on lateral arms; webs between dorsal and ventral arm pairs shallowest. **Web margins extend to tip of arms along ventral margins**. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 120 to 160 suckers on each normal arm. Enlarged suckers present in mature males, 8 to 10 on all arms, starting around the 14th proximal sucker. Gills with 12 to 13 lamellae per demibranch. Funnel organ V V-shaped, outer limbs half length of inner limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Oesophagus with swelling only, no distinct crop. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, 70 to 81% length of opposite arm.

Large, conical and narrow ligula, 10 to 22% of arm length. Calamus tiny, 2 to 6% of ligula length. Hectocotylized arm with 46 to 53 suckers. Spermatophores of moderate size, 75 to 80% of mantle length, produced in moderate numbers (~75). Eggs large, around 14 to 17 mm. **Colour:** Uniform orange-brown dorsally, ventral surfaces of mantle, head and arms lighter in colour. Eyelids gold, often with green iridophore sheen. False-eye spots (ocelli) absent. **Sculpture: Skin densely covered with large star-like patches each of which can produce a raised papilla. Single large unbranched papilla** over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 140 mm; total length to around 375 mm.

Geographical Distribution: Northeastern Pacific from Gulf of Alaska to Baja California, Mexico. Also reported to occur in the Sea of Japan and off Russia (however, see **Remarks**) (Fig. 197).

Habitat and Biology: Depth range from 100 to 900 m. It is a mid-depth cool water species that lives on soft mud and muddy-sand substrates. This species occurs in the hypoxic Santa Barbara Basin where it is able to regulate oxygen consumption down to the limit of detectable oxygen partial pressures. Captive animals forage at night and can move off the bottom to chase fishes, shrimps or crabs. The beaks of juvenile ***'Octopus' californicus*** have been found in stomachs of rockfishes. Males mature at about 60 mm mantle length and females at about 90 mm. Captive females lay between 100 to 500 eggs that are attached singly in small clusters to hard surfaces.



hectocotylus

funnel organ

dorsal view

Fig. 196 ***'Octopus' californicus***

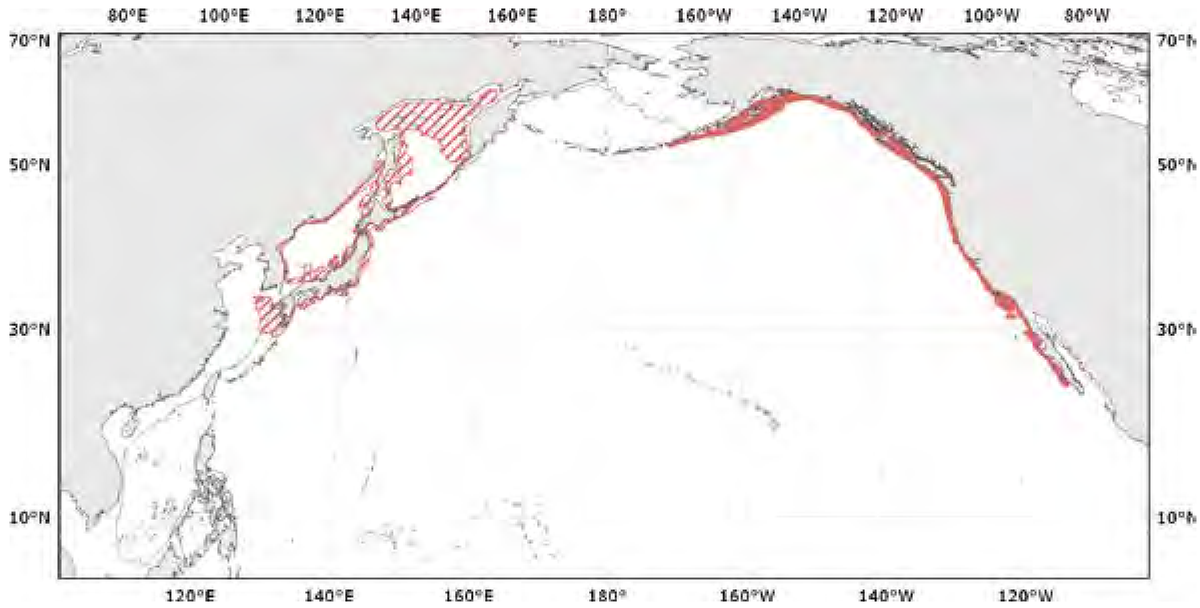


Fig. 197 ***'Octopus' californicus***

🟥 Known distribution ▨ Possible distribution

Interest to Fisheries: No specific statistics available but the species appears to constitute an important by-catch element in the bottom trawl fishery for prawns and groundfishes at depths below 150 m.

Local Names: Unknown.

Remarks: In the northeastern Pacific ***'Octopus' californicus*** is known to occur off Magdalena Bay, Mexico northward to the Gulf of Alaska (Berry, 1912; Phillips, 1933; Morrison, 1944; Talmadge, 1967; Hochberg, 1997a; Hochberg, 1998). The northern limit of the range in the northeastern Pacific is not well documented due to the paucity of specimens in museum collections. ***'Octopus' californicus*** also is reported to occur in the Sea of Japan off Japan and Russia (Kondokov, 1941; Taki, 1944; Akimushkin, 1965) and in the Okhotsk Sea (Bogolepova, 1957; Bogolepova-Dobrokhotova, 1963). Nesis (pers. comm.) has indicated that populations in the eastern and western Pacific may represent a distinct species. Data on depth ranges support Nesis' opinion. ***'Octopus' californicus*** lives at depths of 100-900 m and is the most common deep water species off the coasts of California and Mexico. The highest densities occur between 200-500 m. In southern California, ***'O.' californicus*** overlaps with ***O. rubescens*** in a narrow transition zone from 90 to 145 m. The identity of the juvenile specimen reported by Berry (1912) from over 1800 m off Monterey is questionable. No positively identified specimens are known from waters deeper than 900 m. Off Russia, Akimuskin (1965) reported that ***'O.' californicus*** typically occurs in 20-40 m which is considerably shallower than records from the Eastern Pacific and perhaps is further argument that two distinct species are present. Two species of dicyemid parasites were reported from Russia in ***'O.' californicus*** by Bogolepova (1957) and Bogolepova-Dobrokhotova (1963) in both the Japan and Okhotsk seas. In her publications *Dicyemennea nouveli* McConnaughey, 1959 and *Dicyemodeca dogieli* Bogolepova, 1957 were described. However, judging from the dicyemid species recorded the host species may be either ***Enteroctopus dofleini*** or an as yet undescribed octopod host.

Literature: Robson (1929b), Hochberg (1997a, 1998), Seibel and Childress (2000), Jorgensen (2009).

'Octopus' conispadiceus (Sasaki, 1917) **Fig. 198**

Polypus conispadiceus (Sasaki, 1917), *Annotationes Zoologicae Japonenses*, 9(3): 367. [Type locality: Japan, Hokkaido Island, Sapporo, fish market].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Chestnut octopus; **Fr** — Poulpe casse-noix; **Sp** — Pulpo espadaña.

Diagnostic Features: Large, muscular species. **Arms of moderate length, around 3 times mantle length. Arms approximately equal in length, ventral pair slightly shorter (typically 1=2=3>4)**. Arm autotomy at distinct plane absent. Webs deep, deepest up to 30% of arm length. Web deepest on lateral arms; web sectors of dorsal and ventral arm pairs slightly shallower. Web margins well developed, extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 140 to 190 suckers on each normal arm. Enlarged suckers absent. Gills with 10 to 12 lamellae per demibranch. Funnel organ V V-shaped, lateral limbs slightly shorter than medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Ink sac present. Right third arm of males hectocotylized, 70 to 80% length of opposite arm. **Ligula very large, muscular and cylindrical, 15 to 20% of arm length. Calamus small and pointed, around 12% of ligula length**. Hectocotylized arm with 52 to 58 suckers. Spermatophores long, around 110 to 140 mm, produced in high numbers (~100). Eggs very large, up to 28 to 30 mm in length. **Colour:** Bluish green-brown with numerous yellow spots and dark mottles. **Narrow, transverse, white line across head.** False-eye spots (ocelli) absent. White to pink on ventral surfaces. **Sculpture:** Skin generally smooth with small low warts scattered over head. Ventral surfaces smooth. Single papilla above each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 210 mm; total length to at least 1.2 m.

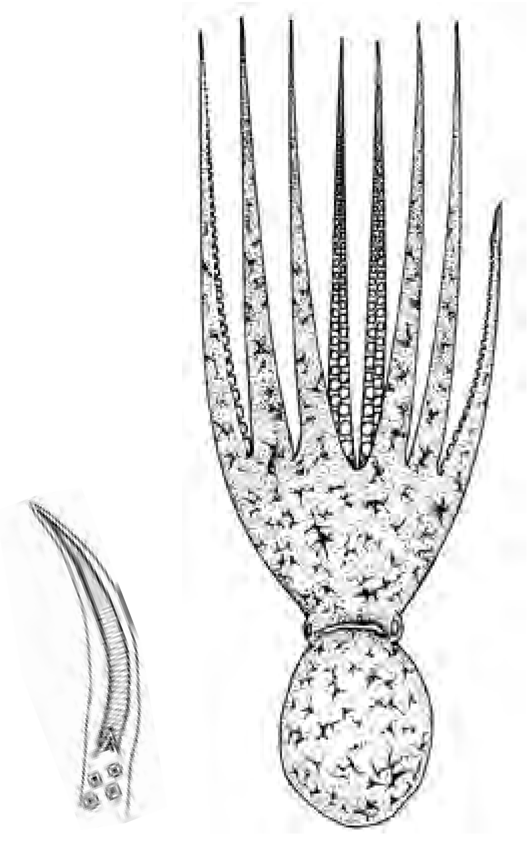


Fig. 198 *'Octopus' conispadiceus*

Geographical Distribution: Northwestern Pacific off northern Japan and Kuril Islands (Fig. 199).

Habitat and Biology: Depth range from 50 to >100 m. A benthic shelf species that lives on sandy to muddy substrates. It migrates seasonally in response to changes in temperature, tending to alternate between deeper waters in summer and shallower waters in the colder seasons. Mating takes place during the inshore migration. Females lay up to 1 200 large eggs. The large eggs indicate hatchlings are benthic. Lifespan is suggested to be around 3 to 4 years.

Interest to Fisheries: Harvested in large numbers by trawl, bottom longline, and trap in northern Japan and as bycatch in Soviet bottom trawl fishery in the Japan Sea and around the southern Kuril Islands. It is the second most common species in Hokkaido markets after ***Enteroctopus dofleini***.

Local Names: JAPAN: Yanagidako.

Literature: Sasaki (1929), Okutani *et al.* (1987), Gleadall (1993).

Fig. 199 *'Octopus' conispadiceus*

🟥 Known distribution

'Octopus' cyanea Gray, 1849

Fig. 200; Plate VII, 56

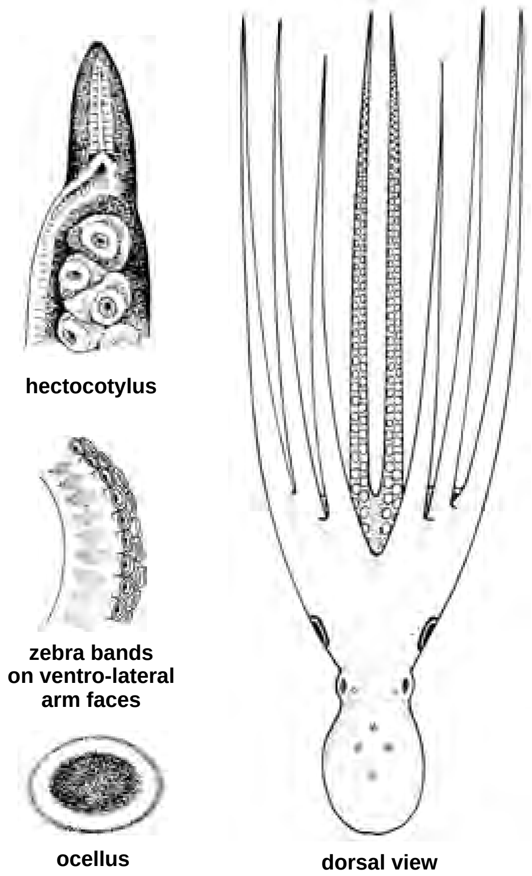
Octopus cyanea Gray, 1849, *Catalogue Mollusca ... British Museum*: 15. [Type locality: "Coast of New Holland" (= Australia)].

Frequent Synonyms: *Octopus tonganus* Hoyle, (in part) 1885; *Octopus marmoratus* Hoyle, 1885; *Octopus horsti* Joubin, 1898; *Polypus herdmani* Hoyle, 1904; *Callistoctopus magnocellatus* Taki, 1964.

Misidentifications: None.

FAO Names: En — Big blue octopus; **En** — Gros poulpe bleu; **Sp** — Pulpo azulòn.

Diagnostic Features: Large, robust, muscular species. Arms moderate to long, 4 to 6 times mantle length. Lateral arms longest (typically 4=3=2>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 15 to 23% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Web margins extend along ventral border of arms to tips. Interbrachial web pouches absent. Two rows of suckers on each arm. **In larger animals, around 450 to 500 suckers on each normal arm**. Enlarged suckers present in mature males, 2 to 4 on arms 2 and 3, starting around the 6th to 7th proximal sucker. Gills with 9 to 11 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, 70 to 90% length of opposite arm. **Ligula tiny, triangular, 1 to 2% of arm length**. Calamus small and blunt, 35 to 40% of ligula length. Hectocotylized arm


hectocotylus

zebra bands on ventro-lateral arm faces

ocellus

dorsal view

Fig. 200 *'Octopus' cyanea*

with 180 to 230 suckers. Spermatophores small, around 30 to 50 mm, 30 to 50% of mantle length, produced in large numbers (in hundreds, to at least 300). Spermatophores unarmed. Eggs small, around 2 to 3 mm, ~2% of mantle length. **Colour:** Variable colour patterns from uniform white to various mottled patterns to uniform dark chocolate brown. Excellent at camouflage against numerous backgrounds. **False-eye spots (ocelli) present as dark oval patches within a dark narrow outer ring.** Ocellus without iridescent ring. **Regular short dark bars along ventro-lateral faces of all arms adjacent to suckers. Arm tips with 3 to 7 longitudinal rows of small white spots, often pronounced against dark base colour** (Plate VII, 56)**.** Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle ('dorsal mantle white spots' *sensu* Packard and Sanders, 1971). **Sculpture:** Skin with patch and groove texture **forms large circles on dorsal arm crown**. Four large primary papillae in diamond arrangement on dorsal mantle; single large supraocular papilla present over each eye. Skin ridge absent around lateral margin of mantle.

Size: Mantle length to 160 mm; total length to greater than 1 m; body weight to at least 6 kg.

Geographical Distribution: Tropical Indo-West Pacific from the east coast of Africa to Hawaii, southern Japan to northern Australia (Fig. 201).

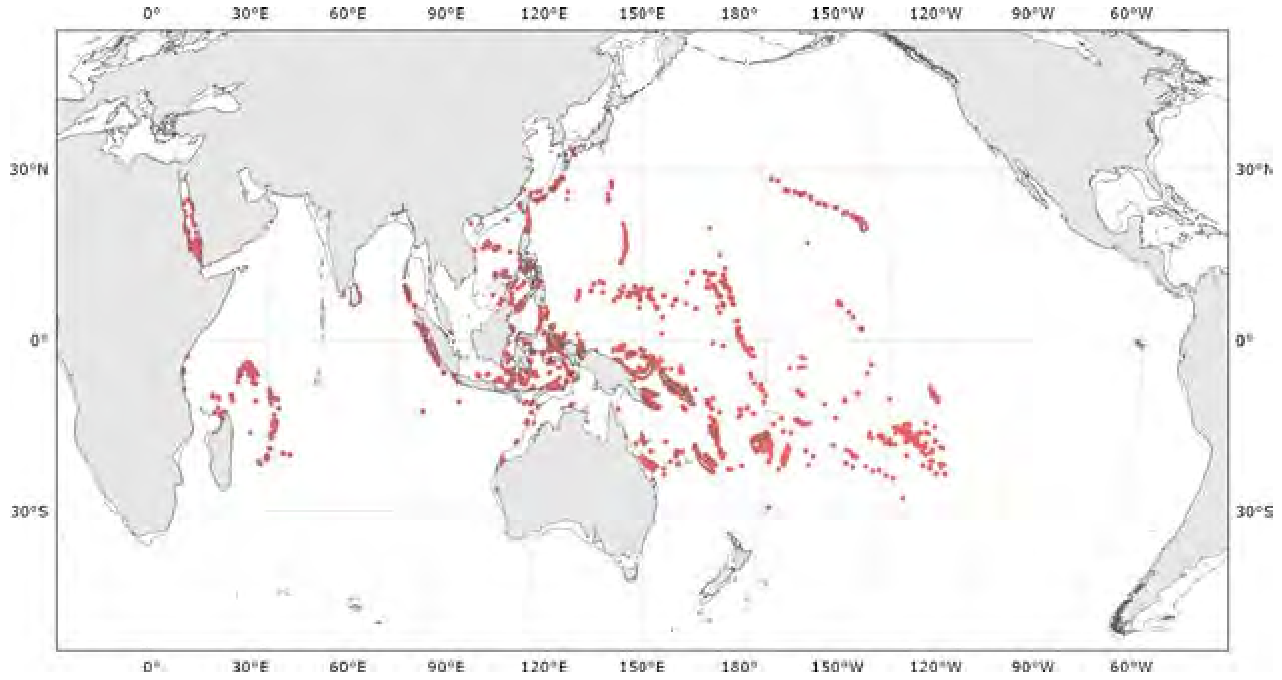


Fig. 201 ***'Octopus' cyanea***

🟥 Known distribution

Habitat and Biology: This species occurs on tropical coral reefs from intertidal flats to at least 22 m deep. It is a day-active species with higher activity peaks at dusk and dawn. It occupies lairs in coral bedrock, live and dead coral heads and excavations in sand and rubble. Males and females can occupy adjacent dens. Established lairs often are discernible by the scattering of empty crab carapaces surrounding the opening. Prey remains around established lairs consist solely of crab remains. Carapaces to 120 mm wide were found around lairs of larger octopuses. Captive animals readily feed on dead prawns and fishes. There is no evidence of inclusion of bivalves or gastropods in the diet. No mollusc shells were observed around lairs and captive animals would not feed on live or dead molluscs. Stomach contents of 49 ***'Octopus' cyanea*** from Hawaiian waters contained 89% crab remains, 41% stomatopods, 27% alpheid shrimps, 10% fish bones and in one individual, remains of a small moray eel. The small size of the eggs indicates hatchlings are planktonic. This species is eaten by the Hawaiian monk seal in Hawaii. Sexual cannibalism was reported in this species.

Interest to Fisheries: Taken in subsistence and local catches throughout its range for human consumption. Primarily collected with spears or lures.

Local Names: HAWAII: He'e; AUSTRALIA, INDONESIA, PAPUA NEW GUINEA: Day octopus.

Remarks: Guzik *et al.* (2005) demonstrated that this species is not a member of the genus ***Octopus*** *sensu stricto* (i.e. ***O. vulgaris*** group). It shows stronger affinities with the genus ***Abdopus***. At this stage, its generic placement remains unresolved.

Literature: Van Heukelem (1983a), Norman (1992a), Forsythe and Hanlon (1997), Young and Harman (1997), Goodman-Lowe *et al.* (1999), Guzik *et al.* (2005), Hanlon and Forsythe (2008), Sauer *et al.* (2011).

'Octopus' kaurna Stranks, 1990

Fig. 202; Plate VIII, 59

Octopus kaurna Stranks, 1990, *Memoirs of the Museum of Victoria*, 50 (2): 460. [Type locality: Australia, Victoria, Hobsons Bay].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Southern sand octopus; **Fr** — Poulpe du sable meridional; **Sp** — Pulpo de l'arena austral.

Diagnostic Features: Moderate-sized, elongate species. Arms long and fine, to 7 times mantle length. Dorsal arms longest (1>2>3>4). Arm autotomy at distinct plane absent. Webs shallow, deepest around 10 to 20% of arm length. Web deepest on dorsal arms, webs between ventral arms shallowest. Web margins extend approximately 30% along arms. Interbrachial web pouches absent. Two rows of suckers on each arm. Enlarged suckers absent. Gills with 9 to 11 lamellae per demibranch. Funnel organ V V-shaped, outer limbs around 75% of length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Ink sac present. Right third arm of males hectocotylized, 55 to 70% length of opposite arm. Ligula small and narrow, 5 to 8% of arm length. Calamus of moderate length, 33 to 48% of ligula length. Hectocotylized arm with 66 to 129 suckers. Spermatophores of moderate size, around 80% of mantle length. Eggs large, around 9 to 11 mm. **Colour: Base colour of uniform orange-cream to maroon red. Sometimes forage while exhibiting an elongate form and pink base colour with a dark maroon stripe on each side from the mantle to the arm tips, running through the eye**. False-eye spots (ocelli) absent. **Sculpture:** Skin texture generally smooth or covered with numerous tiny bumps. Larger scattered low papillae present on lateral faces of mantle. supraocular papillae absent. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 85 mm; total length to around 420 mm.

Geographical Distribution: Southern Australia from eastern Victoria and northern Tasmania west to the Great Australia Bight (Fig. 203).

hectocotylus dorsal view

Fig. 202 *'Octopus' kaurna*

Habitat and Biology: Depth range to 50 m. Shallow-water species found on sand, mud, and seagrass beds. Remains buried during the day in a burrow in the sand formed using mucous to bind the sand grains together. Emerges at night to forage for small crustacean prey. Novel peptides have been reported as venoms in this species.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Stranks (1990), Norman (2000), Fry *et al.* (2009).

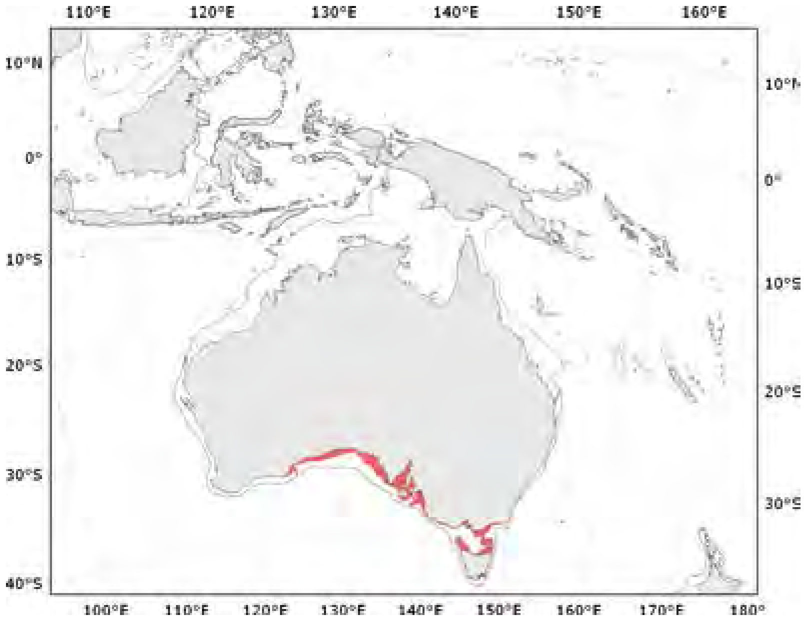


Fig. 203 *'Octopus' kaurna*

🟥 Known distribution

‘*Octopus*’ *maorum* Hutton, 1880

Fig. 204; Plate VIII, 60

Octopus maorum Hutton, 1880, *Manual of the New Zealand Mollusca, Colonial Museum and Geological Survey Department, Wellington*, p. 1. [Type locality: New Zealand, Dunedin].

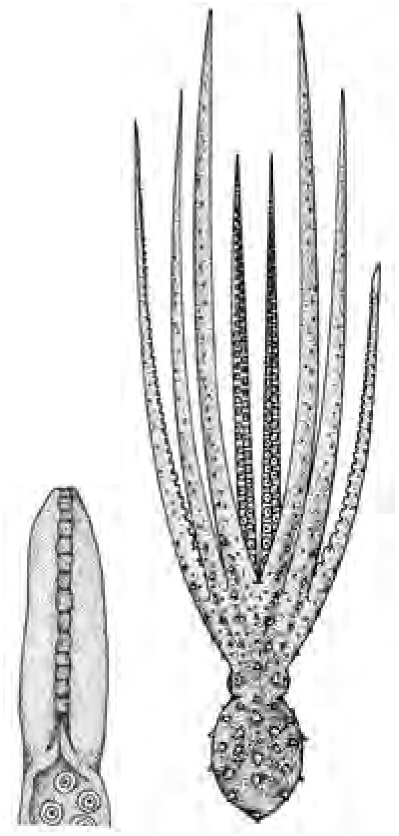
Frequent Synonyms: *Octopus communis* Park, 1885; *O. flindersi* Cotton, 1932.

Misidentifications: *Pinnoctopus cordiformis* Quoy and Gaimard, 1832.

FAO Names: En — Maori octopus; **Fr** — Poulpe maori; **Sp** — Pulpo maori.

Diagnostic Features: Large, muscular species. Arms long, to 5.5 times mantle length. **Dorsal arms longest and thickest (1>2>3>4)**. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20% of arm length. Web deepest on dorsal arms; webs between ventral arms shallowest. Web margins wide and fleshy extend to the arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. Enlarged suckers present in mature males and females, around 6 on all arms, starting around the 15th proximal sucker. Gills with 13 to 15 lamellae per demibranch. Funnel organ W-shaped, outer limbs approximately 75% length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, 60 to 80% length of opposite arm. Ligula small and narrow, around 5% of arm length. Calamus of moderate size and pointed, around 25% of ligula length. Hectocotylized arm with 95 to 135 suckers. Eggs of moderate size, around 6 to 7 mm. **Colour: Orange brown to dark brick red base colour with numerous small white spots scattered over mantle and dorsal arm crown. Orange lateral faces of arms**. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of small irregular patches and papillae over all dorsal and lateral surfaces. **More than 20 large spike-like papillae can be raised on the body and upper arm crown.** Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 300 mm; total length to around 1 m; body weight to around 10 kg.



hectocotylus dorsal view

Fig. 204 ‘*Octopus*’ *maorum*

Geographical Distribution: New Zealand and southern Australia from eastern Victoria to Perth, Western Australia (Fig. 205).

Habitat and Biology: Depth range from 0 to 549 m. This large, muscular octopus occurs on rocky reefs, kelp forests and seagrass beds. Smaller animals are generally night active while larger adults can be seen actively foraging during the day. They are speculative foragers, engulfing crevices and weed within their extensive webs and flushing prey with their arm tips. The diet includes large crabs, rock lobster, abalone, mussels, fish and other octopuses. Lairs often have fresh abalone and mussel shells scattered around the entrance. This species has been recorded in the diet of fur seals in Australia and seals and albatrosses in New Zealand.

Interest to Fisheries: This species is collected by hand and seine nets in Tasmania. It is captured occasionally on

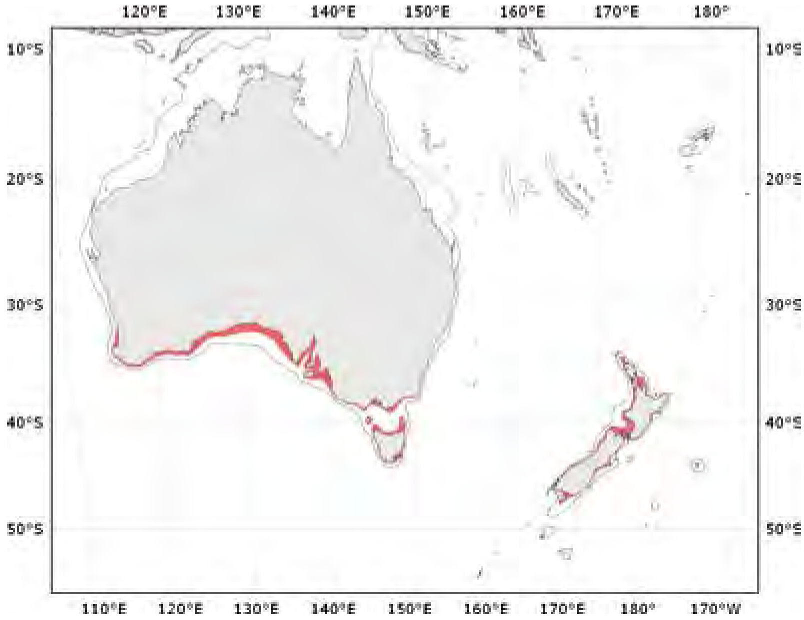


Fig. 205 ‘*Octopus*’ *maorum*

🟥 Known distribution

line by recreational fishers. This octopus species harms the rock lobster pot fisheries as it enters the pots, consumes the lobsters and departs leaving empty carapaces. Introduction of escape hatches in lobster pots in some Australian states in recent years has prevented lobster fishers' harvests of the octopuses as bycatch used for bait. This species is popular for human consumption in the form of Greek-style pickled octopus.

Local Names: Unknown.

Remarks: O'Shea (1999) treats this octopus species under the name ***Pinnoctopus cordiformis*** Quoy and Gaimard, 1832, a previously unresolved name based on a poorly preserved type specimen. The generic name ***Pinnoctopus*** refers to a preservation artefact in the type specimen where the skin had become soft around the mantle and flattened out in the form of an apparent ridge or fin around the body. The original description for ***P. cordiformis*** describes the arms as subequal, with the third arm pair slightly shorter. This species can not possibly be ***'Octopus' maorum*** as the dorsal arms of ***'Octopus' maorum*** are significantly larger and thicker than the other arms, with the ventral arm pair being the shortest and thinnest. It is more likely that ***P. cordiformis*** is the same as O'Shea's ***Enteroctopus zealandicus***, a large species with arms of subequal length. The latter species has been collected close to the type locality for ***P. cordiformis***: Tasman Bay at the top of the South Island, New Zealand. A freshly dead ***E. dofleini*** observed by the authors in Santa Barbara, California exhibited the wide flange of loose skin around the mantle. Robson made ***maorum*** the type species for his genus ***Macroctopus***. Until the phylogenetic relationships of this species are determined (particularly in relation to members of the genus ***Callistoctopus***), we choose to treat this species as an unplaced ***'Octopus'*** species.

Literature: Stranks (1988a), Anderson (1999), O'Shea (1999; as ***Pinnoctopus cordiformis***), Grubert *et al.* (1999), Fea *et al.* (1999), Grubert and Wadley (2000), Brock and Ward (2004), Hume *et al.* (2004), Hunter *et al.* (2005), Norman and Hochberg (2005a), Harrington *et al.* (2006), Doubleday *et al.* (2008, 2009), Lalas (2009).

'Octopus' minor (Sasaki, 1920)

Fig. 206; Plate VIII, 61

Polypus macropus var. *minor* Sasaki, 1920, *Proceedings of the U.S. National Museum*, 57: 181. [Type locality: Japan, Idzu Province, Suruga Bay 34°40'45"N, 138°18'30"E].

Frequent Synonyms: *Polypus variabilis* var. *typicus Sasaki*, 1929; *Octopus variabilis* (Sasaki, 1929).

Misidentifications: *Octopus macropus* Risso, 1826.

FAO Names: En — Whiparm octopus; **Fr** — Poulpe fouet; **Sp** — Pulpo antenado.

Diagnostic Features: Small to moderate, elongate species. **Arms long and slender**, around 4 to 5 times mantle length. **Dorsal arms significantly longer and thicker, twice length of third or fourth arms (1>2>3=4)**. Arm autotomy at distinct plane absent. Webs shallow and poorly developed, deepest around 10% of arm length. Web deepest on dorsal arms; webs between ventral arms shallowest. Web margins poorly developed. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 180 suckers on each normal arm. **Enlarged suckers present in mature males, around level of 8th or 9th sucker pair, largest on dorsal arms (to 17% of mantle length)**. Gills with 10 to 12 lamellae per demibranch. Funnel organ V V shape, outer limbs slightly shorter than medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates, 2 (rarely 3) lateral cusps on each side of rachidian tooth. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 50% length of opposite arm. **Ligula large (around 18 to 23% of arm length) and spoon-like with wide hollow groove, incurled lips and 10 to 14 well marked transverse grooves**. Calamus small and pointed, <20% of ligula length. Hectocotylized arm with around 40 to 60 suckers. Spermatophores around 42 mm long and very thick throughout. Sperm cord coiled in around 40 whorls. Eggs of moderate size, around 8 mm. **Colour:** Live animals red-brown with light yellow spots on dorsal surfaces. False-eye spots (ocelli) absent. **Sculpture:** Skin soft and typically smooth but capable of raising irregular warty texture. Skin ridge around lateral margin of mantle absent.

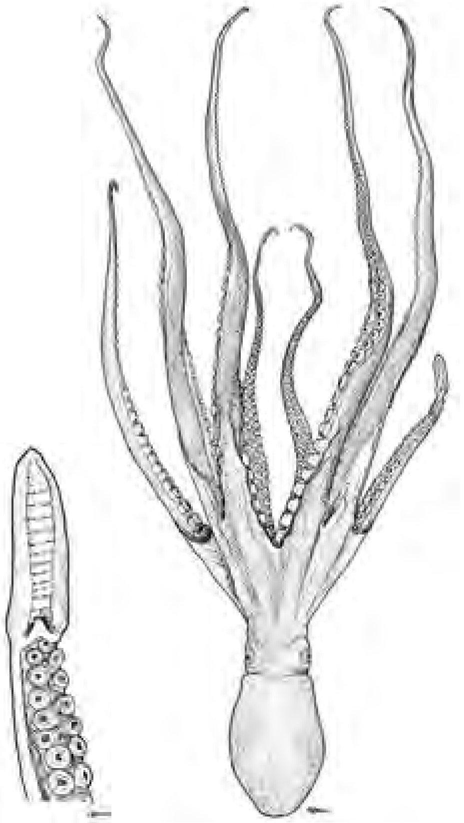


Fig. 206 ***'Octopus' minor***

Size: Mantle length to 80 mm; total length to around 700 mm.

Geographical Distribution: Sakhalin (Russia) to all Japanese waters and potentially south to China, Hong Kong SAR (see **Remarks** below) (Fig. 207).

Habitat and Biology: Depth range unknown. This elongate octopus occurs on soft sediments around Japan, the Korean Peninsula and China.

Interest to Fisheries: This species is an important commercial species in Japan where it was reported by Sasaki (1929) as common in Honshu, especially Seto-umi. Optimal fishing effort was reported by Kim (2008). Heavy metal concentrations have been reported in this species from off the Republic of Korea (Lee and Kim, 2010).

Local Names: Unknown.

Remarks: ***'Octopus' minor*** is in urgent need of review. There is a high likelihood that this name is being applied to a suite of related soft-bodied, long-armed species from the cooler waters of Russia and northern Japan to the warmer waters of southern coastal China.

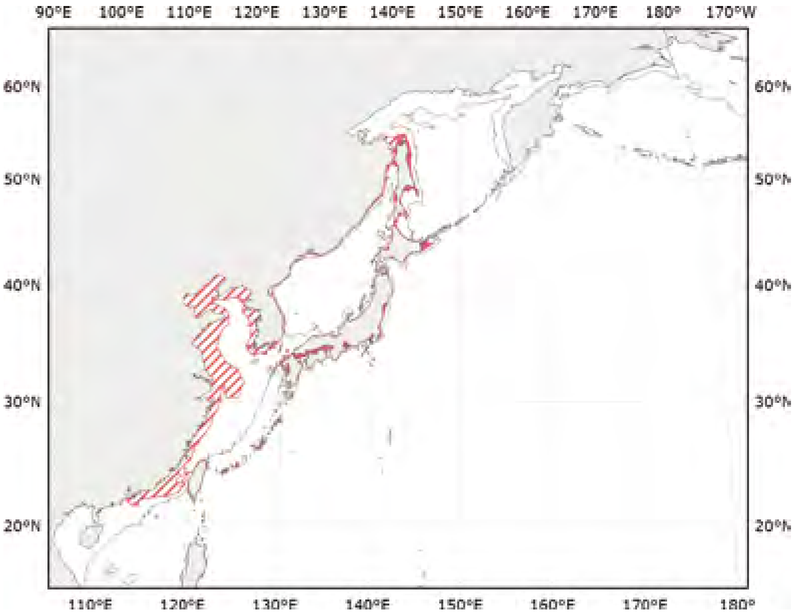


Fig. 207 ***'Octopus' minor***

🟥 Known distribution ▨ Possible distribution

Literature: Sasaki (1929; as ***Polypus variabilis*** var. ***typicus***), Roper *et al.* (1984; as ***Octopus variabilis***), Okutani *et al.* (1987), Furuya *et al.* (1992), Chang and Kim (2003), Kim and Kim (2006, 2007), Kim (2008), Lee and Kim (2010).

'Octopus' pallidus Hoyle, 1885

Fig. 208

Octopus pallidus Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 15: 223. [Type locality: Australia, Victoria, off East Moncoeur Island (39°10'S, 146°37'E)].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Pale octopus; **Fr** — Poulpe blême; **Sp** — Pulpo pálido.

Diagnostic Features: Moderate-sized, squat, muscular species. Arms short, around 2.5 times mantle length. Ventral or lateral arms longest (typically 4>3>2>1). Arm autotomy at distinct plane absent. Webs deep, deepest around 25 to 40% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Web margins extend to arm tips. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 200 suckers on each normal arm. Enlarged suckers absent. Gills with 7 to 9 lamellae per demibranch. Funnel organ V V-shaped, outer limbs approximately 75% length of medial limbs. Radula with 9 elements, 7 rows of teeth plus marginal plates. Ink sac present. Right third arm of males hectocotylized, 80 to 90% length of opposite arm. Ligula cylindrical and robust, 10 to 16% of arm length. Calamus of moderate size, 30 to 50% of ligula length. Hectocotylized arm with 72 to 86 suckers. Spermatophores of moderate length, around 80% of mantle length. Eggs large, around 11 to 13 mm.

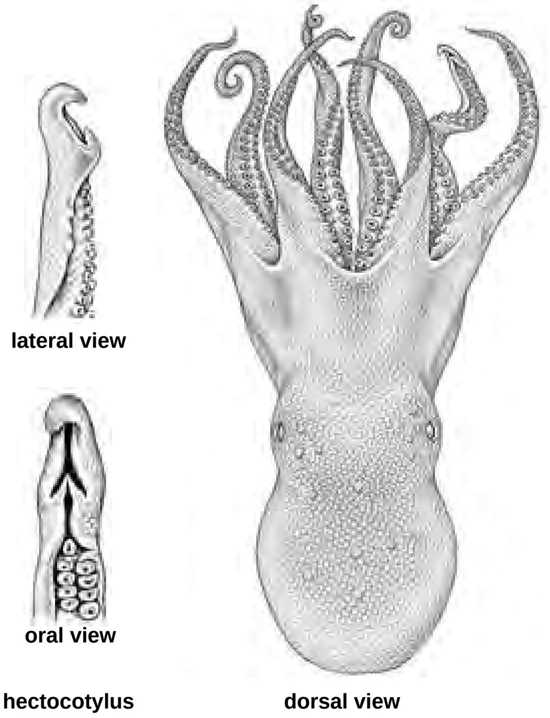


Fig. 208 ***'Octopus' pallidus***

Colour: Typically mottled cream and orange-brown. Capable of becoming uniformly dark brown. False-eye spots (ocelli) absent. **Sculpture: Skin texture of close-set regular "rosette" patches forming tile-like skin sculpture. More than 20 large branched papillae can be raised on all dorsal surfaces, including several large papillae over each eye**. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 150 mm; total length to around 540 mm.

Geographical Distribution: Southeast Australia from central New South Wales to Tasmania and the Great Australian Bight (Fig. 209).

Habitat and Biology: Depth range from 0 to 600 m. Typically found on sand and mud substrates, often in association with sponge gardens or tunicate beds. Diet consists mainly of bivalves which are pulled apart or drilled. Large eggs hatch into benthic young. This species has been reported in the diet of Australian fur seals. ***'Octopus' pallidus*** has been used as an indicator species for toxic pollutants. Influence of temperature on juvenile growth has also been examined.

Interest to Fisheries: This species is harvested on a small scale in pot fisheries in Victoria, primarily for bait. Leporati *et al.* (2009) examined stock status and the effectiveness of CPUE as an assessment tool.

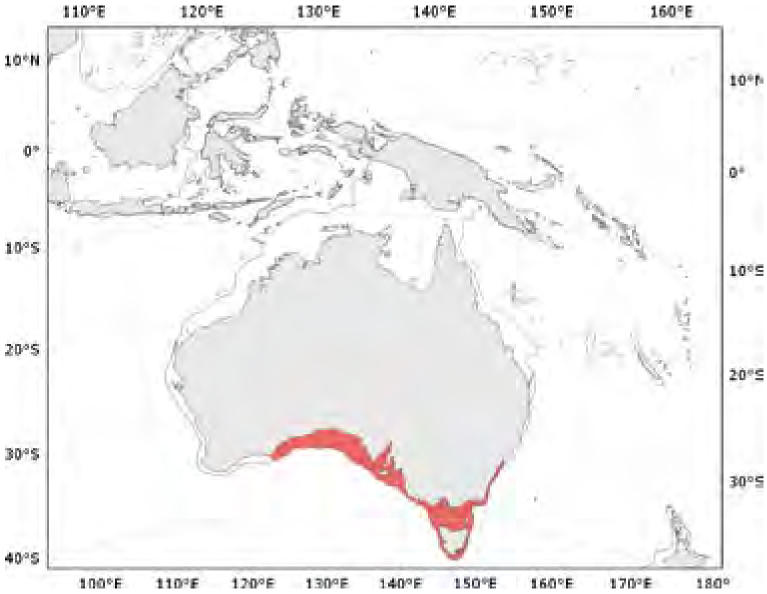


Fig. 209 *'Octopus' pallidus*

🟥 Known distribution

Local Names: Unknown.

Literature: Stranks (1988b), Cheah *et al.* (1995), Norman (2000), Long and Holdway (2002), Hume *et al.* (2004), Doubleday *et al.* (2006, 2008), Leporati *et al.* (2007, 2008a, 2008b, 2009), Andre *et al.* (2008, 2009), Doubleday and Semmens (2011), Semmens *et al.* (2011).

'Octopus' rubescens Berry, 1953

Fig. 210; Plate VIII, 62

Octopus rubescens Berry, 1953, *Leaflets in Malacology*, 1: 51. [Type locality: Mexico, Pacific coast of northern Baja California, off South Coronado Island].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Red octopus; **Fr** — Poulpe rouge; **Sp** — Pulpo rojo.

Diagnostic Features: Small, muscular species. Arms slender and of moderate length, 3.5 to 4.5 times mantle length. Lateral arms longest (typically 2>3>4>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20 to 30% of arm length. Web deepest on lateral arms, webs between dorsal arms shallowest. Web margins extend along 50% of arm length. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 150 to 190 suckers on each normal arm. Enlarged suckers present in mature males, 1 to 2 on arms 1 to 3, typically starting around the 10th sucker. **Gills with 11 to 13 lamellae per demibranch**. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, around 70 to 90% length of opposite arm. **Ligula well developed, elongate and conical with distinct groove, 8 to 11% of arm length**. Calamus small, around 20% of ligula length. Hectocotylized arm with around 80 to 110 suckers. Spermatophores of moderate size, around 80 to 130% of mantle length, produced in moderate numbers (~10 to 15). Spermatophores unarmed. Eggs small, around 3 to 4 mm. **Colour: Reddish on dorsal surfaces of head, mantle and arms, with darker red-brown reticulate pattern**, often mottled with white. Arms with row of white spots down each side. Paler ventrally, often orange-ish. Bluish iridescence around eyes. False-eye spots (ocelli) absent. Transverse pair of white spots present on dorsal mantle, slightly anterior to midpoint of mantle (‘dorsal mantle white spots’ *sensu* Packard and Sanders, 1971). **Sculpture: Skin texture of patch and groove system, patches small, round or circular.** Often textured with tessellate pattern of low relief, inflated or raised patches (“blister-like welts” Hochberg, 1998). Four primary papillae in diamond pattern on dorsal mantle. One large papilla on mid-posterior dorsal mantle and one over each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 100 mm; total length to around 250 mm; body weight to around 400 g.

Geographical Distribution: Gulf of California, Mexico north to Gulf of Alaska (Fig. 211).

Habitat and Biology: Depths range from 0 to 300 m. ***‘Octopus’ rubescens*** probably is the most common species of octopus in the northeastern Pacific. The species typically occupies a depth range intermediate between ***Octopus bimaculatus/bimaculoides*** inshore and ***‘O’. californicus*** in deeper water offshore. The species lives in rocky areas or inhabits large shells of dead gastropods or barnacles, empty bottles, and cans. The life cycle spans 12 to 18 months. It is a migratory species, moving offshore in winter months. Mating occurs at depth in the spring followed by an onshore migration prior to spawning. Depending on the size of the female from 20 000 to 50 000 small eggs are laid in the spring and fall. Paralarvae are thought to remain in the plankton for 1 to 2 months. Juveniles up to 20 mm ML have been reported in the plankton in large numbers. The animals are nocturnally active and feed principally on crustaceans, molluscs, and occasionally fishes. The species is known to bite when handled or disturbed and is capable of injecting a potent toxin via the salivary proboscis.

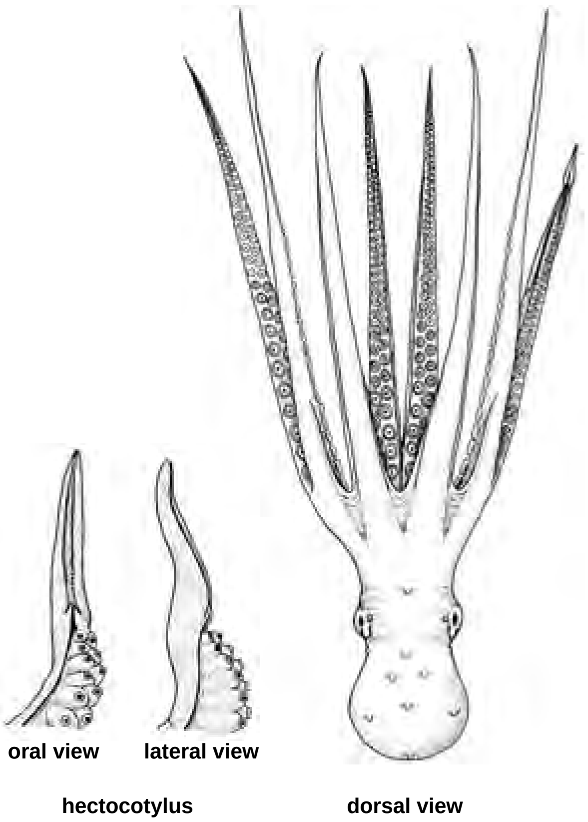


Fig. 210 ***‘Octopus’ rubescens***

Interest to Fisheries: There is no significant harvest of this species. It occasionally appears as bycatch in inshore groundfish trawls.

Local Names: Unknown.

Literature: Hochberg (1997b, 1998), Jorgensen (2009).

Fig. 211 ***‘Octopus’ rubescens***

🟥 Known distribution

‘Octopus’ selene Voss, 1971

Fig. 212

Octopus selene Voss, 1971a, *Bulletin of Marine Science*, 21(1): 11. [Type locality: Pacific Ocean, Panama, NE of Punta Mala, 7°50 2’N, 79°50 5’W].

Frequent Synonyms: None.

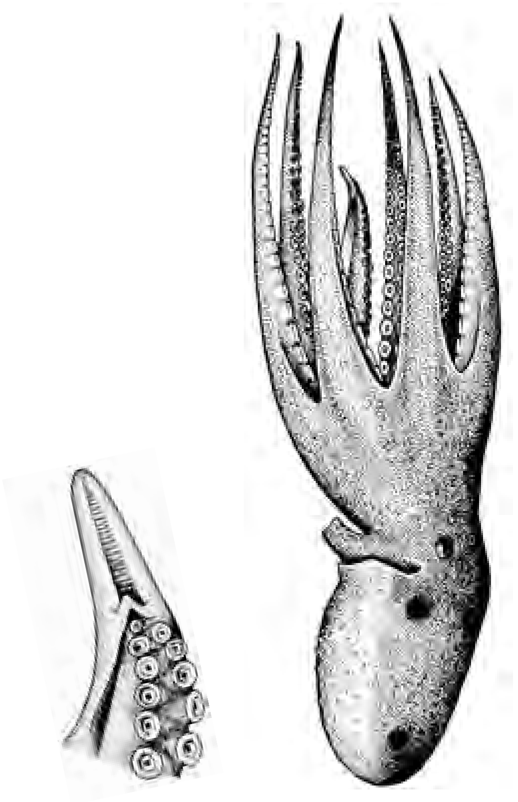
Misidentifications: None.

FAO Names: En — Moon octopus; **Fr** — Poulpe lune; **Sp** — Pulpo lunero.

Diagnostic Features: Moderately small, muscular species. Arms short, 1.7 to 2.5 times mantle length. Lateral arms typically longest (typically 3>2>4>1). Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 20 to 30% of arm length. Web generally deepest on lateral arms. Web margins extend around two thirds of arm length. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 80 to 90 suckers on each normal arm. **Single slightly enlarged sucker at web junction on all arms of male**. **Gills with 12 to 16 lamellae per demibranch**. Funnel organ W-shaped, limbs of approximately equal length. Radula with 9 elements, 7 rows of teeth plus marginal plates. Distinct crop present as side-branch off oesophagus. Ink sac present. Anal flaps present. Right third arm of males hectocotylized, 70 to 85% length of opposite arm. Ligula small, narrow and pointed, 5 to 10% of arm length. Calamus small, 15 to 25% of ligula length. Hectocotylized arm with 23 to 48 suckers. Spermatophores not described. Eggs small, around 1.6 mm. **Colour:** Light to dark reddish purple on the dorsal surfaces, light to pale brown on ventral surfaces **with four dark spots on the mantle, a pair at the posterior tip and an anterior pair close to the opening of the mantle aperture**. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of numerous low papillae over all dorsal surfaces. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 60 mm; total length to around 200 mm.

Geographical Distribution: Gulf of Panama; limits of distribution unknown (Fig. 213).



hectocotylus **lateral view**

Fig. 212 *‘Octopus’ selene*

Fig. 213 *‘Octopus’ selene*

🟥 Known distribution

Habitat and Biology: Depth range from 50 to 210 m. Typically found on sandy and rocky bottoms. Small eggs hatch into planktonic young. This octopus was so numerous at several stations in the Gulf of Panama that densities were calculated at 1.5 octopuses per square metre.

Interest to Fisheries: Some fisheries potential has been predicted due to the high densities in some locations.

Local Names: Unknown.

Remarks: The relationship of this octopus with the similar ***'Octopus' veligero*** has not been resolved.

Literature: No additional literature.

'Octopus' tehuelchus d'Orbigny, 1834 [*In* 1834-1847]

Fig. 214

Octopus tehuelchus d'Orbigny, 1834 [*In* 1834-1847], *Voyage dans l'Amerique Meridionale*, 5(3): 27. [Type locality: Coast of Patagonia, 40°S, inside large bay of San Blas].

Frequent Synonyms: *Octopus lobensis* Castellanos and Menni (1969).

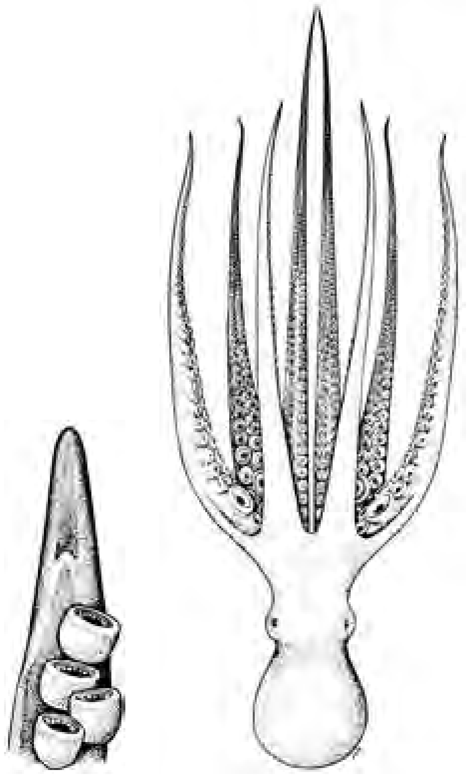
Misidentifications: None.

FAO Names: En — Tehuelche octopus; **Fr** — Poulpe tehuelche; **Sp** — Pulpo tehuelche.

Diagnostic Features: Small to moderate-sized, muscular species. Arms of moderate length, 3 to 4 times mantle length. Lateral arms longest, first two pairs of dorsal arms shortest. Arm autotomy at distinct plane absent. Webs of moderate depth, deepest around 30% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Interbrachial web pouches absent. Two rows of suckers on each arm. Sucker counts unknown. **Enlarged suckers present in mature males, 1 to 3 on arms 2 and 3. Gills with 6 lamellae per demibranch. Funnel organ W-shaped, limbs of approximately equal length**. Radula with 7 rows of teeth plus marginal plates. Rachidian tooth with 2 to 3 lateral cusps in asymmetrical series, migrating over 3 to 4 rows. Ink sac present. Anal flaps present. Right third arm of males hectocotylized. Ligula small, 3.4 to 4.5% of arm length. Calamus small, approximately 15% of ligula length. Hectocotylized arm sucker count unknown. Spermatophores 23 to 30 mm long. **Eggs large, 9 to 12 mm long, attached singly to shelter. Colour:** Preserved material dark brown or purplish black. Live animal colour patterns not described. **Sculpture:** Preserved material described as smooth with minute granulations above the eyes. Skin sculpture of live animals not described. Skin ridge around lateral margin of mantle absent.

Size: Total length to 200 mm; body weight to at least 120 g.

Geographical Distribution: Southwest Atlantic from southern Brazil (30°S) to northern Patagonia (44°S) (Fig. 215).



hectocotylus **dorsal view**

Fig. 214 *'Octopus' tehuelchus*

Fig. 215 *'Octopus' tehuelchus*

🟥 Known distribution

Habitat and Biology: This small octopus lives in intertidal and shallow subtidal habitats (reef and sand areas) where it uses crevices, boulders and empty gastropod and bivalve shells as shelter. It shows prey selection for grapsid crabs and small bivalves. This species also drills gastropod shells to extract resident hermit crabs. This species is a major component of the diet of juvenile school shark in Argentinean waters.

Interest to Fisheries: There is a small-scale artisinal fishery for this species in Patagonia where fishermen harvest during daytime low tides by turning over rocks or extracting octopuses from crevices using a 30 to 40 cm long gaff. Catch is sold to buyers who process and freeze it for distribution around Argentinean cities. A significant decline in catch from the early 1970's to the present has been suggested to be caused by degradation of fishing areas from increased tourism degrading habitat, consequent increased competition between fishers and/or decrease in number of skilled fishers.

Local Names: BRAZIL: Pulpo.

Remarks: Iribarne and Fernandez (1994) clarified that ***Octopus lobensis*** is a junior synonym of this species.

Literature: Castellanos and Menni (1969), Palacio (1977), Pollero and Iribarne (1988), Iribarne (1990, 1991a,b), Iribarne *et al.* (1991, 1993), Iribarne and Fernandez (1994), Klaich *et al.* (2006), Lucifora *et al.* (2006), Narvarte (2006, 2007), Storero *et al.* (2010).

'Octopus' veligero Berry, 1953

Fig. 216

Octopus veligero Berry, 1953, *Leaflets in Malacology*, 1(10): 57. [Type locality: Northeastern Pacific Ocean, Mexico (Baja California Sur), off San Juanico].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Veiled octopus; **Fr** — Poulpe veilé; **Sp** — Pulpo velado.

Diagnostic Features: Moderate-sized, muscular species. **Arms short, 2 to 2.5 times mantle length**. Lateral arms longest (typically 2>3>4>1). Arm autotomy at distinct plane absent. Webs thin, delicate and easily torn, of moderate depth, deepest around 30% of arm length. Web deepest on lateral arms; webs between dorsal arms shallowest. Web margins extend to arm tips as thin diaphanous flaps. Interbrachial web pouches absent. Two rows of suckers on each arm. In larger animals, around 120 to 160 suckers on each normal arm. Enlarged suckers absent. **Gills with 15 to 17 lamellae per demibranch**. **Funnel organ in three parts, IΛI-shaped, limbs of approximately equal length.** Right third arm of males hectocotylized, around 75% length of opposite arm. Ligula small and conical, around 5% of arm length. Calamus small, around 5% of ligula length. Hectocotylized arm with 57 suckers. Spermatophores not described. Eggs small. **Colour: Mottled red-brown with gold and silver iridescence around the eyes and along the sides of the head. Four dark spots can be displayed on the dorsal mantle**. False-eye spots (ocelli) absent. **Sculpture:** Skin texture of closely set papillae of different sizes. Larger erectile papillae present on dorsal mantle and above each eye. Skin ridge around lateral margin of mantle absent.

Size: Mantle length to 70 mm; total length to around 150 mm.

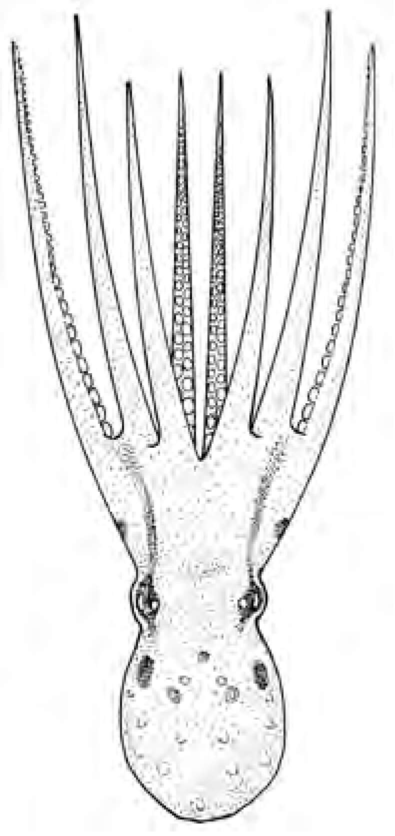


Fig. 216 ***'Octopus' veligero***

Geographical Distribution: Northeast Pacific Ocean, Mexico from Punta Eugenia to tip of Baja California and into Gulf of California to La Paz (Fig. 217).

Habitat and Biology: Depth range from 90 to 200 m. The biology and behaviour are not known.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Remarks: The taxonomic relationship of this octopus with the similar ***'Octopus' selene*** has not been resolved.

Literature: No additional literature.

Fig. 217 ***'Octopus' veligero***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

'Octopus' argus Krauss, 1848

Octopus argus Krauss, 1848, *Die sudafrikanischen Mollusken*: 132. [Type locality: South Africa, Natal Province].

Size: Mantle length to 18 mm.

Geographical Distribution: Southwest Atlantic, off Africa.

Habitat and Biology: Depth range unknown.

Literature: Norman and Finn (2001).

'Octopus' balboai Voss, 1971

Octopus balboai Voss, 1971a, *Bulletin of Marine Science*, 21(1): 16. [Type locality: Gulf of Panama, Panama, Chame Point].

Size: Mantle length to 34 mm.

Geographical Distribution: Central Pacific Ocean, El Salvador and Panama.

Habitat and Biology: Depth range from intertidal to shallow subtidal.

Literature: No additional literature.

'Octopus' berenice Gray, 1849

Octopus berenice Gray, 1849, *Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Antepedia*, 11. [Type locality: unknown].

Size: Mantle length 17 mm (female type specimen).

Geographical Distribution: Indian Ocean and Singapore; limits unknown.

Habitat and Biology: Depth range unknown.

Remarks: Pygmy species.

Literature: Robson (1929a).

'Octopus' bocki Adam, 1941

Octopus bocki Adam, 1941, *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 17(35): 1. [Type locality: Viti Levu, Fiji].

Size: Mantle length to 25 mm; body weight to 9 g.

Geographical Distribution: Currently reported only from Fiji, Philippines, Moorea and Tonga.

Habitat and Biology: Depth range from 0 to 10 m.

Remarks: Pygmy species.

Literature: Norman and Sweeney (1997), Cheng (1996), Caldwell (2005), Huffard (2007a).

'Octopus' bulbus Norman, 2001

Octopus bulbus Norman, 2001, *Memoirs of the Queensland Museum*, 46(2): 680. [Type locality: Australia, southern Queensland, east of Mooloolaba].

Size: Mantle length to 53 mm; total length to 340 mm total length, weight to 47 g.

Geographical Distribution: Australia, off southern Queensland; known from only three specimens.

Habitat and Biology: Depth range from 18 to 195 m.

Literature: No additional literature.

'Octopus' campbelli (Smith, 1902)

Polypus campbelli (Smith, 1902), *Report on the Collections of Natural History made in the Antarctic Regions during the Voyage of the Southern Cross, 7: 201*. [Type locality: New Zealand, Campbell Island, (52°30'S, 169°E)].

Size: Mantle length to 34 mm; total length to 135 mm.

Geographical Distribution: Southern New Zealand to Campbell Island.

Habitat and Biology: Depth range from 43 to 600 m.

Literature: Stranks and Norman (1993), O'Shea (1999).

'Octopus' chierchiae Jatta, 1889 **Plate VII, 55**

Octopus chierchiae Jatta, 1889, *Bollettino della Società dei Naturalisti in Napoli*, series 1, 3(1): 64. [Type locality: Pacific coast of Panama].

Size: Mantle length to 25 mm; total length to 40 mm.

Geographical Distribution: Gulf of California, Mexico to Ecuador.

Habitat and Biology: Depth range from 0 to 30 m.

Literature: Rodaniche (1984), Hofmeister *et al.* (2011).

'Octopus' diminutus Kaneko and Kubodera, 2008

Octopus diminutus Kaneko and Kubodera, 2008, *Molluscan Research*, 28(3): 150. [Type locality: Ryuku Archipelago, Japan (24°50'N, 125°46'E)].

Size: Mantle length to 17 mm.

Geographical Distribution: Known only from the type locality, off Japan.

Habitat and Biology: Depth 364 m.

Remarks: Pygmy species.

Literature: No additional literature.

'Octopus' favonius Gray, 1849

Octopus favonius Gray, 1849, *Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Antepedia*: 9. [Type locality: Singapore].

Size: Mantle length to 55 mm.

Geographical Distribution: Currently known only from Singapore.

Habitat and Biology: Depth range intertidal.

Literature: Robson (1929a).

'Octopus' fitchi Berry, 1953

Octopus fitchi Berry, 1953, *Leaflets in Malacology*, 1(10): 54. [Type locality: Gulf of California, Mexico, Baja California, Punta San Felipe].

Size: Mantle length to 45 mm; total length to 150 mm; body weight to 20 g.

Geographical Distribution: Gulf of California, Mexico to Ecuador.

Habitat and Biology: Depth range from 0 to 20 m.

Literature: No additional literature.

'Octopus' gardineri (Hoyle, 1905)

Polypus gardineri Hoyle, 1905, *Fauna and Geography of the Maldive and Laccadive Archipelago*, 2(1): 976. [Type locality: Indian Ocean, Maldive Islands, Male Atoll].

Size: Mantle length to 18 mm.

Geographical Distribution: Indian Ocean, Maldive Islands.

Habitat and Biology: Depth range unknown.

Remarks: Pygmy species.

Literature: Robson (1929a).

'Octopus' gorgonus Huffard, 2007

Plate VIII, 57

Octopus gorgonus Huffard, 2007a, *Molluscan Research*, 27(3): 148. [Type locality: Tonga, Atata Island].

Size: Mantle length to 24 mm.

Geographical Distribution: Known only from Tongan Islands, Pacific Ocean.

Habitat and Biology: Depth range from 10 to 30 m.

Remarks: Pygmy species.

Literature: No additional literature.

'Octopus' harpedon Norman, 2001

Octopus harpedon Norman, 2001, *Memoirs of the Queensland Museum*, 46(2): 677. [Type locality: Australia, Gulf of Carpentaria, near Weipa, Albatross Bay].

Size: Mantle length to 86 mm; total length to 1 m; body weight to 104 g.

Geographical Distribution: Known from only two specimens, both collected in Australia from the eastern Gulf of Carpentaria.

Habitat and Biology: Depth range to 2 m.

Literature: No additional literature.

'Octopus' hattai (Sasaki, 1929)

Polypus hattai Sasaki, 1929, *Journal of the College of Agriculture, Hokkaido Imperial University,* 20 (supplement), 87. [Type locality: Japan, Izu Province, Kominato].

Size: Mantle length to 120 mm; total length to 750 mm.

Geographical Distribution: Northwest Pacific Ocean, Japan.

Habitat and Biology: Depth range unknown.

Literature: Toll and Voss (1998).

'Octopus' hawiiensis Eydoux and Souleyet, 1852

Octopus hawiiensis Eydoux and Souleyet, 1852, *Voyage Autour du Monde Exécuté pendant.... 1836 et 1837 sur... la Bonite, Commandée par M. Vaillant, Zoologie*, 2: 9. [Type locality: Sandwich Islands (Hawaiian Island)].

Size: Mantle length to 30 mm; total length to >100 mm.

Geographical Distribution: Hawaii.

Habitat and Biology: Depth range from 0 to over 10 m.

Literature: Norman (2000).

'Octopus' hongkongensis (Hoyle 1885)

Polypus hongkongensis Hoyle, 1885, *Annals and Magazine of Natural History*, (series 5), 15: 224. [Type locality: Japan, off Sagami Bay, Enoshima Island, 35°11'N, 139°28'E].

Synonyms: *Polypus madokai* Berry, 1921; *P. tenuicurris* Sasaki, 1929; *Octopus megalops* Taki, 1964.

Size: Mantle length of type 90 mm; total length to 1 m.

Geographical Distribution: Northwest Pacific, Japan; limits unknown.

Habitat and Biology: Depth range from 150 to 630 m.

Remarks: This species (or species group) is in need of thorough revision. Despite the species name, there is no record of this species from China, Hong Kong SAR. The scientific name was borrowed by Hoyle on the basis of similarities between his Japanese material and description of a China, Hong Kong SAR species in an unpublished Steenstrup manuscript. Hoyle's species was described from deep-water material collected around 630 m. Octopuses treated under this name are reported to be of some commercial fishery value (Okutani *et al.,* 1987; Gleadall, 1993).

Literature: Emanuel and Martin (1956), Okutani *et al.* (1987, as ***Paroctopus megalops*** and ***P. tenuicirrus***), Gleadall (1993), Toll and Voss (1998).

'Octopus' humilis Huffard, 2007

Octopus humilis Huffard, 2007a, *Molluscan Research*, 27(3): 153. [Type locality: Tonga, Atata Island].

Size: Mantle length to 26 mm.

Geographical Distribution: Known only from Tongan Islands.

Habitat and Biology: Depth range from 8 to 20 m.

Remarks: Pygmy species.

Literature: No additional literature.

'Octopus' huttoni (Benham, 1943)

Plate VIII, 58

Robsonella huttoni Benham, 1943, *Transactions and Proceedings of the Royal Society of New Zealand*, 73(1): 53. [Type locality: New Zealand, Otago].

Synonym: *Octopus adamsi* Benham, 1944: 259.

Size: Mantle length to 57 mm; total length to 240 mm.

Geographical Distribution: New Zealand.

Habitat and Biology: Depth range from 0 to 260 m.

Literature: O'Shea (1999).

'Octopus' incella Kaneko and Kubodera, 2007

0ctopus incella Kaneko and Kubodera, 2007, *Zootaxa*, 1440: 40. [Type locality: Japan, Okinawa Island].

Size: Mantle length to 31 mm.

Geographical Distribution: Northwest Pacific, Japan, Okinawa Island.

Habitat and Biology: Depth range from 0 to 1 m.

Remarks: Intertidal species.

Literature: No additional literature.

'Octopus' joubini Robson, 1929

Octopus joubini Robson, 1929a, *A Monograph of the Recent Cephalopoda, I: Octopodinae*: 161. [Type locality: Danish West Indies (Virgin Islands), St. Thomas Island].

Size: Mantle length to 45 mm; total length to 135 mm.

Geographical Distribution: Gulf of Mexico and Caribbean Sea.

Habitat and Biology: Depth range from 0 to >10 m.

Remarks: Sometimes appears in aquarium trade (C. Huffard, pers. comm.). A distinct large-egg pygmy species in the genus ***Paroctopus*** often is incorrectly identified as this species.

Literature: Forsythe and Toll (1991), Hanlon (1983b).

'Octopus' kaharoa O'Shea, 1999

Octopus kaharoa O'Shea, 1999, *NIWA Biodiversity Memoir*, 112: 174. [Type locality: New Zealand, North Island].

Size: Mantle length to 90 mm; total length to 390 mm.

Geographical Distribution: Northern half of New Zealand.

Habitat and Biology: Depth range from 7 to 540 m.

Literature: No additional literature.

‘Octopus’ kermadecensis (Berry, 1914)

Polypus kermadecensis Berry, 1914, *Transactions and Proceedings of the New Zealand Institute*, 46(24): 138. [Type locality: Kermadec Islands, Sunday (= Raoul) Island].

Size: Mantle length to 80 mm; total length to 420 mm.

Geographical Distribution: Kermadec Islands.

Habitat and Biology: Depth range unknown; type specimen washed up dead on the beach.

Literature: O’Shea (1999; as ***Pinnoctopus kermadecensis***).

‘Octopus’ laqueus Kaneko and Kubodera, 2005

Octopus laqueus Kaneko and Kubodera, 2005, *Bulletin of the National Science Museum, Tokyo*, series A, 31(1): 8. [Type locality: Japan, Okinawa Island].

Size: Up to 48 mm mantle length.

Geographical Distribution: Japan, Okinawa Island and Australia, northern Great Barrier Reef.

Habitat and Biology: Depth range from 0 to 18 m.

Literature: Norman (2000; as ***Octopus*** sp. 15), Kaneko and Kubodera (2005), Kaneko *et al.* (2006).

‘Octopus’ mariles Huffard, 2007

Octopus mariles Huffard, 2007a, *Molluscan Research,* 27(3): 157. [Type locality: Tonga, Uoleva Island].

Size: Mantle length to 25 mm.

Geographical Distribution: Known only from Tongan Islands.

Habitat and Biology: Depth range <7 m.

Remarks: Pygmy species.

Literature: No additional literature.

‘Octopus’ mernoo O’Shea, 1999

Octopus mernoo O’Shea, 1999, *NIWA Biodiversity Memoir*, 112: 165. [Type locality: East of New Zealand].

Size: Mantle length to 85 mm; total length to 260 mm.

Geographical Distribution: Eastern New Zealand and Chatham Rise.

Habitat and Biology: Depth range from 368 to 550 m.

Literature: No additional literature.

‘Octopus’ microphthalmus Goodrich, 1896

Octopus microphthalmus Goodrich, 1896, *Transactions of the Linnaean Society of London, Zoology*, 7(1): 20. [Type locality: Andamans, Port Blair].

Size: Mantle length to 110 mm.

Geographical Distribution: Singapore to Andaman Islands.

Habitat and Biology: Depth range unknown.

Literature: Robson (1929a).

'Octopus' micropyrsus Berry, 1953

Octopus micropyrsus Berry, 1953, *Leaflets in Malacology*, 1(10): 52. [Type locality: Northeastern Pacific Ocean, United States, California, La Jolla Cove].

Size: Mantle length to 28 mm; total length to 100 mm; body weight to 12 g.

Geographical Distribution: Northeast Pacific, United States, from central California to Baja California, Mexico.

Habitat and Biology: Depth range from 0 to 20 m.

Literature: Hochberg and Fields (1980), Haaker (1985), Lang (1997).

'Octopus' micros Norman, 2001

Octopus micros Norman, 2001, *Memoirs of Queensland Museum*, 46(2): 683. [Type locality: Australia, southern Queensland, east of Moololaba].

Size: Mantle length to 25 mm; total length to 91 mm; body weight to 6 g.

Geographical Distribution: Australia, southern Queensland.

Habitat and Biology: Depth range of capture of type specimen 166 to 195 m.

Remarks: Pygmy species.

Literature: No additional literature.

'Octopus' mutilans Taki, 1942

Octopus mutilans Taki, 1942, *Venus*, 12(1-2): 71. [Type locality: Japan, Seto Sea, Mutsushima].

Size: Mantle length to 55 mm.

Geographical Distribution: Japan.

Habitat and Biology: Depth range unknown.

Literature: Tsuchiya *et al.* (2002).

'Octopus' nanus Adam, 1973

Octopus nanus Adam, 1973, *Bulletin of the Sea Fisheries Research Station, Haifa*, 60: 42. [Type locality: Red Sea, Cundabilu].

Size: Mantle length to 13 mm.

Geographical Distribution: Red Sea.

Habitat and Biology: Depth range from 2 to 8 m.

Remarks: Pygmy species.

Literature: Toll (1998).

'Octopus' oliveri (Berry, 1914)

Polypus oliveri Berry, 1914, *Transactions and Proceedings of the New Zealand Institute*, 46(24): 136. [Type locality: Kermadec Islands, Sunday Island].

Size: Mantle length to 70 mm; total length to 260 mm.

Geographical Distribution: Kermadec Islands.

Habitat and Biology: Depth range unknown.

Remarks: To date all specimens collected from intertidal rock pools.

Literature: O'Shea (1999).

'Octopus' parvus (Sasaki, 1917)

Polypus parvus Sasaki, 1917, *Annotationes Zoologicae Japonenses*, 9(3): 365. [Type locality: Japan, Satsuma Prefecture].

Size: Mantle length to 40 mm.

Geographical Distribution: Northwest Pacific, Japan.

Habitat and Biology: Depth range unknown.

Literature: Norman (2000), Tsuchiya *et al.* (2002), Furuya *et al.* (2004).

'Octopus' penicillifer Berry, 1954

Octopus penicillifer Berry, 1954, *Leaflets in Malacology*, 1(11): 66. [Type locality: Gulf of California, Mexico, off Punta Arena].

Size: Mantle length to 40 mm.

Geographical Distribution: Gulf of California, Mexico, south to Panama.

Habitat and Biology: Depth range from 30 to 35 m.

Literature: No additional literature.

'Octopus' pumilus Norman and Sweeney, 1997

Octopus pumilus Norman and Sweeney, 1997, *Invertebrate Taxonomy*, 11: 127. [Type locality: Philippines, southern tip of Negros Island].

Size: Mantle length to 31 mm; body weight to 12 g.

Geographical Distribution: Philippines, southern Negros, Siquijor Island, Batangas, Luzon.

Habitat and Biology: Depth range from 0 to 3 m.

Remarks: Pygmy species.

Literature: No additional literature.

'Octopus' pyrum Norman, Hochberg and Lu, 1997

Octopus pyrum Norman, Hochberg and Lu, 1997, *Mémoires du Muséum Nationale d'Histoire Naturelle*, 172: 365. [Type locality: Banda Sea, off Kai Islands, 5°21'S, 132°30'E].

Size: Mantle length to 35 mm; total length to 170 mm; body weight to 19 g.

Geographical Distribution: Indonesia, Banda and Arafura Seas; northeastern Australia, off Brisbane.

Habitat and Biology: Depth range from 329 to 511 m.

Literature: No additional literature.

'Octopus' salutii Verany, 1839

'Octopus' salutii Verany, 1839, *Memorie della Reale Accademia delle Scienze di Torino*, series 2, I: 93. [Type locality: Western Mediterranean Sea, France, off Nice].

Size: Mantle length to 165 mm; body weight to 750 g.

Geographical Distribution: Mediterranean Sea and northeastern Atlantic.

Habitat and Biology: Depth range from ~100 to 700 m; typically 250 to 500 m.

Literature: Quetglas *et al.* (2005).

'Octopus' superciliosus Quoy and Gaimard, 1832

Octopus superciliosus Quoy and Gaimard, 1832, *Voyage de Découvertes de l'Astrolabe pendant les Annees 1826-1829*, *Zoologie*, 2(1): 88. [Type locality: New Holland (Australia), Bass Strait, Victoria, Western Port].

Size: Mantle length to 26 mm; total length to 94 mm.

Geographical Distribution: Southeast Australia.

Habitat and Biology: Depth range from 0 to 69 m.

Remarks: Pygmy species.

Literature: Stranks (1998).

'Octopus' vitiensis Hoyle, 1885 **Plate VIII, 63**

Octopus vitiensis Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 15: 226. [Type locality: Fiji, Kandavu, on reefs].

Size: Mantle length to 60 mm; total length to 250 mm.

Geographical Distribution: At present known from Fiji, Tonga, and Papua New Guinea.

Habitat and Biology: Depth range from 0 to about 20 m.

Literature: Norman (2000), Huffard (2007a).

'Octopus' warringa Stranks, 1990

Octopus warringa Stranks, 1990, *Memoirs of the Museum of Victoria*, 50(2): 457. [Type locality: Australia, Tasmania, Maria Island].

Size: Mantle length to 35 mm; total length to 125 mm.

Geographical Distribution: Southeastern Australia.

Habitat and Biology: Depth range from 0 to 144 m.

Remarks: Small to pygmy species. O'Shea (1999) proposes that this species is a junior synonym of ***Octopus huttoni*** (Benham, 1943).

Literature: Stranks (1998), O'Shea (1999).

'Octopus' wolfi (Wülker, 1913)

Polypus wolfi (Wülker, 1913), *Abhandlungen Hrsg. von der Senckenbergischen Naturforschenden Gesellschaft*, 34: 458. [Type locality: Tahiti, Popeete (sic)].

Size: Mantle length to 15 mm; total length to 45 mm.

Geographical Distribution: Indo-Pacific from Red Sea to Tahiti.

Habitat and Biology: Depth range from 0 to 30 m.

Remarks: Pygmy species.

Literature: Norman and Sweeney (1997), Huffard (2007a).

'Octopus' zonatus Voss, 1968

Octopus zonatus Voss, 1968, *Bulletin of Marine Science*, 18(3): 647. [Type locality: Northwestern Atlantic Ocean, Colombia, off Punta Caribana, 8°51.2'N, 77°01.6'W].

Size: Mantle length to 30 mm; total length to 88 mm.

Geographical Distribution: Western Atlantic and Caribbean from Venezuela west to the Gulf of Darien.

Habitat and Biology: Depth range from 30 to 75 m.

Literature: Voss and Toll (1998).

Ctenoglossan octopods

by Mark D. Norman and Julian K. Finn

In members of this tribe mantle and arms are transparent and gelatinous. Fins and shell are absent. Suckers occur in a single row on the arms. Eyes are significantly modified in some species, from elongate or rectangular to telescopic (***Amphitretus***). The name of this tribe (Ctenoglossa) refers to the comb-like teeth in the radula of most member species. Large, simple chromatophores are present in some species.

Size: Members of all three families are small, typically less than 150 mm total length.

Habitat and Biology: Pelagic residents of the open ocean, present at tropical and temperate latitudes worldwide.

Interest to Fisheries: None, due to rarity of capture and gelatinous flesh.

Remarks: This group of gelatinous pelagic octopods collectively is known as the ctenoglossans, a term referring to the comb-like teeth found in the radula of these octopods. The group contains three families* : Amphitretidae, Vitreledonellidae and Bolitaenidae. Recent molecular studies (Strugnell *et al.* 2004) suggest that the ctenoglossans have evolved via an evolutionary step by the transparent planktonic young of the familiar benthic octopuses (family Octopodidae). The ancestors of these pelagic octopuses appear to be planktonic young that never returned to the seafloor, instead carrying out their entire life cycle in midwater. Many of their morphological features are shared with the planktonic juveniles of benthic octopuses, particularly transparent flesh, simple chromatophores and teeth on the rostrum of the beak.

Two relatives of the argonauts also are gelatinous in consistency and may be confused with ctenoglossans. ***Tremoctopus gelatus*** Thomas, 1977 (family Tremoctopodidae) and ***Haliphron atlanticus*** Steenstrup, 1861 (family Alloposidae) are easily separated from ***Amphitretus*** in that they have normal (non-telescopic) eyes. They are distinct from bolitaenids and ***Vitreledonella*** in that they possess two rows of suckers on each arm compared with the single row present in these two ctenoglossan families.

Literature: Naef (1923).

Key to families of ctenoglossan octopods*:

1a. Eyes telescopic and situated close together on dorsal surface of head; body and arms soft, semi-gelatinous; funnel fused to ventral head to form two openings to the mantle cavity . . . . **Family Amphitretidae**

1b. Eyes lateral, round to oblong, not telescopic; funnel free from ventral head, single opening to mantle cavity......→ **2**

2a. Arms longer than mantle length . . . . **Family Vitreledonellidae**

2b. Arms shorter than mantle length. . . . . **Family Bolitaenidae**

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* At the time of going to print, Strugnell *et al.* (2013) used molecular evidence to merge these families into a single family Amphitretidae (see that work).

2.1.2 **Family AMPHITRETIDAE** Hoyle, 1886

by Mark D. Norman and Julian K. Finn

Amphitretidae Hoyle, 1886, *Report on the Scientific Results of the Voyage of H.M.S. Challenger… 1873-76, Zoology*, 16(44): 67.

Type Genus: *Amphitretus* Hoyle, 1885.

FAO Names: En — Telescope octopods; **Fr** — Poulpes téléscopes; **Sp** — Pulpos telescópicos.

Diagnostic Features: Small to moderate-sized, gelatinous octopods. Mantle, arms and webs transparent. Internal shell absent. Each of the eight arms possesses one row of suckers for the majority of the arm length, with two rows present on distal tips beyond the margins of the webs. Eyes telescopic, tubular in shape, oriented vertically. Ventral mantle fused to funnel restricting mantle aperture to two lateral openings. Digestive gland (liver) elongate and narrow, oriented vertically in live animal to minimise silhouette seen by predators from below. Digestive viscera dorsal to digestive gland. Radula comb-like with multiple cusps on central and first two lateral teeth rows. Ink sac present. Third right arm of male modified, consisting of distinct calamus and whip-like distal tip.

Size: Mantle length to 135 mm; total length to ~300 mm.

Geographical Distribution: Tropical and subtropical.

Habitat and Biology: Depth range from 0 to around 2 000 m. Little is known of the biology of these rarely encountered octopods. They are pelagic inhabitants of midwater in the open ocean always over deep water. It is likely that females brood the eggs within their arm crown as has been reported for ***Vitreledonella***.

Remarks: Two species are currently recognized within this family: ***Amphitretus pelagicus*** and ***A. thielei***.

Literature: O'Shea (1999).

Amphitretus Hoyle, 1885

Amphitretus Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 15: 271.

Type Species: *Amphitretus pelagicus* Hoyle, 1885.

Diagnostic Features: With characters of the family. Monogeneric.

Size: Mantle length to 100 mm; total length to around 300 mm.

Geographical Distribution: Tropical to subtropical waters of Indo-Pacific region, temperate waters of southern Indo-Pacific region.

Habitat and Biology: Pelagic species of open waters, from near surface depths to at least 2 000 m.

Remarks: The two member species of this genus are semi-gelatinous, transparent, mesopelagic octopuses easily distinguished by their telescopic eyes used to detect prey above them in the water column.

Literature: Young (1991).

Amphitretus pelagicus Hoyle, 1885

Fig. 218; Plate IX, 72

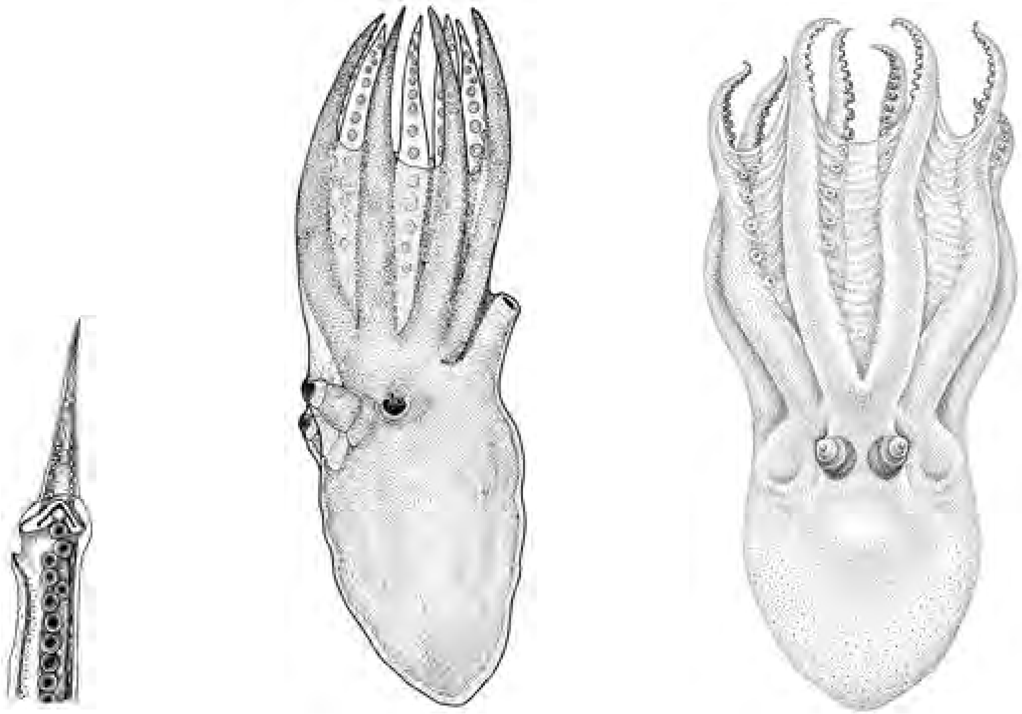
Amphitretus pelagicus Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 15: 235. [Type locality: South Pacific Ocean, off Kermadec Islands, 29°55'S, 178°14'W].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Telescope octopod; **Fr** — Poulpe téléscope; **Sp** — Pulpo telescópico.

Diagnostic Features: Small to medium-sized, gelatinous species. **Mantle, arms and webs transparent. Ventral mantle fused with funnel so that mantle aperture consists of two lateral slits, one below each eye. Eyes telescopic with bases close together in V-shaped arrangement.** Suckers in single row to web margin, forming two rows in distal tips. Normal arms with 22 to 32 suckers. **Males with modified third right arm consisting of whip-like tip bearing two rows of low papillae and a distinct calamus.** Hectocotylized arm with 27 to 28 suckers. Webs very deep, greater than 60% of arm length. Gills with 10 lamellae in the outer demibranch. Cigar-shaped elongate liver, always held in vertical orientation in live animal.



hectocotylus **lateral view** **dorsal view**

Fig. 218 *Amphitretus pelagicus*

Size: Mantle length to 100 mm; total length to around 300 mm.

Geographical Distribution: Tropical and subtropical waters of Indo-Pacific region (Fig. 219).

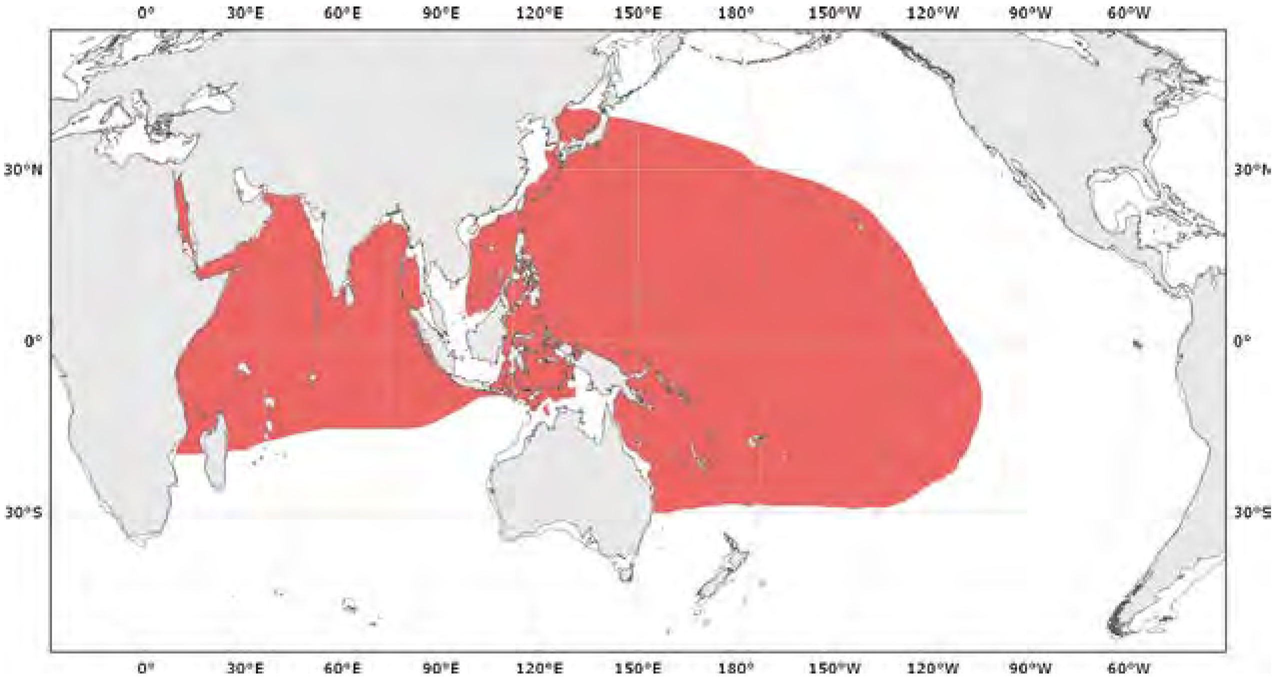


Fig. 219 *Amphitretus pelagicus*

🟥 Known distribution

Habitat and Biology: Depth range from 100 to 2 000 m. This midwater species lives at depths between the epipelagic and bathypelagic zones. The telescopic eyes are always oriented upwards, presumably used to detect the silhouettes of prey from below. The octopus minimises its own silhouette by being mostly transparent and by maintaining both eyes and the digestive gland (liver) in a vertical orientation. Juveniles appear to occur in shallower water.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Thore (1949), Young (1989), O'Shea (1999), Johnsen (2001).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Amphitretus thielei Robson, 1930

Amphitretus thielei Robson, 1930, *Discovery Reports*, II: 372. [Type locality: Southeastern Atlantic Ocean, South Africa, off west coast].

Size: Mantle length to 135 mm; total length to >200 mm.

Geographical Distribution: Poorly known, at this stage recorded from cooler waters off South Africa, southern Australia and New Zealand.

Habitat and Biology: Depth range from near surface to 1 145 m.

Literature: O'Shea (1999).

2.1.3 Family BOLITAENIDAE Chun, 1911

by Mark D. Norman and Julian K. Finn

Bolitaenidae Chun, 1911, *Cirrothauma, ein Blinder Cephalopod*. 210 pages. Doctoral dissertation, University of Leipzig: 20.

Type Genus: *Bolitaena* Steenstrup, 1859.

FAO Names: En — Pelagic octopods; **Fr** — Poulpes pélagiques; **Sp** — Pelagopulpos.

Diagnostic Features: Small, gelatinous and mostly transparent octopods. Arms short, shorter than mantle length. Single row of suckers. Internal shell absent. Eyes lateral and laterally compressed. The long axis of the digestive gland (liver) is parallel to the body axis. Digestive viscera posterior to digestive gland. Radula comb-like with multiple cusps on central and first two lateral teeth rows. Mature females possess a circular light organ that forms a ring surrounding the mouth. Large chromatophores scattered over body, arms and webs.

Size: Mantle length to 85 mm; total length to around 160 mm.

Geographical Distribution: Tropical and temperate latitudes of all oceans.

Habitat and Biology: Meso- to bathypelagic in open ocean to depths of 1 400 m. Little is known of the biology and behaviour of these small pelagic octopods. Females are presumed to use the circumoral light organ to attract males at depths greater than 1 000 m. Females brood the eggs by holding the egg mass within their arm crown. Eggs are stalked with the stalks attached to the capsules of other eggs, thus holding the egg mass together. Off Hawaii, young are released around 800 m and move up to shallower waters (150 to 250 m). As they grow they descend gradually to adult depths of around 800 to 1 400 m.

Remarks: Two genera are recognized, each with a single species: ***Bolitaena pygmaea*** and ***Japetella diaphana***.

Literature: Thore (1949), Young (1978), Robison and Young (1981), Boucaud-Camou and Roper (1995), Haimovici *et al.* (2002).

Bolitaena Steenstrup, 1859

Bolitaena Steenstrup, 1859. *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjobennavn*, 1858: 183.

Type Species: *Bolitaena pygmaea* (Verrill, 1884).

Diagnostic Features: Small gelatinous species. Arm length less than mantle length. **Eyes small and extended away from brain on long optic stalks. Mature males with third left arm hectocotylized with an elongate ligula.** Third right arm in males also modified with 1 to 3 greatly enlarged suckers. **Mature females with circumoral light organ.**

Size: Mantle length to around 60 mm.

Geographical Distribution: Throughout tropical and subtropical waters worldwide.

Habitat and Biology: Semi-transparent pelagic species occurring midwater between 100 and 1 400 m, typically over deeper water.

Remarks: Single widely distributed species.

Literature: Young (1972b, 1978).

Bolitaena pygmaea (Verrill, 1884)

Fig. 220; Plate X, 73

Eledonella pygmaea Verrill, 1884, *Transactions of the Connecticut Academy of Sciences*, 6(1): 145. [Type locality: Northwestern Atlantic Ocean, United States, off Virginia, 37°12'20"N, 69°39'W].

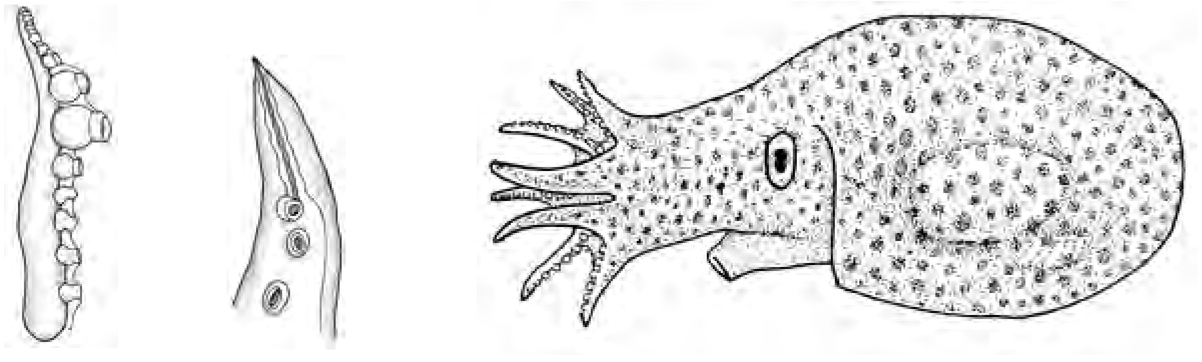
Frequent Synonyms: *Eledonella pygmaea* (Verril 1884); *Bolitaena microcotyla* Steenstrup *In* Hoyle, 1886.

Misidentifications: None.

FAO Names: En — Pygmy pelagic octopod; **Fr** — Poulpe pélagique pygmée; **Sp** — Pelagopulpo pigmeo.

Diagnostic Features: With characters of the genus. Monotypic.

Size: Mantle length to around 60 mm.



arm tip

hectocotylus

lateral view

Fig. 220 ***Bolitaena pygmaea***

Geographical Distribution: Throughout tropical and subtropical waters worldwide (Fig. 221).

Habitat and Biology: Depth range from 100 to 1 400 m. These small pelagic octopods typically live over deeper water. Young animals tend to occur in the shallower end of the range. As members of this species reach sexual maturity the iridescence of the digestive gland and eyes is lost and animals migrate to deeper darker waters. Pigmentation greatly increases in females as they mature and the arms become relatively longer. Increased pigmentation may be associated with the need to mask output from the female's circumoral light organ. This light organ may be used for reproductive signalling to males. The posterior salivary glands of mature males are greatly enlarged and have been suggested to produce a chemical attractant for females.

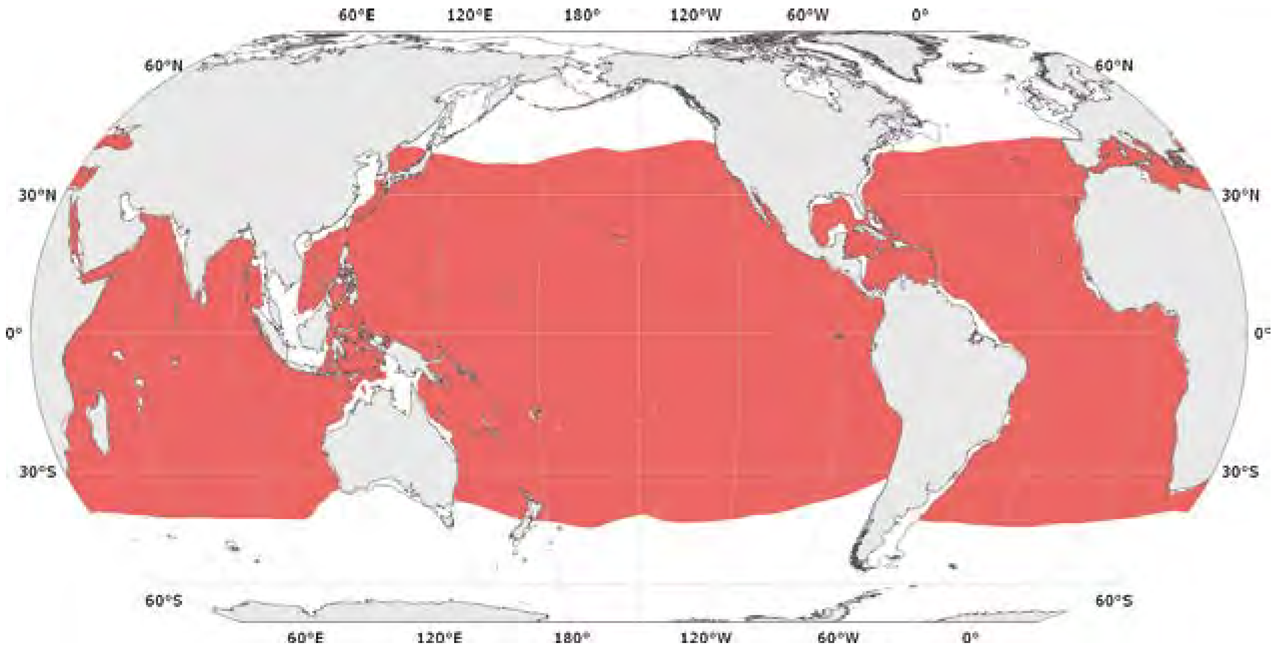


Fig. 221 ***Bolitaena pygmaea***

🟥 Known distribution

Interest to Fisheries: Unknown.

Local Names: Unknown.

Remarks: Confusion exists relating to the identification of animals in this family and whether more than one species is valid. Often placed in the genus ***Eledonella*** or identified as ***Bolitaena microcotyla***.

Literature: Chun (1910), Thore (1949), Young (1972b, 1978), Robison and Young (1981), Young (1991; as ***Eledonella***), Hochberg *et al.* (1992), Voight (1995; as ***E. pygmaea***), O'Shea (1999), Jorgensen (2009).

Japetella Hoyle, 1885

Japetella Hoyle, 1885. *Narrative of the Challenger Expedition. Report on the Scientific Results of the Voyage of the H.M.S. Challenger during the Years 1873-76*, *Narrative*, 1(1): 271.

Type Species: *Japetella diaphana* Hoyle, 1885.

Diagnostic Features: Small gelatinous species. Arm length less than mantle length. **Eyes relatively large, diameter approximately equal with optic stalk length. Mature males without hectocotylized arm.** Third right arm in mature males modified with enlargement of distal suckers, not as extreme as in ***Bolitaena***. **Mature females with circumoral light organ.**

Size: Mantle length to 85 mm; total length to around 160 mm.

Geographical Distribution: Throughout tropical and subtropical waters worldwide; extends into boreal waters in the North Pacific Ocean.

Habitat and Biology: Pelagic residents of water column in the open ocean at depths between 200 and 1 000 m, typically over deeper water.

Remarks: Single species.

Literature: Kubodera *et al.* (2007).

Japetella diaphana Hoyle, 1885

Fig. 222; Plate X, 74

Japetella diaphana Hoyle, 1885, *Annals and Magazine of Natural History*, series 5, 15: 232. [Type locality: Southwestern Pacific Ocean, north of Papua New Guinea, 00°42'S, 147°E].

Frequent Synonyms: None.

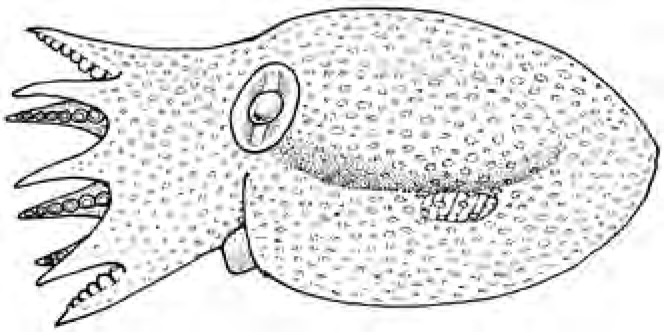
Misidentifications: None.

FAO Names: En — Diaphanous pelagic octopod; **Fr** — Poulpe pélagique translucide; **Sp** — Pelagopulpo translucido.

Diagnostic Features: With characters of the genus. Monotypic.

Size: Mantle length to 85 mm; total length to around 160 mm.

Geographical Distribution: Throughout tropical and subtropical waters worldwide; extends into boreal waters in the north Pacific Ocean (Fig. 223).



lateral view

Fig. 222 ***Japetella diaphana***

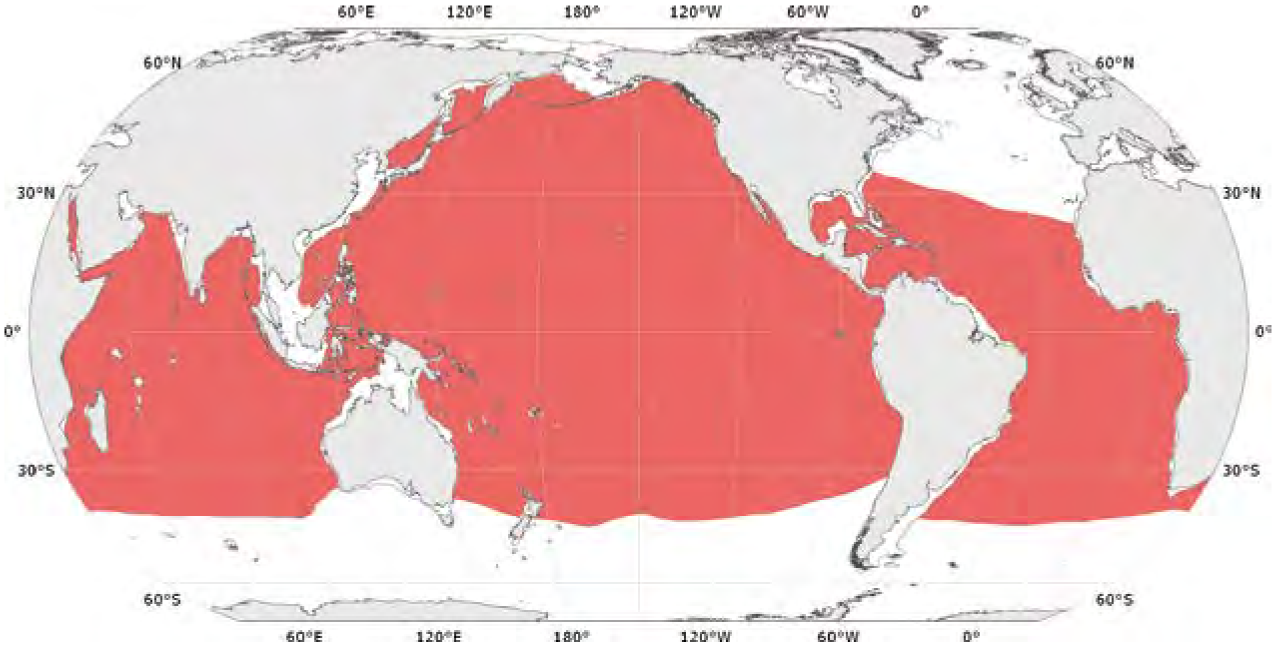


Fig. 223 ***Japetella diaphana***

🟥 Known distribution

Habitat and Biology: Depth range from 200 to 1 000 m. These small pelagic octopods typically occur over deeper water as adults. Young animals tend to occur in the shallower end of the range. As members of this species reach sexual maturity the iridescence of the digestive gland and eyes is lost, and animals migrate to deeper darker waters in the later stages of the life cycle. Nearly mature males have salivary glands that are much larger than those of comparable females. As in ***Bolitaena***, salivary products may be used as a chemical attractant for females. The female light organ may be used for reproductive signalling to males.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Thore (1949), Young (1978), Robison and Young (1981), Young (1989), Seibel *et al.* (1997; as ***Japetella heathi***), Santos *et al.* (2001a), Kubodera *et al.* (2007), Jorgensen (2009), Zylinski (2011).

2.1.4 Family VITRELEDONELLIDAE Robson, 1932

by Mark D. Norman and Julian K. Finn

Vitreledonellidae Robson, 1932, *A Monograph of the Recent Cephalopoda. Part II. Octopoda.* London, British Museum (Natural History): 321.

Type Genus: *Vitreledonella* Joubin, 1918.

FAO Names: En — Glass octopods; **Fr** — Poulpes vitreux; **Sp** — Pulpos vitreos.

Diagnostic Features: Small to moderate-sized, gelatinous, pelagic octopods with transparent mantle, arms and webs. Ventral mantle edge free from funnel (i.e. not fused). Single wide mantle opening. Internal shell absent. Each arm possesses one row of suckers. Eye shape in form of vertical rectangle with lateral lens. Tapered rostrum present on ventral surface of eye. Optic lobes of brain widely spaced with long optic nerve stalks. Gills with outer demibranch only. ***Vitreledonella*** differs from other members of the Tribe Ctenoglossa in that the lateral teeth of the radula do not bear numerous cusps (i.e. are not comb-like). The first lateral tooth bears an extra cusp compared with the radula of the more familiar benthic octopuses (family Octopodidae). Digestive gland elongate and narrow, held vertically in live animal to minimise silhouette from below. Digestive viscera dorsal to digestive gland. Ink sac present. Third left arm of mature male modified as bulbous oval tip bearing a slender papilla. Simple chromatophores present.

Size: Mantle length to 100 mm; total length to 450 mm.

Geographical Distribution: Tropical and subtropical regions of the world's oceans.

Habitat and Biology: Depth range from near the surface to at least 1 000 m, typically over deep water (beyond continental shelf). Little is known of the biology and behaviour of this rarely encountered pelagic octopod. Video sequences from submersibles suggest that the male envelops the female within his webs during mating. Females are thought to brood their eggs within their arm crown.

Remarks: This family contains a single species, ***Vitreledonella richardi***.

Literature: Joubin (1918, 1937).

Vitreledonella Joubin, 1918

Vitreledonella richardi Joubin, 1918, *Bulletin de l'Institute Oceanographique, Monaco,* 340: 1.

Type Species: *Vitreledonella richardi* Joubin, 1918.

Diagnostic Features: With characters of the family. Monotypic.

Size: Mantle length to 110 mm; total length to around 450 mm.

Geographical Distribution: Tropical and temperate waters worldwide.

Habitat and Biology: As above for the family.

Remarks: Single species, ***Vitreledonella richardi***.

Literature: No additional literature.

Vitreledonella richardi Joubin, 1918

Fig. 224; Plate X, 75

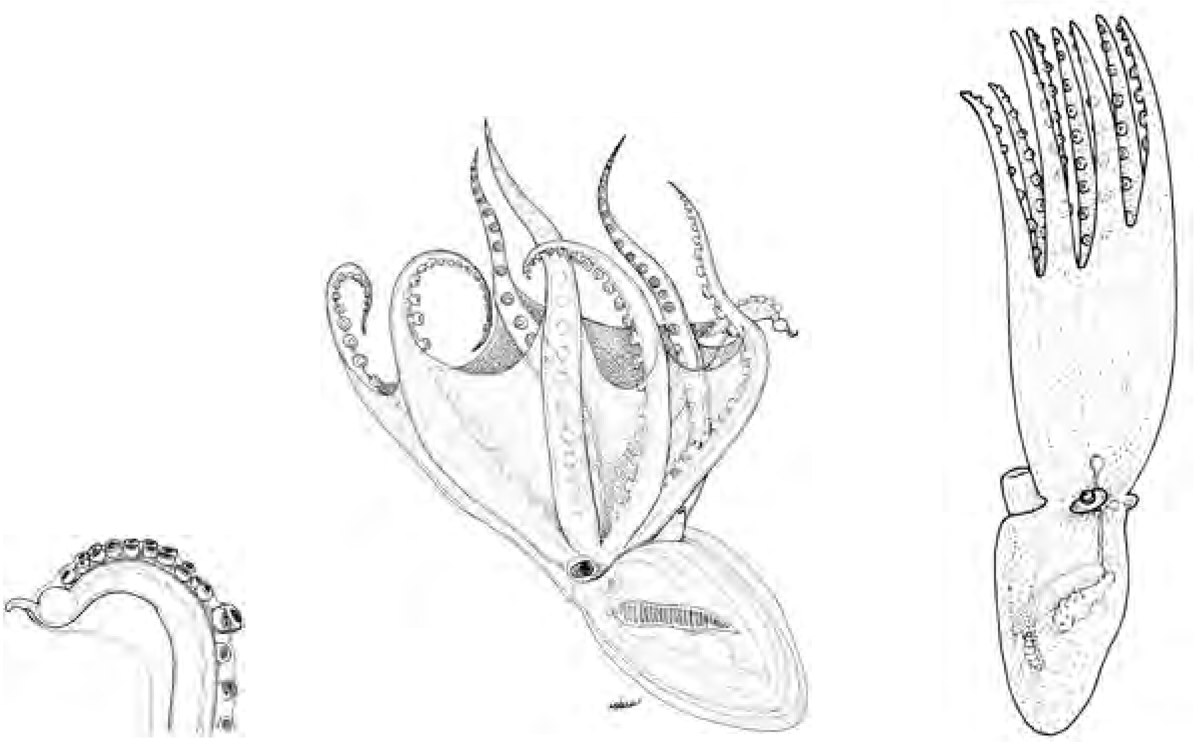
Vitreledonella richardi Joubin, 1918, *Bulletin de l'Institute Oceanographique, Monaco,* 340: 1. [Type locality: Atlantic Ocean, 36º36'N, 26º14'W].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Glass octopod; **Fr** — Poulpe vitreux; **Sp** — Pulpo vitreo.

Diagnostic Features: Small to medium-sized, gelatinous species. **Body, arms and webs transparent. Eyes as vertical rectangles with lateral lens. Single row of suckers on arms, suckers significantly larger in diameter in distal portion, beyond limit of webs.** Webs deep, approximately 60% of arm length. Gills with 7 lamellae in outer demibranch, inner demibranch absent. Scattering of simple orange chromatophores over mantle, arms and webs.



hectocotylus **male - lateral view** **female - dorsolateral view**

Fig. 224 ***Vitreledonella richardi***

Size: Mantle length to 110 mm; total length to around 450 mm.

Geographical Distribution: Tropical and temperate waters worldwide (Fig. 225).

Habitat and Biology: As above for the family.

Interest to Fisheries: Unknown.

Local Names: Unknown.

Literature: Joubin (1918, 1937), Thore (1949), Young (1989), Land (1992), Voight (1996), Santos *et al.* (2001b).

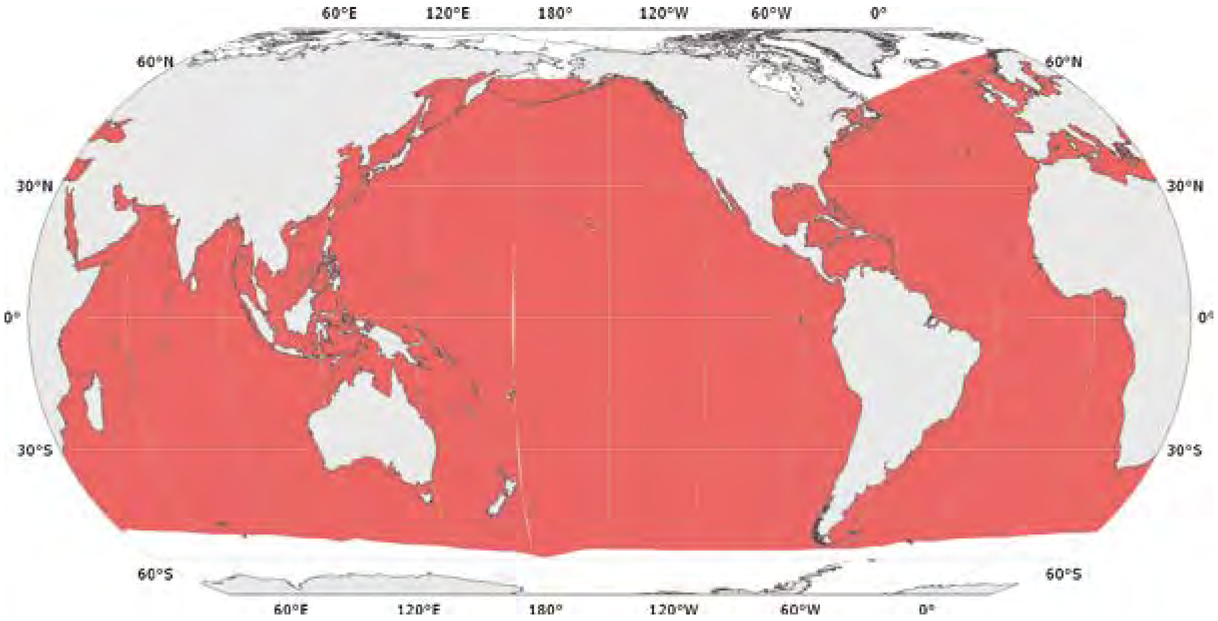


Fig. 225 ***Vitreledonella richardi***

🟥 Known distribution

Argonautoid octopods

by Julian K. Finn

Argonautoid octopods encompass four families of pelagic octopods believed to have derived from a benthic origin. Morphological modifications suited to a benthic habitat (e.g. the presence of corneas; absence of a shell, fins, and cirri; fully formed inferior frontal lobe system, albeit reduced; and brooding) indicate that their ancestral mode was a benthic lifestyle.

All members of this group are united by the presence of the following characters:

(1) marked sexual size dimorphism (females much larger than males);
(2) in males one arm of third pair developed in a specialized sac, completely hectocotylized, autotomous;
(3) funnel locking apparatus present in both sexes.

The presence or absence of paired cephalic water pores (a character unique to some argonautoid families; also known as 'aequiferous pores') can be helpful in distinguishing argonautoid families. Cephalic water pores are essentially oval holes in the skin located ventrally (on the surface of the head, adjacent to the opening of the funnel, at the base of the fourth arms) and/or dorsally (on the surface of the head, slightly anterior to the eyes, at the base of the first arms). The precise function of cephalic water pores remains unknown.

Key to families of argonautoid octopods:

1a. Cephalic water pores absent . . . . → **2**
1b. Cephalic water pores present . . . . → **3**

2a. Body gelatinous; funnel embedded in head tissue; web deep between all arms; third right arm of male hectocotylized, developed in inconspicuous sac in front of right eye . . . . **Family Alloposidae**
2b. Body muscular; funnel not fused in head; web shallow between all arms; dorsal arms of female with distal (terminal) expansion for secretion of an external shell; third left arm of male hectocotylized, developed in sac under left eye. . . . . **Family Argonautidae**

3a. One pair of cephalic water pores (ventral only); first and fourth arm pairs longer than other arms; male hectocotylus in sac that extends from base of third right arm. . . . . **Family Ocythoidae**
3b. Two pairs of cephalic water pores (dorsal and ventral); first and second arms of female longest, connected by a broad web; male hectocotylus develops in sac embedded between funnel and right eye (note: right ventral cephalic water pore of males may be crowded and degenerate due to development of hectocotylus in pouch below right eye)......... . . . . **Family Tremoctopodidae**

Literature: Naef (1923), Young *et al.* (1998).

2.1.5 Family ALLOPOSIDAE Verrill, 1881 by Julian K. Finn

Alloposidae Verrill, 1881, *Transactions of the Connecticut Academy of Sciences*, 5(6): 365.

Type Genus: *Haliphron* Steenstrup, 1861.

FAO Names: En — Gelatinous giant octopods; **Fr** — Poulpes gelées gèants; **Sp** — Megapulpos gelatinosos.

Diagnostic Features: Body tissue gelatinous, smooth; cephalic water pores absent; stylets present; funnel embedded in head tissue; funnel locking apparatus simple, fused in adults; ink sac present; webs deep between all arms; suckers in two rows, can form single row in basal portion of arms; male third right arm hectocotylized, developed in inconspicuous sac in front of right eye.

Size: Mantle length of females to 690 mm; males to over 100 mm; total length of females estimated to reach 4 m; males estimated to 210 mm.

Geographical Distribution: Circumglobal in the Atlantic, Indian, and Pacific oceans between 43°N and 45°S; extends northerly in the Atlantic Ocean to off Ireland (52°N), Scotland (59°N), and Norway (60-68°N).

Habitat and Biology: Members of the family Alloposidae are commonly known as the 'seven-arm octopus', due to the completely embedded hectocotylized arm of males that gives them the appearance of possessing only seven arms, or 'giant octopus', on account of the female's gigantic maximum size. Female alloposids attain the largest size of all argonautoids with a mantle length of at least 690 mm and an estimated total length of 4 m. Male alloposids are similarly the largest of all argonautoid males, attaining a mantle length of at least 100 mm and an estimated total length of over 200 mm. Female alloposids are characteristically gelatinous — their large mass unable to retain form when out of the water and prone to damage and fragmentation in fishing nets. Unlike other argonautoids, which are presumed to be entirely pelagic, it is believed that alloposids may spend only short periods in the open ocean, soon returning to a life on the sea floor, particularly on continental slopes. The remains of alloposids have been recovered from the stomachs of a range of predators including fishes, marine mammals and seabirds.

Remarks: The suggestion in the literature that the family Alloposidae must be corrected to Haliphronidae (Hochberg *et al.,* 1992) is inconsistent with the recent International Code of Zoological Nomenclature (1999), Article 40.1. A single species, ***Haliphron atlanticus***, is currently recognized in this family.

Literature: Verrill (1881), Thore (1949), Lu and Roper (1979), Hochberg *et al.* (1992), Norman (2000), Vecchione and Pohle (2002), O'Shea (2004).

Haliphron Steenstrup, 1861

Haliphron Steenstrup, 1861, *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn*, 1860: 332.

Type species: *Haliphron atlanticus* Steenstrup, 1861.

Frequent Synonyms: *Alloposus* Verrill, 1880.

Diagnostic Features: With characters of the family. Monotypic.

Haliphron atlanticus Steenstrup, 1861

Fig. 226; Plate X, 79

Haliphron atlanticus Steenstrup, 1861, *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn*, 1860: 332. [Type locality: Atlantic Ocean, 38°N, 34°W].

Frequent Synonyms: *Alloposus mollis* Verrill, 1880.

Misidentifications: None.

FAO Names: En — Gelatinous giant octopod; **Fr** — Poulpes gelée gèant; **Sp** — Megapulpo gelatinoso.

Diagnostic Features: Largest of all argonautoids. **Body tissues gelatinous**, densely pigmented, concealing underlying musculature. Mantle short and broad. Mantle aperture wide. Head wide, width equal to or greater than mantle width. Eyes large; diameter up to one-third mantle length. **Cephalic water pores absent**. Arms short. Arm length formula 1>2>3>4. **Webs deep between all arms.** Suckers small, mostly in two series but may be in single series near mouth. Enlarged suckers absent. Funnel long, **entirely embedded in head tissue**, opening anterio-ventrally to eyes. Funnel organ

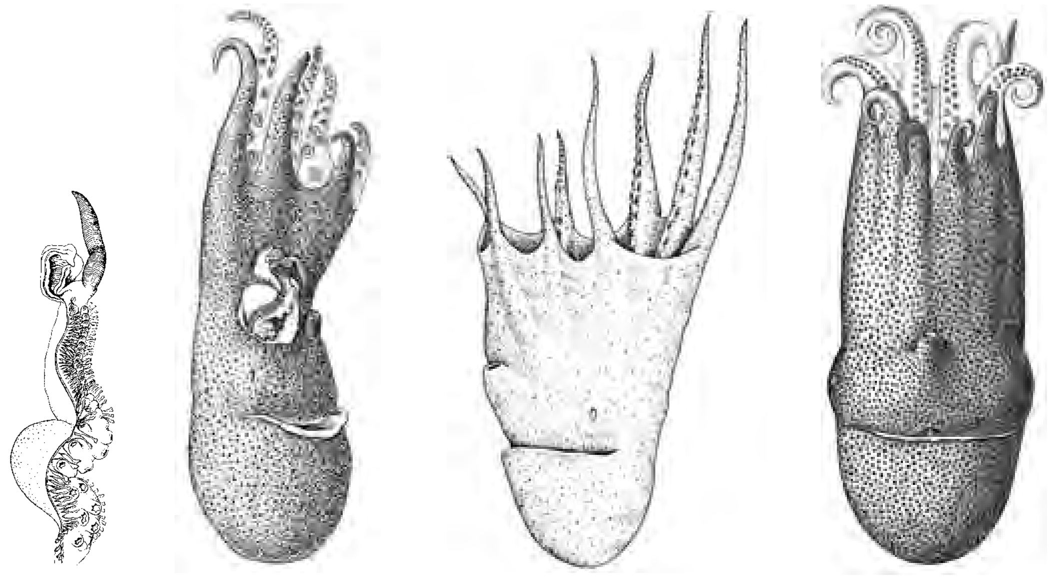

hectocotylus
male - lateral view
female - lateral view
female - ventral view

Fig. 226 *Haliphron atlanticus*

W-shaped. Funnel locking apparatus present, consists of hook-like muscular folds on funnel corners with corresponding ridge/groove system on the mantle, fused in adults. Visceral sac small. Ink sac present. Stylets relatively small, wide, thick, drop-like bodies of soft consistency embedded in lateral walls of mantle. **Males much smaller than females but not dwarfed**. Third right arm of males hectocotylized; develops in inconspicuous pocket produced by interbrachial membrane in front of right eye; male appears to have only seven arms. **Spermatophore groove completely formed; leads to terminal spermatophore reservoir branched off arm at base of penile filament;** penile filament hangs free, not enclosed within sac; 2 rows of large suckers present; papillate lateral fringes from base to spermatophore reservoir.

Size: Mantle length of females to 690 mm; males to over 100 mm; total length of females estimated to reach 4 m; males estimated to 210 mm.

Geographical Distribution: Widespread pelagic species. Circumglobal in the Atlantic, Indian, and Pacific oceans between 43°N and 45°S; extends northerly in the Atlantic Ocean to off Ireland (52°N), Scotland (59°N), and Norway (60-68°N) (Fig. 227).

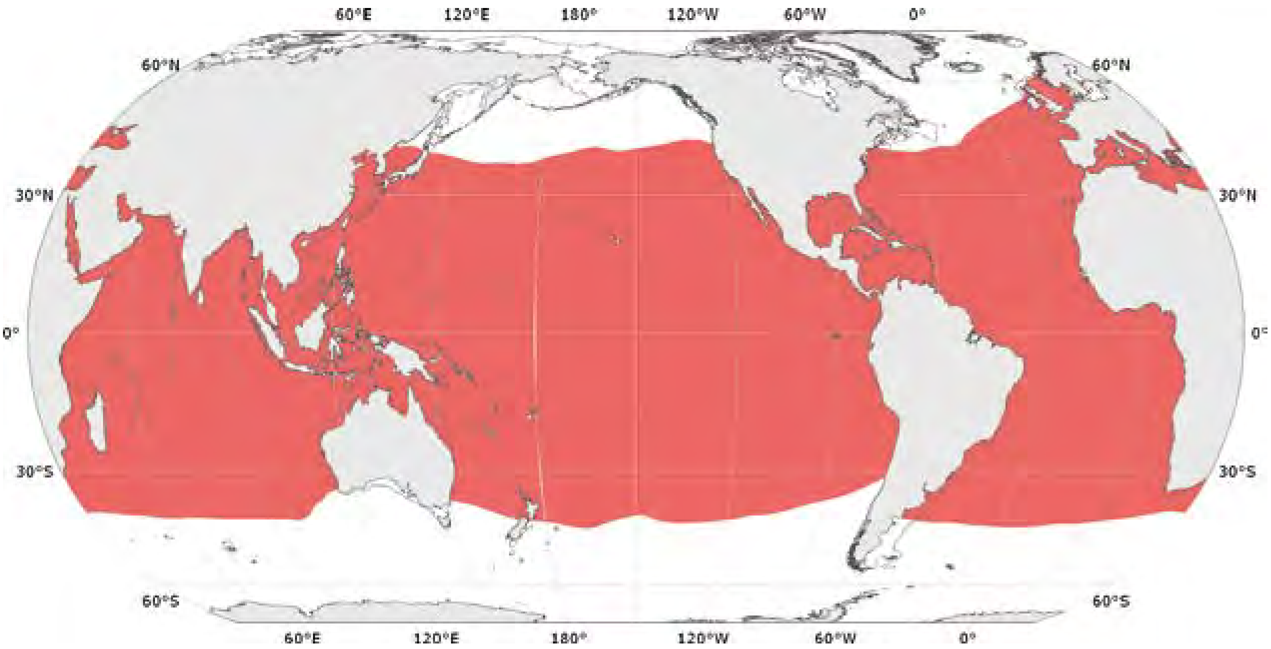


Fig. 227 ***Haliphron atlanticus***

🟥 Known distribution

Habitat and Biology: Reported to occupy a depth range in open-ocean from the surface to at least 1 260 m, over depths of up to 6 787 m. Collected in bottom trawls on continental shelves and slopes at depths of 100 to 3 173 m. It has been proposed that ***Haliphron atlanticus*** may not be entirely pelagic, but might pass only relatively short periods of its life cycle in the open waters, soon returning to a life at the bottom especially on continental slopes. A limited number of captures with opening/closing nets suggest that ***H. atlanticus*** may undertake diel migration with some animals being caught from the surface to 100 m at night and at 600 to 700 m during the day. Based on small number of captures in the western Atlantic Ocean, displaying an increase in individual size from February through to September, it has been proposed that spawning may occur in the northern hemisphere during winter (December to February). Females are reported to brood their eggs, attached to the oral side of the arm bases near the mouth. Variation in the size of immature ovarian eggs indicates that ***H. atlanticus*** may be an intermittent spawner. The locomotion methods employed by female ***H. atlanticus*** appear to vary with size. Small females are reportedly fast swimmers, based on both musculature and direct swimming observations. Observations of a young female swimming faster than a net towed in direct pursuit has lead to the proposal that this apparent net avoidance could be the reason for scarcity of material captured in trawls. By contrast, large females are very ‘soft and flabby’ and it has been doubted, based on body consistency and water resistance, that they are fast swimmers. The body of a 767 mm total length female was reported to be so soft and gelatinous that when out of water it could not retain its natural form. When placed in a large pan it flattened out and filled the vessel like a mass of rather stiff jelly. It has been proposed that the deep umbrella formed by the arms and webs of female ***H. atlanticus*** serves as the main organ of locomotion. This proposal is consistent with morphological examinations that reveal reduction of the stylets and live observations from a submersible of an adult female swimming with slow medusoid motion (using the arms and web to swim in a manner similar to the bell swimming of medusae) just above the sea floor. When mature and before being autotomized, the hectocotylus of males protrudes from the pouch opening on the inner surface of web between the second and fourth pairs of arms. ***Haliphron atlanticus*** is reported to feed on crustaceans and cephalopods.

Interest to Fisheries: Limited fisheries interest due to scarcity of encounters. The gelatinous flesh of this species is not considered palatable. Occasional landings have netted multiple individuals, e.g. a single otter trawl fished at 682 m caught 26 large specimens. Occasionally taken as by-catch in commercial fishing trawls. Gelatinous consistency of flesh can result in large trawled specimens being badly fragmented.

Local Names: JAPAN: Kantendako.

Literature: Verrill (1880, 1881, 1884), Sasaki (1929), Thore (1949), Voss (1956), Lu and Clarke (1975a, 1975b), Nesis (1975) according to Bizikov (2004), Roper and Young (1975), Lu and Roper (1979), Alvariño and Hunter (1981), Willassen (1986), Nixon (1987), Gonçalves (1991), Vecchione and Roper (1991), Hochberg *et al.* (1992), Young (1995, 2013), Clarke (1996b), Collins *et al.* (1997), Norman *et al.* (1997), Norman (2000), Bakken and Holthe (2002), Vecchione and Pohle (2002), Nixon and Young (2003), Bizikov (2004), Moore *et al.* (2004), O'Shea (2004).

2.1.6 **Family ARGONAUTIDAE** Tryon, 1879

by Julian K. Finn

Argonautidae Tryon, 1879, *Manual of Conchology; Structural and Systematics*, 1: 133.

Type Genus: *Argonauta* Linnaeus, 1758.

FAO Names: En — Argonauts, Paper nautiluses; **Fr** — Argonautes papier; **Sp** — Argonautas.

Diagnostic Features: Body tissue muscular, smooth; cephalic water pores absent; stylets absent; funnel not embedded in head tissue; funnel locking apparatus developed by funnel corners hooked into mantle; ink sac present; all arms with 2 rows of suckers; webs shallow between all arms; first (dorsal) pair of arms of females with expanded broad membranous webs, used to secrete shell; third left arm of males hectocotylized, developed in sac under left eye (males with third right arm hectocotylized reported, but extremely rare).

Habitat and Biology: Argonauts are most commonly recognized by the brittle white 'shells' of females, commonly known as a 'paper nautilus'. Unlike the true shells of other molluscs, the 'paper nautilus' shell is actually a brood case, secreted by webs at the distal tips of the female's dorsal arms, and used for protection of long strands of eggs laid within. Similarity in external appearance with the shells of chambered nautiluses (family Nautilidae) regularly leads to confusion between these two distantly related families. In life, the female is typically positioned within the shell with her head forward and her lateral and ventral arms bent backwards adhering to the inside of the shell faces. The expanded lobes on the dorsal arms either cover the outside faces of the shell or are held within. In the event that a shell is damaged a female argonaut can repair the shell or where necessary completely rebuild it. Male argonauts are tiny dwarves that never develop a shell. Their third left arm is a modified hectocotylus that develops in a sac under the left eye. Mature female argonauts are often found with multiple male hectocotyli (each from a different male) wrapped around the gills inside their mantle cavities. Intact males also have been found within female shells. Eggs are laid in long festoons and mature in up to five batches at different stages of development. Egg strings are anchored to the innermost coil of the shell.

Argonauts generally are considered to be epipelagic in oceanic waters, as they are collected in surface tows, midwater trawls, oblique hauls, and hand-netted at the surface. Adult females are most regularly encountered at the surface during the day, at dusk and at night, while males and juvenile females have been reported from the surface to at least 200 and 300 m respectively. Female argonauts have a tendency to cling to objects floating or drifting on the water surface. Female argonauts have been observed 'riding' jellyfishes, attached to floating seaweed, or attached to each other forming large chains of up to 20 to 30 individuals. Males and juvenile females also have been observed riding inside the salp, *Pegea socia*, behaviour more commonly associated with the football octopus (family Ocythoidae). The remains of argonauts have been recovered from the stomachs of a range of predators including squids, fishes, marine mammals, penguins and other marine birds.

Remarks: This family contains a single genus (***Argonauta***) and four species (***A. argo***, ***A. hians***, ***A. nodosus*** and ***A. nouryi***).

Literature: Adams and Reeve (1848), Verrill (1884), Benedict (1886), Holder (1909), Robson (1932), Whitley *In* Allan (1950), Kramp (1956), Jones (1963), Akimushkin (1965), Voss (1967), Voss and Williamson (1971), Lu and Clarke (1975a), Roper and Young (1975), Nesis (1977), Roper (1977), Banas *et al.* (1982), Alliston (1983), Boletzky (1983), Brandt (1983), Bello and Rizzi (1990), Heeger *et al.* (1992), Vecchione (1998), Strickland *In* Norman (2000), Kubodera (2001), Chesalin and Zuyev (2002), Diekmann and Piatkowski (2002), Finn (2009, 2013), Mangold *et al.* (2010a), Rosa and Seibel (2010).

Argonauta Linnaeus, 1758

Argonauta Linnaeus, 1758, *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species cum Characteribus, Differentiis, Synonymis, Locis*, Holmiae: 708.

Type species: *Argonauta argo* Linnaeus, 1758.

Frequent Synonyms: None.

Diagnostic Features: With characters of the family. Monogeneric.

Remarks: Variations in female shell shape within species have caused considerable confusion to taxonomists over the centuries and have resulted in a large number of synonymous species names. At present four species within the single genus ***Argonauta*** are recognized: ***A. argo***, ***A. hians***, ***A. nodosus*** and ***A. nouryi*** (see Finn, 2009, 2013).

Key to species in the genus *Argonauta* based on characters of the female argonaut:

1a. Fourth arms longer than second arms . . . . ***A. argo***
1b. Second arms longer than fourth arms . . . . **→ 2**

2a. Sucker numbers: 280 to 360 on first arms, 140 to 220 on second and third arms, and 80 to 135 on fourth arms; 14 to 21 gill lamellae per demibranch . . . . ***A. nodosus***
2b. Sucker numbers: 135 to 210 on first arms, 70 to 120 on second and third arms, and 30 to 70 on fourth arms; 9 to 15 gill lamellae per demibranch . . . . **→ 3**

3a. Sucker numbers: 135 to 160 on first arms, 70 to 115 on second and third arms, and 30 to 50 on fourth arms; 9 to 13 gill lamellae per demibranch; (absent from the eastern Pacific Ocean) . . . . ***A. hians***
3b. Sucker numbers: 145 to 210 on first arms, 75 to 120 on second and third arms, and 45 to 70 on fourth arms; 13 to 15 gill lamellae per demibranch; (restricted to the eastern Pacific Ocean) . . . . ***A. nouryi***

Key to species in the genus *Argonauta* based on characters of the female argonaut's shell:

1a. Lateral ribs tuberculated (composed of rows of separate tubercles) . . . . ***A. nodosus***
1a. Lateral ribs smooth, continuous. . . . . **→ 2**

2a. Keel thin, with consistent width; keel tubercles of consistent size and shape . . . . ***A. argo***
2b. Keel width and keel tubercle size increase with shell growth . . . . **→ 3**

3a. Keel tuberculation never present; argonaut does not occur in the eastern Pacific Ocean . . . . ***A. hians***
3b. Keel tuberculation expressed in some shells; argonaut occurs in the eastern Pacific Ocean . . . . . . ***A. nouryi***

Key to species in the genus *Argonauta* based on characters of the male argonaut* :

1a. Sucker numbers: 17 to 20 on all normal arms, 58 to 64 on hectocotylized arm; 8 to 10 gill lamellae per demibranch . . . . ***A. nodosus***
1b. Sucker numbers: 10 to 11 on all normal arms, 37 to 44 on hectocotylized arm; 6 to 7 gill lamellae per demibranch. . . . . ***A. hians***
1c. Sucker numbers: 12 to 13 on normal arms, approximately 95 on hectocotylized arm; number of gill lamellae per demibranch unknown . . . . ***A. argo***

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* Details of male ***A. nouryi*** currently unknown

Argonauta argo Linnaeus, 1758

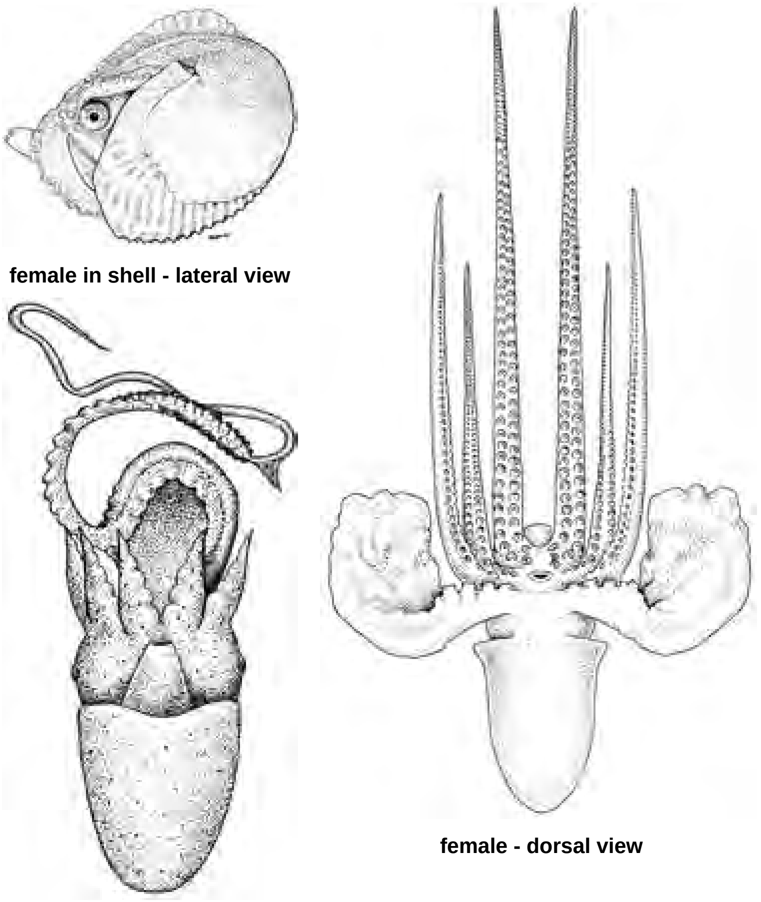
Fig. 228; Plate X, 76

Argonauta argo Linnaeus, 1758, *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species cum Characteribus, Differentiis, Synonymis, Locis,* Holmiae: 708. [Type locality: Mediterranean Sea].

Frequent Synonyms: *Argonauta cygnus* Monterosato, 1889; *A. pacifica* Dall, 1871.

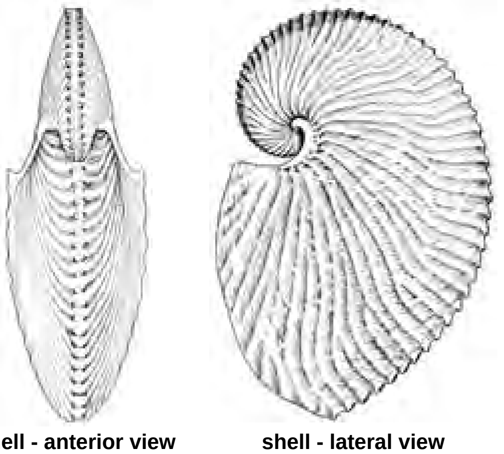
Misidentifications: None.

FAO Names: En — Greater argonaut **Fr** — Argonaute papier; **Sp** — Argonauta común.


female in shell - lateral view

male - ventral view

female - dorsal view


shell - anterior view

shell - lateral view

Fig. 228 *Argonauta argo*

Diagnostic Features: Body muscular. Skin smooth. Cephalic water pores absent. Funnel organ conspicuous, \/\/-shaped with elongate ovate limbs, outer limbs slightly shorter than median limbs. Funnel locking apparatus present, well developed, consists of small, ovate, cartilaginous pits on funnel corners, with corresponding posterior-directed nodules on inner surface of mantle. Suckers small, in two rows. Adult female large in size. Mantle roughly conical, widest anteriorly, flattened laterally, posterior with sharp upward torsion (most pronounced in animals preserved within shells), deep crease in ventral mantle posterior to funnel locking apparatus. Mantle-opening wide. Stylets absent. Head small, embedded within mantle. Eyes large, protrude from level of head, separated by distinct constriction at base. Funnel broad-based and muscular, extremely long, anterior opening projects between fourth arms. Arms long, typically 2 to 3.5 times mantle length in adult females. First (dorsal) arms long, wide, terminate with conspicuous wide lobes used for shell secretion/formation. In female argonauts, first arm lengths are extremely variable due to varied constriction of the shell-secreting lobes and hence are of limited diagnostic value. Other arms unequal in length (**arm formula: 4>2>3**). **Fourth (ventral) arms longest, over 3 times mantle length and 20 to 30% longer than second arms.** Suckers of moderate size, largest on dorsal arms, approximately 7 to 8% of mantle length. Webs shallow between all arms. Gills with approximately 16 to 17 lamellae per demibranch. Colour in life variable from deep maroon to silver; dorsal mantle adorned with large chromatophores, smaller chromatophores present on ventral mantle. Shells large, thin walled, laterally compressed, calcareous, with one chamber. Ribs present on lateral surfaces, formed by corrugations in shell walls, radiate out from central axis, smooth (not a series of tubercles), continuous (from axis to keel) or branched. **Aperture narrow**. Ears (i.e. lateral extensions of shell axis beyond surfaces of shell) may be present in smaller shells, become less conspicuous with increased size. **Keel width consistent around circumference of shell** (does not increase significantly during growth of shell), **extremely narrow**, smooth (without inter-keel tuberculation). **Keel tubercles paired** (ridge present across keel between opposing tubercles), **consistent in size and shape around**

circumference of shell. Surface may appear polished or matt. Colour white, approximate first third of keel tubercles stained black. Eggs extremely small (approximately 1.5 mm long), attached in long strands to internal axis of female's shell, brooded until hatching. Males tiny, dwarfed, shell-less, with third left arm hectocotylized. Hectocotylus detaches from interbrachial membrane early in development; smaller specimens appear to have only seven arms. Hectocotylized arm develops in sac under left eye; as a result male appears asymmetrical; once developed it projects free between arms, enclosed in sac formed from web. Hectocotylus with 2 rows of suckers; proximal spermatophore reservoir formed from spermatophore groove; spermatophore duct visible as shiny muscular tube on aboral side of hectocotylus; terminal motile penis not enclosed in sac; papillate lateral fringes absent. Males with **12 to 13 suckers on normal arms,** and **approximately 95 suckers on hectocotylized arm**.

Size: Female mantle length to at least 97 mm; total length to 438 mm; shell length to at least 300 mm. Male total length to 15 mm (excluding hectocotylus).

Geographical Distribution: Widespread tropical-subtropical cosmopolitan species. Circumglobal distribution in the northern and southern hemispheres (between approximately 40°N and 40°S), incorporating the waters of the Atlantic Ocean, Indian Ocean and Pacific Ocean. Known as far south as South Africa, Western Australia, southern Peru and Brazil, and as far north as the Mediterranean Sea, Japan and California (Fig. 229).

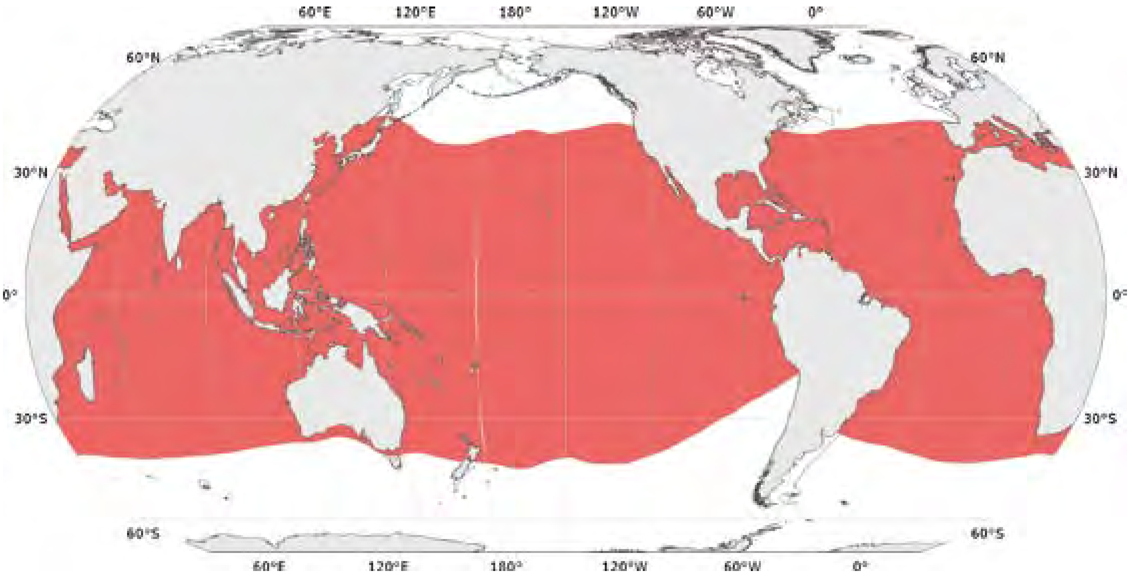


Fig. 229 ***Argonauta argo***

🟥 Known distribution

Habitat and Biology: Mating has not been observed. On contact with the female it is presumed that the male autotomizes the hectocotylus. Multiple hectocotyli can persist in shells and mantle cavities of females for extended periods. Eggs of up to five different developmental stages may be present within a single shell. Females use the shell to trap air, gathered at the sea surface, to attain neutral buoyancy.

Interest to Fisheries: The fisheries potential of this species is limited due to the scarcity and infrequency of encounters. Females occasionally are found in markets in India, Japan, and Taiwan Province of China. Although there are no directed fisheries, fortuitous catches can exceed several hundred kilograms. Between June 17 and July 3, 1982, an estimated 6 300 female ***A. argo*** weighing some 600 kg were caught in set nets in the western Sea of Japan and sold at market. The flesh is known to be edible. Shells have a high value and are regularly sold through the shell trade worldwide.

Local Names: CHINA: Baak Hoi Ma Chau (White Sea-horse's Nest); ITALY: Argonauta; JAPAN: Aoigai.

Remarks: The name ***Argonauta cygnus*** Monterosato, 1889 often is attributed to specimens of ***A. argo*** obtained from the Mediterranean. The name ***A. pacifica*** Dall, 1871 commonly is applied to specimens resembling ***A. argo*** when encountered in California. Both names (***cygnus, pacifica)*** are considered to be synonyms of ***A. argo*** (see Finn, 2009, 2013).

Literature: Naef (1923), Sasaki (1929), Robson (1932), Wagner and Abbott (1982), Okutani and Kawaguchi (1983), Finn (2009, 2010, 2013), Jorgensen (2009), Finn and Norman (2010).

Argonauta hians [Lightfoot], 1786 **Fig. 230; Plate X, 77**

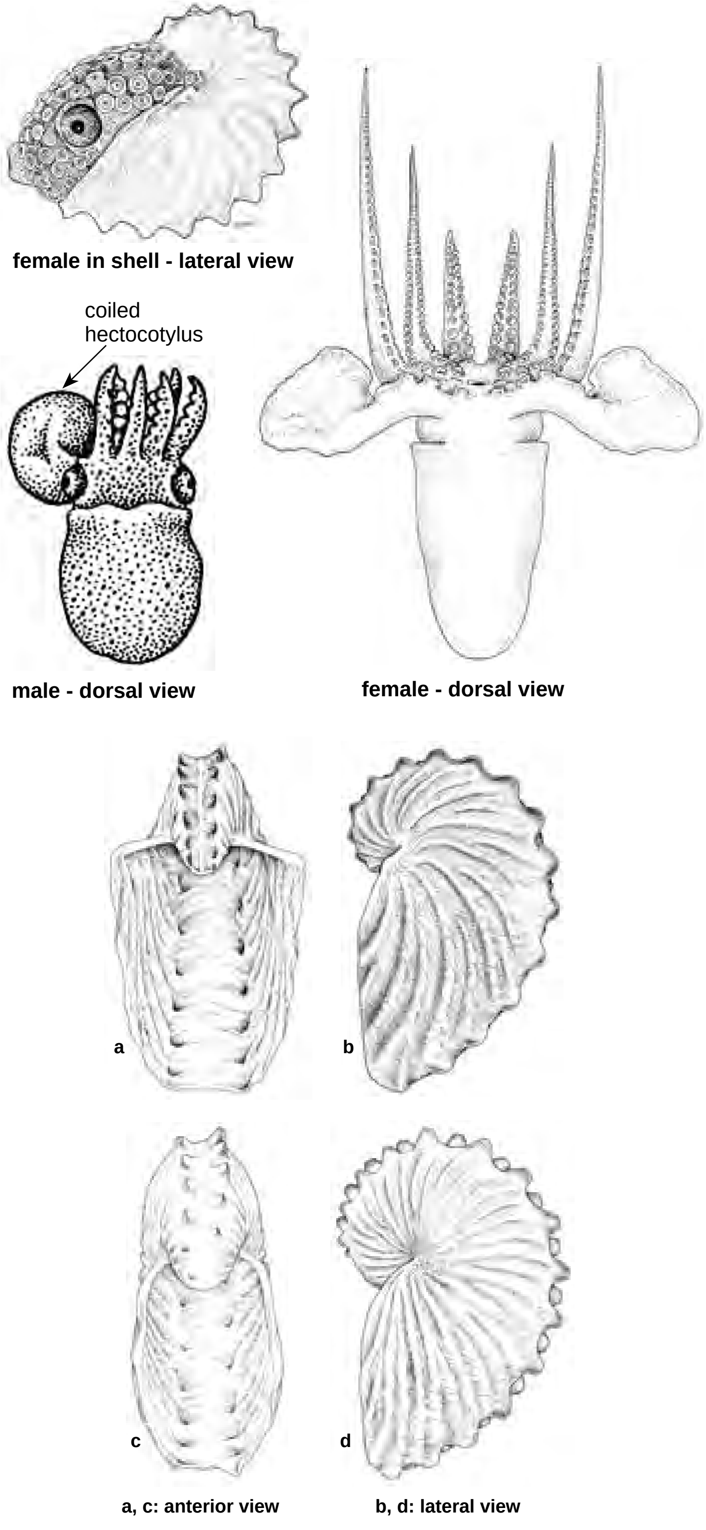
Argonauta hians [Lightfoot], 1786, *A Catalogue of the Portland Museum*, London, 44, 139, 174. [Type locality: Indonesia, Ambon].

Frequent Synonyms: *Argonauta boetgeri* Maltzan, 1881.

Misidentifications: None.

FAO Names: En — Lesser argonaut; **Fr** — Argonaute mineur; **Sp** — Argonauta menor.

Diagnostic Features: Body muscular. Skin smooth. Cephalic water pores absent. Funnel organ conspicuous, \/\/-shaped with elongate ovate limbs; outer limbs slightly shorter than median limbs. Funnel locking apparatus present, well developed; consists of small, ovate, cartilaginous pits on funnel corners, with corresponding posterior-directed nodules on inner surface of mantle. Females large. Mantle roughly conical, widest anteriorly, flattened laterally, posterior with sharp upward torsion (most pronounced in animals preserved within shells), deep crease in ventral mantle posterior to funnel locking apparatus. Mantle-opening wide. Stylets absent. Head small, embedded within mantle. Eyes large, protrude from level of head, separated by distinct constriction at base. Funnel broad-based and muscular, extremely long; anterior end projects between fourth arms. Arms of moderate length; **typically 1 to 2 times mantle length** in adult females. First (dorsal) arms long, wide, distal ends with conspicuous wide lobes used for shell secretion/formation. In female argonauts, first arm lengths are extremely variable due to varied constriction of the shell-secreting lobes and hence are of limited diagnostic value. Other arms unequal in length; arm formula: 2≥3>4. **Second arms longest, 1.4 to 2 times mantle length;** fourth (ventral) arms shortest, 1 to 1.3 times mantle length and 50-80% second arm length. Suckers moderate in size, largest on dorsal arms, approximately 7 to 8% of mantle length; with **approximately 140 to 160 suckers on first arms, 80 to 110 on second arms, 70 to 110 on third arms, 30 to 50 on fourth arms.** Webs shallow between all arms. Gills with approximately **9 to 13 lamellae per demibranch**. Colour in life variable from deep maroon to silver; dorsal mantle adorned with large chromatophores, smaller chromatophores present on ventral mantle. Shell thin walled, calcareous, with one chamber; medium in size. Ribs present on lateral faces, formed by corrugations in shell walls, radiate out from central axis, smooth (series of tubercles not present), continuous (from axis to keel) or branched. **Aperture wide; width approximately 60 to 90% aperture length**. Ears (i.e. lateral extensions of shell axis beyond surfaces of shell) may be present. **Keel wide; width 20 to 30% shell length**, increases during shell growth, smooth (without inter-keel tuberculation). Keel tubercles increase in size around circumference of shell, alternate on opposing surfaces. Surface may appear polished or matt. Colour off-white to brown, approximately first third of keel tubercles



female in shell - lateral view

male - dorsal view

female - dorsal view

a, c: anterior view

b, d: lateral view

shell - top: Type 1; bottom: Type 2

Fig. 230 ***Argonauta hians***

stained black. Eggs extremely small, attached in long strands to the axis of the female's shell; eggs brooded until hatching. Males tiny, dwarfed, shell-less; third left arm hectocotylized. Hectocotylus detached from interbrachial membrane early in development; smaller specimens appear to have only seven arms. Hectocotylized arm develops in sac under left eye; as a result male appears asymmetrical; once developed the hectocotylus projects free between arms, enclosed in sac formed by web. Hectocotylus with 2 rows of suckers; proximal spermatophore reservoir formed from spermatophore groove; spermatophore duct visible as shiny muscular tube on aboral side of hectocotylus; terminal motile penis not enclosed in sac; papillate lateral fringes absent. Males with **6 to 7 gill lamellae per demibranch; normal arms with 10 to 11 suckers, hectocotylized arm with approximately 37 to 44 suckers**.

Size: Female mantle length to at least 40 mm; total length to at least 118 mm; shell length to 106 mm. Male mantle length to at least 7 mm; total length to at least 12 mm (excluding hectocotylus), and 40 mm (including hectocotylus).

Geographical Distribution: Widespread pelagic species. Occurs from South Africa in the west, to Papua New Guinea in the east, and Japan in the north — incorporating at least the north Indian Ocean, Arabian Sea, Andaman Sea, Moluccas, Philippines and China Sea. Absent from eastern Pacific Ocean (Fig. 231).

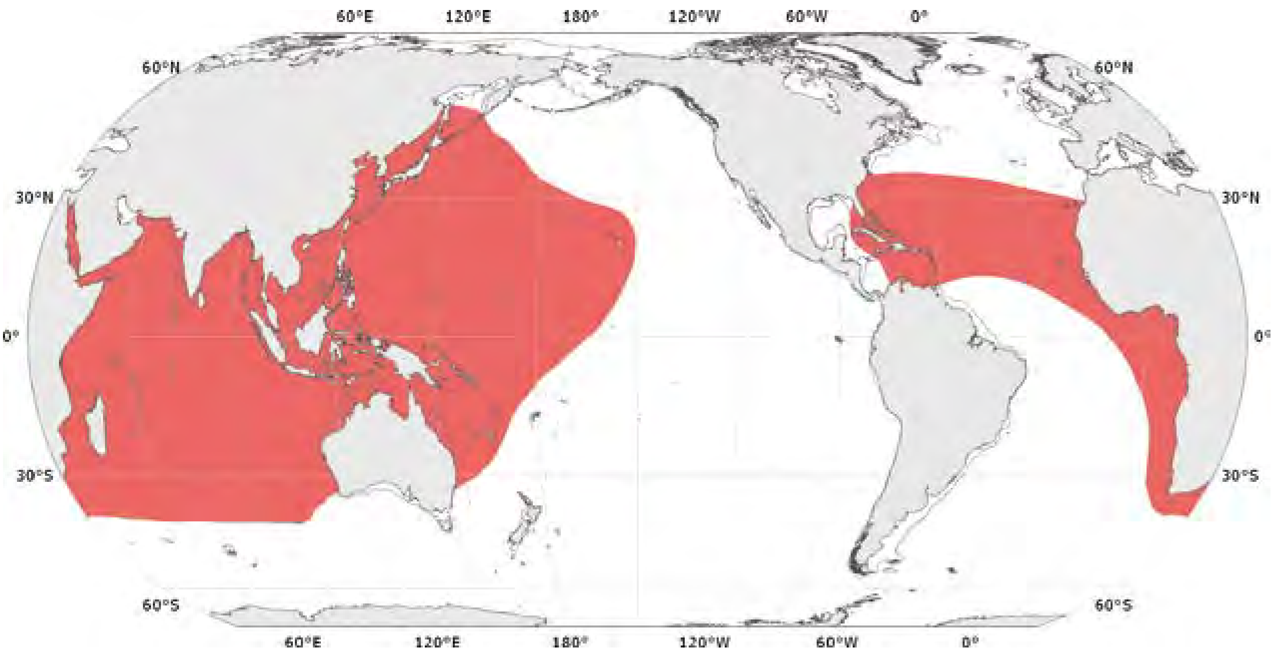


Fig. 231 ***Argonauta hians***

🟥 Known distribution

Habitat and Biology: Mating behaviour has not been observed. On contact with the female it is presumed that the male autotomizes the hectocotylus. Multiple hectocotyli can persist in the mantle cavity of females for extended periods. Australian females were found to mature between 17 mm ML (27 mm shell length) and 19 mm ML (29 mm shell length). Egg laying commences between 19 mm ML (29 mm shell length) and 21 mm ML (31 mm shell length). Females attain a maximum size of at least 40 mm ML (52 mm shell length). Eggs of up to three different developmental stages may be present within a single female's shell. Females have been observed 'riding' jellyfish. Female ***Aronauta hians*** are specialized consumers of pelagic molluscs, chiefly heteropods and pteropods, in addition to octopods (possibly male Argonautidae), crustaceans, comb jellies and fishes.

Interest to Fisheries: Fisheries potential limited due to scarcity of encounters. Shells occasionally sold through shell trade.

Local Names: CHINA: Fooi Hoi Ma Chau (Grey Sea-horse's Nest); JAPAN: Takobuné.

Remarks: While Lightfoot (1786) mentioned China as a locality, designation of a lectotype by Moolenbeek (2008) makes the type locality "Amboina" (Ambon, Indonesia). The name ***Argonauta boetgeri*** Maltzan, 1881 is often attributed to specimens of ***A. hians*** with 'ear-less' shells (i.e. shells without lateral extensions of the shell axis). Lateral extensions are a variable character in this species and ***A. boetgeri*** is considered to be synonym of ***A. hians*** (Finn, 2009).

Literature: Sasaki (1929), Robson (1932), Okutani (1960), Nesis (1977), Heeger *et al.* (1992; as ***Argonauta argo***), Norman (2000), Sukhsangchan and Nabhitabhat (2007), Moolenbeek (2008), Sukhsangchan *et al.* (2008, 2009)**,** Finn (2009, 2013).

Argonauta nodosus [Lightfoot], 1786

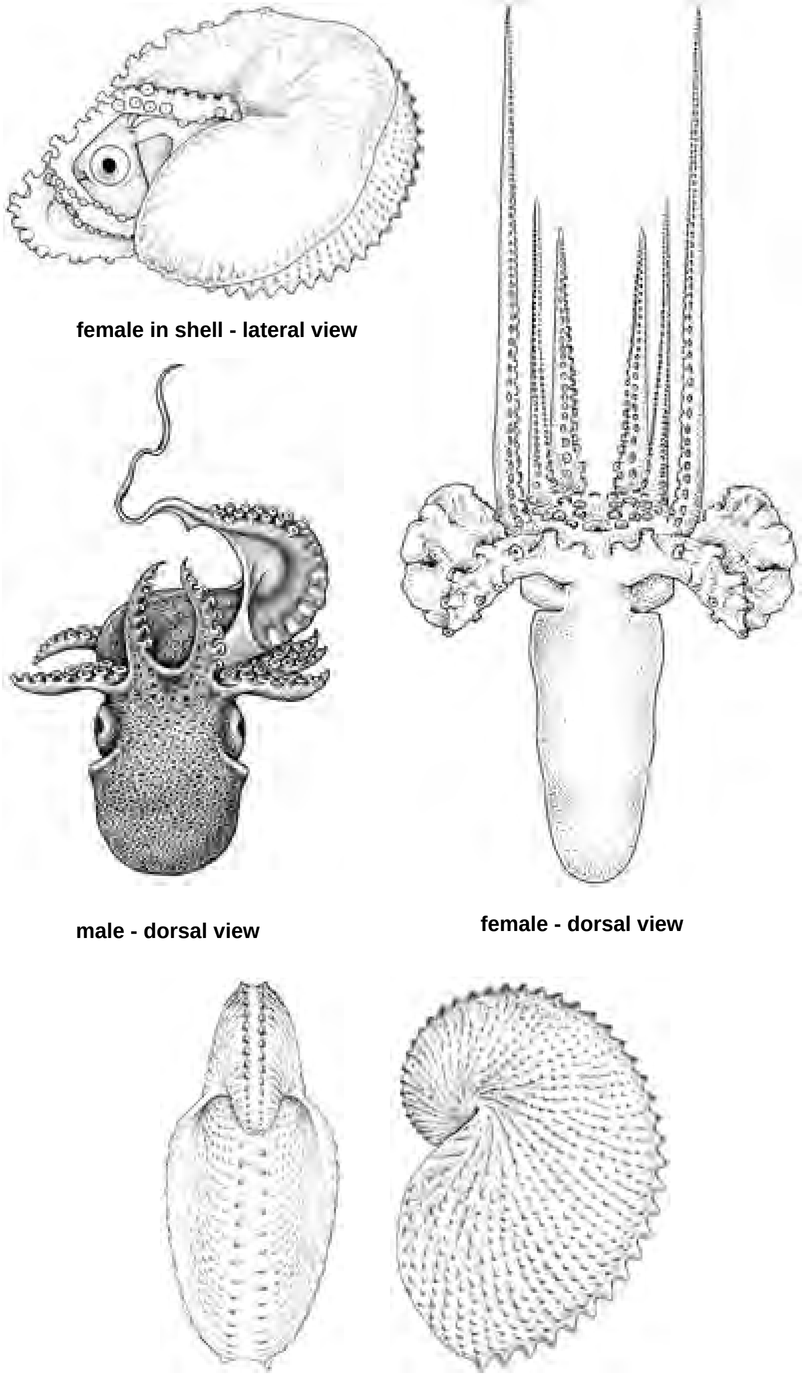
Fig. 232; Plate X, 78

Argonauta nodosa [Lightfoot], 1786, *A Catalogue of the Portland Museum*, London: 96, 172. [Type locality: Africa, Cape of Good Hope].

Frequent Synonyms: *Argonauta tuberculata* [Röding], 1798.

Misidentifications: None.

FAO Names: En — Knobbed argonaut; **Fr** — Argonaute noueux; **Sp** — Argonauta nodoso.


female in shell - lateral view

male - dorsal view

female - dorsal view

anterior view

lateral view

shell

Fig. 232 *Argonauta nodosus*

Diagnostic Features: Body muscular. Skin smooth. Cephalic water pores absent. Funnel organ conspicuous, W-shaped with elongate ovate limbs; outer limbs slightly shorter than median limbs. Funnel locking apparatus present, well developed, consists of small, ovate, cartilaginous pits on funnel corners, with corresponding posterior-directed nodules on inner surface of mantle. Female large. Mantle roughly conical, widest anteriorly, flattened laterally; posterior with sharp upward torsion (most pronounced in animals preserved within shells), deep crease in ventral mantle posterior to funnel locking apparatus. Mantle aperture wide. Stylets absent. Head small, embedded within mantle. Eyes large, protrude from level of head, separated by distinct constriction at base. Funnel broad-based and muscular, extremely long; anterior end projects between fourth arms. Arms of moderate length, **typically 1.5 to 2.5 times mantle length** in adult females. First (dorsal) arms long, wide; distal ends with conspicuous wide lobes used for shell secretion/formation. In female argonauts, first arm lengths are extremely variable due to varied constriction of the shell-secreting lobes and hence are of limited diagnostic value. Other arm pairs unequal in length (arm formula: 2>3≥4 or 2>4≥3). **Second arms longest, 2 to 2.8 times mantle length;** fourth (ventral) arms short, 1.3 to 2 times mantle length and 60-80% of second arm length. Suckers of moderate size, largest on dorsal arms, approximately 6 to 8% of mantle length. Sucker counts: **approximately 280 to 360 on first arms, 190 to 220 on second arms, 180 to 210 on third arms, 110 to 140 on fourth arms.** Webs shallow between all arms. Gills with approximately **17 to 21 lamellae per demibranch**. Colour in life variable, from deep maroon to silver; dorsal mantle adorned with large chromatophores, grading to smaller chromatophores on ventral mantle. Shell thin-walled, calcareous, with one chamber, medium in size. Ribs present on lateral faces, formed by corrugations in shell walls, radiate out from central axis, **tuberculated (series of tubercles present)**, continuous (from axis to keel) or branched. **Aperture moderately wide; width approximately 50 to 60% aperture length**. Ears (i.e. lateral extensions of shell axis beyond surfaces of shell) may be present. **Keel moderately wide**, **width 10 to 14% shell length,** width increases with shell size; smooth (without inter-keel tuberculation). Keel tubercles increase in size around circumference of shell, alternate on opposing surfaces. Surface may appear polished or matt. Colour white, approximately the first third of keel tubercles stained black. Eggs extremely small, attached in long strands to axis of female's shell, brooded until hatching. Males tiny, dwarfed, shell-less; third left arm hectocotylized. Hectocotylus detached from interbrachial membrane early in development; smaller specimens appear to have only seven arms. Hectocotylized arm develops in sac under left eye, as a result, male appears asymmetrical; once developed the hectocotylus projects freely between arms, enclosed in sac formed by web. Hectocotylus with 2 rows of suckers; proximal spermatophore reservoir formed from spermatophore groove; spermatophore duct visible as shiny muscular tube on aboral side of hectocotylus; terminal motile penis not enclosed in sac; papillate lateral fringes absent. Males with **8 to 10 gill lamellae per demibranch; normal arms with 17 to 21 suckers; hectocotylized arm with approximately 57 to 64 suckers**.

Size: Female mantle length to at least 138 mm; total length to 497 mm; shell length to 292 mm. Male mantle length to at least 11 mm; total length to 20 mm (excluding hectocotylus), and 62 mm (including hectocotylus).

Geographical Distribution: Widespread pelagic species. Circumglobal distribution in the Southern Hemisphere, between 10°S and 44°S incorporating the southern extremities of South Africa, Australia, New Zealand and south America, north to Brazil, Indo-West Pacific, and south Pacific islands. Most common in Australia and New Zealand (Fig. 233).

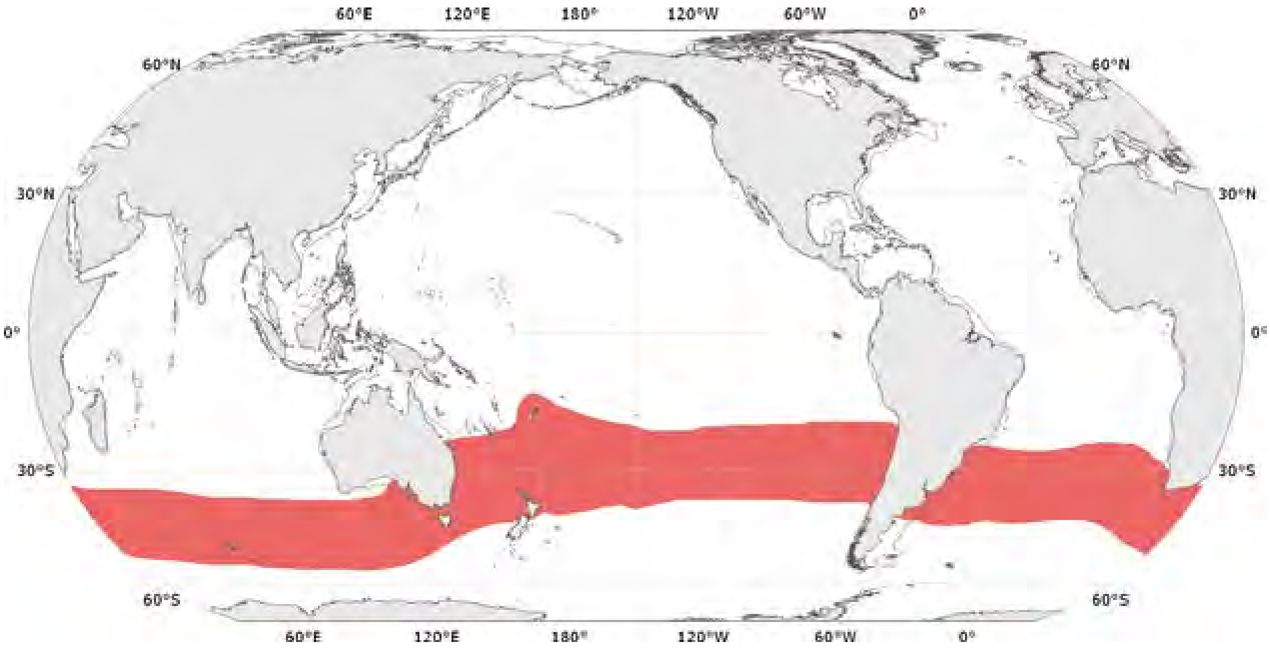


Fig. 233 ***Argonauta nodosus***

🟥 Known distribution

Habitat and Biology: Mating behaviour unknown. On contact with the female it is presumed that the male autotomizes the hectocotylus. Multiple hectocotyli can persist in the mantle cavities of females for extended periods. Eggs of up to five different developmental stages may be present within a single shell. Captive females have been observed to feed on euphausiids, and the presence of female argonauts in southern Australian waters is believed to coincide with euphausiid schools. Female ***Argonauta nodosus*** have been observed 'riding' jellyfishes. It is presumed that females of this species use air trapped in their shells to regulate their buoyancy. Mass strandings have been recorded in New Zealand, southern Australia and Uruguay.

Interest to Fisheries: Fisheries potential limited due to scarcity of encounters. Shells sold occasionally through the shell trade. Beach-cast animals reportedly used as bait in eastern Australia.

Local Names: Unknown.

Remarks: In compliance with the International Code of Zoological Nomenclature (1999) the species name ***nodosa*** is corrected here to the masculine form ***nodosus*** (Article 34.2).

Literature: Robson (1932), Cotton (1948), Allan (1950), Dell (1952), Jones (1956), Tarlton and Doak (1968), Penniket and Moon (1970), Wagner and Abbott (1982), Reid (1989), O'Shea (1999), Norman (2000), Demicheli *et al.* (2006), Finn (2009, 2010, 2013), Finn and Norman (2010), Vidal *et al.* (2010b).

Argonauta nouryi Lorois, 1852

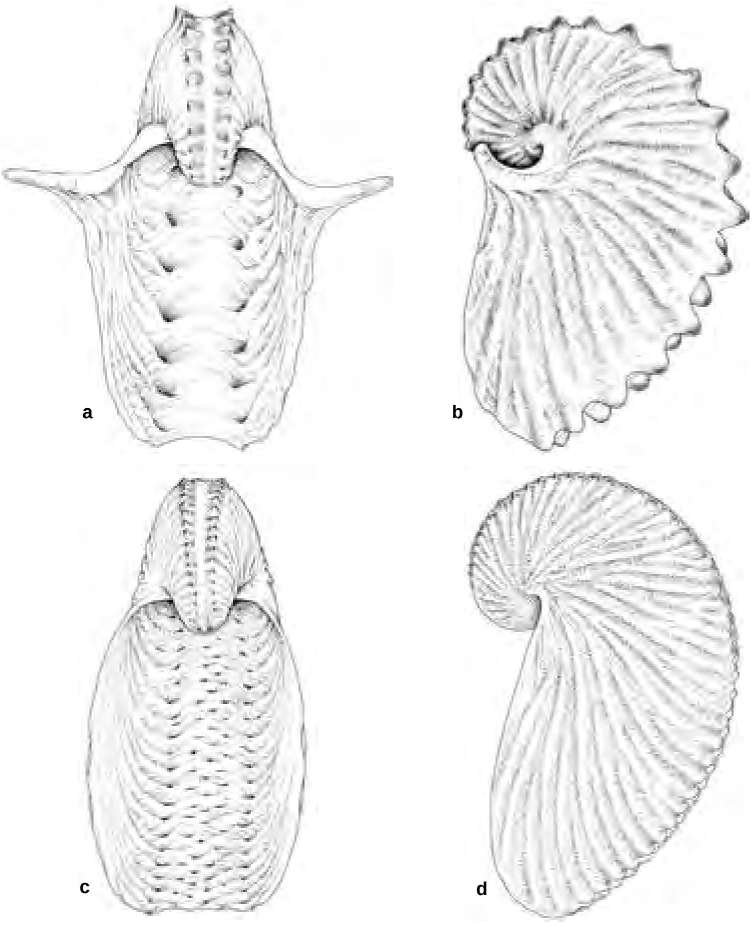
Fig. 234

Argonauta nouryi Lorois, 1852, *Revue et Magasin de Zoologie*, series 2, 4: 10. [Type locality: East of Marquesas].

Frequent Synonyms: *Argonauta gruneri* Dunker, 1852; *A. cornuta* Conrad 1854; *A. expansa* Dall, 1872.

Misidentifications: None.

FAO Names: En — Rough-keeled argonaut; **Fr** — Argonaute tuberculé; **Sp** — Argonauta tuberculado.



a, c: anterior view
b, d: lateral view

shell - top: Type 1; bottom: Type 2

Fig. 234 *Argonauta nouryi*

Diagnostic Features: Body muscular. Skin smooth. Cephalic water pores absent. Funnel organ conspicuous, \Λ/-shaped with elongate ovate limbs; outer limbs slightly shorter than median limbs. Funnel locking apparatus present, well-developed; consists of small, ovate, cartilaginous pits on funnel corners, with posterior-directed nodules on inner surface of mantle. Suckers small, in two rows. Female large in size. Mantle roughly conical, widest anteriorly, flattened laterally, a sharp upward torsion posteriorly (most pronounced in animals preserved within shells), a deep crease in ventral mantle posterior to funnel locking apparatus. Mantle-opening wide. Stylets absent. Head small, embedded within mantle. Eyes large, protrude from head, separated by distinct constriction at base. Funnel broad-based and muscular, extremely long; anterior end projects between fourth arms. Arms of moderate length, **typically 1 to 2.4 times mantle length** in adult females. First (dorsal) arms long, wide, with conspicuous wide lobes distally, used for shell secretion/ formation. In female argonauts, first arm lengths are extremely variable due to varied constriction of the shell-secreting lobes and hence are of limited diagnostic value. Other arm pairs unequal in length (arm formula: 2≥3≥4). **Second arms longest, 1.2 to 2.4 times mantle length;** fourth (ventral) arms shortest, 1 to 1.5 times mantle length and 60 to 90% second arm length. Webs shallow between all arms. Suckers of moderate size, largest on dorsal arms, approximately 9 to 11% of mantle length. Sucker counts: **approximately 150 to 210 on first arms, 80 to 120 on second arms, 80 to 110 on third arms, 50 to 70 on fourth arms.** Gills with approximately **13 to 15 lamellae per demibranch**. Colour in life variable from deep maroon to silver, dorsal mantle adorned with large chromatophores, that grade to smaller chromatophores on ventral mantle. Shell thin walled, calcareous, with one chamber, medium in size. Ribs present on lateral faces, formed by corrugations in shell walls, radiate out from central axis, smooth (series of tubercles absent), continuous (from axis to keel) or branched. **Aperture moderately wide, width approximately 45 to 70% of aperture length**. Ears (i.e. lateral extensions of shell axis beyond surfaces of shell) may be present. **Keel moderately wide; width 10 to 14% shell length;** width increases with shell size, **inter-keel tuberculation present in some shells**. Keel tubercles increase in size around circumference of shell and alternate on opposite faces. Surface may appear polished or matt. Colour white, approximately first third of keel tubercles stained black. Eggs extremely small, attached in long strands to axis of female's shell; brooded until hatching. Males tiny, dwarfed, shell-less; third left arm hectocotylized. Hectocotylus detached from interbrachial membrane early in development, smaller specimens appear to have only seven arms. Hectocotylized arm develops in sac under left eye; as a result male appears asymmetrical; once developed it projects free between arms, enclosed in sac formed by web. Hectocotylus with 2 rows of suckers; proximal spermatophore reservoir formed from spermatophore groove; spermatophore duct visible as shiny muscular tube on aboral side of hectocotylus; terminal motile penis not enclosed in sac; papillate lateral fringes absent. Details of the intact males of this species are unknown.

Size: Female mantle length to at least 52 mm; total length to 174 mm; shell length to 94 mm. Male size unknown.

Geographical Distribution: Pelagic species restricted to the equatorial eastern Pacific Ocean. Eastern Pacific Ocean from Marquesas Islands to the west coast of North and South America, from southern California south to Peru (Fig. 235).

Habitat and Biology: Mating behaviour unknown. On contact with the female presumably the male autotomizes the hectocotylus. Multiple hectocotyli can persist in the mantle cavities of females for extended periods. Eggs of up to three different developmental stages may be present within a single shell. Large numbers of females have been observed at the surface in open-ocean during daylight hours. Females may attach to each other forming large chains of up to 18 individuals. Females are known to strand on beaches in the southern Gulf of California, Mexico, during late winter and early spring (January to March).

Interest to Fisheries: Fisheries potential limited due to scarcity of encounters. Shells occasionally sold through shell trade.

Local Names: Unknown.

Remarks: Females of this species produce shells of varied appearance that are regularly attributed to the synonyms ***Argonauta cornuta*** and ***A. expansa*** (Finn, 2009). Description of this species and designation of the species name ***A. nouryi*** Lorois (1852) preceded the description and erection of the species name ***A. gruneri*** Dunker (1852), by a period of two months (Keen, 1971).

Literature: Dunker (1852), Conrad (1854), Dunker (1858), Dall (1902, 1908), Robson (1932), Keen (1958, 1971), Reeve (1860), Voss (1971a), Garcìa-Domìnguez and Castro-Aguirre (1991), Paredes *et al.* (1999), Gonzáles-Peralta (2006), Finn (2009, 2013), Rosa and Seibel (2010).

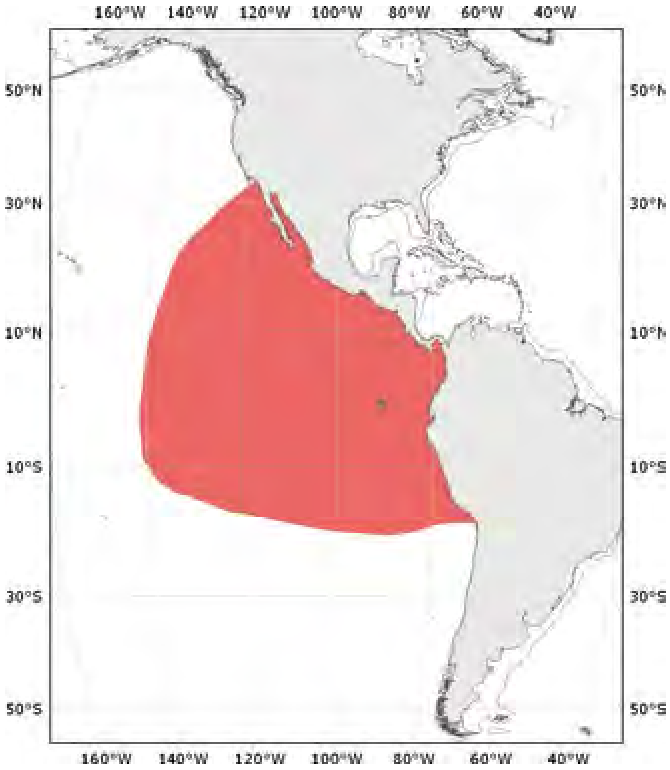


Fig. 235 ***Argonauta nouryi***

🟥 Known distribution

2.1.7 Family OCYTHOIDAE Gray, 1849

by Julian K. Finn

Ocythoidae Gray, 1849, *Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Antepedia*. 30-34. London: British Museum (Natural History).

Type Genus: *Ocythoe* Rafinesque, 1814.

FAO Names: En — Football octopods; **Fr** — Poulpes balonné; **Sp** — Pulpos abalonados.

Diagnostic Features: Body tissue muscular; ventral surface of mantle sculptured in females; cephalic water pores present, one pair opening on ventral side of head; stylets absent; funnel not embedded in head tissue; funnel locking apparatus developed; funnel corner coiled into snail-like knob enclosed in mantle depression; webs absent between all arms; third right arm of males hectocotylized, developed in sac that extends from base of third right arm.

Habitat and Biology: Members of the family Ocythoidae are commonly known as the 'football octopod' based on the size and shape of the female's mantle. Very little is known about this rarely encountered pelagic octopod. The ventral mantle of adult females is adorned with reticular sculpture of crossing skin ridges and tubercles of cartilage under the skin — its function is unknown. Female ocythoids possess functional swim bladders. A specialized dorsal sac on top of the visceral mass is connected to the mantle cavity by a posterior duct. Gas stored in the swim bladder allows the female to attain and regulate buoyancy. The swim bladder is well developed in females that are heavy with young and is absent in dwarf males. Mating behaviour is unknown. The hectocotylus is freed from the sac before being filled with spermatophores prior to copulation. Hectocotyli retrieved from the mantle cavity of females often have a penile filament that is still coiled within its sac. Female ocythoids are the only cephalopods known to be ovoviviparous, giving birth to live young that hatch internally within greatly elongated oviducts from encapsulated eggs. Mature female ocythoids are considered to be continuous spawners. The potential fecundity of a medium-sized female is reported to be approximately 200,000 eggs, while the fecundity of the largest females is thought to be much higher — potentially as high as one million eggs. The remains of ocythoids have been recovered from the stomachs of a range of predators including squids, fishes, marine mammals, penguins and other marine birds.

Remarks: The family Ocythoidae is monotypic, consisting of a single species, ***Ocythoe tuberculata***.

Literature: Naef (1923), Packard and Wurtz (1994), Laptikhovsky and Salman (2003).

Ocythoe Rafinesque, 1814

Ocythoe Rafinesque, 1814, *Précis des découvertes et travaux somiologiques de Mr. C.S. Rafinesque-Schmaltz… zoologie et en botanique*, Palermo, 29.

Type species: *Ocythoe tuberculata* Rafinesque, 1814.

Frequent Synonyms: None.

Diagnostic Features: With characters of the family. Monotypic.

Ocythoe tuberculata Rafinesque, 1814

Fig. 236; Plate X, 80

Ocythoe tuberculata Rafinesque, 1814, *Précis des découvertes et travaux somiologiques de Mr. C. S. Rafinesque-Schmaltz entre 1800 et 1814; ou choix raisonné de ses principales découvertes en zoologie et en botanique, pour servir d'introduction á ses ouvrages futurs,* Palermo: 29. [Type locality: Mediterranean Sea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Football octopod; **Fr** — Poulpe balonné; **Sp** — Pulpo abalonado.

Diagnostic Features: Body muscular. Cephalic water pores present, one pair only, on ventral surface of head at base of fourth arms in both sexes; not present on dorsal surface. Arms long, **dorsal (first) and ventral (fourth) arms much longer than lateral (second and third) arms at all growth stages**. Suckers small, in 2 rows. Web almost completely absent between bases of all arms; arm fringe absent. Funnel very long; funnel organ IΛI-shaped. Locking apparatus well developed, strong; funnel corner coiled into snail-like knob, firmly enclosed in depression in mantle. Stylets absent. Females large; body firm. Adult females with reticular sculpture of criss-crossed skin ridges, tubercles at cross points, on ventral side of mantle. Colour translucent, milky-white, lateral and ventral sides of mantle with bright silvery sheen; predominant tones of blue and violet mainly on dorsal side of mantle, head, and dorsal arms. Males dwarfed; third right arm hectocotylized, developed in sac that extends from base of third right arm. Proximal spermatophore reservoir formed from spermatophore groove. Penile filament coiled within sac attached to terminal end of hectocotylus; end of filament protrudes through opening between last suckers. Hectocotylized arm with suckers in 2 rows; papillate lateral fringes absent. Eggs brooded to hatching within female's elongate oviducts.

Size: Female mantle length to 310 mm; total length to at least 960 mm. Males dwarfed; mantle length to 30 mm; total length to at least 69 mm.

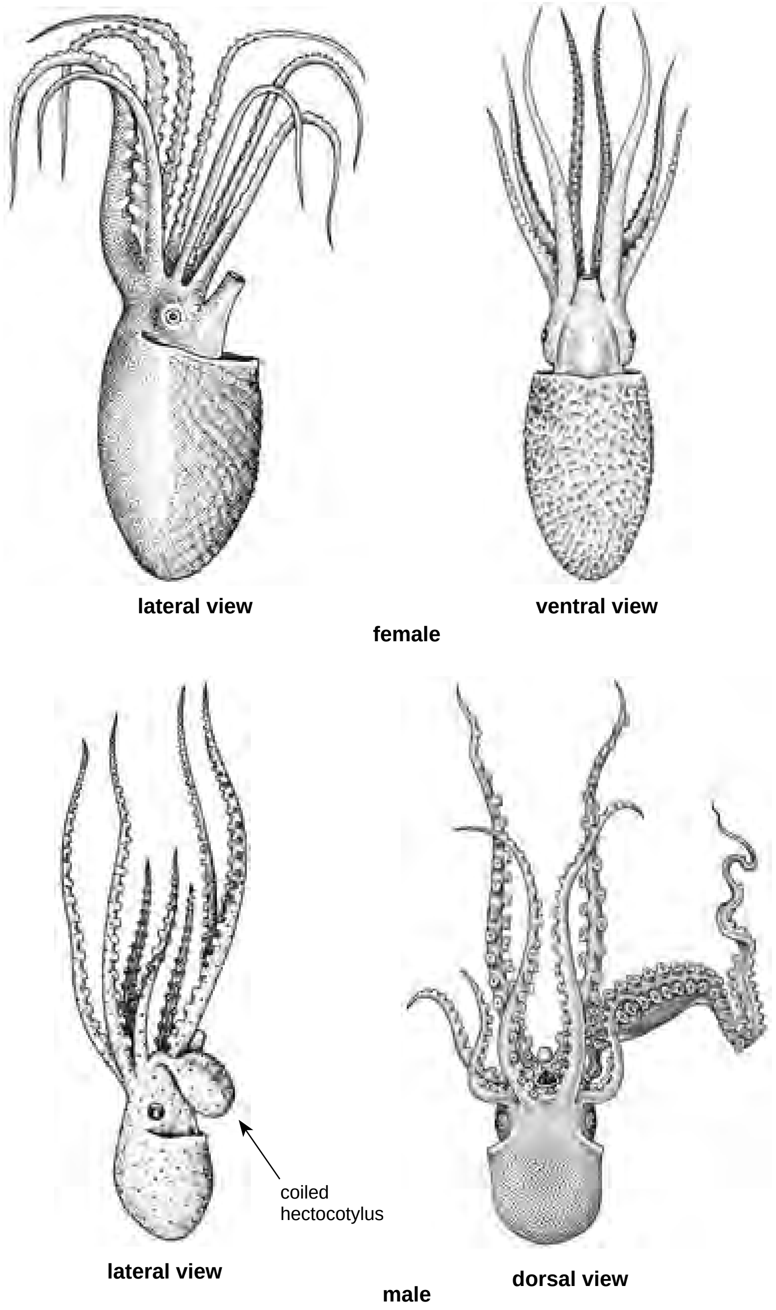


Fig. 236 ***Ocythoe tuberculata***

Geographical Distribution: Temperate latitudes of the world's oceans. Recorded in the northern hemisphere from the Mediterranean Sea, North Atlantic, and North Pacific Oceans. Recorded in the southern hemisphere from the eastern South Atlantic Ocean (off Namibia and South Africa), western South Pacific Ocean (off Australia and New Zealand) and eastern South Pacific Ocean (off Peru). Most frequently encountered in the vicinity of landmasses and islands (Fig. 237).

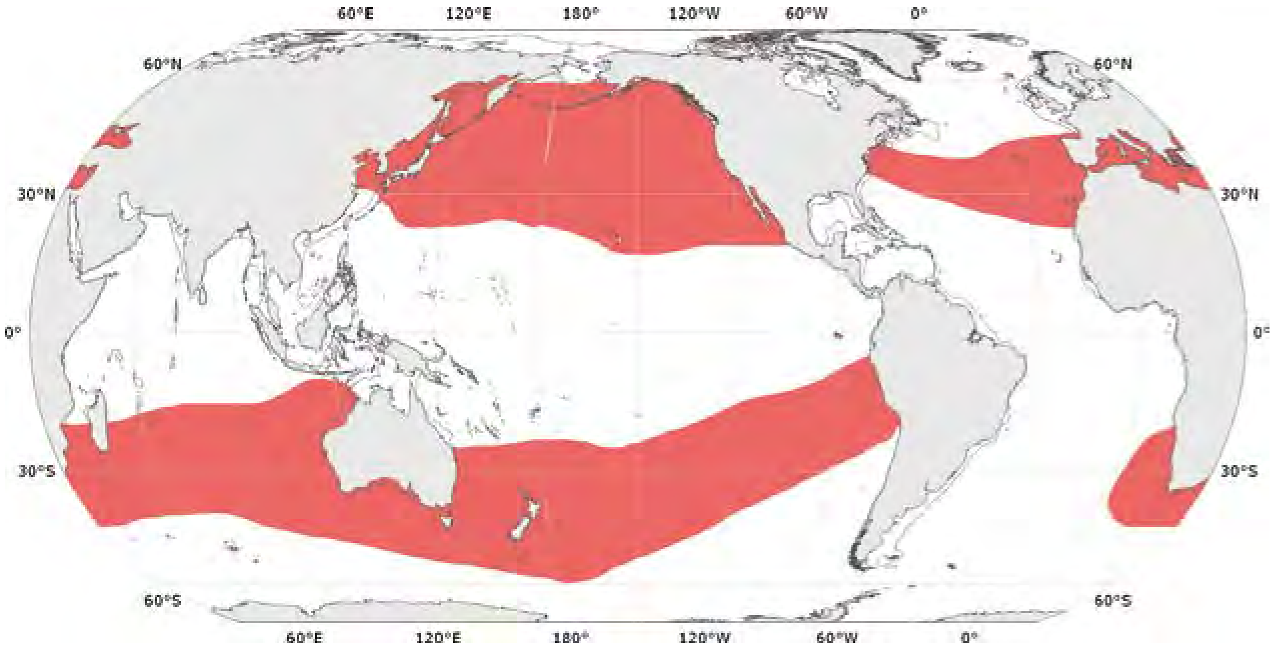


Fig. 237 ***Ocythoe tuberculata***

🟥 Known distribution

Habitat and Biology: Female ***Ocythoe*** typically occupy near-surface waters, having been encountered in the upper 10 m and captured in plankton hauls and on hook and line. While male ***Ocythoe*** have been collected in pelagic tows at the sea surface, they are not restricted to surface waters, having been collected in closing nets at 100 to 200 m. ***Ocythoe*** are reported to be edible. Both male and small female ***Ocythoe*** have been encountered inhabiting tests of the gigantic salp, *Tethys vagina*, in surface waters during the day. ***Ocythoe*** are reported to feed on pteropod and heteropod molluscs, sardines, and crustaceans.

Interest to Fisheries: Limited interest to fisheries due to scarcity of capture. Reported to be edible.

Local Names: ITALY: Polpo pignatta; JAPAN: Amidako.

Remarks: The current distributional records of this species suggest that it may be limited to the temperate latitudes of both hemispheres. If this distribution is correct, it suggests two separate populations and potentially two separate species might exist. The population structure of this group requires further investigation.

Literature: Rafinesque (1840), Naef (1923), Robson (1932), Berry (1955a), Nishimura (1968), Hardwick (1970), Roper and Sweeney (1976), Brandt (1983), Okutani and Osuga (1986), Packard *In* Nixon (1987), Cardoso (1991), Gonçalves (1991), Nesis (1991), Smale *et al.* (1993), Corsini and Lefkaditou (1994), Packard and Wurtz (1994), Cardoso and Paredes (1998), O'Shea (1999), Laptikhovsky and Salman (2003), Lefkaditou *et al.* (2003), Nixon and Young (2003), Caballero-Alfonso *et al.* (2008), Tutman *et al.* (2008), Jorgensen (2009), Mangold *et al.* (2010b).

2.1.8 Family TREMOCTOPODIDAE Tryon 1879 by Julian K. Finn

Tremoctopodidae, Tryon, 1879, *Manual of Conchology; Structural and Systematics, I: Cephalopoda*, Philadelphia: 130.

Type Genus: *Tremoctopus* Delle Chiaje, 1830.

FAO Names: **En** — Blanket octopods; **Fr** — Poulpes manteau; **Sp** — Pulpos manta.

Diagnostic Features: Body tissue muscular or gelatinous, smooth; two pairs of cephalic water pores present, one pair located on dorsal surface of head, slightly anterior to eyes, and second pair located ventrally, adjacent to funnel opening; stylets present; funnel not embedded in head tissue; funnel locking apparatus developed; funnel corner hooked into pocket in mantle; extensive webs between first two pairs of arms of females; male third right arm hectocotylized, developed in sac between funnel and right eye.

Habitat and Biology: Members of the family Tremoctopodidae are commonly known as ‘blanket octopods’ on account of the expanded dorsal webs (or ‘blankets’) that unite the dorsal arms of females. These expansive webs are divided into sequential subunit components, which can be autotomized as long free strips by the animal. Female tremoctopods attain a large size, often reaching 1 m total length, while the mantle length of dwarf males seldom exceeds 15 mm. Males and small females usually carry fragments of nematocyst-bearing tentacles of the siphonophore *Physalia* (Portuguese Man-of-War). The fragments are held on arms 1 and 2 in two rows that correspond to the two rows of suckers. It is not known whether the *Physalia* tentacle fragments are used to aid in food capture and/or defence. *Physalia* tentacles are absent from females greater than 70 mm in total length. The stomach of an Australian specimen was found to contain fish scales, cephalopod flesh, algae and polychaete jaws. The remains of tremoctopods have been recovered from the stomachs of a range of predators including fishes, marine mammals and birds.

Remarks: Four species currently are considered to be valid in the family: ***Tremoctopus violaceus***, ***T. gracilis***, ***T. gelatus*** and ***T. robsoni*** (Mangold *et al.*, 2010c), although the group still requires further revision. Females of three species (***T. violaceus***, ***T. gracilis*** and ***T. robsoni***) are moderately large, muscular, firm-bodied and deeply pigmented with colour patterns of purple dorsally and silver ventrally (counter-shading typical of surface dwellers). The fourth species (***T. gelatus***) is a very gelatinous, fragile, deep-water form of larger size, with few chromatophores and is almost completely transparent (Voss, 1967).

Literature: Naef (1923), Portmann (1952), Jones (1963), Voss (1967), Voss and Williamson (1971), Thomas (1977), Zeidler (1989), O’Shea (1999), Norman *et al.* (2002), Finn (2009), Mangold *et al.* (2010c).

Tremoctopus Delle Chiaje, 1830

Tremoctopus Delle Chiaje, 1830, *Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli*, pls. 70, 71.

Type species: *Tremoctopus violaceus* Delle Chiaje, 1830.

Frequent Synonyms: None.

Diagnostic Features: With characters of the family. Monogeneric.

Literature: No additional literature.

Tremoctopus violaceus Delle Chiaje, 1830

Fig. 238; Plate XI, 81

Tremoctopus violaceus, Delle Chiaje, 1830, *Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli:* pls 70, 71. [Type locality: Mediterranean Sea].

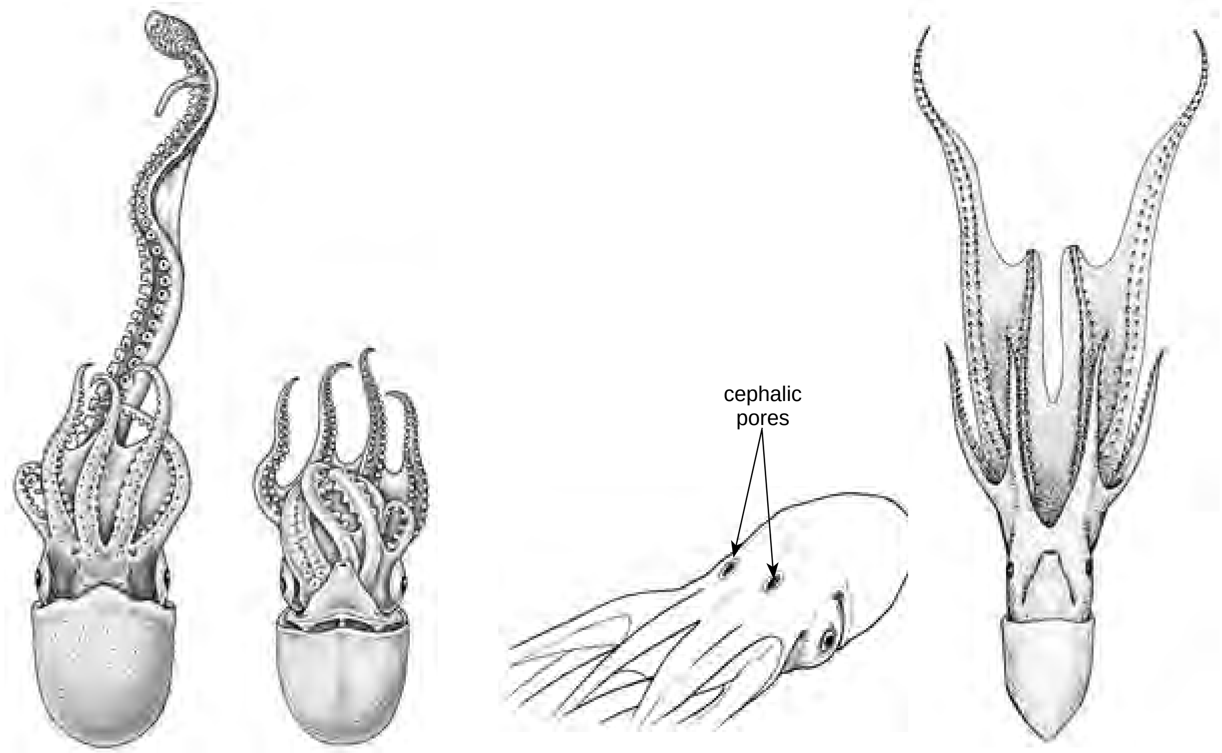
Frequent Synonyms: *Tremoctopus violaceus violaceus* Delle Chiaje, 1830.

Misidentifications: None.

FAO Names: En — Violet blanket octopod; **Fr** — Poulpe manteau violet; **Sp** — Pulpo manta violaceo.

Literature: No additional literature.

Diagnostic Features: Extreme sexual dimorphism by size; males are dwarfed. Mantle smooth, thick, muscular. Cephalic water pores present, conspicuous, oval, in two pairs: dorsal pair on surface of head, slightly anterior to eyes, at base of first arms; ventral pair adjacent to tip of funnel, at base of fourth arms. Arms unequal in length; arm formula 2>1>4>3 or 1>2>4>3. Suckers biserial, elevated on broad bases. Funnel of moderate size, extends beyond level of eyes, distal one quarter free. Funnel-mantle locking apparatus present, consists of rigid recurved portion of posterior margin of funnel that articulates with depression in mantle wall. Funnel organ W-shaped in males and very young females; present as numerous longitudinal, parallel folds of glandular tissue in adult females. Ink sac present. Stylets present.



dorsal view **ventral view**
male

anterodorsal view **ventral view**
female

Fig. 238 ***Tremoctopus violaceus***

Females large. Body firm. Head narrower than mantle, constricted in neck region. Eyes large, laterally directed. Nuchal folds posterior to eyes, 8 to 10 in number. First and second arms much longer than third and fourth arms. First arms very long in young females, suckers on ends arranged in single row spaced widely apart; shallow grooves pass across arms. First arms of adult females truncated. Second arms stout and flattened along oral surface, suckers degenerated in adults and appear as 2 rows of inconspicuous lateral projections. Third and fourth arms exhibit no unusual modifications. Web well developed. Dorsal web deep, extends to tip of truncated arms; V-shaped cleft present medially. Web connects arms of first two pairs, with a wide fringe present on both sides of first arms and on dorsal side of second arms. Web fringe absent on third and fourth arms. Web between third and fourth arms poorly developed. Suckers biserial, elevated on broad bases. Gills with 13 to 16 filaments on outer demibranch. Eggs small, brooded in arm crown attached to “rod” secreted by female. In life dorsal surface of head and body dark bluish-purple; ventral surface iridescent silvery gold colour; web deep maroon. Males dwarfed. Mantle smooth, bowl-shaped and broad posteriorly. Head slightly wider than mantle, separated laterally by prominent constriction. Dorsal surface of head continuous with mantle. Dorsal surface of mantle and head with few scattered chromatophores. Eyes large, laterally directed. Gills with 9 to 11 filaments on outer demibranch. First arms intact and unmodified. Web thin, of uniform structure, without epithelial modifications. Third right arm hectocotylized; develops in pouch between second and fourth right arms. As hectocotylized arm grows, the animal appears asymmetrical. Right ventral cephalic water pore often crowded and degenerate due to development of hectocotylus in pouch. **Proximal half of hectocotylized arm contains approximately 22 to 23 pairs of suckers (in two rows)**. Fringed area with closely spaced filaments (arranged in rows, 4 to 5 filaments per row) located lateral to each sucker pair. **Distal portion of arm with 15 to 19 pairs of suckers**. Spermatophore groove absent; terminal spermatophore reservoir with terminal opening. Penile filament enclosed in sac proximal to spermatophore reservoir between suckers on inner surface of arm; penile filament protrudes from proximal opening in sac. Single large spermatophore typically present.

Size: Female mantle length to 250 mm; total length to approximately 1 m. Frequently cited total length measurements of 2 m are not supported by a known specimen. Male mantle length to at least 15 mm.

Geographical Distribution: Widespread pelagic species found in the Atlantic Ocean, Gulf of Mexico, Caribbean and Mediterranean seas, between latitudes 40°N and 36°S (Fig. 239).

Habitat and Biology: Observed at the surface at night but may undergo small diel vertical migrations. Juveniles have been collected at depths ranging from 0 to 250 m. Females brood eggs within the arm crown and webs, attached as strings to a secreted, mineralized rod. Egg strings at different stages of development indicate prolonged spawning and potentially high fecundity. Up to five different egg stages can be carried by a single female. Female ***Tremoctopus violaceus*** are reported to feed on pteropod molluscs and small fishes. Known to occur, on occasion, in plague proportions.

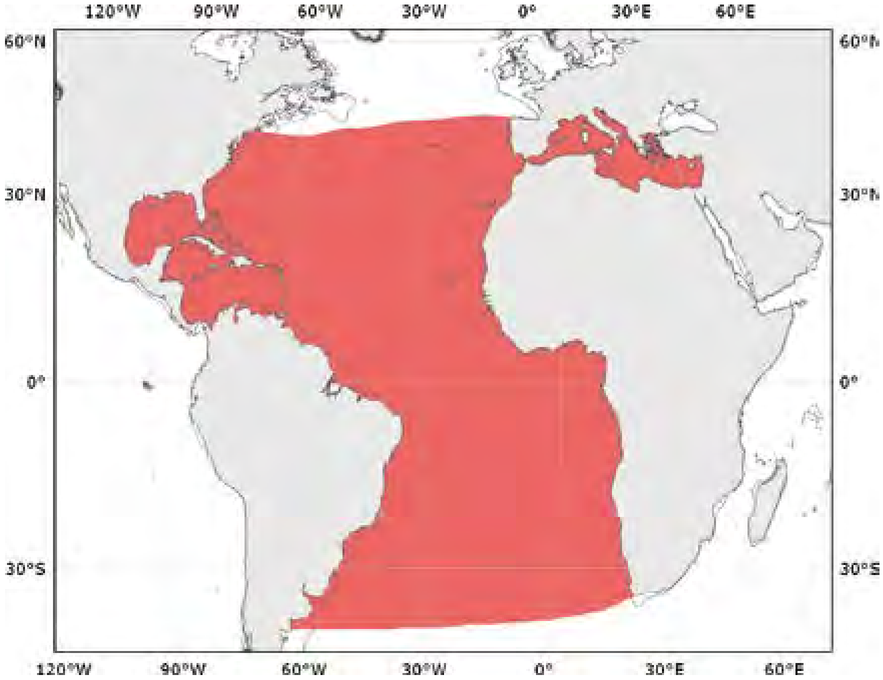


Fig. 239 ***Tremoctopus violaceus***

🟥 Known distribution

Interest to Fisheries: Unknown.

Local Names: ITALY: Polpo palmato.

Literature: d'Orbigny (1840) *in* Ferussac and d'Orbigny (1834-1848), Lane (1957), Jones (1963), Lu and Clarke (1975a), Roper and Young (1975), Thomas (1977), Knudsen (1992), Bello (1993), Vardala-Theodorou (1994), Bizikov (2004), Orsi Relini (2009), Mangold *et al.* (2010c).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Tremoctopus gelatus Thomas, 1977

Tremoctopus gelatus, Thomas, 1977, *Bulletin of Marine Science*, 27(3): 371. [Type locality: Northeastern Atlantic Ocean, USA, Florida, Boynton Beach].

Size: Female mantle length to at least 328 mm. Male mantle length to at least 10 mm.

Geographical Distribution: Western Atlantic Ocean, Indian Ocean, and eastern Pacific Ocean.

Literature: Voss (1967), Thomas (1977), Mangold *et al.* (2010c).

Tremoctopus gracilis (Eydoux and Souleyet, 1852) **Plate XI, 82, 83**

Octopus gracilis, Eydoux and Souleyet, 1852, *Mollusques: Cephalopodes*. *In voyage autour du monde exécuté pendant… 1836 et 1837 sur… la Bonite, commandeé par M. Vaillant, Zoologie, Paris*, 2: 13. [Type locality: Pacific Ocean, 08°N, 106°W of Paris].

Frequent Synonyms: *Tremoctopus violaceus gracilis* (Eydoux and Souleyet, 1852).

Size: Female mantle length to at least 320 mm; total length to approximately 1 m. Male mantle length to 15.5 mm.

Geographical Distribution: Indian and Pacific oceans, between latitudes 39°N and 30°S, and Mediterranean Sea.

Habitat and Biology: Females and males observed live in surface waters at night.

Literature: Jones (1963), Voss and Williamson (1971), Hamabe (1973), Thomas (1977), Zeidler (1989), Norman *et al.* (2002, as ***Tremoctopus violaceus***), Belluscio *et al.* (2004, as ***Tremoctopus*** sp.), Orsi Relini *et al.* (2004), Finn (2009), Mangold *et al.* (2010c).

Tremoctopus robsoni Kirk, 1884

Tremoctopus robsoni, Kirk, 1884, *Transactions and Proceedings of the New Zealand Institute*, 16(1883): 549. [Type locality: New Zealand, Mayor Island].

Size: Female mantle length to 137 mm. Male mantle length to 15.3 mm.

Geographical Distribution: New Zealand waters.

Habitat and Biology: Depths range from 0 to 305 m, over bottom depths of 1 002 to 1 352 m.

Literature: Kirk (1884), O'Shea (1999), Mangold *et al.* (2010c).

2.2 Cirrate octopods

by Frederick G. Hochberg, Mark D. Norman and Julian K. Finn

The cirrate octopods are collectively known as the finned octopods or cirrates. They are medium- to large-sized residents of deep waters. The largest are estimated to be 4 m in total length (Voss, 1988a). They are characterised by soft, semi-gelatinous bodies, a single pair of fins on the mantle and typically deep webs. Their eight arms bear a single row of suckers, each side of which is a row of narrow finger-like projections ("cirri"). All species lack an ink sac and anal flaps. Many species lack a radula. An internal cartilaginous shell* supports and attaches to the fin bases. Sexual dimorphism is minimal. Males lack a hectocotylus, but males of some species possess a series of enlarged suckers. Spermatophores are simple barrel-like structures with an opercular cap on each end. Females have a single oviduct on the left side, and they produce large encapsulated eggs that are laid singly on hard surfaces on the seafloor. Cirrate octopods occur in all deep waters of the world, including both polar regions, at depths from 100 to 7 000 m. Most species associate with the seafloor (benthic, epibenthic or benthopelagic), although individuals sometimes are caught in midwater or close to the surface in cooler (polar) regions.

Remarks: Based on a single mitochondrial gene (16S), Piertney *et al.* (2003) proposed four families within this order: Cirroteuthidae (including Stauroteuthidae), Opisthoteuthidae (for ***Opisthoteuthis***), Grimpoteuthidae (for ***Grimpoteuthis*** and ***Luteuthis***) and a new family, Cirroctopodidae (for ***Cirroctopus***). There was limited support for Grimpoteuthidae in the resulting trees. At this stage we support the three families followed by Vecchione *et al.,* 2014 (Tree of Life website). Based on the pubblication by Collins and Villanueva (2006) we have also included treatment of a fourth family, Cirroctopodidae. In spite of a comprehensive review of the cirrates (Collins and Villanueva, 2006), the systematics and taxonomy of this group continue to be in a state of flux and are in critical need of further molecular and morphological study.

Key to Families:

1a. Web sectors between arms in single layer, not as two separate layers; anterior-posterior elongation of body and arms not pronounced. . . . . **→ 2**

1b. Web sectors between arms in two distinct layers (known as primary and secondary webs), capable of being inflated with water enabling the animal to inflate like a ball ("ballooning" behaviour); anterior-posterior elongation pronounced ... . **→ 3**

2a. Fins small, subterminal; shell U-shaped; . . . . **Family Opisthoteuthidae**

2b. Fins large, paddle-like; shell V-shaped; . . . . **Family Cirroctopodidae**

3a. Mantle opening forms a complete tube around the funnel; shell simple U-shaped. . . . **Family Stauroteuthidae**

3b. Mantle opening as slit opening, not tube-like; shell saddle-shaped, broad with two lobe-like, deeply excavated flared wings . . . . **Family Cirroteuthidae**

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* The internal cartilage structure in the dorsal mantle of cirrate octopods that supports the fin is often referred to as a "shell". It is not a true shell as it is not formed by the true molluscan shell gland. It is more appropriate to refer to this structure as a "fin support cartilage".

Fig. 240 Cirroctopodidae
(Cirroctopus)

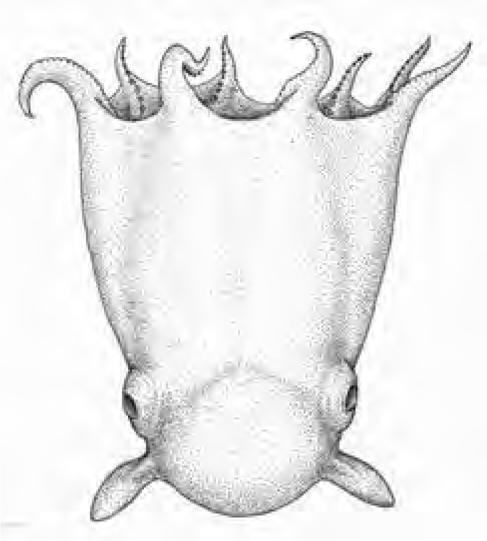


Fig. 241 Opisthoteuthidae
(Opisthoteuthis)

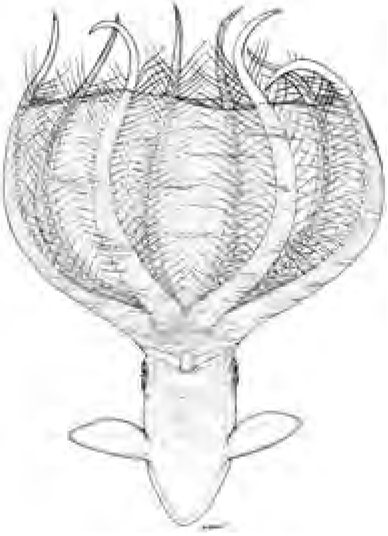


Fig. 242 Stauroteuthidae
(Stauroteuthis)

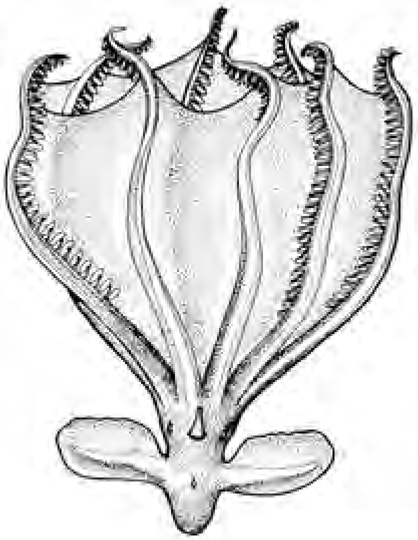


Fig. 243 Cirroteuthidae
(Cirroteuthis)

2.2.1 **Family CIRROCTOPODIDAE** Collins and Villanueva, 2006

by Frederick G. Hochberg,
Mark D. Norman and Julian K. Finn

Cirroctopodidae Collins and Villanueva, 2006, *Oceanography and Marine Biology: An Annual Review*, 44: 300.

Type Genus: *Cirroctopus* Naef, 1923, *Fauna e Flora de Golfo di Napoli*, Monograph 35: 675.

FAO Names: En — Finned octopods; **Fr** — Poulpes à oreilles; **Sp** — Pulpos cirrados.

Diagnostic Features: Relatively muscular species with large fins; anterior-posterior elongation of the body not pronounced. Eyes tilt dorsally; lenses present. Secondary web absent. Gills half-orange form. Ink sac and radula absent. Posterior salivary glands absent. Digestive gland entire. Shell V-shaped with spike-like lateral walls. Suckers relatively small; enlarged suckers absent in mature males. Cirri of moderate length, equal to maximum sucker diameter.

Size: Mantle length to 180 mm; total length to >600 mm.

Geographical Distribution: Restricted to the southern hemisphere.

Remarks: This family contains a single genus and four species.

Literature: Nesis (1999), O’Shea (1999), Collins and Villanueva (2006), Vecchione *et al.* (2014).

Cirroctopus Naef, 1923

Cirroctopus Naef, 1923, *Fauna e Flora del Golfo di Napoli*, Monograph 35: 675

Type species: *Cirroctopus mawsoni* (Berry, 1917).

Frequent Synonyms: *Grimpoteuthis* Robson, 1932.

Diagnostic Features: With characters of the family. Monogeneric.

Remarks: Type species of genus not treated as the descriptor for the genus as it is known only from the original specimen, which is in poor condition.

Literature: No additional literature.

Cirroctopus glacialis (Robson, 1930)

Fig. 244

Grimpoteuthis glacialis Robson, 1930, *Discovery Report, 2:* 375. [Type locality: Southern Ocean, Antarctica, Palmer Archipelago, Schollaert Channel, 64º21'S, 62º58'W].

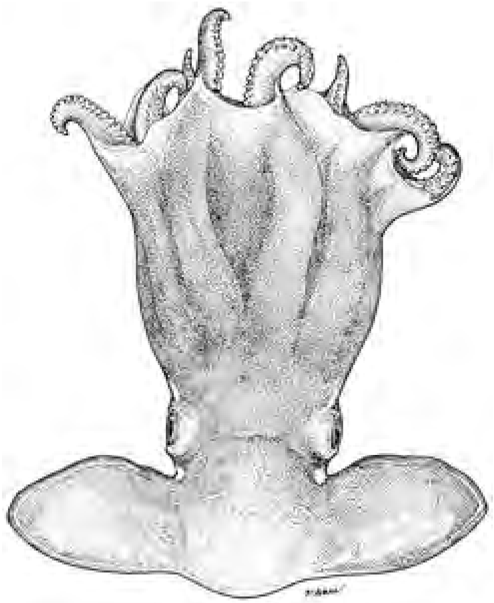
Frequent Synonyms: *Cirroteuthis glacialis* (Robson, 1930).

FAO Names: En — Icy finned octopod; **Fr** — Poulpe à oreilles glacial; **Sp** — Pulpo cirrado glacial.

Diagnostic Features: Medium-sized, relatively muscular species. **Pair of large fins present on mantle; fin length equal to mantle length, width nearly 75% of fin length.** Eyes able to be tilted dorsally. V-shaped shell present, shell surface smooth, basal shelf present. Mantle septum very thick. Gills with 6 primary lamellae. All eight arms have a single row of small suckers, none enlarged in either sex. **Each arm bears a double row of short cirri, each approximately equal in length with sucker diameter.** Longest arm with 74 suckers. Arm formula: 1>2>3>4. Webs deep, extend to near arm tips, formula A>B>C>D>E, sector E half the length of sector A. Ink sac and radula absent. **Colour pattern of large pale triangles on oral webs on each side of midsection of arms.**

Size: Mantle length to 165 mm; total length to >600 mm.

Geographical Distribution: Southern Ocean, off Antarctic Peninsula (Fig. 245).



dorsal view

Fig. 244 *Cirroctopus glacialis*

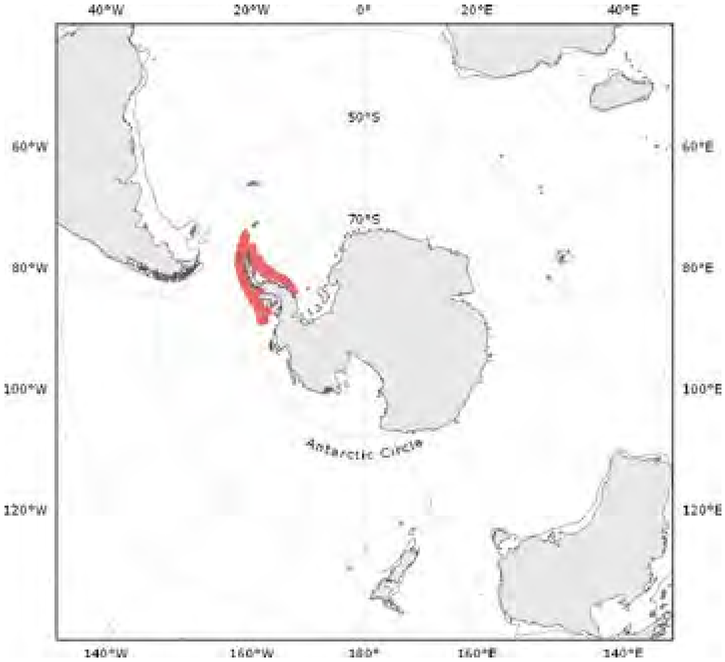


Fig. 245 *Cirroctopus glacialis*

🟥 Known distribution

Habitat and Biology: Depths range from 333 to 879 m. The species occupies a primarily benthic habit, with individuals typically captured living over soft mud substrates. This species swims primarily by fin action. Males tend to be larger than females in total length and body mass for the same mantle length. Males mature at much smaller sizes. Males produce tiny ovoid capsules of sperm. Females lay large eggs (16 x 12 mm) with a sticky outer coating which hardens on contact with seawater to form a hard outer coating. Brood time is estimated to be between 2.5 to 3.5 years. A dicyemid parasite, *Dicyemennea discocephala*, is known to occur in the renal coelom of this cirrate species.

Interest to Fisheries: Unknown.

Remarks: Due to preservation/condition problems with the specimen of ***Cirroctopus mawsoni***, the type species for this genus, ***C. glacialis*** is presented instead as a better-known example of this genus.

Literature: Hochberg and Short (1983), Nesis (1999), O'Shea (1999), Vecchione and Young (2010).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Cirroctopus antarctica (Kubodera and Okutani, 1986)

Grimpoteuthis antarctica Kubodera and Okutani, 1986 *memoirs of the National Institute of Polar Research, Special Issue,* 44: 129. [Type locality: Southern Ocean, off Antarctica, 62º59'S, 62º09'W].

Size: Mantle length to 180 mm (known only from type specimens).

Geographical Distribution: Known only from the type locality, off Antarctica.

Habitat and Biology: Depths of types range from 509 to 804 m.

Remarks: This species is considered to represent a possible junior synonym of ***Cirroctopus glacialis***.

Literature: O'Shea (1999).

Cirroctopus hochbergi O'Shea, 1999

Cirroctopus hochbergi O'Shea, 1999, *NIWA Biodiversity Memoir,* 112: 35. [Type locality: New Zealand, 39º54'S, 178º16'E].

Size: Mantle length to 160 mm; total length to 493 mm.

Geographical Distribution: New Zealand, off east coast of North Island.

Habitat and Biology: Depths range from 700 to 1 350 m.

Literature: No additional literature.

Cirroctopus mawsoni (Berry, 1917)

Stauroteuthis (?) *mawsoni* Berry, 1917, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 69: 8. [Type locality: Southern Ocean, Antarctica, off Mertz Glacier, Adelie Land, 66º55'S, 145º21'E].

Size: Mantle length 12 mm; total length 32 mm; known only from type the specimen.

Geographical Distribution: Known only from the type locality, Antarctica.

Habitat and Biology: Depth of type 527 to 549 m.

Remarks: Type species for genus but known only from original specimen, which is in poor condition.

Literature: No additional literature.

2.2.2 Family CIRROTEUTHIDAE Keferstein, 1866

by Frederick G. Hochberg, Mark D. Norman
and Julian K. Finn

Cirroteuthidae Keferstein, 1866, *Die Klassen und Ordnungen des Thier-reiches: Weichthiere (Malacozoa):* 1307-1464.

Type Genus: *Cirroteuthis* Eschricht, 1836.

FAO Names: En — Cirroctopods; **Fr** — Cirropoulpes; **Sp** — Cirropulpos.

Diagnostic Features: Very fragile, gelatinous, finned octopods; elongate in anterior-posterior axis. Eyes range from very large to small; some taxa have degenerate, barely-functional eyes. Two sets of webs present: primary webs between each arm, and secondary webs as inflatable pouches along arm bases. Cirri very long, up to eight times largest sucker diameter. Cartilaginous shell present; broad saddle-shaped structure at base of fins with flared, deeply excavated wings.

Size: Mantle length to 330 mm; total length to 1.7 m.

Geographical Distribution: North Atlantic, North Pacific and Indian Oceans.

Habitat and Biology: Cirroteuthids are typically found near the seafloor in very deep water but also have been caught in the water column and near the surface in polar waters.

Remarks: Two genera are recognized in this family.

Key to genera in the family Cirroteuthidae:

1a. Eyes well developed with lens and iris . . . . **→ 2**
1b. Eyes reduced without lens or iris . . . . ***Cirrothauma*** (in part)

2a. Arm tips lack suckers; nodules present on webs; shell with saddle more than half shell length in anterior-posterior plane. . . . . ***Cirroteuthis***
2b. Suckers continue to arm tips; nodules absent on webs; shell with saddle length less than half shell length in anterior posterior plane. . . . . ***Cirrothauma*** (in part)

Cirroteuthis Eschricht, 1836

Cirroteuthis Eschricht, 1836, *Nova Acta Physico-Medica Academiae Caesarea Leopoldino-Carolinae Naturae Curiosorum,* 18(2): 633.

Type Species: *Cirroteuthis muelleri* Eschricht, 1836.

Frequent Synonyms: *Sciadephorus* Reinhardt and Prosch, 1846.

Diagnostic Features: Medium to large species. Body soft, gelatinous; elongate in anterior-posterior axis. Pair of large fins present on mantle, attached closer to head than posterior mantle. Eyes well developed; with lenses. **Shell present with broad saddle and wings in anterior-posterior plane. Saddle length more than half shell length. Wings ovoid from lateral view.** The eight subequal arms have a single row of small suckers, none enlarged in either sex. **Each arm bears a double row of long cirri, longest ~9 to 13 times sucker diameter. Suckers and cirri absent from arm tips beyond web limit. Web nodules present.** Webs deep, extend to near arm tips. **Secondary webs present along majority of arm length.**

Size: Total length to 1.5 m.

Geographical Distribution: Northwestern Atlantic Ocean and north Pacific Ocean.

Remarks: Single described species recognized.

Literature: Voss (1988a), Collins *et al*. (2001a), Collins (2002).

Cirroteuthis muelleri Eschricht, 1836

Fig. 246; Plate XI, 86

Cirroteuthis muelleri Eschricht, 1836, *Nova Acta Physico-Medica Academiae Caesarea Leopoldino-Carolinae Naturae Curiosorum,* 18(2): 633. [Type locality: west Greenland, Jacobshavn].

Frequent Synonyms: *Sciadephorus muelleri* (Eschricht, 1836). In the literature the species name is often spelled "*mülleri*" with the umlaut.

FAO Names: En — Müller's cirroctopod; **Fr** — Cirropoulpe de Müller; **Sp** — Cirropulpo de Müller.

Diagnostic Features: With characters of the genus. Monotypic.

Size: Medium to large species; total length to 1.5 m.

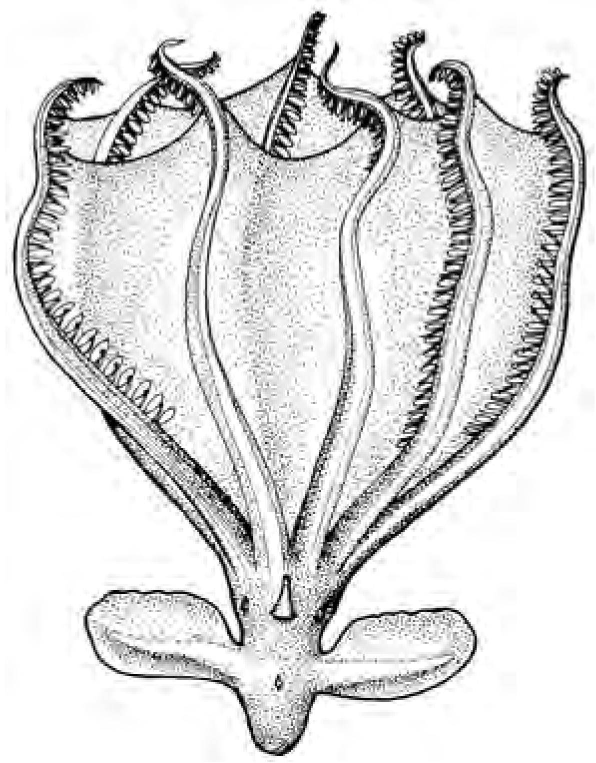
Geographical Distribution: Circum-Arctic, in north Atlantic and north Pacific oceans (Fig. 247).

Habitat and Biology: Depth range from 500 to 4 854 m, with highest abundance around 3 000 to 3 500 m. Most captures have been made near the seafloor. Egg capsules are large (10.5 x 6.5 mm) and protected by a strong chitinous shell. The eggs are laid singly on the bottom and brooding duration is estimated to be about 20 to 32 months.

Interest to Fisheries: Unknown.

Remarks: A similar form, ***Cirroteuthis*** cf. ***muelleri***, has been reported off the Chatham Rise in New Zealand (O'Shea, 1999).

Literature: Reinhardt and Prosch (1846), Robson (1924, 1932), Pearcy and Beal (1973), Nesis (1988, 1999, 2001), Voss (1988b), Voss and Pearcy (1990), Hochberg *et al.* (1992), Guerra *et al.* (1998), O'Shea (1999), Collins *et al.* (2001b), Collins (2002), Knudsen and Roeleveld (2002), Gardiner and Dick (2010a,b).



dorsal view

Fig. 246 *Cirroteuthis muelleri*

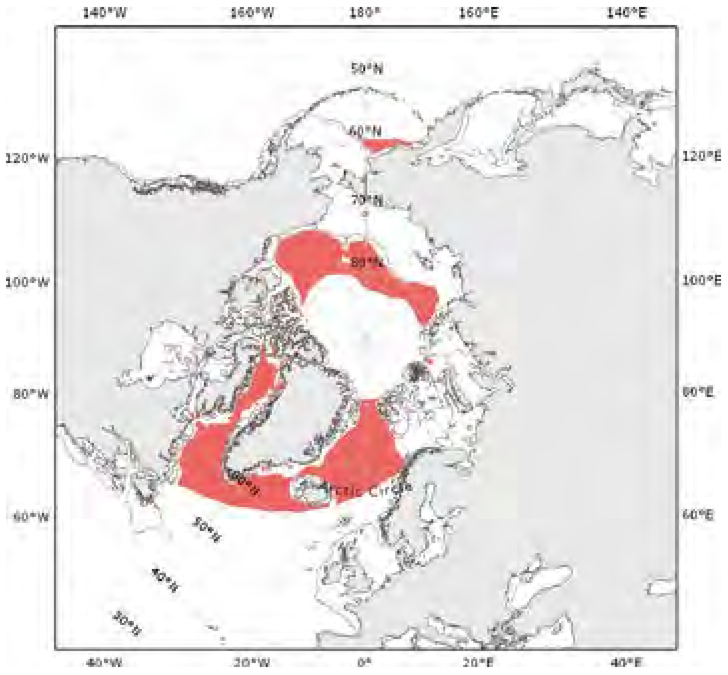


Fig. 247 *Cirroteuthis muelleri*

🟥 Known distribution

Cirrothauma Chun, 1911

Cirrothauma Chun, 1911, *Philosophiae Doctores Dissertation*, *Leipzig*: 5.

Type Species: *Cirrothauma murrayi* Chun, 1911.

Frequent Synonyms: None.

Diagnostic Features: Eyes well developed, lenses present (in *Cirroteuthis magna*), or poorly developed, without lenses (in *C. murrayi*). Web nodules absent. Suckers extend to arm tips. Cirri may extend to arm tip (***C. murrayi***) or terminate at web margin (***C. magna***). Shell saddle-shaped but with a saddle of moderate length. **Shell with anterior-posterior length of wings more than 2.5 times length of saddle antero-posteriorly.** Shell wings triangular in lateral view.

Size: Total length to about 1.7 m.

Geographical Distribution: Reported to be present in all oceans except for the Southern Ocean.

Remarks: Chun erected the genus name in 1913, but it was considered to be preoccupied by prior use of the name in his PhD dissertation in 1911 (see Voss, 1988a).

Literature: Chun (1913); Voss (1988a,b).

Cirrothauma murrayi Chun, 1911

Fig. 248

Cirrothauma murrayi Chun, 1911, *Doctoral dissertation, Leipzig*: 5. [Type locality: mid-Atlantic Ocean, 48º24'N, 6º53'W].

Frequent Synonyms: None.

FAO Names: En — Murray's cirroctopod; **Fr** — Cirropoulpe de Murray; **Sp** — Cirropulpo de Murray.

Diagnostic Features: Medium to large species. Body gelatinous; elongate in anterior-posterior axis. Pair of large fins present on mantle, attached closer to head than posterior mantle. **Eyes poorly developed, lacking lenses and exposed to exterior. Shell with moderate saddle and large, flared wings. Saddle length less than half shell length. Wings triangular from lateral view.** The eight arms have a single row of small suckers, first six sessile, the remainder long and spindle-shaped with gelatinous stalks. **Photophores located in bases of stalked suckers.** Long cirri present**. Web nodules absent**. Webs deep, extend nearly to arm tips. Secondary webs present along majority of arm length.

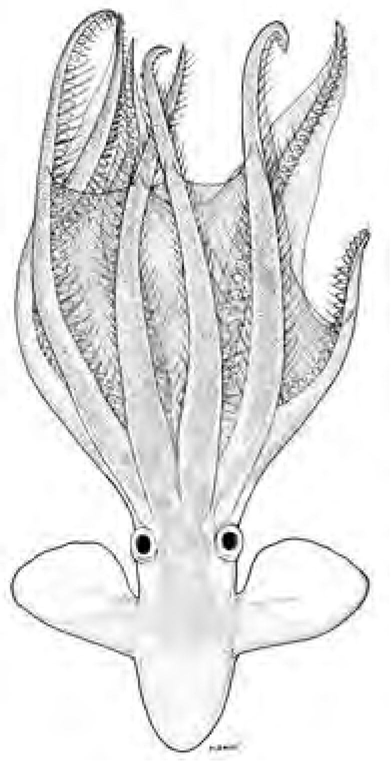
Size: Total length to at least 1 m.

Geographical Distribution: Pacific, Atlantic, and Arctic oceans (Fig. 249).

Habitat and Biology: Depth range from 2 430 to 4 850 m, with most captures deeper than 3 000 m. The poorly developed eyes of this animal indicate that it may be nearly blind. This species has possible light organs in the base of the suckers as reported for ***Stauroteuthis***, the function of which is unknown.

Interest to Fisheries: Unknown.

Remarks: The author and date for this species often are cited as Chun, 1913 but this is preoccupied by the name in Chun, 1911.



dorsal view

Fig. 248 ***Cirrothauma murrayi***

Literature: Chun (1913), Ebersbach (1915), Roper and Brundage (1972), Pearcy and Beal (1973), Roper and Young (1975), Aldred *et al*. (1978, 1982, 1983), Robison and Young (1981), Voss (1988a, b), Hochberg *et al.* (1992), Vecchione and Young (1997), Villanueva and Segonzac (1997), Collins *et al*. (2001b).

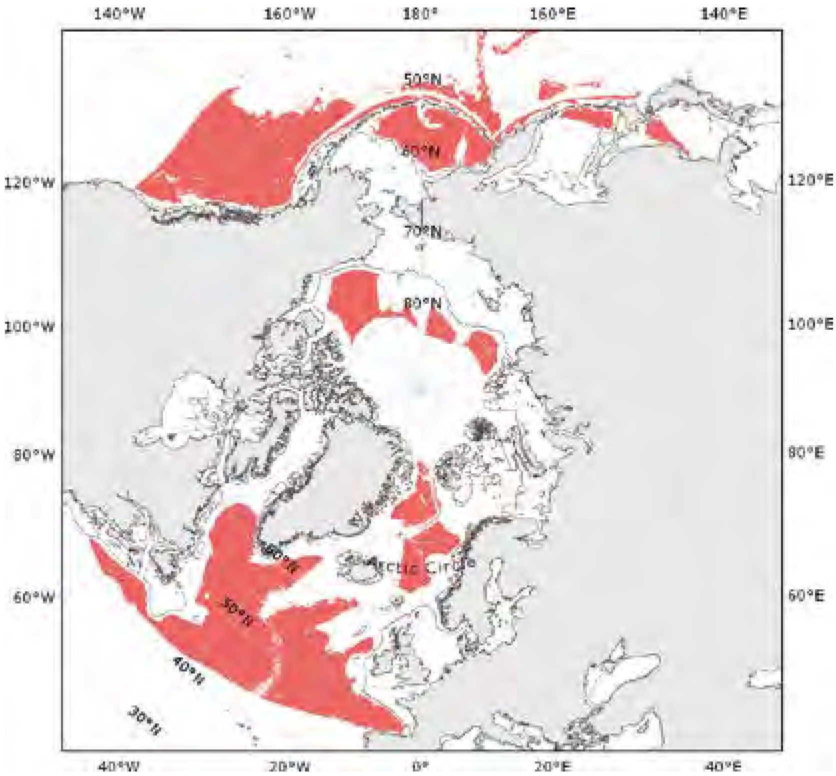


Fig. 249 ***Cirrothauma murrayi***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Cirrothauma magna (Hoyle, 1885)

Cirroteuthis magna Hoyle, 1885a, *Annals and Magazine of Natural History*, series 5, 15: 232. [Type locality: Indian Ocean, between Prince Edward Island and Crozet Island, 45º46'S, 45º31'E].

Size: Mantle length to 330 mm; total length to 1 700 mm.

Geographical Distribution: Atlantic and Indian Oceans.

Habitat and Biology: Depth range from 1 300 to 3 351 m.

Remarks: This species has been placed in the genus ***Cirrothauma*** based on shell shape.

Literature: Villanueva *et al*. (1997), Guerra *et al*. (1998), O'Shea (1999), Collins *et al*. (2001a).

2.2.3 Family OPISTHOTEUTHIDAE Verrill 1896

by Frederick G. Hochberg, Mark D. Norman
and Julian K. Finn

Opisthoteuthidae Verrill, 1896, *American Journal of Science*, 2: 74.

Type Genus: *Opisthoteuthis* Verrill, 1893.

FAO Names: En — Flapjack octopods; **Fr** — Discopoulpes; **Sp** — Discopulpos.

Diagnostic Features: Members of this family are united by anterior-posterior compression, so bodies appear relatively squat or flat. Body gelatinous to fragile; fins small to moderate size. Eyes laterally oriented. Single row of small suckers and two rows of short cirri (0.4 to 2.5 times largest sucker diameter), extending to arm tips. Enlarged suckers present in mature males of several genera. Shells simple U-or W-shaped structures; significantly expanded lateral wings absent. Secondary web absent.

Size: Mantle length to 140 mm; total length to >480 mm.

Geographical Distribution: Worldwide. Present in all oceans.

Remarks: In this work we follow Vecchione *et al.* (2014) in which O'Shea's families Grimpoteuthidae and Luteuthidae are treated as junior synonyms of the Opisthoteuthidae. Collins (2003) recognized Grimpoteuthidae and treated Luteuthidae as a junior synonym of Grimpoteuthidae. Collins (2004) placed his new genus ***Cryptoteuthis*** in the family Grimpoteuthidae. We take the conservative path of recognising only Opisthoteuthidae until a major revision of the group is undertaken.

Literature: Collins (2003, 2004).

Key to genera in the family Opisthoteuthidae:

1a. Shell strongly W-shaped; sucker aperture with tooth-like structures (two very fragile gelatinous species known from only three specimens in China and off New Zealand) . . . . ***Luteuthis***
1b. Shell U- or slightly W-shaped; sucker apertures without tooth-like structures . . . . **→2**

2a. Body form round to slightly elongate, not greatly compressed in anterior-posterior axis; shell U- or slightly W-shaped . . . . **→ 3**
2b. Body extremely compressed in anterior-posterior axis; shell U-shaped . . . . ***Opisthoteuthis***

3a. Moderate compression in anterior-posterior axis; fins of moderate size, length approximately equal with mantle width; cirri ~3.5 times largest sucker diameter; shell U- or slightly W-shaped . . . . ***Grimpoteuthis***
3b. Bell-shaped species; fins small, length ~50% of mantle width; cirri slightly longer than maximum sucker diameter; shell simple, U-shaped (known only from a single immature female from northeast Atlantic Ocean). . . . . ***Cryptoteuthis***

Opisthoteuthis Verrill, 1883

Opisthoteuthis Verrill, 1883, *Bulletin of the Museum of Comparative Zoology*, 11(5): 113.

Type Species: *Opisthoteuthis agassizii* Verrill, 1883.

Frequent Synonyms: None.

Diagnostic Features: With characters of the family. **Cirri commence between suckers 1 and 4. Enlarged suckers present in males. Mantle transversely divided by mantle margin invagination. Shell simple; solid or vacuolate; lateral wings with terminal prolongation into fine tips.** Digestive gland bilobed or entire. Ink sac absent. Radula absent.

Size: Mantle length to 140 mm; total length to greater than 480 mm.

Geographical Distribution: Present in all oceans.

Remarks: O'Shea (1999) divided the genus into 3 'groups' based on a number of distinct morphological differences. It was not specified whether these groups might represent subgenera or distinct genera.

Literature: O'Shea (1999).

Opisthoteuthis agassizii Verrill, 1883

Fig. 250

Opisthoteuthis agassizii Verrill, 1883, *Bulletin of the Museum of Comparative Zoology, Harvard,* 11(5): 113. [Type locality: West Indies, off Grenada, 12º03.30'N, 61º47.10'W)].

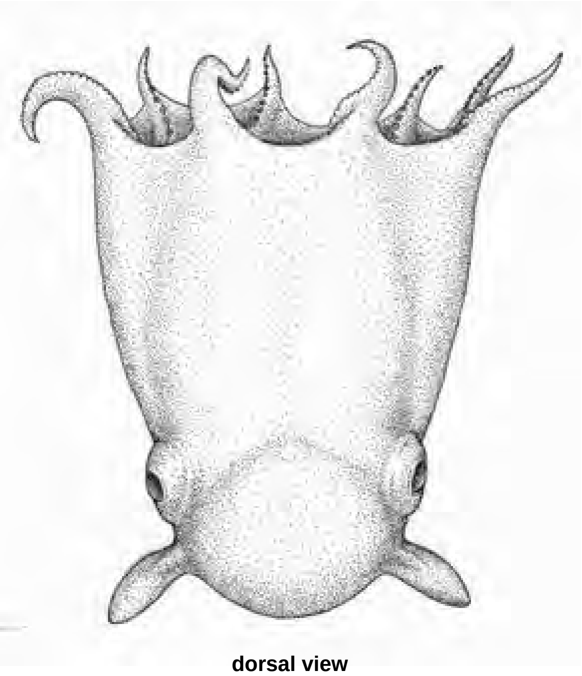
Frequent Synonyms: None.

FAO Names: En — Agassiz's flapjack octopod; **Fr** — Discopoulpe de Agassiz; **Sp** — Discopulpo de Agassiz.

Diagnostic Features: Moderate-sized, gelatinous species. **Pair of relatively small narrow fins present on mantle, length approximately 60% of head width**. Arms approximately equal in length. **U-shaped shell present.** Up to 80 suckers on all arms. Sucker aperture without tooth-like structures. Mature males with enlarged suckers in two fields: 6 to 10 in proximal arms, 7 to 8 in distal arms around level of suckers 30 to 34. Each arm bears a double row of cirri, each approximately 4 to 9% of mantle length. Series of web supports present on ventral margins of arms between suckers 26 and 53. Gills with 6 to 8 (typically 7) large primary lamellae. Ink sac absent. Radula absent. Skin reddish brown in preservation. **Series of white spots (areolae) present on head and 8 to 12 in medial row along arms.**

Size: Mantle length to 55 mm; total length to 186 mm.

Geographical Distribution: Northwestern Atlantic Ocean from Gulf of Mexico and Caribbean Sea north to 40ºN. (Fig. 251).



dorsal view

Fig. 250 ***Opisthoteuthis agassizii***

Fig. 251 ***Opisthoteuthis agassizii***

🟥 Known distribution

Habitat and Biology: Depth range from 227 to 1 935 m. Males mature at about 22 mm ML and females at about 23 mm ML. Mature egg capsules measure 10 x 7 mm. A total of 320 eggs have been reported in the ovary of one female.

Interest to Fisheries: Unknown.

Literature: Morales (1959), Cupka (1970), Alcazar and Ortea (1981), Villanueva and Guerra (1991), Roeleveld *et al.* (1992), Villanueva (1992b), Orsi Relini *et al.* (2001), Villanueva *et al.* (2002a).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Opisthoteuthis albatrossi (Sasaki, 1920)

Stauroteuthis albatrossi Sasaki, 1920, *Proceedings of the United States National Museum,* 57: 169. [Type locality: Northwestern Pacific Ocean, Japan, Rikuzen Prefecture, off Kinkasan].

Size: Mantle length to 36 mm; total length to 200 mm.

Geographical Distribution: North Pacific Ocean from Japan to Sea of Okhotsk.

Habitat and Biology: Depth range from 457 to 3 400 m.

Literature: Sasaki (1929), Kondokov (1941), Katugin *et al.* (2010).

Opisthoteuthis borealis Collins, 2005

Opisthoteuthis borealis Collins, 2005, *Journal of the Marine Biological Association of the United Kingdom*, 85: 1475. [Type locality: Off west coast of Greenland, Davis Strait, 63°10’N, 54°14’W].

Size: Mantle length to 75 mm.

Geographical Distribution: North Atlantic Ocean, off east and west coasts of Greenland.

Habitat and Biology: Depth range from 957 to 1 321 m.

Literature: Collins (2002; as ***Opisthoteuthis*** sp.).

Opisthoteuthis bruuni (Voss, 1982)

Grimpoteuthis bruuni Voss, 1982, *Bulletin of Marine Science*, 32(2): 426. [Type locality: Southeastern Pacific Ocean, Chile, off Antofogasta, 23°41’S, 70°34’W].

Size: Mantle length to 29 mm; known only from 16 juvenile specimens.

Geographical Distribution: Southeastern Pacific Ocean, off the west coast of South America.

Habitat and Biology: Depth range from 250 to 360 m.

Remarks: The female has been briefly described. The species was transferred to the genus ***Opisthoteuthis*** by Collins and Villanueva (2006). What appears to be a similar, or closely related, undescribed species, occurs in the northeastern Pacific Ocean off California.

Literature: Hunt (1999), Collins and Villanueva (2006), Vega-Petkovic (2007).

Opisthoteuthis californiana Berry, 1949

Opisthoteuthis californiana Berry, 1949, *Leaflets in Malacology*, 1(6): 23. [Type locality: Northeastern Pacific Ocean, (United States), California, bearing NW by W of Eureka Bar].

Size: Mantle length to 80 mm; males larger than females.

Geographical Distribution: North Pacific boreal species. In the northeastern Pacific Ocean it has been recorded from off the Aleutian Islands, Alaska [59°N] south to Point Arguello, California [35°N]. In the northwestern Pacific Ocean it has been found off Japan and Russia to the Sea of Okhotsk.

Habitat and Biology: Depth range from 125 to 1 285 m. A copepod parasite, *Cholidyella breviseta*, has been reported from the mantle cavity of this cirrate octopod.

Remarks: Appears very similar to ***Opisthoteuthis albatrossi*** but the two species have not been critically evaluated. Eggs are large 10 x 5 mm capsule length. Development time is estimated to be about 600 days.

Literature: Berry (1952, 1955b, 1966), Taki (1963), Pereyra (1965), Talmadge (1967), Avdeev (1986), Laptikhovsky (1999), Nesis (1999), Bizikov (2008), Jorgensen (2009), Katugin *et al.* (2010).

Opisthoteuthis calypso Villanueva, Collins, Sànchez and Voss, 2002

Opisthoteuthis calypso Villanueva, Collins, Sànchez and Voss, 2002a, *Bulletin of Marine Science*, 71: 946. [Type locality: Northeastern Atlantic Ocean, Cantabric Sea, Bay of Biscay, 43º34.64'N, 2º16.47'W].

Size: Mantle length to 50 mm; total length to 482 mm.

Geographical Distribution: Northeastern Atlantic Ocean and Mediterranean Sea.

Habitat and Biology: Depth range from 365 to 2 208 m.

Literature: Cuccu *et al*. (2009), Rosa *et al.* (2009).

Opisthoteuthis chathamensis O'Shea, 1999

Opisthoteuthis chathamensis O'Shea, 1999, *NIWA Biodiversity Memoir*, 112: 25. [Type locality: Chatham Rise, off New Zealand, 44º15'S, 177º13.01'W].

Size: Mantle length to 54 mm; total length to 180 mm.

Geographical Distribution: Southwestern Pacific Ocean, New Zealand, off east coast, and Chatham Rise.

Habitat and Biology: Depth range from 900 to 1 438 m.

Literature: No additional literature.

Opisthoteuthis depressa Ijima and Ikeda, 1895

Opisthoteuthis depressa Ijima and Ikeda, 1895, *Journal of the College of Science, Imperial University of Tokyo,* 8(2): 323. [Type locality: Northwest Pacific Ocean, Japan, Sagami Prefecture, south of Misaki].

Size: Mantle length to 38 mm.

Geographical Distribution: Northwestern Pacific Ocean, off Japan.

Habitat and Biology: Depth range from 130 to 1 100 m.

Remarks: Appears very similar to ***Opisthoteuthis japonica***, but these species have not been critically evaluated.

Literature: Meyer (1906a,b), Sasaki (1929), Takumiya *et al*. (2005).

Opisthoteuthis dongshaensis Lu, 2010

Opisthoteuthis dongshaensis Lu, 2010, *Zoological Studies,* 49(3): 406. [Type locality: South China Sea, China, off Dong Sha Island, 19º25'N, 114º02'E].

Size: Mantle length to 46 mm; total length to 226 mm.

Geographical Distribution: Known only from vicinity of type locality, South China Sea.

Habitat and Biology: Depth range from 660 to 1 015 m.

Literature: No additional literature.

Opisthoteuthis extensa Thiele, *in* Chun, 1915

Opisthoteuthis extensa Thiele, *In* Chun, 1915, *Wissebschaftliche ergebnisse der deutschen tiefsee expedition auf dem dampfer "Valdivia" 1898-1899*, 18: 537 [Type locality: Indian Ocean, off west coast of Sumatra, Mentawei-Becken [=Mentawai Basin], 0º57.5'S, 99º51.1'E].

Size: Not indicated.

Geographical Distribution: Known only from the type locality.

Habitat and Biology: Depth of type 768 m.

Remarks: Systematic status unresolved. Appears to be similar to *Grimpoteuthis meangensis* but both species have not been critically evaluated.

Literature: Glaubrecht and Salcedo-Vargas (2000), Vecchione and Collins (2002).

Opisthoteuthis grimaldii (Joubin, 1903)

Plate XI, 85

Cirroteuthis grimaldii Joubin, 1903, *Compte Rendu des Seances de l'Academie des Sciences,* 136(2): 100. [Type locality: Central Atlantic Ocean, Azores Islands, NNW of Fayal, 39º30'N, 29º02'W].

Size: Mantle length to 50 mm; total length to 250 mm.

Geographical Distribution: Eastern Atlantic Ocean from Namibia to Rockall Trench.

Habitat and Biology: Depth range from 1 135 to 2 287 m.

Literature: Joubin (1912, 1920), Boyle *et al.* (1998), Boyle and Daly (2000), Collins *et al.* (2001b), Villanueva (2000), Villanueva *et al*. (2002a).

Opisthoteuthis hardyi Villanueva, Collins, Sànchez and Voss, 2002

Opisthoteuthis hardyi Villanueva, Collins, Sànchez and Voss, 2002, *Bulletin of Marine Science,* 71: 963. [Type locality: Southern Ocean, NW of South Georgia Island, 53º18'S, 42º12'W].

Size: Mantle length to 64 mm; total length to 285 mm.

Geographical Distribution: Known from the type locality off South Georgia Island north to the southwestern Atlantic Ocean on the Patagonian Slope near the Falkland Islands.

Habitat and Biology: Depth range from 630 to 1 390 m.

Literature: Collins *et al.* (2010).

Opisthoteuthis japonica Taki, 1962

Opisthoteuthis japonica Taki, 1962, *Dobutsu-Gaku Zasshi,* 71: 397. [Type locality: Northwest Pacific Ocean, Japan, Wakayama Prefecture, off Minabe].

Size: Mantle length to 45 mm.

Geographical Distribution: Northwestern Pacific Ocean, off Japan.

Habitat and Biology: Depth of types 152 m.

Remarks: Appears very similar to ***Opisthoteuthis albatrossi*, *O. depressa*** and ***O. californiana***, but these species have not been critically evaluated.

Literature: Taki (1963).

Opisthoteuthis massyae (Grimpe, 1920)

Cirroteuthis (*Cirroteuthopsis*) *massyae* Grimpe, 1920, *Zoologischer Anzeiger,* 51(11): 230. [Type locality: Northeastern Atlantic Ocean, off Ireland, 50º31'N, 11º31'W].

Size: Mantle length to 76 mm; total length to 350 mm.

Geographical Distribution: Eastern Atlantic Ocean from Ireland to Namibia.

Habitat and Biology: Depth range from 1 226 to 1 450 m.

Remarks: ***Opisthoteuthis vossi*** Sànchez and Guerra (1989) has been reported to be a junior synonym (Villanueva *et al*. 2002).

Literature: Massy (1924), Sànchez and Guerra (1989), Collins *et al.* (2001b), Villanueva *et al*. (2002a).

Opisthoteuthis medusoides Thiele, *In* Chun, 1915

Opisthoteuthis medusoides Thiele, *In* Chun, 1915, *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer Valdivia 1898-1899*, 18: 538. [Type locality: western Indian Ocean, off Tanzania, 6º39.1'S, 39º30.8'E].

Size: Known only from juveniles.

Geographical Distribution: Known only from the type locality off Tanzania.

Habitat and Biology: Depth of types 400 m.

Literature: No additional literature.

Opisthoteuthis mero O'Shea, 1999

Opisthoteuthis mero O'Shea, 1999 *NIWA Biodiversity Memoir,* 112: 17. [Type locality: New Zealand, off northern coast, 36º54.84'S, 176º19.15'E].

Size: Mantle length to 90 mm; total length to 340 mm.

Geographical Distribution: New Zealand.

Habitat and Biology: Depth range from 360 to 1 000 m.

Literature: No additional literature.

Opisthoteuthis persephone Berry, 1918

Opisthoteuthis persephone Berry, 1918, *Biological Results of the Fishing Experiments Carried on by the F.I.S. Endeavour, 1909-1914*, 4(5): 290. [Type locality: Australia, Victoria, Bass Straits, 42 miles South and East of Genoa Peak].

Size: Total length to >200 mm.

Geographical Distribution: Southern Australia.

Habitat and Biology: Depth range from 277 to 554 m.

Literature: Healy (1993).

Opisthoteuthis philipii Oommen, 1976

Opisthoteuthis philipii Oommen, 1976, *Journal of the Marine Biological Association of India,* 18(2): 368. [Type locality: Indian Ocean, Arabian Sea, 9º32'N, 75º45'E].

Size: Mantle length to 140 mm; total length to 470 mm.

Geographical Distribution: Arabian Sea.

Habitat and Biology: Depth range from 275 to 365 m.

Literature: No additional literature.

Opisthoteuthis pluto Berry, 1918

Opisthoteuthis (Teuthidiscus) pluto Berry, 1918, *Biological Results of the Fishing Experiments Carried on by the F.I.S. Endeavour, 1909-1914*, 4(5): 284. [Type locality: Great Australian Bight, South Australia].

Size: Arm span to 540 mm.

Geographical Distribution: Southern Australia.

Habitat and Biology: Depth range from 275 to 830 m.

Literature: Nesis (1987), O'Shea (1999).

Opisthoteuthis robsoni O'Shea, 1999

Opisthoteuthis robsoni O'Shea, 1999, *NIWA Biodiversity Memoir,* 112: 28. [Type locality: New Zealand, off east coast, NW Mernoo Slope, 42º41.7'S, 174º28.0'E].

Size: Mantle length to 65 mm; total length to 362 mm.

Geographical Distribution: Known only from the type locality off New Zealand.

Habitat and Biology: Depth of types 1 180 to 1 723 m.

Literature: No additional literature.

Cryptoteuthis Collins, 2004

Cryptoteuthis Collins, 2004, *Journal of Molluscan Studies*, 70: 263.

Type Species: *Cryptoteuthis brevibracchiata* Collins, 2004.

Frequent Synonyms: None.

Diagnostic Features: Bell-shaped species, with small fins and short arms. Gills with 7 broad lamellae. Suckers broad; cirri moderate in length. Optic nerve passes through white body in single bundle. Posterior salivary glands absent. Radula absent. Ink sac absent. **Digestive gland entire.**

Size: Mantle length 35 mm; total length 121 mm; known only from immature female specimen.

Geographical Distribution: Known only from the northeast Atlantic Ocean.

Remarks: This genus is considered midway between ***Opisthoteuthis*** and ***Grimpoteuthis***. Body shape and short fins are similar to ***Opisthoteuthis***; shell, suckers, and cirri are similar to ***Grimpoteuthis***.

Literature: No additional literature.

Cryptoteuthis brevibracchiata Collins, 2004

Fig. 252

Cryptoteuthis brevibracchiata Collins, 2004, *Journal of Molluscan Studies*, 70: 263. [Type locality: Northeastern Atlantic Ocean, Porcupine Seabight, 49º54'N, 12º21'W].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En — Short-arm flapjack octopod; **Fr** — Discopoulpe aux bras courts; **Sp** — Discopulpo de brazos cortos.

Diagnostic Features: Fins small and round; length equal to about half of head width. Eyes lateral. **Simple U-shape shell.** Gills with 7 primary lamellae. Arms with single row of small suckers, none enlarged in female type. Each arm with double row of short cirri; each cirrus slightly longer than largest sucker diameter. Longest arm with 48 suckers. Arm formula of 1>2>3>4. Webs approximately half of arm length; formula A>B>C>D>E. Ink sac and radula absent. Gelatinous body semi-transparent. Oral web and fin tips darkly pigmented.

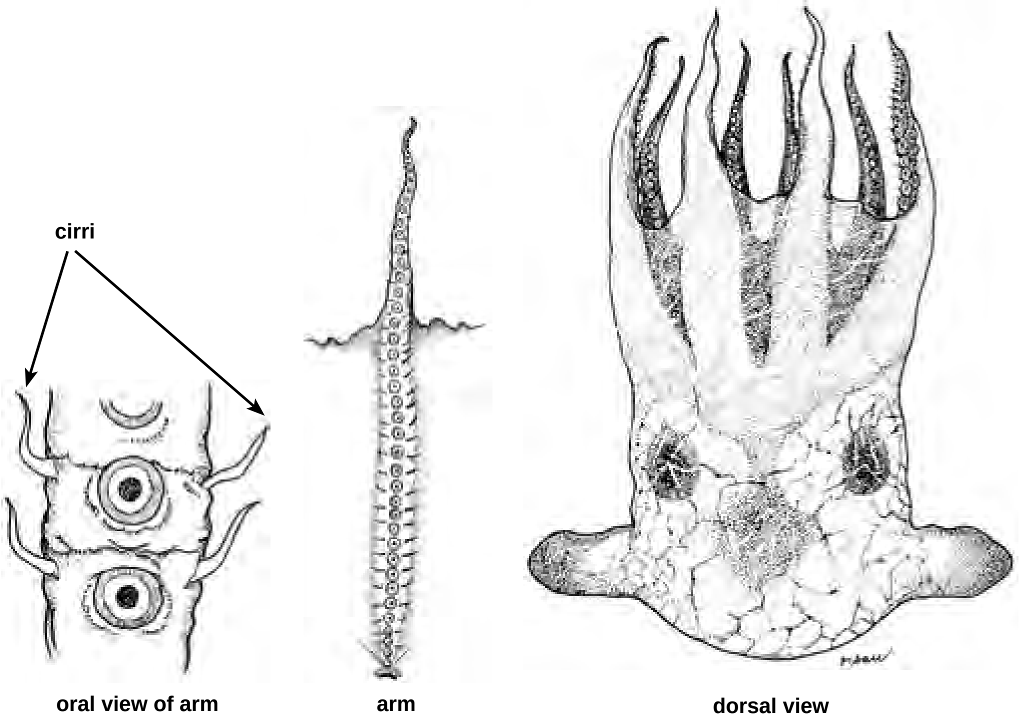


Fig. 252 ***Cryptoteuthis brevibracchiata***

Size: Mantle length 35 mm; total length 121 mm (known only from an immature female type specimen).

Geographical Distribution: Known only from the type locality, northeastern Atlantic Ocean (Fig. 253).

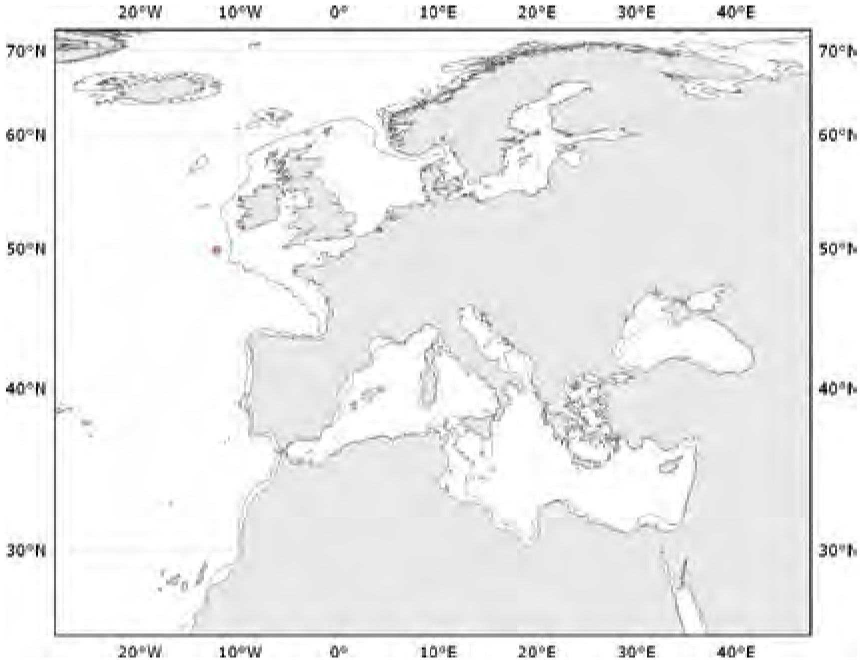


Fig. 253 ***Cryptoteuthis brevibracchiata***

🟥 Known distribution

Habitat and Biology: Depth range of type specimen 2 274 to 2 300 m.

Interest to Fisheries: Unknown.

Literature: No additional literature.

Grimpoteuthis Robson, 1932

Plate XI, 84

Grimpoteuthis Robson, 1932, *A Monograph of the Recent Cephalopoda*, Part II: 136.

Type Species: *Grimpoteuthis umbellata* (Fischer, 1883).

Frequent Synonyms: *Stauroteuthis* Verrill, 1836; *Cirroteuthis* Eschricht, 1836.

Diagnostic Features: Small to large octopods with bell-shaped semi-gelatinous body. **Primary web thick; intermediate (secondary) web absent. Fins medium to large, lateral, with distinct lobe near anterior fin insertion. Shell U-shaped; lateral sides parallel, not tapered to fine points.** Radula homodont or absent. Ink sac absent. **Sucker sexual dimorphism present in some species, but with single enlarged field.**

Size: Mantle length to 115 mm; total length to 475 mm.

Geographical Distribution: Species reported from the North Atlantic and both the north and south Pacific Oceans.

Habitat and Biology: Depth range from 280 to 4 870 m.

Remarks: Over the years, species recognized herein and placed in the genus ***Grimpoteuthis***, formerly have been treated under several other generic names: ***Stauroteuthis***, ***Cirroteuthis*** and ***Enigmatiteuthis***. Type species of the genus is not treated as the descriptor for the genus as it is poorly known.

Literature: Villanueva *et al*. (1997b), Collins (2003).

Grimpoteuthis wuelkeri (Grimpe, 1920)

Fig. 254

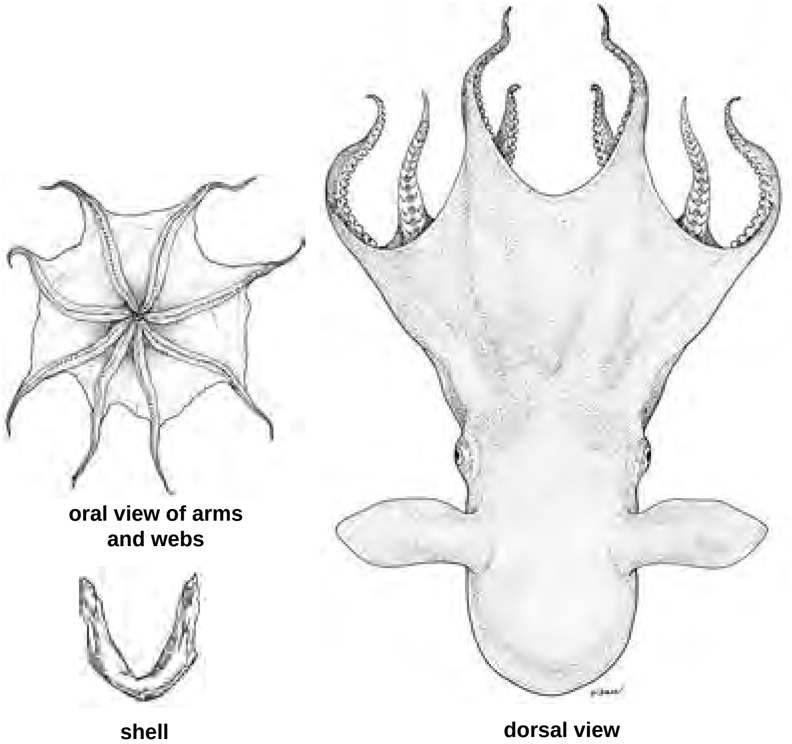
Stauroteuthis wuelkeri Grimpe, 1920, *Zoologischer Anzeiger*, 51: 235. [Type locality: Northeastern Atlantic Ocean, off Morocco, 35°46'N, 8°16'W].

Frequent Synonyms: In the literature the species name often is spelled "*wülkeri*" with the umlaut.

Misidentifications: None.

FAO Names: En — Wülker's flapjack octopod; **Fr** — Discopoulpe de Wülker; **Sp** — Discopulpo de Wülker.

Diagnostic Features: Medium-sized, relatively gelatinous species. **Pair of large fins present on mantle; fin span 70% of total length.** Shell U-shaped; lateral edges of wings almost parallel. Gills with 6 to 7 primary lamellae. Arms long, subequal in length. Single row of small suckers present on each arm; **none enlarged in either sex**. A double row of short cirri present on each arm. Longest arm with 62 to 70 suckers. Arm formula of 1>2>3>4. Webs deep, 2/3rd of arm length; formula A=B>C=D>E. **Single web nodule present on ventral side of each arm, located around level of suckers 22 to 28.** Ink sac absent. Radula present, poorly developed.


oral view of arms and webs

shell

dorsal view

Fig. 254 *Grimpoteuthis wuelkeri*

Size: Mantle length to 115 mm; total length to 400 mm.

Geographical Distribution: Northeast Atlantic Ocean (Fig. 255).

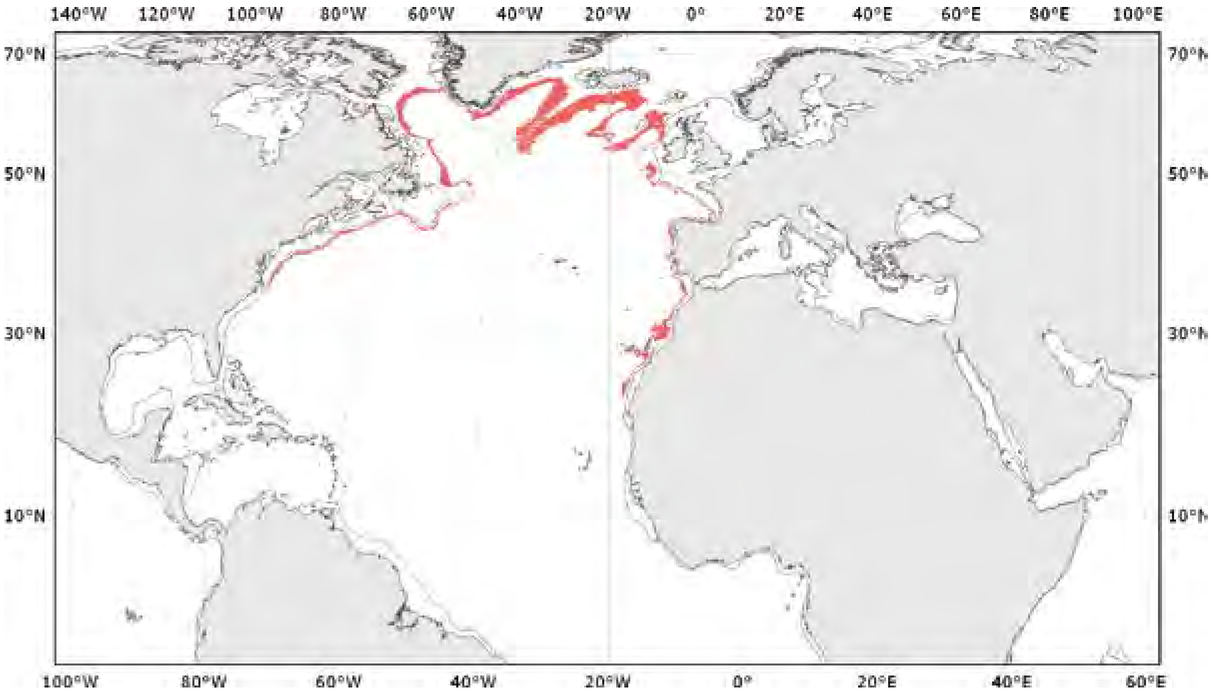


Fig. 255 *Grimpoteuthis wuelkeri*

🟥 Known distribution

Habitat and Biology: Depth range for type specimen 1 550 to 2 056 m. Little information is available on this species. An egg from the oviducal gland of the single available female measured 14 mm in diameter.

Interest to Fisheries: Unknown.

Remarks: Due to condition/preservation problems with ***Grimpoteuthis umbellata*** (Fischer, 1883), the type species for this genus, ***G. wuelkeri*,** is presented instead as a better known example of this genus.

Literature: Collins (2003), Piatkowski and Diekmann (2005).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Grimpoteuthis abyssicola O'Shea, 1999

Grimpoteuthis abyssicola O'Shea, 1999, *NIWA Biodiversity Memoir,* 112: 46. [Type locality: West of New Zealand, off Lord Howe Rise, 35°35'S, 160°57'E].

Size: Mantle length to 75 mm; total length to 305 mm; known only from the female type specimen.

Geographical Distribution: Known only from the type locality Tasman Sea.

Habitat and Biology: Depth range of type specimen 3 154 to 3 180 m.

Literature: Collins (2003).

Grimpoteuthis bathynectes Voss and Pearcy, 1990

Grimpoteuthis bathynectes Voss and Pearcy, 1990, *Proceedings of the California Academy of Sciences*, 47(3): 57. [Type locality: Northeastern Pacific Ocean, United States, off Oregon, 45°01'N, 135°12'W].

Size: Mantle length to 85 mm; total length to 240 mm.

Geographical Distribution: Northeastern Pacific, off Oregon, Cascadia and Tufts Abyssal plains.

Habitat and Biology: Depth range from 2 816 to 3 932 m.

Literature: Collins (2003).

Grimpoteuthis boylei Collins, 2003

Grimpoteuthis boylei Collins, 2003, *Zoological Journal of the Linnean Society*, 139: 105. [Type locality: Northeastern Atlantic Ocean, Porcupine Abyssal Plain, 48°47'N, 16°30'W].

Size: Mantle length to 115 mm; total length to 470 mm.

Geographical Distribution: Northeastern Atlantic Ocean.

Habitat and Biology: Depth range from 4 190 to 4 848 m.

Literature: No additional literature.

Grimpoteuthis challengeri Collins, 2003

Grimpoteuthis challengeri Collins, 2003, *Zoological Journal of the Linnean Society,* 139: 110. [Type locality: Northeastern Atlantic Ocean, Porcupine Abyssal Plain, 48º56'N, 15º45'W].

Size: Mantle length to 75 mm; total length to 370 mm.

Geographical Distribution: Northeastern Atlantic Ocean.

Habitat and Biology: Depth range from 4 800 to 4 850 m.

Literature: No additional literature.

Grimpoteuthis discoveryi Collins, 2003

Grimpoteuthis discoveryi Collins, 2003, *Zoological Journal of the Linnean Society,* 139: 116. [Type locality: Northeastern Atlantic Ocean, Porcupine Seabight, 49º35'N, 14º01'W].

Size: Mantle length to 58 mm; total length to 210 mm.

Geographical Distribution: Northeastern Atlantic Ocean.

Habitat and Biology: Depth range from 2 600 to 4 870 m.

Literature: No additional literature.

Grimpoteuthis hippocrepium (Hoyle, 1904)

Stauroteuthis hippocrepium Hoyle, 1904, *Bulletin of the Museum of Comparative Zoology at Harvard College,* 43: 6. [Type locality: Northeastern Pacific Ocean, off Colombia, SW of Malpelo Island, 2º35'N, 83º53'W].

Size: Total length ~80 mm; known only from the type specimen.

Geographical Distribution: Known only from the type locality, off Colombia.

Habitat and Biology: Depth of type 3 332 m.

Literature: Voss and Pearcy (1990), O'Shea (1999), Vecchione and Collins (2002), Collins (2003), Collins and Villanueva (2006).

Grimpoteuthis innominata (O'Shea, 1999)

Enigmatiteuthis innominata O'Shea, 1999, *NIWA Biodiversity Memoir,* 112: 48. [Type locality: Chatham Rise, off New Zealand, 42º37'S, 176º10'W].

Size: Mantle length to 43 mm; total length to 156 mm (all specimens immature).

Geographical Distribution: Chatham Rise, off New Zealand.

Habitat and Biology: Depth range from 1 705 to 2 002 m.

Remarks: O'Shea (1999) coined the genus ***Enigmatiteuthis*** to contain this species. Collins (2003) treated ***Grimpoteuthis*** as the senior synonym of O'Shea's genus.

Literature: Collins (2003).

Grimpoteuthis meangensis (Hoyle, 1885)

Cirroteuthis meangensis Hoyle, 1885, *Annals and Magazine of Natural History,* series 5, 15: 234. [Type locality: Near the Philippines [South Philippines, Kepulauan Talaud], off Meangis Islands, (4º33'N, 127º06'E)].

Size: Mantle length to 53 mm; total wet weight to at least 1 345 g.

Geographical Distribution: Philippines and Sumatra (as synonym ***extensa*** Thiele, 1915).

Habitat and Biology: Depth range from 280 to 1 050 m.

Remarks: The generic placement of this taxon is currently in review.

Literature: Collins (2003).

Grimpoteuthis megaptera (Verrill, 1885)

Cirroteuthis megaptera Verrill, 1885, *Transactions of the Connecticut Academy of Sciences*, 6(2): 405. [Type locality: Northwestern Atlantic Ocean, United States, off North Carolina].

Size: Total length to 107 mm.

Geographical Distribution: Known only from the type locality northwestern Atlantic Ocean.

Habitat and Biology: Depth of type 4 592 m.

Literature: Collins (2003).

Grimpoteuthis pacifica (Hoyle, 1885)

Cirroteuthis pacifica Hoyle, 1885, *Annals and Magazine of Natural History,* series 5, 15: 235. [Type locality: Southwestern Pacific Ocean, Papua New Guinea, 13°50'S, 151°49'E].

Size: Fin length 55 mm; known only from damaged type specimen.

Geographical Distribution: Known only from the type locality off Papua New Guinea.

Habitat and Biology: Depth of type 4 463 m.

Literature: Guerra *et al.* (1998), Collins (2003).

Grimpoteuthis plena (Verrill, 1885)

Cirroteuthis plena Verrill, 1885, *Transactions of the Connecticut Academy of Sciences,* 6(2): 404. [Type locality: Northwestern Atlantic Ocean, United States, off New Jersey, 39°35'00"N, 71°18'45"W].

Size: Mantle length to 57 mm; total length to 185 mm; known only from the type specimen.

Geographical Distribution: Known only from the type locality, northwestern Atlantic Ocean.

Habitat and Biology: Depth of type 1 963 m.

Remarks: The latitude as originally published by Verrill (37°35'N) is incorrect.

Literature: Vecchione and Collins (2002), Collins (2003).

Grimpoteuthis tuftsi Voss and Pearcy, 1990

Grimpoteuthis tuftsi Voss and Pearcy, 1990, *Proceedings of the California Academy of Sciences,* 47(3): 63. [Type locality: Northeastern Pacific Ocean, United States, off Oregon, 45°05.2'N, 134°43.4'W].

Size: Mantle length to 102 mm; total length to 475 mm.

Geographical Distribution: Northeastern Pacific Ocean, off Oregon, Tufts Abyssal Plain.

Habitat and Biology: Depth range from 3 585 to 3 900 m.

Remarks: Generic placement in need of critical review.

Literature: O'Shea and Lu (2002), Collins (2003).

Grimpoteuthis umbellata (Fischer, 1883)

Cirroteuthis umbellata Fischer, 1883, *Journal de Conchologie,* 31: 404. [Type locality: Northeastern Atlantic Ocean, Azores and Morocco].

Size: Mantle length to 46 mm; total length to 250 mm.

Geographical Distribution: North Atlantic Ocean.

Habitat and Biology: Depth range from 2 235 m.

Remarks: Although this species represents the type of the genus ***Grimpoteuthis*** it is poorly known.

Literature: Voss (1955), Collins (2003).

Luteuthis O'Shea, 1999

Luteuthis O'Shea, 1999, *NIWA Biodiversity Memoir,* 112: 56.

Type Species: *Luteuthis dentatus* O'Shea, 1999.

Frequent Synonyms: None.

Diagnostic Features: Cephalopodal mass with pronounced anteroposterior elongation; areolar spots absent. Web simple; web nodules absent. Cirri very short; commence between suckers 1 and 2; extend to arm tip. Sucker aperture crenulate. Interpallial septum thick, short. Gills of 'half-orange' type, **Shell W-shaped; lateral wings with inrolled margins, taper to acute points; basal shelf deflected beneath saddle.** Ink sac and salivary glands absent. Radular and palatine teeth present; palatine teeth large.

Size: Mantle length to 98 mm; total length to 524 mm.

Geographical Distribution: South China Sea and off west coast of New Zealand.

Remarks: Two member species from depths between 754 to 991 m.

Literature: O'Shea and Lu (2002), Collins (2003).

Luteuthis dentatus O'Shea, 1999

Fig. 256

Luteuthis dentatus O'Shea, 1999, *NIWA Biodiversity Memoir,* 112: 57. [Type locality: New Zealand (off west coast), 40º01.3'S, 167º49.9'E].

Frequent Synonyms: None.

FAO Names: En — Toothed flapjack octopod; **Fr** — Discopoulpe denté; **Sp** — Discopulpo dentado.

Diagnostic Features: Relatively gelatinous. **Pair of small fins present on mantle; fin length less than mantle width**. Mantle and funnel attached entirely to head. **W-shaped shell present.** Dorsal arms 75% of total length; ventral arms 38% of total length. **Sucker apertures with inward pointing skin projections forming star shape.** Each arm bears a double row of short cirri, each approximately a half sucker diameter. Up to 58 suckers on all arms. Web nodules absent. Gills with 7 large primary lamellae. Ink sac and salivary glands absent. Radula present.

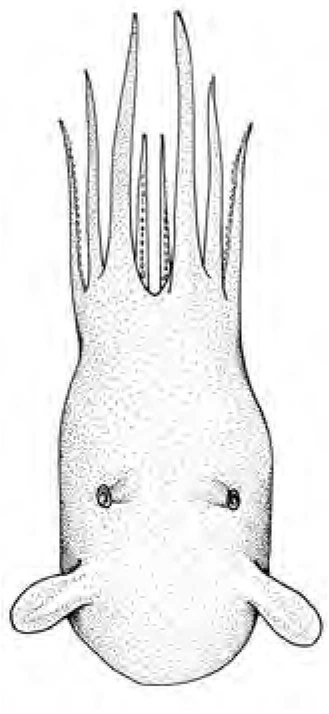
Size: Mantle length 98 mm; total length 524 mm.

Geographical Distribution: Known only from the type locality (Fig. 257).

Habitat and Biology: Depth of type 991 m.

Interest to Fisheries: Unknown.

Literature: Collins (2003).



dorsal view

Fig. 256 ***Luteuthis dentatus***

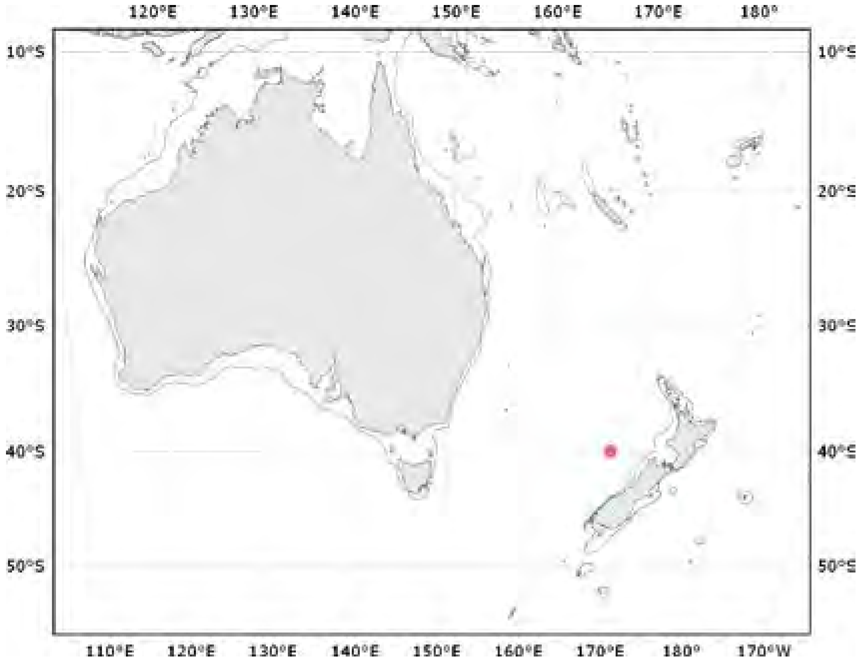


Fig. 257 ***Luteuthis dentatus***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Luteuthis shuishi O'Shea and Lu, 2002

Luteuthis shuishi O'Shea and Lu, 2002, *Zoological Studies*, 41: 120. [Type locality, South China Sea, off Pratas Islands, 19º30'N, 114º10'E].

Size: Mantle length 87.5 mm; total length >300 mm; known only from type the specimen.

Geographical Distribution: Known only from the type locality.

Habitat and Biology: Depth range of type 754 to 767 m.

Literature: No additional literature.

2.2.4 Family STAUROTEUTHIDAE Grimpe, 1916

by Frederick G. Hochberg, Mark D. Norman and Julian K. Finn

Stauroteuthidae Grimpe, 1916, *Zoologische Anzeiger*, 46(12): 349-359.

Type Genus: *Stauroteuthis* Verrill, 1879.

FAO Names: En — Balloon octopods; **Fr** — Poulpes ballons; **Sp** — Pulpos globo.

Diagnostic Features: Distinctive gelatinous octopods. Body elongate in anterior-posterior axis. **Mantle aperture highly modified, forms complete tube around funnel**; funnel can be withdrawn from tube into mantle cavity. **Eyes well developed, with lenses**. Deep primary webs and well-developed secondary webs present; web nodules absent. Bell-shaped posture in life; webs can be inflated to form “balloon” posture. Gills distinctive in appearance; secondary and tertiary lamellae branched to form cauliflower-like appearance, i.e. primary lamellae not in symmetrical series as in other octopods. Shell U-shaped. Suckers small, enlarged in mature males. Cirri long, more than twice arm diameter; absent from arm tips beyond suckers 18 to 24.

Size: Mantle length to 114 mm; total length to 540 mm.

Geographical Distribution: Atlantic Ocean.

Remarks: This family contains a single genus and two species.

Literature: Verrill (1881), Grimpe (1916), Robson (1924, 1932), Boletzky (1978, 1979, 1980, 1982, 1986), Voss (1988a,b), Vecchione and Young (1997), Johnsen *et al*. (1999a,b), Collins and Henriques (2000), Collins (2002).

Stauroteuthis Verrill, 1879

Stauroteuthis Verrill, 1879, *American Journal of Science and Arts*, 18(58): 468.

Type Species: *Stauroteuthis syrtensis* Verrill, 1879.

Frequent Synonyms: *Chunioteuthis* Grimpe, 1916.

Diagnostic Features: With characters of the family. Monogeneric.

Stauroteuthis syrtensis Verrill, 1879

Fig. 258; Plate XI, 87

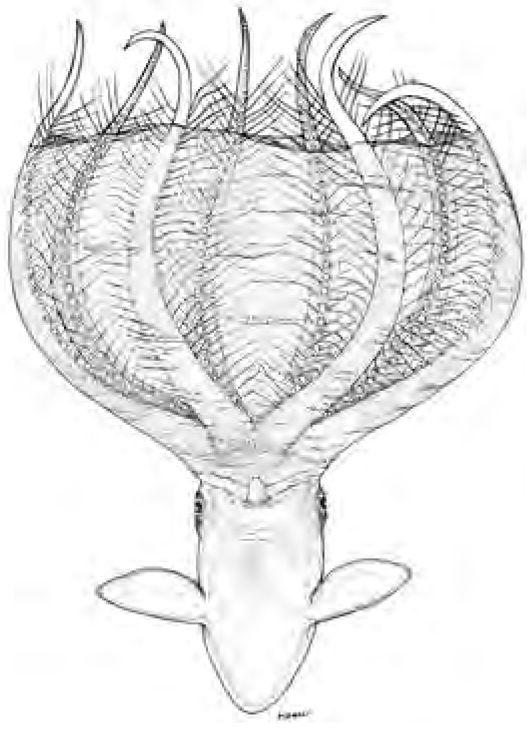
Stauroteuthis syrtensis Verrill, 1879, *American Journal of Science and Arts*, 18(58): 468. [Type locality: Northwest Atlantic Ocean, Canada, off Nova Scotia, 43°54’N, 58°44’W].

Frequent Synonyms: *Chunioteuthis unguiculatus* Blainville, 1826.

FAO Names: En — Balloon octopod; **Fr** — Poulpe ballon; **Sp** — Pulpo globo.

Diagnostic Features: Moderate-sized. Body gelatinous, elongate anterior-posteriorly. Pair of fins present on mantle. **Mantle opening reduced to fused cylinder as sheath around funnel.** Mantle cavity lined with darkly pigmented skin. U-shaped shell present. Arms approximately equal in length. Suckers small and cylindrical; enlarged suckers present in males. Total of 55 to 65 suckers on each arm. Each arm with double row of long cirri; longest more than twice arm diameter. Primary and secondary webs present; enable ballooning behaviour. **Gills in distinctive cauliflower form without obvious boundaries between primary lamellae.** Ink sac absent. Radula absent.

Size: Mantle length to 114 mm; total length to 500 mm.



dorsal view

Fig. 258 *Stauroteuthis syrtensis*

Geographical Distribution: Widespread in the North Atlantic Ocean (Fig. 259).

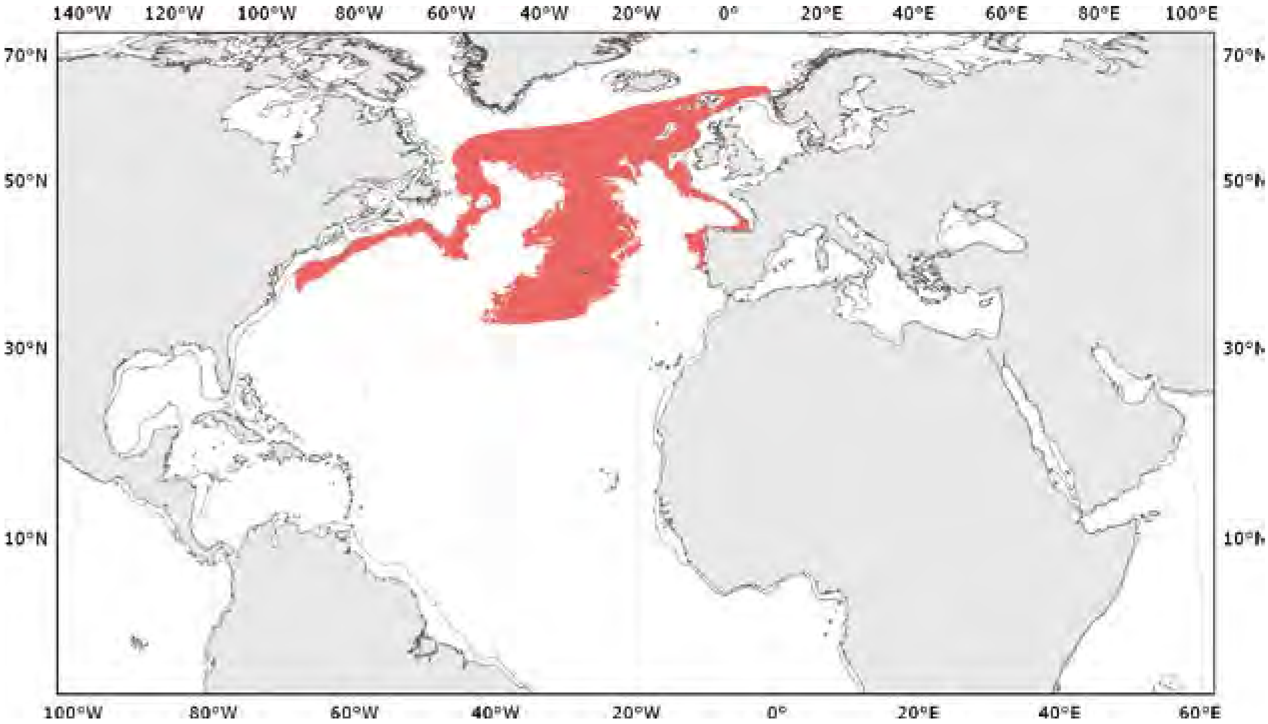


Fig. 259 ***Stauroteuthis syrtensis***

🟥 Known distribution

Habitat and Biology: Depths range from 450 to 4 000 m. Typically captured within about 100 m off the bottom. Bioluminescence has been reported from the sucker bases of this octopod. The function of this light production is unknown. A cestode parasite, *Tentacularia coryphaenae*, has been reported from this species of cirrate.

Interest to Fisheries: Unknown.

Literature: Verrill (1879, 1885), Grimpe (1916), Robson (1932), Dollfus (1967), Boletzky (1978-1979, 1980, 1982, 1986), Voss (1988b), Vecchione and Young (1997), Johnsen *et al*. (1999a,b), Collins and Henriques (2000), Collins (2002), Jacoby *et al*. (2009).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Stauroteuthis gilchristi (Robson, 1924)

Cirroteuthis gilchristi Robson, 1924, *Annals and Magazine of Natural History*, series 9, 13: 204. [Type locality: Southeastern Atlantic Ocean, South Africa, SW of Cape Town].

Size: Mantle length to 70 mm; total length to 540 mm.

Geographical Distribution: Southern Atlantic Ocean.

Habitat and Biology: Depth of type locality 2 561 m.

Literature: Robson (1932), Nesis (1987), Collins and Henriques (2000).

2.3 Vampire squids

by Mark D. Norman and Julian K. Finn

This group contains a single family (Vampyroteuthidae) with a single unique species, ***Vampyroteuthis infernalis***, which lives in the deep waters of the open ocean. It has many unusual features and is thought to be related to the ancestors of the octopuses. It is characterized by a jelly-like consistency, black pigmentation, fins on the body (two pairs in juveniles), eight arms with deep webs and a pair of long, thin, filament-like, limbs which can retract into pits on the outer arm crown, between the first and second arm pair.

2.3.1 **Family VAMPYROTEUTHIDAE** Thiele, *In* Chun, 1915

Vampyroteuthidae, Thiele *in* Chun, 1915. *Wissebschaftliche Ergebnisse der Deutschen Tiefsee Expedition auf dem Dampfer "Valdivia" 1898-1899*, 18(2): 534.

Type Genus: *Vampyroteuthis* Chun, 1903.

FAO Names: En — Vampire squids, vampires; **Fr** — Calmars vampire; **Sp** — Calamars vampiro.

Diagnostic Features: Small to medium-sized species. Body gelatinous, with black pigmentation. Fins present on mantle: one pair on adults, two pairs on juveniles. The eight arms have a single row of stalked suckers starting from half way along their length that extend to arm tips. Horny sucker rings absent. Each arm bears a double row of long thin fingers of skin (cirri). **Pair of pits in web between bases of arms 1 and 2, each pit contains a long thread-like filament.** Webs very deep; extend to near arm tips. Ink sac absent. Females store sperm in deep receptacles in front of each eye. **Pair of large light organs present on the posterior mantle at the base of the adult fins.** These light organs can be masked using black shutter-like lids. Other light organs present on the tips of the arms and in a scatter of small light organs on the ventral side of the head, body and arms. Arm tips capable of exuding bioluminescent particles.

Size: Mantle length to 130 mm; total length to ~300 mm.

Geographical Distribution: Tropical and temperate waters worldwide, between approximately 35°N and 35°S.

Remarks: Single genus containing single species.

Literature: Robson (1929c), Pickford (1939, 1949a,b).

Vampyroteuthis Chun, 1903

Vampyroteuthis, Chun, 1903. *Aus den Tiefen des Weltmeeres*. 592 pages. Jena: Gustav Fischer, second edition: 88, text-fig.

Frequent Synonyms: None.

Diagnostic Features: With characters of the family. Monogeneric.

Literature: No additional literature.

Vampyroteuthis infernalis Chun, 1903

Fig. 260; Plate XI, 88

Vampyroteuthis infernalis Chun, 1903, *Aus den Tiefen des Weltmeeres, Gustav Fischer, Jena*: 88. [Type locality: Gulf of Guinea, West Africa].

Frequent Synonyms: None.

FAO Names: En — Vampire squid; **Fr** — Calmar vampire; **Sp** — Calamar vampiro.

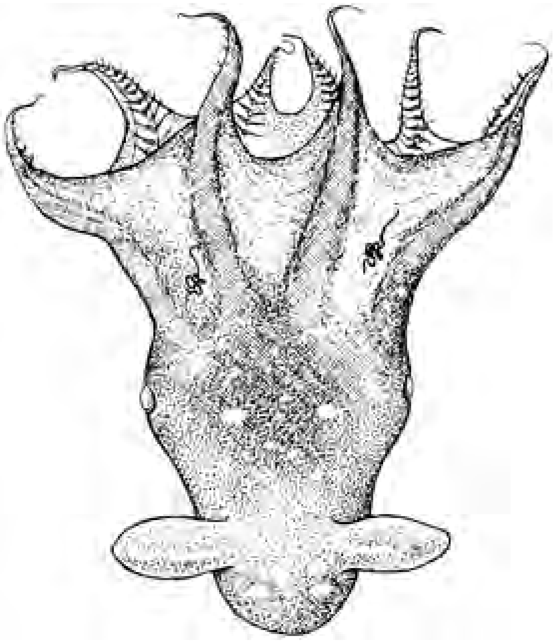
Diagnostic Features: With characters of the family and genus. Monotypic.

Size: Mantle length to 130 mm; total length to ~300 mm.

Geographical Distribution: Tropical and temperate waters worldwide, between approximately 35°N and 35°S (Fig. 261).

Habitat and Biology: Depths range from 600 to 1 200 m. This is a mid-water species. The long filaments in pits between the first two arm pairs may be used to feel for or chemically detect prey. Live animals observed *in situ* typically orient in the water column with the dorsal mantle surface facing upwards and one filament extended well beyond the arms. Disturbed animals pull the arms and webs over their body to take on an inverted shape that exposes the black skin and cirri, on the oral surfaces of the webs. In addition to the large four photophores, this species can produce light on its arm tips and squirt luminous clouds from the arm tips consisting of discrete glowing particles, which can glow for up to 10 minutes. The physiological source of these particles is unknown.

Interest to Fisheries: Unknown.



dorsal view

Fig. 260 *Vampyroteuthis infernalis*

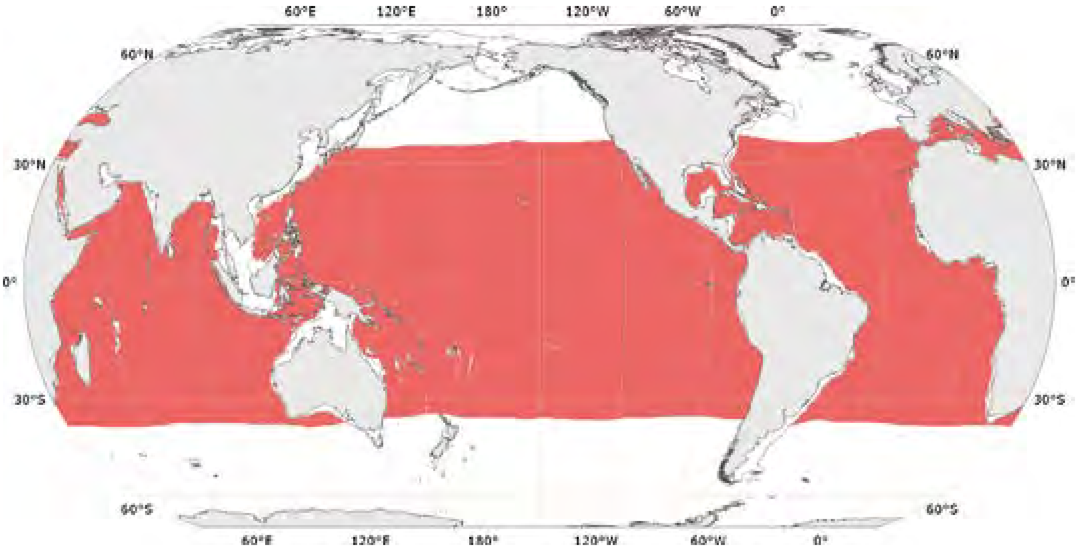


Fig. 261 *Vampyroteuthis infernalis*

🟥 Known distribution

Remarks: Young (1964, 1972a) indicated that there are distinct morphological differences in specimens he examined from near the type locality and off California, which suggests that more than one species may be present in this genus.

Literature: Pickford (1949a, b), Young (1964, 1972a), Healy (1989, 1990), Herring *et al*. (1994), Seibel *et al*. (1998), Robison *et al*. (2004), Jorgensen (2009).

3. LIST OF NOMINAL SPECIES

The following list gives information (horizontally) in the order (i) the scientific name as it originally appeared, in alphabetical order according to the specific name; (ii) the author(s); (iii) date of publication; and (iv) present allocation of valid species.

NOMINAL SPECIES	PRESENT ALLOCATION
ALLOPOSIDAE Verrill, 1881	
Haliphron atlanticus Steenstrup, 1861	*Haliphron atlanticus*
AMPHITRETIDAE Hoyle, 1886	
Amphitretus pelagicus Hoyle, 1885	*Amphitretus pelagicus*
Amphitretus thielei Robson, 1930	*Amphitretus thielei*
ARGONAUTIDAE Tryon, 1879	
Argonauta argo Linnaeus, 1758	*Argonauta argo*
Argonauta hians [Lightfoot, 1786]	*Argonauta hians*
Argonauta nodosus [Lightfoot, 1786]	*Argonauta nodosus*
Argonauta nouryi Lorois, 1852	*Argonauta nouryi*
BOLITAENIDAE Chun, 1911	
Eledonella pygmaea Verrill, 1884	*Bolitaena pygmaea*
Japetella diaphana Hoyle, 1885	*Japetella diaphana*
CIRROCTOPODIDAE Collins and Villanueva, 2008	
Cirroctopus hochbergi O'Shea, 1999	*Cirroctopus hochbergi*
Grimpoteuthis antarctica Kubodera and Okutani, 1986	*Cirroctopus antarctica*
Grimpoteuthis glacialis Robson, 1930	*Cirroctopus glacialis*
Stauroteuthis (?) *mawsoni* Berry, 1917	*Cirroctopus mawsoni*
CIRROTEUTHIDAE Keferstein, 1866	
Cirroteuthis muelleri Eschricht, 1836	*Cirroteuthis muelleri*
Cirroteuthis magna Hoyle, 1885	*Cirrothauma magna*
Cirrothauma murrayi Chun, 1911	*Cirrothauma murrayi*
OCTOPODIDAE d'Orbigny, 1840 [*In* Ferussac and d'Orbigny, 1834-1848]	
Abdopus undulatus Huffard, 2007	*Abdopus undulatus*
Adelieledone piatkowski Allcock, Hochberg, Rodhouse and Thorpe, 2003	*Adelieledone piatkowski*
Ameloctopus litoralis Norman, 1992	*Ameloctopus litoralis*
Amphioctopus arenicola Huffard and Hochberg, 2005	*Amphioctopus arenicola*
Atlantoctopus pseudonymus Grimpe, 1922	*Benthoctopus pseudonymus*
Bathypolypus pugniger Muus, 2002	*Bathypolypus pugniger*
Bathypolypus rubrostictus Kaneko and Kubodera, 2008	*Bathypolypus rubrostictus*
Bathypurpurata profunda Vecchione, Allcock and Piatkowski, 2005	*Bathypurpurata profunda*
Benthoctopus berryi Robson, 1924	*Benthoctopus berryi*
Benthoctopus canthylus Voss and Pearcy, 1990	*Benthoctopus canthylus*
Benthoctopus clyderoperi O'Shea, 1999	*Benthoctopus clyderoperi*

Benthoctopus fuscus Taki, 1964	*Benthoctopus fuscus*
Benthoctopus johnsoniana Allcock, Strugnell, Ruggiero and Collins, 2006	*Benthoctopus johnsoniana*
Benthoctopus karubar Norman, Hochberg and Lu, 1997	*Benthoctopus karubar*
Benthoctopus oregonae Toll, 1981	*Benthoctopus oregonae*
Benthoctopus oregonensis Voss and Pearcy, 1990	*Benthoctopus oregonensis*
Benthoctopus profundorum Robson, 1932	*Benthoctopus profundorum*
Benthoctopus rigbyae Vecchione, Allcock, Piatkowski and Strugnell, 2009	*Benthoctopus rigbyae*
Benthoctopus robustus Voss and Pearcy, 1990	*Benthoctopus robustus*
Benthoctopus sibiricus Loyning, 1930	*Benthoctopus sibiricus*
Benthoctopus tangaroa O'Shea, 1999	*Benthoctopus tangaroa*
Benthoctopus tegginmathae O'Shea, 1999	*Benthoctopus tegginmathae*
Benthoctopus thielei Robson, 1932	*Benthoctopus thielei*
Benthoctopus yaquinae Voss and Pearcy, 1990	*Benthoctopus yaquinae*
Cistopus chinensis Zheng, Lin, Lu and Ma, 2012	*Cistopus chinensis*
Cistopus taiwanicus Liao and Lu, 2009	*Cistopus taiwanicus*
Eledone brevis Hoyle, 1885	*Thaumeledone brevis*
Eledone caparti Adam, 1950	*Eledone caparti*
Eledone charcoti Joubin, 1905	*Pareledone charcoti*
Eledone gaucha Haimovici, 1988	*Eledone gaucha*
Eledone massyae Voss, 1964	*Eledone massyae*
Eledone palari Lu and Stranks, 1992	*‘Eledone’ palari*
Eledone rotunda Hoyle, 1885	*Bentheledone rotunda*
Eledone schultzei Hoyle, 1910	*Eledone schultzei*
Eledone turqueti Joubin, 1905	*Pareledone turqueti*
Eledone verrucosa Verrill, 1881	*Graneledone verrucosa*
Enteroctopus eureka Robson, 1929	*Muusoctopus eureka*
Euaxoctopus panamensis Voss, 1971	*Euaxoctopus panamensis*
Euaxoctopus pillsburyae Voss, 1975	*Euaxoctopus pillsburyae*
Galeoctopus lateralis Norman, Boucher-Rodoni and Hochberg, 2004	*Galeoctopus lateralis*
Graneledone antarctica Voss, 1976	*Graneledone antarctica*
Graneledone boreopacifica Nesis, 1982	*Graneledone boreopacifica*
Graneledone gonzalezi Guerra, Gonzàlez and Cherel, 2000	*Graneledone gonzalezi*
Graneledone macrotyla Voss, 1976	*Graneledone macrotyla*
Graneledone polymorpha Robson, 1930	*Adelieledone polymorpha*
Graneledone setebos Robson, 1932	*Megaleledone setebos*
Graneledone taniwha kubodera O'Shea, 1999	*Graneledone taniwha kubodera*
Graneledone taniwha taniwha O'Shea, 1999	*Graneledone taniwha taniwha*
Graneledone yamana Guerrero-Kommritz, 2000	*Graneledone yamana*
Grimpella thaumastocheir Robson, 1928	*Grimpella thaumastocheir*

Histoctopus discus Norman, Boucher-Rodoni and Hochberg, 2009	*Histoctopus discus*
Histoctopus zipkasae Norman, Boucher-Rodoni and Hochberg, 2009	*Histoctopus zipkasae*
Microeledone mangoldi Norman, Hochberg and Boucher-Rodoni, 2004	*Microeledone mangoldae*
Moschites adelieana Berry, 1917	*Adelieledone adelieana*
Moschites albida Berry, 1917	*Bentheledone albida*
Moschites aurorae Berry, 1917	*Pareledone aurorae*
Moschites challengeri Berry, 1916	*Graneledone challengeri*
Moschites harrissoni Berry, 1917	*Pareledone harrissoni*
Muusoctopus bizikovi Gleadall, Guerro-Kommritz, Hochberg and Laptikhovsky, 2010	*Muusoctopus bizikovi*
Muusoctopus longibrachus akambei Gleadall, Guerro-Kommritz, Hochberg and Laptikhovsky, 2010	*Muusoctopus longibrachus akambei*
Muusoctopus longibrachus longibrachus Ibáñez, Sepúlveda and Chong, 2006	*Muusoctopus longibrachus longibrachus*
Octopus (Abdopus) abaculus Norman and Sweeney, 1997	*Abdopus abaculus*
Octopus aculeatus d’Orbigny, 1834 [*In* Ferrusac and d’Orbigny, 1834-1848]	*Abdopus aculeatus*
Octopus aegina Gray, 1849	*Amphioctopus aegina*
Octopus alecto Berry, 1953	*‘Octopus’ alecto*
Octopus alpheus Norman, 1993	*Callistoctopus alpheus*
Octopus arcticus Prosch, 1847	*Bathypolypus arcticus*
Octopus argus Krauss, 1848	*‘Octopus’ argus*
Octopus aspilosomatis Norman, 1993	*Callistoctopus aspilosomatis*
Octopus australis Hoyle, 1885	*‘Octopus’ australis*
Octopus bairdii Verrill, 1873	*Bathypolypus bairdii*
Octopus balboai Voss, 1971	*‘Octopus’ balboai*
Octopus berenice Gray, 1849	*‘Octopus’ berenice*
Octopus berrima Stranks and Norman, 1993	*‘Octopus’ berrima*
Octopus bimaculatus Verrill, 1883	*Octopus bimaculatus*
Octopus bimaculoides Pickford and McConnaughey, 1949	*Octopus bimaculoides*
Octopus bocki Adam, 1941	*‘Octopus’ bocki*
Octopus briareus Robson, 1929	*‘Octopus’ briareus*
Octopus bulbus Norman, 2001	*‘Octopus’ bulbus*
Octopus bunurong Stranks, 1990	*‘Octopus’ bunurong*
Octopus burryi Voss, 1950	*Amphioctopus burryi*
Octopus californicus Berry, 1911	*‘Octopus’ californicus*
Octopus (Abdopus) capricornicus Norman and Finn, 2001	*Abdopus capricornicus*
Octopus chierchiae Jatta, 1889	*‘Octopus’ chierchiae*
Octopus cirrhosa Lamarck, 1798	*Eledone cirrhosa*
Octopus cyanea Gray, 1849	*‘Octopus’ cyanea*

Octopus defilippi Verany, 1851	*Macrotritopus defilippi*
Octopus dierythraeus Norman, 1993	*Callistoctopus dierythraeus*
Octopus diminutus Kaneko and Kubodera, 2008	*'Octopus' diminutus*
Octopus ergasticus Fischer and Fischer, 1892	*Bathypolypus ergasticus*
Octopus exannulatus Norman, 1993	*Amphioctopus exannulatus*
Octopus digueti Perrier and Rochebrune, 1894	*Paroctopus digueti*
Octopus fangsiao d'Orbigny, 1839-1841 [*In* Ferrusac and d'Orbigny, 1834-1848]	*Amphioctopus fangsiao*
Octopus favonius Gray, 1849	*'Octopus' favonius*
Octopus filosus Howell, 1867	*Octopus filosus*
Octopus fitchi Berry, 1953	*'Octopus' fitchi*
Octopus fontanianus d'Orbigny, 1834 [*In* Ferrusac and d'Orbigny, 1834-1848]	*Robsonella fontanianus*
Octopus gorgonus Huffard, 2007	*'Octopus' gorgonus*
Octopus graptus Norman, 1993	*Callistoctopus graptus*
Octopus harpedon Norman, 2001	*'Octopus' harpedon*
Octopus hawiiensis Eydoux and Souleyet, 1852	*'Octopus' hawiiensis*
Octopus horridus d'Orbigny, 1826	*Abdopus horridus*
Octopus hubbsorum Berry, 1953	*Octopus hubbsorum*
Octopus humilis Huffard, 2007	*'Octopus' humilis*
Octopus incella Kaneko and Kubodera, 2007	*'Octopus' incella*
Octopus indicus Rapp, 1835 [*In* Ferrusac and d'Orbigny, 1834-1848]	*Cistopus indicus*
Octopus insularis Leite and Haimovici *In* Leite, Haimovici, Molina and Warnke, 2008	*Octopus insularis*
Octopus januarii Hoyle, 1885	*Muusoctopus januarii*
Octopus joubini Robson, 1929	*'Octopus' joubini*
Octopus kagoshimensis Ortmann, 1888	*Amphioctopus kagoshimensis*
Octopus kaharoa O'Shea, 1999	*'Octopus' kaharoa*
Octopus kaurna Stranks, 1990	*'Octopus' kaurna*
Octopus laqueus Kaneko and Kubodera, 2005	*'Octopus' laqueus*
Octopus lechenaultii d'Orbigny, 1826	*Callistoctopus lechenaultii*
Octopus levis Hoyle, 1885	*Benthoctopus levis*
Octopus lunulata Quoy and Gaimard, 1832	*Hapalochlaena lunulata*
Octopus macropus Risso, 1826	*Callistoctopus macropus*
Octopus maculosa Hoyle, 1883	*Hapalochlaena maculosa*
Octopus magnificus Villanueva, Sànchez and Compagno, 1992	*Enteroctopus magnificus*
Octopus mariles Huffard, 2007	*'Octopus' mariles*
Octopus maorum Hutton, 1880	*'Octopus' maorum*
Octopus marginatus Taki, 1964	*Amphioctopus marginatus*
Octopus maya Voss and Solis, 1966	*Octopus maya*

Octopus megalocyathus Gould, 1852	*Enteroctopus megalocyathus*
Octopus membranaceus Quoy and Gaimard, 1832	*Amphioctopus membranaceus*
Octopus mercatoris Adam, 1937	*Paroctopus mercatoris*
Octopus mernoo O’Shea, 1999	*‘Octopus’ mernoo*
Octopus microphthalmus Goodrich, 1896	*‘Octopus’ microphthalmus*
Octopus micropyrsus Berry, 1953	*‘Octopus’ micropyrsus*
Octopus micros Norman, 2001	*‘Octopus’ micros*
Octopus mimus Gould, 1852	*Octopus mimus*
Octopus moschata Lamarck, 1798	*Eledone moschata*
Octopus mototi Norman, 1993	*Amphioctopus mototi*
Octopus mutilans Taki, 1942	*‘Octopus’ mutilans*
Octopus nanus Adam, 1973	*‘Octopus’ nanus*
Octopus neglectus Nateewathana and Norman, 1999	*Amphioctopus neglectus*
Octopus nierstraszi Adam, 1938	*Hapalochlaena nierstraszi*
Octopus nocturnus Norman and Sweeney, 1997	*Callistoctopus nocturnus*
Octopus ornatus Gould, 1852	*Callistoctopus ornatus*
Octopus pallidus Hoyle, 1885	*‘Octopus’ pallidus*
Octopus penicillifer Berry, 1954	*‘Octopus’ penicillifer*
Octopus pictus var. *fasciata* Hoyle, 1886	*Hapalochlaena fasciata*
Octopus polyzenia Gray, 1849	*Amphioctopus polyzenia*
Octopus pumilus Norman and Sweeney, 1997	*‘Octopus’ pumilus*
Octopus pyrum Norman, Hochberg and Lu, 1997	*‘Octopus’ pyrum*
Octopus rapanui Voss, 1979	*Callistoctopus rapanui*
Octopus rex Nateewathana and Norman, 1999	*Amphioctopus rex*
Octopus robsoni Adam, 1941	*Amphioctopus robsoni*
Octopus rubescens Berry, 1953	*‘Octopus’ rubescens*
Octopus salutii Verany, 1839	*‘Octopus’ salutii*
Octopus selene Voss, 1971	*‘Octopus’ selene*
Octopus siamensis Nateewathana and Norman, 1999	*Amphioctopus siamensis*
Octopus sponsalis Fischer and Fischer, 1892	*Bathypolypus sponsalis*
Octopus superciliosus Quoy and Gaimard, 1832	*‘Octopus’ superciliosus*
Octopus tehuelchus d’Orbigny, 1834 [*In* Ferrusac and d’Orbigny, 1834-1848]	*‘Octopus’ tehuelchus*
Octopus tenebricus Smith, 1884	*Abdopus tenebricus*
Octopus tetracirrhus Delle Chiaje, 1830	*Pteroctopus tetracirrhus*
Octopus tetricus Gould, 1852	*Octopus tetricus*
Octopus tonganus Hoyle, 1885	*Abdopus tonganus*
Octopus unicirrhus Delle Chiaje, 1839-1841	*Scaeurgus unicirrhus*
Octopus varunae Oommen, 1971	*Amphioctopus varunae*
Octopus veligero Berry, 1953	*‘Octopus’ veligero*

Octopus vitiensis Hoyle, 1885	*‘Octopus’ vitiensis*
Octopus vulgaris Cuvier, 1797	*Octopus vulgaris*
Octopus warringa Stranks, 1990	*‘Octopus’ warringa*
Octopus winckworthi Robson, 1926	*Macrochlaena winckworthi*
Octopus zealandicus Benham, 1944	*Enteroctopus zealandicus*
Octopus zonatus Voss, 1968	*‘Octopus’ zonatus*
Pareledone aequipapillae Allcock, 2005	*Pareledone aequipapillae*
Pareledone albimaculata Allcock, 2005	*Pareledone albimaculata*
Pareledone aurata Allcock, 2005	*Pareledone aurata*
Pareledone cornuta Allcock, 2005	*Pareledone cornuta*
Pareledone felix Allcock, Strugnell, Prodohl, Piatkowski and Vecchione, 2007	*Pareledone felix*
Pareledone framensis Lu and Stranks, 1994	*Pareledone framensis*
Pareledone panchroma Allcock, 2005	*Pareledone panchroma*
Pareledone prydzensis Lu and Stranks, 1994	*Pareledone prydzensis*
Pareledone serperastrata Allcock, 2005	*Pareledone serperastrata*
Pareledone subtilis Allcock, 2005	*Pareledone subtilis*
Polypus abruptus Sasaki, 1920	*Benthoctopus abruptus*
Polypus campbelli Smith, 1902	*‘Octopus’ campbelli*
Polypus conispadiceus Sasaki, 1917	*‘Octopus’ conispadiceus*
Polypus dofleini Wülker, 1910	*Enteroctopus dofleini*
Polypus gardineri Hoyle, 1905	*‘Octopus’ gardineri*
Polypus hattai Sasaki, 1929	*‘Octopus’ hattai*
Polypus hokkaidensis Berry, 1921	*Benthoctopus hokkaidensis*
Polypus hongkongensis Hoyle 1885	*‘Octopus’ hongkongensis*
Polypus hoylei Berry, 1909	*Pteroctopus hoylei*
Polypus kermadecensis Berry, 1914	*‘Octopus’ kermadecensis*
Polypus leioderma Berry, 1911	*Benthoctopus leioderma*
Polypus luteus Sasaki, 1929	*Callistoctopus luteus*
Polypus minor Sasaki, 1920	*‘Octopus’ minor*
Polypus normani Massy, 1907	*Benthoctopus normani*
Polypus oculifer Hoyle, 1904	*Octopus oculifer*
Polypus oliveri Berry, 1914	*‘Octopus’ oliveri*
Polypus ovulum Sasaki, 1917	*Amphioctopus ovulum*
Polypus parvus Sasaki, 1917	*‘Octopus’ parvus*
Polypus salebrosus Sasaki, 1920	*Sasakiopus salebrosus*
Polypus valdiviae Thiele *In* Chun, 1915	*Bathypolypus valdiviae*
Polypus wolfi Wülker, 1913	*‘Octopus’ wolfi*
Praealtus paralbida Allcock, Collins, Piatkowski and Vecchione, 2004	*Praealtus paralbida*
Robsonella huttoni Benham, 1943	*‘Octopus’ huttoni*

Scaeurgus jumeau Norman, Hochberg and Boucher-Rodoni, 2005	*Scaeurgus jumeau*
Scaeurgus nesisi Norman, Hochberg and Boucher-Rodoni, 2005	*Scaeurgus nesisi*
Scaeurgus patagiatus Berry, 1913	*Scaeurgus patagiatus*
Scaeurgus tuber Norman, Hochberg and Boucher-Rodoni, 2005	*Scaeurgus tuber*
Teretoctopus alcocki Robson, 1932	*Teretoctopus alcocki*
Teretoctopus indicus Robson, 1929	*Teretoctopus indicus*
Tetracheledone spinicirrus Voss, 1955	*Tetracheledone spinicirrus*
Thaumeledone gunteri Robson, 1930	*Thaumeledone gunteri*
Thaumeledone marshalli O'Shea, 1999	*'Thaumeledone' marshalli*
Thaumeledone peninsulae Allcock, Collins, Piatkowski and Vecchione, 2004	*Thaumeledone peninsulae*
Thaumeledone zeiss O'Shea, 1999	*'Thaumeledone' zeiss*
Thaumoctopus mimicus Norman and Hochberg, 2005	*Thaumoctopus mimicus*
Tremoctopus scalenus Hoyle, 1904	*Euaxoctopus scalenus*
Velodona togata Chun, 1915	*Velodona togata*
Vosseledone charrua Palacio, 1978	*Vosseledone charrua*
Vulcanoctopus hydrothermalis González and Guerra *In* González, Guerra, Pascual and Briand, 1998	*Vulcanoctopus hydrothermalis*
Wunderpus photogenicus Hochberg, Norman and Finn, 2006	*Wunderpus photogenicus*
OCYTHOIDAE Gray, 1849	
Ocythoe tuberculata Rafinesque, 1814	*Ocythoe tuberculata*
OPISTHOTEUTHIDAE Verrill 1896	
Cirroteuthis grimaldii Joubin, 1903	*Opisthoteuthis grimaldii*
Cirroteuthis (*Cirroteuthopsis*) *massyae* Grimpe, 1920	*Opisthoteuthis massyae*
Cirroteuthis meangensis Hoyle, 1885	*Grimpoteuthis meangensis*
Cirroteuthis megaptera Verrill, 1885	*Grimpoteuthis megaptera*
Cirroteuthis pacifica Hoyle, 1885	*Grimpoteuthis pacifica*
Cirroteuthis plena Verrill, 1885	*Grimpoteuthis plena*
Cirroteuthis umbellata Fischer, 1883	*Grimpoteuthis umbellata*
Cryptoteuthis brevibracchiata Collins, 2004	*Cryptoteuthis brevibracchiata*
Enigmatiteuthis innominata O'Shea, 1999	*Grimpoteuthis innominata*
Grimpoteuthis abyssicola O'Shea, 1999	*Grimpoteuthis abyssicola*
Grimpoteuthis bathynectes Voss and Pearcy, 1990	*Grimpoteuthis bathynectes*
Grimpoteuthis boylei Collins, 2003	*Grimpoteuthis boylei*
Grimpoteuthis bruuni Voss, 1982	*Opisthoteuthis bruuni*
Grimpoteuthis challengeri Collins, 2003	*Grimpoteuthis challengeri*
Grimpoteuthis discoveryi Collins, 2003	*Grimpoteuthis discoveryi*
Grimpoteuthis tuftsi Voss and Pearcy, 1990	*Grimpoteuthis tuftsi*
Luteuthis dentatus O'Shea, 1999	*Luteuthis dentatus*
Luteuthis shuishi O'Shea and Lu, 2002	*Luteuthis shuishi*

Opisthoteuthis agassizii Verrill, 1883	*Opisthoteuthis agassizii*
Opisthoteuthis borealis Collins, 2005	*Opisthoteuthis borealis*
Opisthoteuthis californiana Berry, 1949	*Opisthoteuthis californiana*
Opisthoteuthis calypso Villanueva, Collins, Sànchez and Voss, 2002	*Opisthoteuthis calypso*
Opisthoteuthis chathamensis O'Shea, 1999	*Opisthoteuthis chathamensis*
Opisthoteuthis depressa Ijima and Ikeda, 1895	*Opisthoteuthis depressa*
Opisthoteuthis dongshaensis Lu, 2010	*Opisthoteuthis dongshaensis*
Opisthoteuthis hardyi Villanueva, Collins, Sànchez and Voss, 2002	*Opisthoteuthis hardyi*
Opisthoteuthis japonica Taki, 1962	*Opisthoteuthis japonica*
Opisthoteuthis medusoides Thiele *In* Chun, 1915	*Opisthoteuthis medusoides*
Opisthoteuthis mero O'Shea, 1999	*Opisthoteuthis mero*
Opisthoteuthis persephone Berry, 1918	*Opisthoteuthis persephone*
Opisthoteuthis philipii Oommen, 1976	*Opisthoteuthis philipii*
Opisthoteuthis pluto Berry, 1918	*Opisthoteuthis pluto*
Opisthoteuthis robsoni O'Shea, 1999	*Opisthoteuthis robsoni*
Stauroteuthis albatrossi Sasaki, 1920	*Opisthoteuthis albatrossi*
Stauroteuthis hippocrepium Hoyle, 1904	*Grimpoteuthis hippocrepium*
Stauroteuthis wuelkeri Grimpe, 1920	*Grimpoteuthis wuelkeri*
STAUROTEUTHIDAE Grimpe, 1916	
Cirroteuthis gilchristi Robson, 1924	*Stauroteuthis gilchristi*
Stauroteuthis syrtensis Verrill, 1879	*Stauroteuthis syrtensis*
TREMOCTOPODIDAE Tryon, 1879	
Octopus gracilis Eydoux and Souleyet, 1852	*Tremoctopus gracilis*
Pteroctopus violaceus Delle Chiaje, 1830 *In* 1823-1831	*Tremoctopus violaceus*
Tremoctopus gelatus Thomas, 1977	*Tremoctopus gelatus*
Tremoctopus robsoni Kirk, 1884	*Tremoctopus robsoni*
VAMPYROTEUTHIDAE Thiele *In* Chun, 1915	
Vampyroteuthis infernalis Chun, 1903	*Vampyroteuthis infernalis*
VITRELEDONELLIDAE Robson, 1932	
Vitreledonella richardi Joubin, 1918	*Vitreledonella richardi*

4. LIST OF SPECIES BY MAJOR FISHING AREAS

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Abdopus abaculus	62															●				
Abdopus aculeatus	61															●				
Abdopus capricornicus	62															●				
Abdopus horridus	60										●									
Abdopus tenebricus	62															●				
Abdopus tonganus	63															●				
Abdopus undulatus	63															●				
Adelieledone adelieana	65												●							
Adelieledone piatkowski	65									●										
Adelieledone polymorpha	64									●										
Ameloctopus litoralis	66											●				●				
Amphioctopus aegina	68										●	●		●		●				
Amphioctopus arenicola	83																●			
Amphioctopus burryi	69				●	●														
Amphioctopus exannulatus	71											●				●				
Amphioctopus fangsiao	72													●						
Amphioctopus kagoshimensis	73													●						
Amphioctopus marginatus	75										●	●		●		●				
Amphioctopus membranaceus	83															●				
Amphioctopus mototi	77															●		●		
Amphioctopus neglectus	79										●	●		●		●				
Amphioctopus ovulum	83													●						
Amphioctopus polyzenia	84											●				●				
Amphioctopus rex	80										●	●				●				
Amphioctopus robsoni	84										●									
Amphioctopus siamensis	81											●				●				
Amphioctopus varunae	84										●									
Amphitretus pelagicus	217										●	●		●		●	●	●	●	
Amphitretus thielei	219										●	●						●		
Argonauta argo	230		●	●	●	●	●	●	●		●	●		●		●	●	●	●	
Argonauta hians	232				●	●		●	●		●	●		●		●	●		●	
Argonauta nodosus	234							●	●		●	●		●		●		●		
Argonauta nouryi	236																●		●	
Bathypolypus arcticus	85													●	●					
Bathypolypus bairdii	86		●	●																
Bathypolypus ergasticus	87			●		●														

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Bathypolypus pugniger	87		●	●																
Bathypolypus rubrostictus	87													●						
Bathypolypus sponsalis	87			●		●	●													
Bathypolypus valdiviae	87								●											
Bathypurpurata profunda	88									●										
Bentheledone albida	91												●							
Bentheledone rotunda	90											●								
Benthoctopus abruptus	94													●						
Benthoctopus berryi	94								●											
Benthoctopus canthylus	94														●					
Benthoctopus clyderoperi	94																	●		
Benthoctopus fuscus	95													●						
Benthoctopus hokkaidensis	95													●	●					
Benthoctopus johnsoniana	95			●																
Benthoctopus karubar	92															●				
Benthoctopus leioderma	95													●	●		●			
Benthoctopus levis	96												●							
Benthoctopus normani	96			●																
Benthoctopus oregonae	96				●															
Benthoctopus oregonensis	96														●					
Benthoctopus profundorum	96													●						
Benthoctopus pseudonymus	97			●																
Benthoctopus rigbyae	97									●										
Benthoctopus robustus	97														●		●			
Benthoctopus sibiricus	97	●																		
Benthoctopus tangaroa	97																	●		
Benthoctopus tegginmathae	98																	●		
Benthoctopus thielei	98												●							
Benthoctopus yaquinae	98														●					
Bolitaena pygmaea	220				●	●		●	●		●	●		●		●	●	●	●	
Callistoctopus alpheus	100															●				
Callistoctopus aspilosomatis	102															●				
Callistoctopus dierythraeus	103											●				●				
Callistoctopus graptus	104											●				●				
Callistoctopus lechenaultii	109											●								
Callistoctopus luteus	105															●				
Callistoctopus macropus	106						●													
Callistoctopus nocturnus	107															●				

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Callistoctopus ornatus	99										●	●		●		●	●	●		
Callistoctopus rapanui	108																		●	
Cirroctopus antarctica	247									●										
Cirroctopus glacialis	246									●										
Cirroctopus hochbergi	247																	●		
Cirroctopus mawsoni	247												●							
Cirroteuthis mülleri	249	●	●	●																
Cirrothauma magna	251				●	●					●									
Cirrothauma murrayi	250	●	●	●										●	●					
Cistopus chinensis	112													●						
Cistopus indicus	110															●				
Cistopus taiwanicus	113													●						
Cryptoteuthis brevibracchiata	258			●																
Eledone caparti	121					●			●											
Eledone cirrhosa	117			●			●													
Eledone gaucha	121							●												
Eledone massyae	119							●												
Eledone moschata	114			●			●													
'Eledone' palari	120											●				●		●		
'Eledone' schultzei	121								●											
Enteroctopus dofleini	124													●	●		●			
Enteroctopus magnificus	125								●											
Enteroctopus megalocyathus	122							●												
Enteroctopus zealandicus	126																	●		
Euaxoctopus panamensis	127																●		●	
Euaxoctopus pillsburyae	128				●															
Euaxoctopus scalenus	128																●			
Galeoctopus lateralis	129															●	●			
Graneledone antarctica	132																			●
Graneledone boreopacifica	133													●	●		●			
Graneledone challengeri	133																	●		
Graneledone gonzalezi	133												●							
Graneledone macrotyla	133							●												
Graneledone taniwha kubodera	134																	●		
Graneledone taniwha taniwha	134																	●		
Graneledone verrucosa	131		●	●																
Graneledone yamana	134							●												
Grimpella thaumastocheir	135											●								

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Grimpoteuthis abyssicola	261																	●		
Grimpoteuthis bathynectes	261														●					
Grimpoteuthis boylei	261			●																
Grimpoteuthis challengeri	262			●																
Grimpoteuthis discoveryi	262			●																
Grimpoteuthis hippocrepium	262																		●	
Grimpoteuthis innominata	262																	●		
Grimpoteuthis meangensis	262															●				
Grimpoteuthis megaptera	263				●															
Grimpoteuthis pacifica	263															●				
Grimpoteuthis plena	263		●																	
Grimpoteuthis tuftsi	263														●					
Grimpoteuthis umbellata	263		●	●																
Grimpoteuthis wuelkeri	260			●			●													
Haliphron atlanticus	226		●	●	●	●		●	●		●	●		●	●	●	●	●	●	
Hapalochlaena fasciata	138																	●		
Hapalochlaena lunulata	137											●				●				
Hapalochlaena maculosa	139											●								
Hapalochlaena nierstraszi	140											●								
Histoctopus discus	143															●				
Histoctopus zipkasae	141											●								
Japetella diaphana	222				●	●		●	●		●	●		●	●	●	●	●	●	
Luteuthis dentatus	264																	●		
Luteuthis shuishi	265													●						
Macrochlaena winckworthi	144											●								
Macrotritopus defilippi	146			●			●													
Megaleledone setebos	148									●			●							●
Microeledone mangoldae	150																	●		
Muusoctopus bizikovi	153							●												
Muusoctopus eureka	153							●												
Muusoctopus januarii	151				●			●												
Muusoctopus longibrachus akambei	153							●												
Muusoctopus longibrachus longibrachus	153																		●	
'Octopus' alecto	187																●		●	
'Octopus' argus	207										●									
'Octopus' australis	189																	●		
'Octopus' balboai	207																●			
'Octopus' berenice	208											●				●				

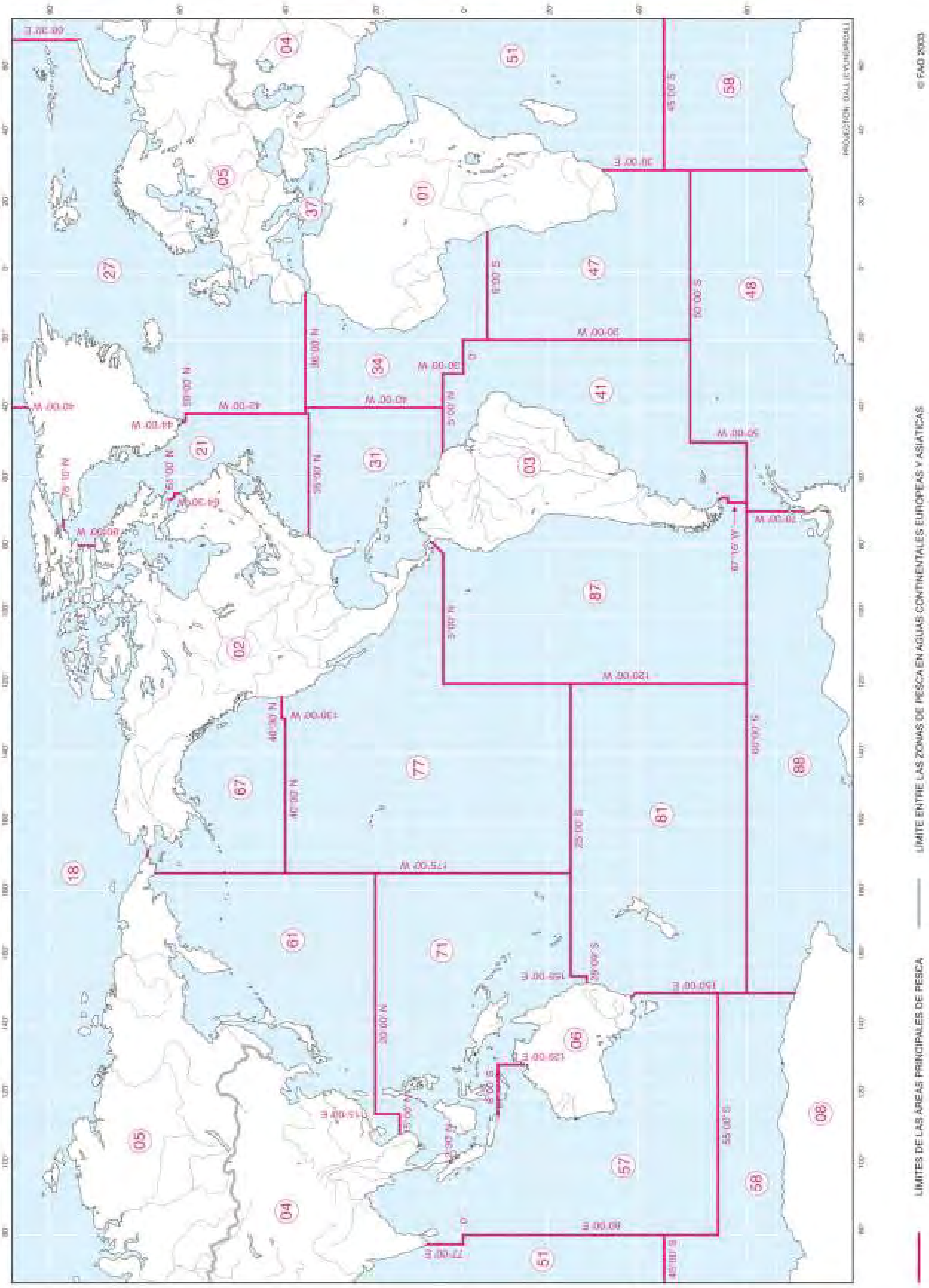
SPECIES	page	GEOGRAPHICAL DISTRIBUTION MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
‘Octopus’ berrima	190											●								
Octopus bimaculatus	47																●			
Octopus bimaculoides	48																●			
‘Octopus’ bocki	208															●	●			
‘Octopus’ briareus	191				●															
‘Octopus’ bulbus	208															●				
‘Octopus’ bunurong	192											●								
‘Octopus’ californicus	193													●	●		●			
‘Octopus’ campbelli	208																	●		
‘Octopus’ chierchiae	208																●			
‘Octopus’ conispadiceus	195													●						
‘Octopus’ cyanea	196										●	●		●		●	●	●		
‘Octopus’ diminutus	209													●						
‘Octopus’ favonius	209															●				
Octopus filosus	58				●															
‘Octopus’ fitchi	209																●			
‘Octopus’ gardineri	209										●									
‘Octopus’ gorgonus	209															●				
‘Octopus’ harpedon	210															●				
‘Octopus’ hattai	210													●						
‘Octopus’ hawiiensis	210																●			
‘Octopus’ hongkongensis	210													●						
Octopus hubbsorum	50																●			
‘Octopus’ humilis	211															●				
‘Octopus’ huttoni	211																	●		
‘Octopus’ incella	211													●						
Octopus insularis	51							●												
‘Octopus’ joubini	211				●															
‘Octopus’ kaharoa	211																	●		
‘Octopus’ kaurna	198											●								
‘Octopus’ kermadecensis	212																	●		
‘Octopus’ laqueus	212													●		●				
‘Octopus’ maorum	199											●						●		
‘Octopus’ mariles	212															●				
Octopus maya	53				●															
‘Octopus’ mernoo	212																	●		
‘Octopus’ microphthalmus	212											●				●				
‘Octopus’ micropyrsus	213																●			

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
'Octopus' micros	213															●				
Octopus mimus	54																		●	
'Octopus' minor	200													●						
'Octopus' mutilans	213													●						
'Octopus' nanus	213										●									
Octopus oculifer	56																		●	
'Octopus' oliveri	213																	●		
'Octopus' pallidus	201											●								
'Octopus' parvus	214													●						
'Octopus' penicillifer	214																●			
'Octopus' pumilus	214															●				
'Octopus' pyrum	214															●				
'Octopus' rubescens	202														●		●			
'Octopus' salutii	214			●			●													
'Octopus' selene	204																●			
'Octopus' superciliosus	215											●								
'Octopus' tehuelchus	205							●												
Octopus tetricus	57											●						●		
'Octopus' veligero	206																●			
'Octopus' vitiensis	215															●				
Octopus vulgaris sensu stricto	42			●		●	●													
Octopus vulgaris type I	44				●			●												
Octopus vulgaris type II	45							●												
Octopus vulgaris type III	45								●		●									
Octopus vulgaris type IV	46											●		●		●				
'Octopus' warringa	215											●								
'Octopus' wolfi	215										●	●				●	●			
'Octopus' zonatus	215				●															
Ocythoe tuberculata	238		●	●			●		●		●			●	●			●	●	
Opisthoteuthis agassizii	253		●		●															
Opisthoteuthis albatrossi	254													●						
Opisthoteuthis borealis	254		●	●																
Opisthoteuthis bruuni	254																		●	
Opisthoteuthis californiana	254													●	●		●			
Opisthoteuthis calypso	255			●																
Opisthoteuthis chathamensis	255																	●		
Opisthoteuthis depressa	255													●						
Opisthoteuthis dongshaensis	255													●						

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Opisthoteuthis extensa	255											●								
Opisthoteuthis grimaldii	256			●		●			●											
Opisthoteuthis hardyi	256							●		●										
Opisthoteuthis japonica	256													●						
Opisthoteuthis massyae	256			●		●			●											
Opisthoteuthis medusoides	256										●									
Opisthoteuthis mero	257																	●		
Opisthoteuthis persephone	257											●								
Opisthoteuthis philipii	257										●									
Opisthoteuthis pluto	257											●								
Opisthoteuthis robsoni	257																	●		
Pareledone aequipapillae	155									●										
Pareledone albimaculata	155									●										
Pareledone aurata	156									●										
Pareledone aurorae	156												●							
Pareledone charcoti	154									●			●							●
Pareledone cornuta	156									●										
Pareledone felix	156									●										
Pareledone framensis	157												●							
Pareledone harrissoni	157												●							
Pareledone panchroma	157									●										
Pareledone prydzensis	157												●							
Pareledone serperastrata	158									●										
Pareledone subtilis	158									●										
Pareledone turqueti	158									●										
Paroctopus digueti	160																●			
Paroctopus mercatoris	161				●															
Praealtus paralbida	162									●										
Pteroctopus hoylei	165																●			
Pteroctopus tetracirrhus	164			●		●	●													
Robsonella fontanianus	166							●											●	
Sasakiopus salebrosus	168													●	●					
Scaeurgus jumeau	172															●				
Scaeurgus nesisi	172															●				
Scaeurgus patagiatus	172													●			●			
Scaeurgus tuber	172															●				
Scaeurgus unicirrhus	170			●	●	●	●	●												
Stauroteuthis gilchristi	267							●	●											

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	**21**	**27**	**31**	**34**	**37**	**41**	**47**	**48**	**51**	**57**	**58**	**61**	**67**	**71**	**77**	**81**	**87**	**88**
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Stauroteuthis syrtensis	266		●	●	●															
Teretoctopus alcocki	174										●	●								
Teretoctopus indicus	173										●									
Tetracheledone spinicirrus	175				●															
Thaumeledone brevis	178							●												
Thaumeledone gunteri	177									●										
'Thaumeledone' marshalli	178																	●		
Thaumeledone peninsulae	178							●												
'Thaumeledone' zeiss	178																	●		
Thaumoctopus mimicus	179										●	●				●				
Tremoctopus gelatus	243				●						●	●					●		●	
Tremoctopus gracilis	243						●				●	●		●		●	●	●	●	
Tremoctopus robsoni	243																	●		
Tremoctopus violaceus	240		●	●	●	●	●													
Vampyroteuthis infernalis	269		●	●	●	●		●	●		●	●		●	●	●	●	●	●	
Velodona togata	181										●									
Vitreledonella richardi	223		●	●	●	●	●	●	●		●	●		●	●	●	●	●	●	
Vosseledone charrua	183							●												
Vulcanoctopus hydrothermalis	184																		●	
Wunderpus photogenicus	186															●				

MAJOR FISHING AREAS FOR STATISTICAL PURPOSES



5. REFERENCES

Adam, W. 1934. Notes sur les Céphalopodes. V. *Ozaena cirrhosa* (Lamarck, 1798) sur la côte belge. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 10(43): 1-3.

Adam, W. 1973. Contributions to the knowledge of the Red Sea. No. 47. Cephalopoda from the Red Sea. *Bulletin of the Sea Fisheries Research Station, Haifa,* 60: 9-47.

Adams, A. & Reeve, L. 1848. Mollusca. *In* A. Adams, ed. *The Zoology of the Voyage of H.M.S. Samarang*, pp. 1-87. London, Reeve and Benham.

Aguado Giménez, F. & García García, B. 2002. Growth and food intake models in *Octopus vulgaris* Cuvier (1797): influence of body weight, temperature, sex and diet. *Aquaculture International,* 10(5): 361-377.

Aguilar-Chavez, S. & Godínez-Domínguez, E. 1997. Presencia del pulpo *Octopus hubbsorum* (Cephalopoda: Octopoda) en el Pacifico Central mexicano. *Revista de Biologia Tropical*, 44(3)/45(1): A & B, 678.

Akimushkin, I.I. 1965. *Cephalopods of the Seas of the U.S.S.R. (Academy of Sciences of the U.S.S.R. - Institute of Oceanology).* Translated from Russian; Jerusalem, Israel Program for Scientific Translations. 223 pp.

Akyol, O. 2003. Retained and trash fish catches of beach-seining in the Aegean coast of Turkey. *Turkish Journal of Veterinary & Animal Sciences*, 27(5): 1111-1117.

Akyol, O., Sen, H. & Kmacigil, H.T. 2007a. Reproductive biology of *Eledone moschata* (Cephalopoda: Octopodidae) in the Aegean Sea (Izmir Bay, Turkey). *Journal of the Marine Biological Association of the United Kingdom*, 87(4): 967-970.

Akyol, O., Ceyhan, T., İlkyaz, A. & Erdem, M. 2007b. Investigations on the set net fishery in Gökova Bay (Aegean Sea). *Anadolu University, Journal of Science and Technology,* 8(1): 139-144.

Alcazar, J. & Ortea, J. 1981. Comentarios sobre *Opisthoteuthis agassizii* Verrill, 1883 (Cephalopoda: Octopoda) en el mar Cantábrico. *Cuadernos del Crinas*, 6: 29-37.

Aldred, R.G., Nixon, M. & Young, J.Z. 1978. The blind octopus, *Cirrothauma*. *Nature*, 275(5680): 547-549.

Aldred, R.G., Nixon, M. & Young, J.Z. 1982. Possible light organs in finned octopods. *Journal of Molluscan Studies,* 48(1): 100-101.

Aldred, R.G., Nixon, M. & Young, J.Z. 1983. *Cirrothauma murrayi* Chun, a finned octopod. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 301: 1-54.

Alejo-Plata, M. del C., Gómez-Márque, J.L., Carrillo, S.R. & Herrera-Galindo, J.E. 2009. Reproducción, dieta y pesquería del pulpo *Octopus* (*Octopus*) *hubbsorum* (Mollusca: Cephalopoda) en la costa de Oaxaca, México. *Revista de Biologia Tropical*, 57(1-2): 63-78.

Allan, J. 1950. *Australian Shells*. Melbourne, Australia, Georgian House. 470 pp.

Allcock, A.L. 2005. On the confusion surrounding *Pareledone charcoti* (Joubin, 1905) (Cephalopoda: Octopodidae): endemic radiation in the Southern Ocean. *Zoological Journal of the Linnean Society,* 143: 75-108.

Allcock, A.L. & Piertney, S.B. 2002. Evolutionary relationships of southern ocean Octopodidae (Cephalopoda: Octopoda) and a new diagnosis of *Pareledone. Marine Biology*, 140(1): 129-135.

Allcock, A.L., Collins, M.A. & Vecchione, M. 2003a. A redescription of *Graneledone verrucosa* (Verrill, 1881) (Octopoda: Octopodidae). *Journal of Molluscan Studies*, 69: 135-143.

Allcock A.L., Hochberg, F.G. & Stranks, T.N. 2003b. Re-evaluation of *Graneledone setebos* (Cephalopoda: Octopodidae) and allocation to the genus *Megaleledone*. *Journal of the Marine Biological Association of the United Kingdom*, 82(2): 319-328.

Allcock, A.L., Brierley, A.S., Thorpe, J.P. & Rodhouse, P.G. 1997. Restricted gene flow and evolutionary divergence between geographically separated populations of the Antarctic octopus *Pareledone turqueti. Marine Biology*, 129(1): 97-102.

Allcock, A.L., Collins, M.A., Piatkowski, U. & Vecchione, M. 2004. *Thaumeledone* and other deep water octopodids from the Southern Ocean. *Deep-Sea Research*, 51: 1883-1901.

Allcock, A.L., Hochberg, F.G., Rodhouse, P.G.K. & Thorpe, J.P. 2003c. *Adelieledone*, a new genus of octopodid from the Southern Ocean. *Antarctic Science*, 15(4): 415-424.

Allcock, A.L., Piatkowski, U., Rodhouse, P.G.K. & Thorpe, J.P. 2001. A study on octopodids from the eastern Weddell Sea, Antarctica. *Polar Biology*, 24(11): 832-838.

Allcock, A.L., Strugnell, J.M., Ruggiero, H. & Collins, M.A. 2006. Redescription of the deep-sea octopod *Benthoctopus normani* (Massy, 1907) and a description of a new species from the Northeast Atlantic. *Marine Biology Research*, 2: 372-387

Allcock, A.L., Strugnell, J.M., Prodohl, P., Piatkowski, U. and Vecchione, M. 2007. A new species of *Pareledone* (Cephalopoda: Octopodidae) from Antarctic Peninsula waters. *Polar Biology*, 30: 883-893.

Allcock, A.L., Barratt, I., Eleaume, M., Linse, K., Norman, M.D., Smith, P.J., Steinke, D., Stevens, D.W. & Strugnell, J.M. 2011. Cryptic speciation and the circumpolarity debate: A case study on endemic Southern Ocean octopuses using the COI barcode of life. *Deep-Sea Research Part II - Topical Studies in Oceanography*, 58(1-2): 242-249.

Alliston, E. 1983. *Escape to an Island*. Melbourne, Australia, Greenhouse Publications. 184 pp.

Alonso, M.K., Crespo, E.A., Pedraza, S.N., Garcia, N.A. & Coscarella, M.A. 2000. Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. *Fishery Bulletin*, 98(2): 250-263.

Alvariño, A. & Hunter, J.R. 1981. New records of *Alloposus mollis* Verrill (Cephalopoda, Octopoda) from the Pacific Ocean. *Nautilus,* 95: 26-32.

Ambrose, R.F. 1981. Observations on the embryonic development and early post-embryonic behavior of *Octopus bimaculatus* (Mollusca: Cephalopoda). *Veliger,* 24: 139-146.

Ambrose, R.F. 1982a. Shelter utilization by the molluscan cephalopod *Octopus bimaculatus*. *Marine Ecological Progress Series*, 7: 67-73.

Ambrose, R.F. 1982b. Octopus Predation and Community Structure of Subtidal Rocky Reefs at Santa Catalina Island, California*.* Ph.D. Dissertation. University of California: Los Angeles, California, USA. 153 pp.

Ambrose, R.F. 1983. Midden formation by octopuses: the role of biotic and abiotic factors. *Marine Behavior and Physiology,* 10: 137-144.

Ambrose, R.F. 1984. Food preferences, prey availability, and the diet of *Octopus bimaculatus* Verrill. *Journal of Experimental Marine Biology and Ecology,* 77: 29-44.

Ambrose, R.F. 1986. Effects of octopus predation on motile invertebrates in a rocky subtidal community. *Marine Ecological Progress Series*, 30: 261-273.

Ambrose, R.F. 1988. Population dynamics of *Octopus bimaculatus*: Influence of life history patterns, synchronous reproduction and recruitment. *Malacologia*, 29(1): 23-39.

Ambrose, R.F. 1997. *Octopus bimaculatus*. *In* Lang, M.A. & F.G. Hochberg, eds. *The Fishery and Market Potential of* Octopus *in California,* Washington, D.C., Smithsonian Institution. (Workshop Proceedings). Pp. 11-22.

Ambrose, R.F. & Nelson, B.V. 1983. Predation by *Octopus vulgaris* in the Mediterranean. *Marine Ecology,* 4(3): 251-261.

Anderson, R.C. & Mather, J.A. 2007. The packaging problem: Bivalve prey selection and prey entry techniques of the octopus *Enteroctopus dofleini*. *Journal of Comparative Psychology*, 121(3): 300-305.

Anderson, R.C., Wood, J.B. & Mather, J.A. 2008. *Octopus vulgaris* in the Caribbean is a specializing generalist. *Marine Ecology Progress Series,* 371: 199-202.

Anderson, R.C., Mather, J.A., Monette, M.Q. & Zimsen, S.R.M. 2010. Octopuses (*Enteroctopus dofleini*) recognize individual humans. *Journal of Applied Animal Welfare Science*, 13(3): 261-272.

Anderson, R.C., Shimek, R., Cosgrove, J.A. & Berthinier, S. 2007. Giant Pacific Octopus, *Enteroctopus dofleini*, attacks on divers. *Canadian Field Naturalist*, 121(4): 423-425.

Anderson, T.J. 1997. Habitat selection and shelter use by *Octopus tetricus*. *Marine Ecology-Progress Series,* 150: 137-148.

Anderson, T.J. 1999. Morphology and biology of *Octopus maorum* Hutton 1880 in northern New Zealand. *Bulletin of Marine Science,* 65: 657-676.

Andre, J., Pecl, G.T., Semmens, J.A. & Grist, E.P.M. 2008. Early life-history processes in benthic octopus: Relationships between temperature, feeding, food conversion, and growth in juvenile *Octopus pallidus*. *Journal of Experimental Marine Biology and Ecology*, 354(1): 81-92.

Andre, J., Pecl, G.T., Grist, E.P.M., Semmens, J.M., Haddon, M. & Leporati, S.C. 2009. Modelling size-at-age in wild immature female octopus: a bioenergetics approach. *Marine Ecology-Progress Series*, 384: 159-174.

Appellof, A. 1886. Japanska Cephalopoder. *Svenska Vetenskaps-Akademiens Handlingar,* 2l(l3): 1-36.

Arai, D., Kurihara, A., Komi, R., Iwamoto, A. & Takeuchi, T. 2008. Effect of feeding various amounts of pacific sandeel flakes on growth, survival and carcass fatty acid composition of common octopus *Octopus vulgaris* paralarvae. *Suisan Zoshoku,* 56: 595-600.

Arancibia, H. & Troncoso, G. 1984. Estudio de talla y peso de primera madurez sexual en el pulpo *Octopus vulgaris* Cuvier, 1797. *Informe Final, Servicio Nacional de Pesca de Chile (SERNAP)*. 56 pp.

Arnold, J.M. & Arnold, K.O. 1969. Some aspects of hole-boring predation by *Octopus vulgaris*. *American Zoologist,* 9(3): 991-996.

Arocha, F. 1989. Cephalopod resources of Venezuela. *Marine Fisheries Review*, 51(2): 47-51.

Arocha, F., Marcano, L. & Cipriani, R. 1991. Cephalopods trawled from Venezuelan waters by the R/V *Dr. Fridtjof Nansen* in 1988. *Bulletin of Marine Science*, 49(1-2): 231-234.

Aronson, R.B. 1989. The ecology of *Octopus briareus* Robson in a Bahamian saltwater lake. *American Malacological Bulletin*, 7(1): 47-56.

Arreguin-Sánchez, F., Sólis-Ramírez, M.J.S. & González de la Rosa, M.E. 2000. Population dynamics and stock assessment for *Octopus maya* (Cephalopoda: Octopodidae) fishery in the Campeche Bank, Gulf of Mexico. *Revista de Biologia Tropical,* 48: 323-331.

Avdeev, G.V. 1986. New harpacticoid copepods associated with Pacific cephalopods. *Crustaceana*, 51: 49-65.

Baeta, F., Pinheiro, A., Corte-Real, M., Costa, J.L., Raposa del Almeida, P., Cabral, H. & Costa, M.J. 2005. Are the fisheries in Tagus estaury sustainable? *Fisheries Research,* 76: 243-251.

Baino, R., Mannini, P. & Volpi C. 1988. Predictive use of length-weight regression in *Eledone cirrhosa*. *Rapports et Proces-verbaux des Reunions Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee*, 32(2): 254.

Bakken, T. & Holthe, T. 2002. *Haliphron antarcticum* (Cephalopoda: Alloposidae) caught in Skjorafjorden (64°N) Norway. *Fauna Norvegica,* 22: 37-38.

Balguerias, E., Hernández-González, C. & Perales-Raya, C. 2002. On the identity of *Octopus vulgaris* Cuvier, 1797 stocks in the Saharan Bank (Northwest Africa) and their spatio-temporal variations in abundance in relation to some environmental factors. *Bulletin of Marine Science,* 71(1): 147-163.

Baltazar, P., Rodríguez, P., Rivera, W. & Valdivieso, V. 2000. Cultivo experimental de *Octopus mimus* Gould, 1852 en el Perú. *Revista Peruana de Biología*, 7(2): 151-160.

Banas, P.T., Smith, D.E. & Biggs, D.C. 1982. An association between a pelagic octopod, *Argonauta* sp. Linnaeus 1758, and aggregate salps. *Fishery Bulletin,* 80: 648-650.

Barratt, I.M. & Allcock, A.L. 2010. Ageing octopods from stylets: development of a technique for permanent preparations. *ICES Journal of Marine Science*, 67: 1452–1457.

Barratt, I.M., Johnson, M.P. & Allcock, A.L. 2007. Fecundity and reproductive strategies in deep-sea incirrate octopuses (Cephalopoda: Octopoda). *Marine Biology*, 150: 387–398.

Barratt, I.M., Johnson, M.P., Collins, M.A. & Allcock, A.L. 2008. Female reproductive biology of two sympatric incirrate octopod species, *Adelieledone polymorpha* (Robson 1930) and *Pareledone turqueti* (Joubin 1905) (Cephalopoda: Octopodidae), from South Georgia. *Polar Biology*, 31(5): 583-594.

Barry, J.P. & Drazen, J.C. 2007. Response of deep-sea scavengers to ocean acidification and the odour from a dead grenadier. *Marine Ecology - Progress Series*, 350: 193-207.

Barry, P.D., Tamone, S.L. & Tallmon, D.A. 2010. Evaluation of the capture efficiency and size selectivity of four pot types in the prospective fishery for North Pacific giant octopus (*Enteroctopus dofleini*). *Fishery Bulletin*, 108 (1): 39-44.

Barry, P.D., Tamone, S.L. & Tallmon, D.A. 2011. A comparison of tagging methodology for North Pacific giant octopus *Enteroctopus dofleini*. *Fisheries Research*, 109 (2-3): 370-372.

Belcari, P., Biagi, F. & Fedi, E. 1990a. Relazione taglia-peso in *Eledone cirrhosa*. *Oebalia Supplement* 16(2): 591-594.

Belcari, P., Fedi, E. & Saston, P. 1990b. Analysis of the sexual development of *Eledone cirrhosa* (Cephalopoda, Octopoda) in the northern Tyrrhenian Sea through two maturity indices. *Rapports et Proces-verbaux des Reunions Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee*, 32(1): 241-248.

Belcari, P., Matricardi, G. & Wurtz, M. 1992. Distribution and abundance of the octopus *Eledone cirrhosa* in the Tyrrhenian Sea, central Mediterranean. *Fisheries Research*, 13(1): 53-66.

Belcari, P., Cuccu, D., González, M., Srairi, A. & Vidoris, P. 2002. Distribution and abundance of *Octopus vulgaris* Cuvier, 1797 (Cephalopoda: Octopoda) in the Mediterranean Sea. *Scientia Marina,* 66: 157-166.

Belcari, P., Tserpes, G., González, M., Lefkaditou, E., Marceta, B., Manfrin, G.P. & Souplet, A. 2002. Distribution and abundance of *Eledone cirrhosa* (Lamarck, 1798) and *E. moschata* (Lamarck, 1798) (Cephalopoda: Octopoda) in the Mediterranean Sea. *Scientia Marina,* 66: 143-155.

Bello, G. 1993. *Tremoctopus violaceus* (Cephalopoda: Tremoctopodidae) in the stomach contents of a swordfish from the Adriatic Sea. *Bolletino Malacologico*, 29(1-4): 45-48.

Bello, G. 2004. First record of paralarvae of *Scaeurgus unicirrhus* (Cephalopoda: Octopodidae). *Journal of Plankton Research*, 26 (12): 1555-1558.

Bello, G. 2006. Signs of multiple spawning in *Graneledone pacifica* (Cephalopoda: Octopodidae). *Journal of The Marine Biological Association of The United Kingdom*, 86(5): 1183-1186.

Bello, G. & Rizzi, E. 1990. Comportamento di tre femmina di *Argonauta argo* in Acquario (Cephalopoda: Argonautidae). *Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano,*131: 450-452.

Belluscio A., Ardizzone G.D., Conticelli M. & Pellicciari C. 2004. Prima documentazione fotografica di una femmina ovigera di *Tremoctopus* sp. (Octopoda, Tremoctopodidae) nel Mediterraneo. *Biologia Marina Mediterranea*, 11(2): 556-559.

Benedict, J.E. 1886. Surface-collecting on the *Albatross*. *Science,* 7: 300-301.

Berry, S.S. 1912. A review of the cephalopods of western North America. *Bulletin U.S. Bureau Fisheries*, 30: 269-336.

Berry, S.S. 1914. The Cephalopoda of the Hawaiian Islands. *Bulletin of the Bureau of Fisheries* 32 (1912), 255-362.

Berry, S.S. 1917. Cephalopoda. *Scientific Reports of the Australasian Antarctic Expeditions, 1911-1914, Zoology & Botany*, 14(2): 1-39.

Berry, S.S. 1918. Report on the Cephalopoda obtained by the F.I.S. “Endeavour” in the Great Australian Bight and other southern Australian localities. *Biological Results of the Fishing Experiments Carried Out by the F.I.S. “Endeavour”, 1909-14*, 4: 201-298.

Berry, S.S. 1949. A new *Opisthoteuthis* from the eastern Pacific. *Leaflets in Malacology*, 1(6): 23-26.

Berry, S.S. 1952. The flapjack devilfish, *Opisthoteuthis*, in California. *California Fish and Game,* 38 (2): 183-188.

Berry, S.S. 1953. Preliminary diagnosis of six west American species of octopus. *Leaflets in Malacology*, 1(10): 51-58.

Berry, S.S. 1955a. On recent Californian occurrences of the rare octopod *Ocythoe*. *California Fish and Game*, 41(2): 177-181.

Berry, S.S. 1955b. The male flapjack devilfish. *California Fish and Game*, 41(3): 219-224.

Berry, S.S. 1966. Additional records of flapjack devilfish from California waters. *California Fish & Game*, 52 (2): 124.

Biandolino, F., Portacci, G. & Prato, E. 2010. Influence of natural diet on growth and biochemical composition of *Octopus vulgaris* Cuvier, 1797. *Aquaculture International,* 18(6): 1163-1175.

Bizikov, V.A. 2004. The shell in Vampyropoda (Cephalopoda): morphology, functional role and evolution. *Ruthenica* (Supplement 3), 2004: 1-88.

Bizikov, V.A. 2008. *Evolution of the Shell in Cephalopoda*. Moscow, Russia, VNIRO Publishing. 448 pp.

Boal, J.G. 1991. Complex learning in *Octopus bimaculoides*. *American Malacological Bulletin*, 9: 75-80.

Boal, J.G., Dunham, A.W., Williams, K.T. & Hanlon, R.T. 2000. Experimental evidence for spatial learning in octopuses (*Octopus bimaculoides*). *Journal of Comparative Psychology*, 114 (3): 246-252.

Bogolepova, I.I. 1957. [Concerning the existence of *Dicyemodeca* Wheeler, 1897]. *Transactions of the Leningrad Society of Naturalists (St. Petersburg)*, 73: 52-57. [In Russian].

Bogolepova-Dobrokhotova, I.I. 1963. [The current classification of the dicyemids]. *Parazitologicheskii Sbornik*, 21: 259-271. [In Russian].

Boletzky, S.v. 1969. Zum vergleich von *Octopus vulgaris*, *O. joubini* und *O. briareus*. *Revue Suisse de Zoologie*, 76: 716-726.

Boletzky, S.v. 1973. Structure et fonctionnement des organes de Kolliker chez les jeunes octopodes (Mollusca, Cephalopoda). *Zeitschrift fur Morphologie der Tiere*, 75: 315-327.

Boletzky, S.v. 1975. Le développement d'*Eledone moschata* (Mollusca, Cephalopoda) élevèe au laboratoire. *Bulletin Societe. zoologique Francaise*, 100: 361-367.

Boletzky, S.v. 1977. Post-hatching behaviour and mode of life in cephalopods. *Symposia of the Zoological Society of London*, 38: 557-567.

Boletzky, S.v. 1978-1979. Nos connaissances actuelles sur le developpement des octopodes. *Vie et Milieu*, 28/29 (series AB): 85-120.

Boletzky, S.v. 1980. Note preliminaire sur quelques embryons d'octopodes cirromorphes (Mollusca, Cephalopoda). *Haliotis*, 10 (2): 23.

Boletzky, S.v. 1982. On eggs and embryos of cirromorph octopods. *Malacologia*, 22 (1-2): 197-204.

Boletzky, S.v. 1983. Laboratory observations on a female *Argonauta argo* (Mollusca: Cephalopoda). *Rapports et Proces-verbaux des Reunions Commission internationale pur l'Exploration Scientifique de la Mer Mediterranee, Monaco,* 28: 289-290.

Boletzky, S.v. 1986. Reproductive strategies in cephalopods: variation and flexibility of life-history patterns. *In* Porchet, M., Andries, J. C., Dhainaut, A. (eds.) *Advances in invertebrate reproduction*, Vol. 4. Elsevier Publishers, New York, p. 379-389.

Boletzky, S.v 1999. Breve mise au point sur la classification des cephalopodes actuels. *Bulletin de la Societé Zoologique de France*, 124(3): 271–278.

Boletzky, S.v., Fuentes, M. & Offner, N. 2002. Developmental features of *Octopus macropus* Risso, 1826 (Mollusca, Cephalopoda). *Vie et Milieu,* 52: 209-215.

Bonichon-Laubier, A. 1971. [Presence of neurosecretory cells in the subpedunculated lobe of a cephalopod, *Pteroctopus tetracirrhus*. Relations to sexual maturation] *Comptes Rendus Hebdomadaires des Séances de L'académie des Sciences. Série D: Sciences Naturelles*, 272(16): 2086-2088 [In French].

Bonnaud, L., Ozouf-Costaz, C. & Boucher-Rodoni, R 2004. A molecular and karyological approach to the taxonomy of *Nautilus*. *Comptes rendus Biologies*, 327(2): 133-138.

Boone, L. 1928. Mollusks from the Gulf of California and the Perlas Islands. *Bulletin of the Bingham Oceanographic Collection*, 2 (5): 1-17.

Borer, K.T. 1971. Control of food intake in *Octopus briareus* Robson. *Journal of Comparative and Physiological Psychology*, 75(2): 171-185.

Boucaud Camou, E. & Roper, C.F.E. 1995. Digestive enzymes in paralarval cephalopods. *Bulletin of Marine Science*, 57 (2): 313-p327.

Boyle, P.R. 1981. Methods for the aquarium maintenance of the common octopus of British waters, *Eledone cirrhosa*. *Laboratory Animals*, 15: 327-331.

Boyle, P.R. 1983. *Eledone cirrhosa*. *In* P.R. Boyle, ed. Cephalopod Life Cycles. Vol. I, Species Accounts. Academic Press, London. Pp. 365-386.

Boyle, P.R. 1986a. A descriptive ecology of *Eledone cirrhosa* (Mollusca: Cephalopoda) in Scottish waters. *Journal of the Marine Biological Association, U.K*., 66: 855-865.

Boyle, P.R. 1986b. Responses to water-borne chemicals by the octopus *Eledone cirrhosa* (Lamarck, 1798). *Journal of Experimental Marine Biology & Ecology*, 104: 23-30.

Boyle, P.R. 1997. *Eledone cirrhosa*: biology and fisheries in the eastern Atlantic and Mediterranean. *In* M.A. Lang & F.G. Hochberg, eds. *The Fishery and Market Potential of* Octopus *in California*. Washington, D.C., Smithsonian Institution. (Workshop Proceedings). Pp. 99-103.

Boyle, P.R. & Chevis, D. 1992. Egg development in the octopus *Eledone cirrhosa*. *Journal of Zoology*, *London*, 227: 623-638.

Boyle, P.R. & Daly, H.I. 2000. Fecundity and spawning in a deep-water cirromorph octopus. *Marine Biology*, 137: 317-324.

Boyle, P.R. & Dubas, F. 1981. Components of body pattern displays in the octopus *Eledone cirrhosa* (Mollusca: Cephalopoda). *Marine Behaviour & Physiology*, 8: 135-148.

Boyle, P.R. & Knobloch, D. 1981. Hole boring of crustacean prey by the octopus *Eledone cirrhosa*. *Journal of Zoology*, 193: 1-10.

Boyle, P.R. & Knobloch, D. 1982a. On growth of the octopus *Eledone cirrhosa*. *Journal of the Marine Biological Association*, *U.K.*, 62: 277-296.

Boyle, P.R. & Knobloch, D. 1982b. Sexual maturation in the octopus *Eledone cirrhosa* Lamarck. *Malacologia*, 22 (1-2): 189-196.

Boyle, P.R. & Knobloch, D. 1983. The female reproductive cycle of the octopus, *Eledone cirrhosa*. *Journal of the Marine Biological Association of the United Kingdom*, 63: 71-83.

Boyle, P.R. & Knobloch, D. 1984a. Male reproductive maturity in the octopus, *Eledone cirrhosa* (Cephalopoda: Octopoda). *Journal of the Marine Biological Association of the United Kingdom*, 64: 573-579

Boyle, P.R. & Knobloch, D. 1984b. Reproductive maturity in fresh and aquarium-held *Eledone cirrhosa* (Cephalopoda: Octopoda). *Journal of the Marine Biological Association of the United Kingdom*, 64: 581-585.

Boyle, P. & Rodhouse, P. 2004. *Cephalopods: ecology and fisheries.* Blackwell Publishers, Iowa. 452 pp.

Boyle, P.R. & Thorpe, R.S. 1984. Optic gland enlargement and female gonad maturation in a population of the octopus *Eledone cirrhosa*: a multivariate analysis. *Marine Biology*, 79 (2): 127-132.

Boyle, P.R., Collins, M.A. & Williamson, G.R. 1998. The cephalopod by-catch of deep-water trawling on the Hebrides Slope. *Journal of the Marine Biological Association of the United Kingdom,* 78: 1023-1026.

Boyle, P.R., Grisley, M.S. & Robertson, G. 1986. Crustacea in the diet of *Eledone cirrhosa* (Mollusca: Cephalopoda) determined by serological methods. *Journal of the Marine Biological Association*, *U.K.*, 66: 867-879.

Boyle, P.R., Mangold, K. & Ngoile, M. 1988. Biological variation in *Eledone cirrhosa* (Cephalopoda: Octopoda): simultaneous comparison of North Sea and Mediterranean populations. *Malacologia*, 29 (1): 77-87.

Bradbury, H.E. 1974. The gross morphology of some aspects of the development of the octopod *Eledone cirrosa* (Lamarck) (Eledoninae, Incirrata). *Memorial University of Newfoundland, Marine Science Research Laboratory*, *Technical Report*, No. 13: 1-30.

Brandt, S.B. 1983. Pelagic squid associations with a warm core eddy of the East Australian Current. *Australian Journal of Marine and Freshwater Research,* 34: 573-585.

Bresciani, J. & Lützen, J. 1994. Morphology and anatomy of *Avdeevia antarctica*, new genus, new species (Copepoda: Harpacticoida: Tisbidae), parasitic on an Antarctic cephalopod. *Journal of Crustacean Biology*, 14 (4): 744-751.

Brock, D.J. 2006. A two-chambered trap reduces within-trap predation by octopus on rock lobsters in aquarium trials. *Fisheries Research*, 80 (2-3): 129-135.

Brock, D.J. & Ward, T.M. 2004. Maori octopus (*Octopus maorum*) bycatch and southern rock lobster (*Jasus edwardsii*) mortality in the South Australian rock lobster fishery. *Fishery Bulletin,* 102: 430-440.

Bustamante, P., Cherel, Y., Caurant, F. & Miramand, P. 1998. Cadmium, copper and zinc in octopuses from Kerguelen Islands, Southern Indian Ocean. *Polar Biology*, 19 (4): 264-271.

Butler, M.J. & Lear, J.A. 2009. Habitat-based intraguild predation by Caribbean reef octopus *Octopus briareus* on juvenile Caribbean spiny lobster *Panulirus argus*. *Marine Ecology-Progress Series*, 386: 115-122.

Cabello, A.M. 2004. Freshness parameters of mollusks. *Revista Cientifica-Facultad de Ciencias Veterinarias*, 14 (5): 457-466.

Caballero-Alfonso, A., Ganzedo-López, U., Díez-Díez, G. & Castro, J.J. 2008. New record of *Ocythoe tuberculata* (Cephalopoda: Ocythoidae) in the North-east Atlantic related to sea warming. *Journal of the Marine Biological Association of the United Kingdom 2 (JMBA2) - Biodiversity Records*, 6153.

Cabranes, C., Fernandez-Rueda, P. & Martínez, J.L. 2008. Genetic structure of *Octopus vulgaris* around the Iberian Peninsula and Canary Islands as indicated by microsatellite DNA variation. *ICES Journal of Marine Science,* 65(1): 12-16.

Caddy, J.F. & Rodhouse, P.G.K. 1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries? *Reviews in Fish Biology and Fisheries*, 8: 431-444.

Cai, H. 2009. Culture Experiment of *Octopus vulgaris* in Lower Tunnel Cement Pool. *Journal of Zhejiang Ocean University (Natural Science],* 2009-02.

Cai, H., Zhuang, D., Ye P. & Lin, L. 2009. Experiment on stock culturing, spawning and hatching of *Octopus vulgaris*. *Marine Fisheries*, 2009-01.

Cai, H., Zhuang, D., Ye, P., Fu, H. & Wang, Y. 2007. Net cage and cement tank culture of common Atlantic octopus *Octopus vulgaris* in Nanji Island, Zhejiang Province. *South China Fisheries Science*, 2007-02.

Caldwell, R.L. 2005. An observation of inking behavior protecting adult *Octopus bocki* from predation by green turtle (*Chelonia mydas*) hatchlings. *Pacific Science*, 59 (1): 69-72.

Canali, E., Ponte, G., Belcari, P., Rocha, F. & Fiorito, G. 2011. Evaluating age in *Octopus vulgaris*: estimation, validation and seasonal differences. *Marine Ecology Progress Series,* 441: 141-149.

Cardoso, F. 1991. First record of net collected *Ocythoe tuberculata* (Cephalopoda, Octopoda) from Peruvian Waters. *American Malacological Bulletin,* 8: 143-144.

Cardoso, F. & Paredes, C. 1998. Family Ocythoidae (Cephalopoda: Octopoda) in Peru. *Revista Peruana de Biología*, 5: 129-137.

Cardoso, F., Villegas, P. & Estrella, **C.** 2004. Observacions sobre la biología de *Octopus mimus* (Cephalopoda: Octopoda) en la costa peruana. *Revista Peruana de Biología*, 11(1): 45-50.

Carrasco, J.F., Arronte, J.C. & Rodríguez, C. 2006. Paralarval rearing of the common octopus, *Octopus vulgaris* (Cuvier). *Aquaculture Research,* 37(15): 1601-1605.

Carreira, G.P. & Gonçalves, J.M. 2009. Catching *Octopus vulgaris* with traps in the Azores: first trials employing Japanese baited pots in the Atlantic. *Marine Biodiversity Records,* 2: e114.

Carvalho, J.M.N. & Reis, C.S. 2003. Contributions to knowledge on the maturation and fertility of the common octopus *Octopus vulgaris* Cuvier, 1797 on the Portuguese coast. *Biologia,* 19(1-4): 473-482.

Casaux, R., Baroni, A. & Carlini, A. 1997. The diet of the Weddell seal *Leptonychotes weddelli* at Harmony Point, South Shetland Islands. *Polar Biology*, 18 (6): 371-375.

Castellanos, Z.A. de & Menni, R. 1969. Sobre dos pulpos costeros de la Argentina. *Neótropica,* 15(47): 89-94, I-VIII.

Castley, J.G., Cockcroft, V.G. & Kerley, G.I.H. 1991. A note on the stomach contents of fur seals *Arctocephalus pusillus pusillus* beached on the south east coast of South Africa. *South African Journal of Marine Science,* 11: 573-577.

Castro-Fuentes, H., Olivares-Paz, A., Quintana-Fellay, A. & Zuñiga- Romero, O. 2002. Descripción del desarrollo embrionario y paralarvas de *Octopus mimus* Gould, 1852 (Mollusca: Cephalopoda) en cautiverio. *Estudios Oceanológicos*, 21: 13-25.

Casu, M., Maltagliati, F., Meloni, M., Casu, D., Cossu, P., Binelli, G., Curini-Galletti, M. & Castelli, A. 2002. Genetic structure of *Octopus vulgaris* (Mollusca, Cephalopoda) from the Mediterranean Sea as revealed by a microsatellite locus. *Italian Journal of Zoology,* 69(4): 295-300.

Caverivière, A., Domain, F. & Diallo, A. 1999. Observations on the influence of temperature on the length of embryonic development in *Octopus vulgaris* (Senegal). *Aquatic Living Resources,* 12(2): 151.

Caverivière, A. Thiam, M. & Jouffre, D., eds. 2002. Le Poulpe *Octopus vulgaris*: Sénégal et Côtes Nord-Ouest Africaines. Paris, France, IRD Editions. 385 pp.

Ceriola, L., Accadia, P., Mannini, P., Massa, F., Milone, N. & Ungaro, N. 2008. A bio-economic indicators suite for the appraisal of the demersal trawl fishery in the southern Adriatic Sea (central Mediterranean). *Fisheries Research*, 92 (2-3): 255-267.

Chang, D.J. & Kim, D.A. 2003. Characteristics by the Behaviour and Habits of the Common Octopus (*Octopus minor*). *Journal - Korean Fisheries Society*, 36: 735-742.

Chapela, A., González, A.F., Dawe, E.G., Rocha, F.J. & Guerra, A. 2006. Growth of common octopus (*Octopus vulgaris*) in cages suspended from rafts. *Scientia Marina,* 70(1): 121-129.

Cheah, D.M.Y., Wright, P.F.A., Holdway, D.A. & Ahokas, J.T. 1995. *Octopus pallidus* Cytochrome-P-450 - characterization and induction studies with Beta-Naphthoflavone and Aroclor-1254. *Aquatic Toxicology,* 33: 201-214.

Chédia, J., Widien, K. & Amina, B. 2010. Role of sea surface temperature and rainfall in determining the stock and fishery of the common octopus (*Octopus vulgaris*, Mollusca, Cephalopoda) in Tunisia. *Marine Ecology-an Evolutionary Perspective,* 31(3): 431-438.

Cheng, M.A.W. 1996. *The Reproductive Biology of Two Species of Pygmy Octopuses*, *Hapalochlaena lunulata* and *Octopus bocki*. Berkeley, California, University of California. (Ph.D. dissertation).

Cheng, M.A.W. & Caldwell, R.L. 2000. Sex identification and mating in the blue-ringed octopus, *Hapalochlaena lunulata*. *Animal Behaviour,* 60: 27-33.

Cherel, Y., Weimerskirch, H. & Trouvé, C. 2000. Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. *Marine Ecology-Progress Series*, 207: 183-199.

Cherel, Y., Weimerskirch, H. & Trouvé, C. 2001. Dietary evidence for spatial foraging segregation in sympatric albatrosses (*Diomedea* spp.) rearing chicks at Iles Nuageuses, Kerguelen. *Marine Biology*, 141(6): 1117-1129

Chesalin, M.V. & Zuyev, G.V. 2002. Pelagic cephalopods of the Arabian Sea with an emphasis on *Sthenoteuthis oualaniensis. Bulletin of Marine Science,* 71: 209-221.

Childerhouse, S., Dix, B. & Gales, N. 2001. Diet of New Zealand sea lions (*Phocarctos hookeri*) at the Auckland Islands. *Wildlife Research*, 28 (3): 291-298.

Chotiyaputta, C. 1993. Cephalopod resources of Thailand. *In* T. Okutani, R.K. O'Dor & T. Kubodera (Eds), *Recent Advances in Fisheries biology.* (Tokai University Press: Tokyo). Pp. 71-80.

Chotiyaputta, C., Nootmorn, P. & Jirapunpipat, K. 2002. Review of cephalopod fishery production and long term changes in fish communities in the Gulf of Thailand. *Bulletin of Marine Science*, 71(1): 223-238.

Chun, C. 1910. Die Cephalopoden. Oegopsida. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee Expedition auf dem Dampfer "Valdivia" 1898-1899*, 18(1): 1-401.

Chun, C. 1911. *Cirrothauma, ein Blinder Cephalopod*. Doctoral dissertation Leipzig. 210 pp.

Chun, C. 1913. Cephalopoda from the "Michael Sars" North Atlantic Deep-sea Expedition, 1910. *Report of the Scientific Results of the "Michael Sars" North Atlantic Deep-Sea Expedition, 1910, Zoology*, 3 (1): 1-28.

Chun, C. 1915. Die Cephalopoden II: Myopsida, Octopoda. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899*, 18 (2): 405-552.

Cigliano, J.A. 1993. Dominance and den use in *Octopus bimaculoides*. *Animal Behaviour*, 46: 677-684.

Clarke, M.R. 1996. The role of cephalopods in the world's oceans: general conclusions and the future. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences,* 351: 1105-1112.

Clarke, M.R. 1988. Evolution of recent cephalopods. *In* M.R. Clarke & E.R. Trueman, eds. *The Mollusca. Palaeontology and Neontology of Cephalopods*. Academic Press, London, Vol. 12: 331–340.

Cobb, C.S., Pope S.K. & Williamson, R. 1995a. Circadian rhythms to light-dark cycles in the Lesser octopus, *Eledone cirrhosa*. *Marine and Freshwater Behaviour & Physiology*, 26 (1): 47-58.

Cobb, C.S., Williamson, R. & Pope, S.K. 1995b. The responses of the epistellar photoreceptors to light and their effect on circadian rhythms in the lesser octopus, *Eledone cirrhosa*. *Marine and Freshwater Behaviour & Physiology*, 26(1): 59-70.

Cockcroft, V.G., Haschick, S.L. & Klages, N.T.W. 1993. The diet of Risso's dolphin, *Grampus griseus* (Cuvier, 1812), from the east coast of South Africa. *International Journal of Mammalian Biology,* 58(5): 286-293.

Collins, M.A. 2002. Cirrate octopods from Greenland and Iceland waters. *Journal of the Marine Biological Association of the United Kingdom*, 82: 1035-1036.

Collins, M.A. 2003. The genus *Grimpoteuthis* (Octopoda: Grimpoteuthidae) in the north-east Atlantic, with descriptions of three new species. *Zoological Journal of the Linnean Society*, 139: 93-127.

Collins, M.A. 2004. *Cryptoteuthis brevibracchiata*: a new species and genus of cirrate octopod (Octopoda: Cirrata). *Journal of Molluscan Studies*, 70: 263-267.

Collins, M.A. 2005. *Opisthoteuthis borealis*: A new species of cirrate octopod from Greenland waters. *Journal of the Marine Biological Association of the United Kingdom*, 85: 1475-1479.

Collins, M.A. & Henriques, C. 2000. A revision of the Family Stauroteuthidae (Octopoda: Cirrata) with redescriptions of *Stauroteuthis syrtensis* and *S. gilchristi*. *Journal of the Marine Biological Association of the United Kingdom*, 80: 685-697.

Collins, M.A. & Villanueva, R. 2006. Taxonomy, ecology and behaviour of the cirrate octopods. *Oceanography and Marine Biology: An Annual Review*, 44: 277-322.

Collins, M.A., Allcock, A.L. & Belchier, M. 2004. Cephalopods of the South Georgia slope. *Journal of the Marine Biological Association of the United Kingdom*, 84: 415-419.

Collins, M.A., Laptikhovsky, V. & Strugnell, J.M. 2010. Expanded description of *Opisthoteuthis hardyi* based on new specimens from the Patagonian slope. *Journal of the Marine Biological Association of the United Kingdom*, 90: 605-611.

Collins, M.A., O'Dea, M. & Henriques, C. 2001a. A large *Cirroteuthis magna* (Cephalopoda: Cirrata) caught on the Cape Verde Terrace (North Atlantic) *Journal of the Marine Biological Association of the United Kingdom*, 81: 357-358.

Collins, M.A., Yau, C., Allcock, A.L. & Thurston, M.H. 2001b. Distribution of deep-water benthic and bentho-pelagic cephalopods from the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 81: 105-117.

Collins, M.A., Lordan, C., Flannery, K., Quigley, D.T.G. & Howard, F.G. 1997. New records of cephalopods caught in Irish and Scottish waters. *Journal of the Marine Biological Association of the United Kingdom*, 77: 561-564.

Collins, M.A., Yau, C., Boyle, P.R., Friese, D., Piatkowski, U. 2002. Distribution of cephalopods from plankton surveys around the British Isles. *Bulletin of Marine Science*, 71(1): 239-254.

Conners, E. 2010. Field trials of octopus tagging: pot gear a success. *Quarterly Report of the Alaska Fisheries Science Center*, April 2010: 26-27.

Conrad, T.A. 1854. Monograph of the genus *Argonauta* Linne, with descriptions of five new species. *Journal of the Academy of Natural Sciences of Philadelphia,* 2: 331-334.

Corsini, M. & Lefkaditou, E. 1994. Occurrence of *Ocythoe tuberculata* (Cephalopoda: Ocythoidae) in Greek waters. *Bolletino Malacologico*, 30: 304-310

Cortez, T. & Cotton, W. 1992. Diagnóstico de las Pesquerías del Pulpo de la I Región de Chile. *Informe Final, Proyecto SERPLAC/UNAP, Iquique, Chile*. (Diciembre, 1992). 200 pp.

Cortez, T. & González, A.F. 1988. Aspectos Biológico-Pesqueros del Pulpo en la Primera Región (Tarapacá) de Chile. *Informe Final, Departamento de Ciencias del Mar, Universidad Nacional Arturo Prat (UNAP), Iquique, Chile*. 38 pp.

Cortez, T., Castro, B.G., & Guerra, A. 1995a. Feeding dynamics of *Octopus mimus* (Mollusca, Cephalopoda) in northern Chile Waters. *Marine Biology,* 123: 497-503.

Cortez, T., Castro, B.G., & Guerra, A. 1995b. Reproduction and condition of female *Octopus mimus* (Mollusca, Cephalopoda). *Marine Biology,* 123: 505-510.

Cortez, T., Castro, B.G., & Guerra, A. 1998. Drilling behaviour of *Octopus mimus* Gould. *Journal of Experimental Marine Biology and Ecology,* 224: 193-203.

Cortez, T., González, A.F. & Guerra, A. 1999a. Growth of cultured *Octopus mimus* (Cephalopoda, Octopodidae). *Fisheries Research,* 40: 81-89.

Cortez, T., González, A.F. & Guerra, A. 1999b. Growth of *Octopus mimus* (Cephalopoda, Octopodidae) in wild populations. *Fisheries Research,* 42: 31-39.

Cosgrove, J.A. 2003. An *in situ* observation of webover hunting by the Giant Pacific Octopus, *Enteroctopus dofleini* (Wülker, 1910). *Canadian Field Naturalist*, 117(1): 117-118.

Cosgrove, J.A. & McDaniel, N. 2009. *Super Suckers: The Giant Pacific Octopus and Other Cephalopods of the Pacific Coast*. Madeira Park, British Columbia, Canada, Harbour Publishing. 208 pp.

Costa, P.A.S. & Fernandes, F.D. 1993. Seasonal and spatial changes of cephalopods caught in the Cabofrio (Brazil) upwelling ecosystem. *Bulletin of Marine Science*, 52 (2): 751-759.

Costa, P.R., Rosa, R., Pereira, J. & Sampayo, M.A.M. 2005. Detection of domoic acid, the amnesic shellfish toxin, in the digestive gland of *Eledone cirrhosa* and *E. moschata* (Cephalopoda, Octopoda) from the Portuguese coast. *Aquatic Living Resources*; 18 (4): 395-400.

Cotton, B.C. 1948. Paper nautilus. *The South Australian Naturalist,* 25: 8.

Crook, R. 2008. Behavioral correlates of learning and memory in chambered nautilus, *Nautilus pompilius*. *Dissertation Abstracts International*, 69, (5, suppl. B): 196.

Cuccu, D., Damele, F., Follesa, M.C., Murenu, M. & Cau, A. 2003. Aspetti biologici di *Eledone cirrhosa* (Cephalopoda Octopoda) nei mari circostanti la Sardegna. *Biologia Marina Mediterranea*: 10 (1): 119-126.

Cuccu, D., Mereu, M., Follesa, M.C., Deiana, A.M. & Cau, A. 2011. *Bathypolypus sponsalis* (Cephalopoda: Octopoda) from the central western Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 91 (2): 549–553.

Cuccu, D., Mereu, M., Cannas, R., Follesa, M.C., Cau, A. & Jereb, P. 2009. Morphology, biology and molecular characterizations of *Opisthoteuthis calypso* (Cephalopoda: Octopoda) from the Sardinian Channel (central western Mediterranean). *Journal of the Marine Biological Association of the United Kingdom*, 89 (8): 1709–1715.

Cuccu D., Mereu M., Cau Al., Pesci P. & Cau A. 2013a. Reproductive development versus estimated age and size in a wild Mediterranean population of *Octopus vulgaris* (Cephalopoda: Octopodidae), *Journal of the Marine Biological Association of the United Kingdom*, 93(3): 843-849.

Cuccu D., Mereu M., Porcu C., Follesa M.C., Cau Al. & Cau A. 2013b. Development of sexual organs and fecundity in *Octopus vulgaris* Cuvier, 1797 from the Sardinian waters (Mediterranean Sea). *Mediterranean Marine Science*, 14 (2): 270-277.

Cupka, D.M. 1970. Observations on the Biology and Bathymetric Distribution of the Bathybenthic Octopod*, Opisthoteuthis agassizii* (Cephalopoda: Octopoda) in the Gulf of Mexico*.* M.Sc. Thesis. Tallahassee, Florida, USA, Florida State University. 108 pp.

Cuvier, G. 1797. `Tableau élémentaire de l’histoire naturelle des animaux.’ (Paris.) 710 pp.

Czaker R. 2002. Virus-like particles in an Antarctic *Aggregata* sp.: I. Sporogonial stages. *Journal of Submicroscopic Cytology and Pathology*, 34 (2): 191-197.

Dall, W.H. 1902. Illustrations and descriptions of new, unfigured, or imperfectly known shells chiefly American in the U.S. National Museum. *Proceedings of the U.S. National Museum,* 24: 499-566.

Dall, W.H. 1908. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California….XIV. The Mollusca and Brachiopoda. *Bulletin of the Museum of Comparative Zoology, Harvard,* 43: 205-487.

Daly, H.I. & Peck, L.S. 2000. Energy balance and cold adaptation in the octopus *Pareledone charcoti*. *Journal of Experimental Marine Biology and Ecology*, 245(2): 197-214.

Daly, H.I. & Rodhouse, P.G. 1994. Comparative morphology of 2 sympatric *Pareledone* species from South Georgia. *Antarctic Science*, 6(2): 163-169.

Daneri, G.A., Carlini, A.R. & Rodhouse, P.G.K. 2000. Cephalopod diet of the southern elephant seal, *Mirounga leonina*, at King George Island, South Shetland Islands. Antarctic Science,12(1) 16-19.

Davis, L. E. 2005. *Nautilus*; portrait of a living fossil. *The Compass*, 79 (2): 45-51.

Defeo, O. & Castilla, J.C. 1998. Harvesting and economic patterns in the artisanal *Octopus mimus* (Cephalopoda) fishery in a northern Chile cove. *Fisheries Research,* 38: 121-130.

Delgado, M., Gairin, J.I., Carbo, R. & Aguilera, C. 2011. Growth of *Octopus vulgaris* (Cuvier, 1797) in tanks in the Ebro Delta (NE Spain): effects of temperature, salinity and culture density. *Scientia Marina,* 75(1): 53-59.

Dell, R.K. 1952. The Recent Cephalopoda of New Zealand. *Dominion Museum Bulletin,* 16: 1-157.

Delle Chiaje, **S.** 1839-1841. *In* A.E. de Férussac & A. d’Orbigny. 1834-1848. *Histoire naturelle générale et particulière Céphalopodes Acétabulifères Vivants et Fossiles*. Paris, J.B. Balliere. 361 pp. + 144 pls, p. 70.

Demarcq, H. & Faure, V. 2000. Coastal upwelling and associated retention indices derived from satellite SST. Application to *Octopus vulgaris* recruitment. *Oceanologica Acta,* 23(4): 391-408.

Demicheli, M., Martínez, A., Ortega, L., Scarabino, F., Maytía, S. & Demicheli, A. 2006. Mass stranding of *Argonauta nodosa* Lightfoot, 1786 (Cephalopoda, Argonautidae) along the Uruguayan coast (southwestern Atlantic). *Revista de Biología Marina y Oceanografía,* 41: 147-153.

De Rusha, R.H., Forsythe, J.W. & Hanlon, R.T. 1987. Laboratory growth, reproduction and life span of the Pacific Pygmy Octopus, *Octopus digueti*. *Pacific Science*, 41: 104-121 (1987).

De Wolf, T., Lenzi, S. & Lenzi, F. 2011. Paralarval rearing of *Octopus vulgaris* (Cuvier) in Tuscany, Italy. *Aquaculture Research,* 42(9): 1406-1414.

Diallo, M., Jouffre, D., Caveriviere, A. & Thiam, M. 2002. The demographic explosion of *Octopus vulgaris* in Senegal during the summer 1999. *Bulletin of Marine Science,* 71(2): 1063-1065.

Diekmann, R. & Piatkowski, U. 2002. Early life stages of cephalopods in the Sargasso Sea: Distribution and diversity relative to hydrographic conditions. *Marine Biology,* 141: 123-130.

Dollfus, R.-P. 1967. Enumeration des cestodes du plancton et des invertebres marins (7e contribution). Ann. Parasit. 42:155-178.

Domain, F., Jouffre, D. & Caverivière, A. 2000. Growth of *Octopus vulgaris* from tagging in Senegalese waters. *Journal of the Marine Biological Association of the United Kingdom,* 80(4): 699-705.

Domingues, P., García, S. & Garrido, D. 2010a. Effects of three culture densities on growth and survival of *Octopus vulgaris* (Cuvier, 1797). *Aquaculture International,* 18(2): 165-174.

Domingues, P., García, S., Hachero-Cruzado, I., Lopez, N. & Rosas, C. 2010b. The use of alternative prey (crayfish, *Procambarus clarki*, and hake, *Merlucius gayi*) to culture *Octopus vulgaris* (Cuvier 1797). *Aquaculture International,* 18(3): 487-499.

Dong, Z. 1976. On three new species of the genus *Octopus* (Octopoda, Cephalopoda) from the Chinese waters. *Studia Marina Sinica*, 11: 211-215.

Doubleday, Z.A. & Semmens, J.M. 2011. Quantification of the age-pigment lipofuscin in known-age octopus (*Octopus pallidus*): A potential tool for age determination. *Journal of Experimental Marine Biology and Ecology*, 397(1): 8-12.

Doubleday, Z.A., Pecl, G.T., Semmens, J.M. & Danyushevsky, L. 2008. Stylet elemental signatures indicate population structure in a holobenthic octopus species, *Octopus pallidus*. *Marine Ecology-Progress Series*, 371: 1-10.

Doubleday, Z., Semmens, J.M., Pecl, G. & Jackson, G. 2006. Assessing the validity of stylets as ageing tools in *Octopus pallidus*. *Journal of Experimental Marine Biology and Ecology*, 338(1): 35-42.

Drazen, J.C., Goffredi, S.K., Schlining, B. & Stakes, D.S. 2003. Aggregations of egg-brooding deep-sea fish and cephalopods on the Gorda Escarpment: a reproductive hot spot. *Biological Bulletin*, 205(1): 1-7.

Dubas, F. & Boyle, P.R. 1985. Chromatophore motor units in *Eledone cirrhosa* (Cephalopoda: Octopoda). *Journal of Experimental Biology*, 117: 415-431.

Dunker, W. 1852. *Argonauta gruneri* Dunker. *Zeitschrift für Malakozoologie,* 1852: 48.

Dunker, W. 1858. *Novitates Conchologicae. Mollusca Marina*. Cassel, Germany, Theodor Fischer. 144 pp.

Dunstan, A. J., Ward, P. D. & Marshall, N J. 2011. *Nautilus pompilius* life history and demographics at the Osprey Reef. *PloSone*, Z6(2):e16312 (doi:10.1371/journal.pone.0016312)

Duysak, Ö., Sendão, J., Borges, T., Tureli, C. & Erdem, Ü. 2008. Cephalopod distribution in Iskenderun Bay (eastern Mediterranean Turkey). *Journal of Fisheries Sciences.com*, 2(2): 118-125.

Ebersbach, A. 1915. Zur Anatomie von *Cirroteuthis umbellata* Fischer and *Stauroteuthis* sp. *Zeitschrift. Wissenschaftliche Zoologie*, 113: 361-483.

Ebert, D.A., Compagno, L.J.V. & Cowley, P.D. 1992. A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of southern Africa. *South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap,* 12: 601-609.

Edgar, G.J., Banks, S., Farina, J.M., Calvopina, M. & Martinez, C. 2004. Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos Archipelago. *Journal of Biogeography*, 31: 1107-1124.

Emanuel, C.F. & Martin, A.W. 1956. The composition of octopus renal fluid. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology*, 39(2): 226-234.

Engeser, T. & Bandel, K. 1988. Phylogenetic classification of coleoid cephalopods. *In* J. Wiedman & J. Kullman, eds. *Cephalopods Present and Past*. Schweizerbartsche Stuttgart, pp. 105–115.

Eschricht, D.F. 1836. *Cirroteuthis mulleri*, eine neue Gattung der Cephalopoden bildend. *Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum*, 18(2): 625-634.

Espino-Barr, E., Jiménez-Quiroz, M.C., Garcia-Boa, A. Cabral-Solis, E. & Puente-Gómez, M. 2007. Aspectos generales de la pesca del pulpo *Octopus hubbsorum* en la costa sur de Jalisco. *In* E. Rios-Jara, M.C. Esqueda-González & C.M. Galván-Villa, eds. *Estudios sobre Malacologia y Conquiliologia en México*, pp. 225-227. Guadalajara, Mexico, Universidad de Guadalajara.

FAO. 2012 *Fisheries and acquaculture statistics 2010.* FAO Yearbook. Rome. 78 pp.

Faraj, A. & Bez, N. 2007. Spatial considerations for the Dakha stock of *Octopus vulgaris*: indicators, patterns and fisheries impacts. *ICES Journal of Marine Science*, 64: 1820-1828.

Farias, A., Navarro, J.C., Cerna, V., Pino, S. & Uriarte, I. 2011. Effect of broodstock diet on the fecundity and biochemical composition of eggs of the Patagonian red octopus (*Enteroctopus megalocyathus* Gould, 1852). *Ciencias Marinas*, 37(1): 11-21.

Farias, A., Pereda, S.V., Uriarte, I., Dorner, J., Cuzon, G. & Rosas, C. 2010. Evaluating the effects of formulated moist diets on juveniles of Patagonian octopus *Enteroctopus megalocyathus* (Gould 1852). *Journal of Shellfish Research*, 29(4): 793-798.

Farias, A., Uriarte, I., Hernandez, J., Pino, S., Pascual, C., Caamal, C., Domingues, P. & Rosas, C. 2009. How size relates to oxygen consumption, ammonia excretion, and ingestion rates in cold (*Enteroctopus megalocyathus*) and tropical (*Octopus maya*) octopus species*. Marine Biology*, 156(8): 1547-1558.

Faure, V., Inejih, C.A., Demarcq, H. & Cury, P. 2000. The importance of retention processes in upwelling areas for recruitment of *Octopus vulgaris*: the example of the Arguin Bank (Mauritania). *Fisheries Oceanography,* 9(4): 343-355.

Fea, N.I., Harcourt, R. & Lalas, C. 1999. Seasonal variation in the diet of New Zealand fur seals (*Arctocephalus forsteri*) at Otago Peninsula, New Zealand. *Wildlife Research,* 26: 147-160.

Fernandez-Rueda, P. 2007. *Octopus vulgaris* (Mollusca: Cephalopoda) fishery management assessment in Asturias (north-west Spain). *Fisheries Research*, 83(2-3): 351-354.

Férussac, A.E. de & d'Orbigny, A. 1834-1848. *Histoire naturelle générale et particulière Céphalopodes Acétabulifères Vivants et Fossiles*. Paris, J.B. Balliere. 361 pp., 144 pls.

Feyjoo, P., Riera, R., Felipe, B. C., Skalli, A. & Almansa, E. 2011. Tolerance response to ammonia and nitrite in hatchlings paralarvae of *Octopus vulgaris* and its toxic effects on prey consumption rate and chromatophores activity. *Aquaculture International,* 19(1): 193-204.

Finn, J.K. 2009. *Systematics and Biology of the Argonauts or 'Paper Nautiluses' (Cephalopoda: Argonautidae).* Ph.D. dissertation. Bundoora, Victoria, Australia, La Trobe University. 548 pp.

Finn, J.K. 2010. Sinking Aristotle's sailing octopus. *Australasian Science*, 31(8): 25-27.

Finn, J.K. 2013. Taxonomy and biology of the argonauts (Cephalopoda: Argonautidae) with particular reference to Australian material. *Molluscan Research*., 33(3): 143-222.

Finn, J.K. & Norman, M.D. 2010. The argonaut shell: gas-mediated buoyancy control in a pelagic octopus. *Proceedings of the Royal Society of London B: Biological Sciences*, 277: 2967-2971.

Finn, J.K., Tregenza, T. & Norman, M.D. 2009. Defensive tool use in a coconut-carrying octopus. *Current Biology*, 19(23): R1069-R1070.

FIS (Fish Information and Services), 2009. First-ever octopus bred in captivity. 27 July 2009. http://www.fis.com/fis/worldnews.

Fonseca, T., Campos, A., Afonso-Dias, M., Fonesca, P. & Pereira, J. 2008. Trawling for cephalopods off the Portuguese coast - fleet dynamics and landings composition. *Fisheries Research*, 92(2-3): 180-188.

Forsythe, J.W. 1983. Observation on the reproductive biology of *Octopus burryi*. *American Malacological Bulletin*, 2: 92.

Forsythe, J.W. & Hanlon, R.T. 1985. Aspects of egg development, post-hatching behavior, growth and reproductive biology of *Octopus burryi* Voss, 1950 (Mollusca, Cephalopoda). *Vie et Milieu*, 35(3/4): 273-285.

Forsythe, J.W. & Hanlon, R.T. 1988a. Behavior, body patterning and reproductive biology of *Octopus bimaculoides* from California. *Malacologia* 29, 46-56.

Forsythe, R.W. & Hanlon, R.T. 1988b. Effect of temperature on laboratory growth, reproduction and life span of *Octopus bimaculoides. Marine Biology*, 98: 369-379.

Forsythe, J.W., & Hanlon, R.T. 1997. Foraging and associated behaviour by *Octopus cyanea*, 1849 on a coral atoll, French Polynesia. *Journal of Experimental Marine Biology and Ecology,* 209: 15–31.

Forsythe, J.W. & Toll, R.B. 1991. Clarification of the Western Atlantic Ocean pygmy octopus complex - the identity and life-history of *Octopus joubini* (Cephalopoda, Octopodinae). *Bulletin of Marine Science*, 49(1-2): 88-97,

Fry, B.G., Roelants, K. & Norman, J.A. 2009. Tentacles of Venom: Toxic Protein Convergence in the Kingdom Animalia. *Journal of Molecular Evolution*, 68: 311–321.

Fuentes, D. 1974. Pesca del pulpo en México. *Boletín Informativo, Secretaria de Pesca*, 10 pp.

Fuentes, L. & Iglesias, J. 2010. Release experiments with *Octopus vulgaris* Cuvier, 1797 in Galicia, NW Spain. First results on recapture rate, distribution and growth. *Life and Environment,* 60(1): 65-71.

Furuya, H. 2006. Three new species of dicyemid mesozoans (phylum Dicyemida) from *Amphioctopus fangsiao* (Mollusca: Cephalopoda), with comments on the occurrence patterns of dicyemids. *Zoological Science*, 23(1): 105-19.

Furuya, H. 2008. Redescription of *Dicyemennea nouveli* (Phylum: Dicyemida) from *Enteroctopus dofleini* (Mollusca: Cephalopoda: Octopoda). *The Journal of Parasitology*, 94(5): 1064-1070.

Furuya, H. 2010. A new dicyemid from *Benthoctopus sibiricus* (Mollusca: Cephalopoda: Octopoda). *The Journal of Parasitology*, 96(6): 1123-1127.

Furuya, H. & Hochberg, F.G. 2002. New species of Dicyemennea (Phylum: Dicyemida) in deep-water *Graneledone* (Mollusca: Cephalopoda: Octopoda) from the Antarctic. *Journal of Parasitology*, 88(2): 330-336.

Furuya, H. & Tsuneki, K. 2005. The occurrence pattern of dicyemid mesozoans (phylum Dicyemida) in *Amphioctopus fangsiao*. *Zoological Science*, 22(12):1432.

Furuya, H., Hochberg, F.G. & Short, R.B. 2002. *Dicyemennea canadensis* n.sp. (phylum Dicyemida) from *Bathypolypus arcticus* (Mollusca: Cephalopoda: Octopoda). *Journal of Parasitology*, 88(1): 119-123.

Furuya, H., Tsuneki, K. & Koshida, Y. 1992. 2 new species of the genus *Dicyema* (Mesozoa) from octopuses of Japan with notes on d-misakiense and d-acuticephalum. *Zoological Science*, 9(2): 423-437.

Furuya, H., Ota, M., Kimura, R. & Tsuneki, K. 2004. Renal organs of cephalopods: A habitat for dicyemids and chromidinids. *Journal of Morphology*, 262(2): 629-643.

Galarza-Munoz, G., Soto-Morales, S.I., Holmgren, M. & Rosenthal, J.J.C. 2011. Physiological adaptation of an Antarctic Na+/K+-ATPase to the cold. *Journal of Experimental Biology*, 214(13): 2164-2174.

García, S., Domingues, P., Navarro, J.C., Hachero, I., Garrido, D. & Rosas, C. 2011. Growth, partial energy balance, mantle and digestive gland lipid composition of *Octopus vulgaris* (Cuvier, 1797) fed with two artificial diets. *Aquaculture Nutrition,* 17(2): E174-E187.

Garcia-Dominguez, F. & Castro-Aguirre, L. 1991. Cuatro registros y algunas notas sobre la biologia del pulpo pelagico *Tremoctopus violaceus gracilis* (Eydoux y Souleyet, 1852) (Octopoda: Tremoctopodidae) en Mexico y en Golfo de California. *Investigaciones Marinas Centro Interdisciplinario de Ciencias Marinas,* 6: 229-233.

García García, B. & Aguado-Giménez, F. 2002. Influence of diet on ongrowing and nutrient utilization in the common octopus (*Octopus vulgaris*). *Aquaculture,* 211(1-4): 171-182.

García García, B. & Valverde, J. C. 2006. Optimal proportions of crabs and fish in diet for common octopus (*Octopus vulgaris*) ongrowing. *Aquaculture,* 253(1-4): 502-511.

García García, B., Valverde, J.C., Aguado-Giménez, F., García García, J. & Hernández, M. D. 2009. Growth and mortality of common octopus *Octopus vulgaris* reared at different stocking densities in Mediterranean offshore cages. *Aquaculture Research,* 40(10): 1202-1212.

García García, B., Valverde, J.C., Gómez, E., Hernández, M.D. & Aguado-Giménez, F. 2011. Ammonia excretion of octopus (*Octopus vulgaris*) in relation to body weight and protein intake. *Aquaculture,* 319(1-2): 162-167.

García-Garrido, S., Hachero-Cruzado, I., Domingues, P., López, N. & Rosas, C. 2011. Effects of fish hydrolysate (CPSP®) on growth and digestive gland lipid composition of *Octopus vulgaris* (Cuvier, 1797) juveniles. *Aquaculture Nutrition,* 17(4): e825-e839.

Gardiner, K. & Dick, T.A. 2010a. A concentration of large forms of five common cephalopods from the Canadian Arctic. *Marine Biodiversity Records*, 3(1): special section 1-6.

Gardiner, K. & Dick, T.A. 2010b. Arctic cephalopod distributions and their associated predators. *Polar Research*, 29: 209–227.

Garofalo, G., Ceriola, L., Gristina, M., Fiorentino, F. & Pace, R. 2010. Nurseries, spawning grounds and recruitment of *Octopus vulgaris* in the Strait of Sicily, central Mediterranean Sea. *ICES Journal of Marine Science,* 67(7): 1363-1371.

Gascuel, D., Labrosse, P., Meissa, B., Taleb Sidi, M.O. & Guénette, S. 2007. Decline of demersal resources in North-West Africa: an analysis of Mauritanian trawl-survey data over the past 25 years. *African Journal of Marine Science*, 29(3): 331–345.

Gestal, C., Pascual, S. & Hochberg, F.G. 2010. *Aggregata bathytherma* sp. nov. (Apicomplexa: Aggregatidae), a new coccidian parasite associated with a deep-sea hydrothermal vent octopus. *Diseases of Aquatic Organisms*, 91(3): 237-242.

Gil-de-Sola Simarro, L. 1992. Bottom catches along continental shelf of Western Mediterranean (Spain) of curled octopus (*Eledone cirrhosa* Lam.) fishery. *Rapports et Proces-verbaux des Reunions Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee*, 33: 294 (extended abstract).

Gillespie, G.E., Parker, G. & Morrison, J. 1998. A review of octopus fisheries biology and British Columbia octopus fisheries. *Canadian Stock Assessment Secretariat Research Document*, 98/87: 1-66.

Giordano, D., Bottari, T., Perdichizzi, A., Pirrera, L., Profeta, A., Busalacchi, B. & Rinelli, P. 2010. Distribution and some aspects of the biology of *Scaeurgus unicirrhus* (Cephalopoda: Octopodidae) in the Southern Tyrrhenian Sea (Central Mediterranean). *Vie et Milieu - Life And Environment*, 60(4): 291-297.

Giordano, D., Busalacchi, B., Bottari, T., Perdichizzi, F., Profeta, A., Perdichizzi, A., Pirrera, L., Modica, L. & Rinelli, P. 2010. Population dynamics and distribution of *Eledone cirrhosa* (Lamarck, 1798) in the southern Tyrrhenian Sea (Central Mediterranean). *Cahiers de Biologie Marine*, 51(3): 213-227.

Glaubrecht, M. & Salcedo-Vargas, M.A. 2000. Annotated type catalogue of the Cephalopoda (Mollusca) in the Museum fur Naturkunde, Humboldt University of Berlin. *Zoosystematics and Evolution*, 76(2): 269-282.

Gleadall, I. 1993. Identification of the long-ligula octopuses of Japan: a status report. *In* T. Okutani, R. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Biology*, pp. 145-158. Tokyo, Tokai University Press.

Gleadall, I.G. 2004. Some old and new genera of octopus. *Interdisciplinary Information Sciences*, 10: 99-112.

Gleadall, I.G. & Naggs, F.C. 1991. The Asian ocellate octopuses. II. The validity of *Octopus fangsiao* d'Orbigny. *Annals of Applied Information Sciences*, 16(2): 173-180.

Gleadall, I.G., Guerrero-Kommritz, J., Hochberg, F.G. & Laptikhovsky, V.V. 2010. The inkless octopuses (Cephalopoda: Octopodidae) of the southwest Atlantic. *Zoological Science,* 27: 528–553.

Gonçalves, J.M. 1991. The Octopoda (Mollusca: Cephalopoda) of the Azores. *Arquipelago, Life and Earth Sciences,* 9: 75-81.

González, Á.F., Guerra, Á., Pascual, S. & Briand, P. 1998. *Vulcanoctopus hydrothermalis* gen. et. sp. nov. (Mollusca, Cephalopoda): an octopus from deep-sea hydrothermal vent site. *Cahiers de Biologie Marine*, 39(2): 169-184

González, Á.F., Guerra, Á., Pascual, S. & Segonzac, M. 2008a. Female description of the hydrothermal vent cephalopod *Vulcanoctopus hydrothermalis*. *Journal of the Marine Biological Association of the United Kingdom*, 88(2): 375-379.

González, Á.F., Guerra, Á., Rocha, F. & Briand, P. 2002. Morphological variation in males of *Vulcanoctopus hydrothermalis* (Mollusca, Cephalopoda). *Bulletin of Marine Science*, 71(1): 289-298.

González, Á.F., Otero, J., Guerra, Á., Prego, R., Rocha, F.J. & Dale, A.W. 2005. Distribution of common octopus and common squid paralarvae in a wind-driven upwelling area (Ria of Vigo, northwestern Spain). *Journal of Plankton Research,* 27(3): 271-277.

González, M.L., Arraigada, S.E., López, D.A. & Pérez, M.C. 2008b. Reproductive aspects, eggs and paralarvae of *Robsonella fontanianus* (d'Orbigny, 1834). *Aquaculture Research*, 39(14): 1569-1573.

González, M.L., Pérez-Schultheiss, J. & López, D.A. 2011. Exotic amphipods in aquaculture systems: presence and potential use. *Crustaceana*, 84(7): 769-775.

González, M. & Sánchez, P. 2002. Cephalopod assemblages caught by trawling along the Iberian Peninsula Mediterranean coast. *Scientia Marina*, 66(2): 199-208.

Gonzáles-Peralta, A. 2006. Mass stranding of *Argonauta* spp. (Cephalopoda: Argonautidae) in the Gulf of California, Mexico. *In Cephalopod Life Cycles, CIAC '06, Program & Abstracts*, p. 75. Hobart, Australia.

González-Rendón, R., Mejía, B., Lizárraga, F. & Lizárraga, S. 1990. Artes y Métodos de Captura para el Pulpo en la Bahía de Mazatlán, Sinaloa, México. Memoria. Escuela de Ciencias del Mar. Universidad Autónoma de Sinaloa. Mazatlán, Sinaloa. 69 pp. [In Spanish]

Goodman-Lowe, G.D., Carpenter, J.R., Atkinson, S. & Ako, H. 1999. Nutrient, fatty acid, amino acid and mineral analysis of natural prey of the Hawaiian Monk Seal, *Monachus schauinislandi*. *Comparative Biochemistry and Physiology,* 123(2): 137-146.

Greatorex, E.C., Jones, C.S., Murphy, J., Key, L.N., Emery, A.M. & Boyle, P.R. 2000. Microsatellite markers for investigating population structure in *Octopus vulgaris* (Mollusca : Cephalopoda). *Molecular Ecology,* 9(5): 641-642.

Grimpe, G. 1916. *Chunioteuthis* eine neue Cephalopodéngattung. *Zoologische Anzeiger*, 46(12): 349-359.

Grimpe, G. 1925. Zur kenntnis der Cephalopodenfauna der Nordsee. *Wissenschaftliche Meeresunkrsuchungen Abteilung Helgoland, Neue Folge*, 16(3): 1-124.

Grisley, M.S., Boyle, P.R. & Key, L.N. 1996. Eye puncture as a route of entry for saliva during predation on crabs by the octopus *Eledone cirrhosa* (Lamarck). *Journal of Experimental Marine Biology and Ecology*, 202(2): 225-237.

Grisley, M.S., Boyle, P.R., Pierce, G.J. & Key, L.N. 1999. Factors affecting prey handling in lesser octopus (*Eledone cirrhosa*) feeding on crabs (*Carcinus maenas*). *Journal of the Marine Biological Association of the United Kingdom*, 79(6): 1085-1090.

Gristina, M., Sinopoli, M., Fiorentino, F., Garofalo, G. & Badalamenti, F. 2011. Shelter selection of the spiny lobster *Palinurus elephas* under different levels of *Octopus vulgaris* predation threat. *Marine Biology,* 158(6): 1331-1337.

Groeneveld, J.C., Maharaj, G. & Smith, C.D. 2006. *Octopus magnificus* predation and bycatch in the trap fishery for spiny lobsters *Palinurus gilchristi* off South Africa. *Fisheries Research,* 79: 90-96.

Grubert, M.A. & Wadley, V.A. 2000. Sexual maturity and fecundity of *Octopus maorum* in southeast Tasmania. *Bulletin of Marine Science,* 66: 131-142.

Grubert, M.A., Wadley, V.A. & White, R.W.G. 1999. Diet and feeding strategy of *Octopus maorum* in southeast Tasmania. *Bulletin of Marine Science,* 65: 441-451.

Guard, M & Mgaya, Y.D. 2002. The artisinal fishery for *Octopus cyanea* Gray in Tanzania. *Ambio*, 31(7-8): 528-536.

Guerra, Á. 1981. Spatial distribution pattern of *Octopus vulgaris*. *Journal of Zoology, London,* 195: 133-146.

Guerra, Á. 1997. *Octopus vulgaris*: review of the world fishery. *In* M.A. Lang & F.G. Hochberg, eds. *The Fishery and Market Potential of Octopus in California*, pp. 91-97. Washington, D.C., Smithsonian Institution. (Workshop Proceedings). Pp. 91-97.

Guerra, Á. & Fernández, M.T. 1990. Pesquerías de pulpo en Chile. *Industrias Pesqueras*, No. 1508: 9-10.

Guerra, Á., Cortez, T. & Rocha, F. 1999. Redescription of the Changos' octopus, *Octopus mimus* Gould, 1852, from coastal waters of Chile and Peru (Mollusca, Cephalopoda). *Iberus,* 17(2): 37-57. [In Spanish]

Guerra, Á., González, Á.F. & Cherel, Y. 2000. *Graneledone gonzalezi* sp. nov. (Mollusca: Cephalopoda): a new octopod from the Îles Kerguelen. *Antarctic Science*, 12(1): 33-40.

Guerra, Á., Portela, J.M. & del Rio, J.L. 2011. Cephalopods caught in the outer Patagonian shelf and its upper and medium slope in relation to the main oceanographic features. *Fisheries Research*, 109(1): 179-186.

Guerra, Á., Villanueva, R., Nesis, K.N. & Bedoya, J. 1998. Redescription of the deep-sea cirrate octopod *Cirroteuthis magna* Hoyle, 1885, and considerations on the genus *Cirroteuthis* (Mollusca: Cephalopoda). *Bulletin of Marine Science*, 63: 51-81.

Guerra, Á., Roura, Á., González, Á. F., Pascual, S., Cherel, Y. & Pérez-Losada, M. 2010. Morphological and genetic evidence that *Octopus vulgaris* Cuvier, 1797 inhabits Amsterdam and Saint Paul Islands (southern Indian Ocean). *ICES Journal of Marine Science,* 67(7): 1401-1407.

Guzik, M.T., Norman, M.D. & Crozier, R. 2005. Molecular phylogeny of the benthic shallow-water octopuses (Cephalopoda: Octopodinae). *Molecular Phylogenetics and Evolution*, 37: 235-248.

Haaker, P.L. 1985. Observations of a dwarf octopus, *Octopus micropyrsus*. *Shells and Sea Life*, 17(1): 39-40.

Haas, W. 2002. The evolutionary history of the eight-armed Coloidea. *In* H. Summesberger, Histon, & A. Daurer, eds. *Cephalopods - Present and Past*. Gabhandlungen der Geologischen Bundesanstalt, 57:341-351.

Hadjisolomou, S.P. & Grasso, F.W. 2010. Evidence for inter-sucker coordination in the Giant Pacific *Octopus Enteroctopus dofleini*. *Integrative and Comparative Biology*, 50: E237

Haimovici, M. 1988. *Eledone gaucha*, a new species of eledonid octopod (Cephalopoda: Octopodidae) from southern Brazil. *Nautilus*, 102(2): 82-87.

Haimovici, M. & Andriguetto Fo, J.M. 1986. Cefalópodes costeiros capturados na pesca de arrasto do litoral sul do Brasil. *Arq. Biol. Tecnol. Parana,* 29(3): 473-495.

Haimovici, M. & Perez, J.A.A. 1992. Coastal cephalopod fauna of southern Brazil. *Bulletin of Marine Science*, 49(1-2): 221-230 (1991).

Haimovici, M., Santos, R.A. & Fischer, L.G. 2009. Class Cephalopoda. *In* E. de Rios (ed.). *Compendium of Brazilian Sea Shells*. Rio Grande, RS: Evangraf, pp 610-649.

Haimovici, M., Piatkowski, U. & Santos, R.A.d. 2002. Cephalopod paralarvae around tropical seamounts and oceanic islands off the north-eastern coast of Brazil. *Bulletin of Marine Science*, 71(1): 313–330.

Hamabe, M. 1973. Egg mass and newborns of *Tremoctopus violaceus* Delle Chiaje, caught in the Harbour of Kasumi, Hyogo Prefecture. *Bulletin of Tokai Region Fisheries Research Laboratory*, 72: 1-5.

Hamasaki K. & Morioka, T. 2002. Effects of temperature on egg incubation period, and paralarval survival and growth of common octopus, *Octopus vulgaris* Reared in the Laboratory. *Suisan Zoshoku,* 50(4): 407-413.

Hamasaki, K. & Takeuchi, T. 2001. Dietary value of *Artemia* enriched with omega-yeast or shark eggs as feed for planktonic larvae of *Octopus vulgaris*. *Saibai Gyogyo Gijutsu Kaihatsu Kenkyu,* 28(2): 65-68.

Hanlon, R.T. 1983a. *Octopus briareus*. *In* P.R. Boyle, ed. *Cephalopod Life Cycles*, *Volume 1. Species Accounts*. London: Academic Press. Pp. 251-266.

Hanlon, R.T. 1983b. *Octopus joubini*. *In* P.R. Boyle, ed. *Cephalopod Life Cycles*, *Volume 1. Species Accounts*. London: Academic Press. Pp. 293-310.

Hanlon, R.T. 1988. Behavioral and body patterning characters useful in taxonomy and field identification of cephalopods. *Malacologia*, 29(1): 247-264.

Hanlon, R.T. & Forsythe, J.W. 1985. Advances in the laboratory culture of octopuses for biomedical research. *Laboratory Animal Science*, 1985: 33-40.

Hanlon, R.T. & Forsythe, J.W. 2008. Sexual cannibalism by *Octopus cyanea* on a Pacific coral reef. *Marine and Freshwater Behaviour and Physiology*, 41(1): 19-28.

Hanlon, R.T. & Hixon, R.F. 1980. Body patterning and field observations of *Octopus burryi*, Voss, 1950. *Bulletin of Marine Science*. 30(4): 749-755.

Hanlon, R.T. & Wolterding, M.R. 1989. Behavior, body patterning, growth and life history of *Octopus briareus* cultured in the laboratory. *American Malacological Bulletin*, 7(l): 21-45.

Hanlon, R.T., Conroy, L. & Forsythe, J.W. 2008. Mimicry and foraging behaviour of two tropical sand-flat octopus species off North Sulawesi, Indonesia. *Biological Journal of the Linnean Society*, 93(1): 23-38.

Hanlon, R.T., Forsythe, J.W. & S.v. Boletzky. 1985. Field and laboratory behavior of "macrotritopus larvae" reared to *Octopus defillipi* Verany, 1851 (Mollusca: Cephalopoda). *Vie milieu*, 35: 237-242.

Hanlon, R.T., Watson, A.C. & Barbosa, A. 2010. A "Mimic Octopus" in the Atlantic: flatfish mimicry and camouflage by *Macrotritopus defilippi*. *Biological Bulletin*, 218(1): 15-24.

Hardwick, J.E. 1970. A note on the behavior of the octopod *Ocythoe tuberculata. California Fish and Game,* 56: 68-70.

Harrington, J.J., Semmens, J.M., Gardner, C. & Frusher, S.D. 2006. Predation of trap-caught southern rock lobsters, *Jasus edwardsii* (Hutton, 1875), in Tasmanian waters by the Maori octopus, *Octopus maorum* (Hutton, 1880): spatial and temporal trends. *Fisheries Research,* 77: 10-16.

Hartwick, E.B. 1983. *Octopus dofleini*. *In* P.R. Boyle, ed. *Cephalopod Life Cycles. Volume 1, Species Accounts*. New York, Academic Press. Pp. 277-291.

Hartwick, E.B. & Barriga, I. 1997. *Octopus dofleini*. *In* M.A. Lang & F.G. Hochberg, eds. *The Fishery and Market Potential of Octopus in California*. Washington, D.C., Smithsonian Institution. (Workshop Proceedings). Pp. 45-56.

Harvey, A. W., Mooi R & Gosliner, T. M. 1999. Phylogenetic taxonomy and the status of *Allonautilus* Ward and Saunders, 1997. Journal of Paleontology, 73: 1214-1217.

Hastie, L.C., Pierce, G.J., Wang, J., Bruno, I., Moreno, A., Piatkowski, U. & Robin, J.P. 2009. Cephalopods in the north-eastern Atlantic: species, biogeography, ecology, exploitation and conservation. *Oceanography and Marine Biology: An Annual Review*, 47: 111-190.

Healy, J.M. 1989. Spermatozoa of the deep-sea cephalopod *Vampyroteuthis infernalis* Chun: ultrastructure and possible phylogenetic significance. *Philosophical Transactions of the Royal Society, Series B, Biological Sciences*, 323(1219): 589-600.

Healy, J.M. 1990. Ultrastructure of spermiogenesis in *Vampyroteuthis infernalis* Chun – a relict cephalopod mollusc. *Helgoländer Meeresuntersuchungen*, 44: 95-107.

Healy, J.M. 1993. Sperm and spermiogenesis in *Opisthoteuthis persephone* (Octopoda: Cirrata): ultrastructure, comparison with other cephalopods and evolutionary significance. *Journal of Molluscan Studies*, 59: 105-115.

Heeger, T., Piatkowski, U. & Moller, H. 1992. Predation on jellyfish by the cephalopod *Argonauta argo. Marine Ecology Progress Series,* 88: 293-296.

Henderson, A.C., Dunne, J. & Flannery, K. 2002. Stomach contents of spiny dogfish *Squalus acanthias* L. off the west coast of Ireland. *The Irish Naturalists Journal*, 27(3): 101-105.

Hermosilla, C., Rocha, F. & Valavanis, V.D. 2011. Assessing *Octopus vulgaris* distribution using presence-only model methods. *Hydrobiologia,* 670(1): 35-47.

Hernández-García, V., Hernández-López, J.L. & Castro, J.J. 1998. The octopus (*Octopus vulgaris*) in the small-scale trap fishery off the Canary Islands (Central-East Atlantic). *Fisheries Research,* 35(3): 183-189.

Hernández-García, V., Hernández-López, J. L. & Castro-Hdez, J. J. 2002. On the reproduction of *Octopus vulgaris* off the coast of the Canary Islands. *Fisheries Research,* 57(2): 197-203.

Hernández-García, V., Martín, A.Y. & Castro, J.J. 2000. Evidence of external digestion of crustaceans in *Octopus vulgaris* paralarvae. *Journal of the Marine Biological Association of the United Kingdom,* 80(3): 559.

Herring, P.J., Dilly, P.N. & Cope, C. 1994. The bioluminescent organs of the deep-sea cephalopod *Vampyroteuthis infernalis* (Cephalopoda: Vampyromorpha). *Journal of Zoology, London*, 233: 45-55.

Hochberg, F.G. 1980. Class Cephalopoda. *In* R.C. Brusca, ed. *Common Intertidal Invertebrates of the Gulf of California*. Tucson, Arizona, University of Arizona Press. Pp. 201-204.

Hochberg, F.G. 1983. The parasites of cephalopods: A review. *In* C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. *Proceedings of the Workshop on the Biology and Resource Potential of Cephalopods*. *Memoirs of the National Museum of Victoria*, No. 44. Pp. 108-145.

Hochberg, F.G. 1989. Les Parasites. *In* K. Mangold, ed. *Traité De Zoologie. Anatomie, Systématique, Biologie. Tome V. Métazoaires,* Fasc. 4. *Céphalopodes.* Paris, Masson. Pp. 589-608.

Hochberg, F.G. 1990. Diseases of Mollusca: Cephalopoda. Diseases caused by protistans and metazoans. *In* O. Kinne, ed. *Diseases of Marine Animals. Introduction, Cephalopoda, Annelida, Crustacea, Chaetognatha, Echinodermata, Urochordata.* Vol. III, 47-227. Hamburg, *Biologische Anstalt Helgoland*.

Hochberg, F.G. 1997a. *Octopus californicus*. *In* M.A. Lang & F.G. Hochberg, eds. *The Fishery and Market Potential of Octopus in California*, Washington, D.C., Smithsonian Institution, (Workshop Proceedings). Pp. 23-28.

Hochberg, F.G. 1997b. *Octopus rubescens*. *In* M.A. Lang & F.G. Hochberg, eds. *The Fishery and Market Potential of Octopus in California*, Washington, D.C., Smithsonian Institution, (Workshop Proceedings). Pp. 29-38.

Hochberg, F.G. 1998. Class Cephalopoda. *In* P. Valentich-Scott & J.A. Blake, eds. *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 8. The Mollusca. Part 1, The Aplacophora, Polyplacophora, Scaphopoda, Bivalvia and Cephalopoda*. Santa Barbara, California, Santa Barbara Museum of Natural History. Pp. 175-236.

Hochberg, F.G. & Fields, W.G. 1980. Cephalopoda: the squids and octopuses. *In* R.H. Morris, D.P. Abbott & E.C. Haderlie, eds. *Intertidal Invertebrates of California*. Stanford, California, Stanford University Press. Pp. 429-444.

Hochberg, F.G. & Short, R.B. 1970. *Dicyemennea littlei* sp. n. and *Dicyema benthoctopi* sp. n.: Dicyemid Mesozoa from *Benthoctopus magellanicus*. *Transactions of the American Microscopical Society*, 89(2): 216-224.

Hochberg, F.G., Nixon, M. & Toll, R.B. 1992. Order Octopoda Leach, 1818. *In* M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. *"Larval" and Juvenile Cephalopods: A Manual for their Identification. Smithsonian Contributions to Zoology*, 513: 213-280.

Hochberg, F.G., Norman, M.D. & Finn, J.K. 2006. *Wunderpus photogenicus* n. gen. and sp., a new octopus from the shallow waters of the Indo-Malayan Archipelago (Cephalopoda: Octopodidae). *Molluscan Research*, 26(3): 128-140.

Hofmeister, J.K., Alupay, J.S., Ross, R. & Caldwell, R.L. 2011. Observations on mating behavior and development in the lesser Pacific striped octopus, *Octopus chierchiae* (Jatta, 1889). *Integrative and Comparative Biology*, 51: E58.

Holder, C.F. 1909. A tame nautilus. *Scientific American*, October: 293.

Hormiga, J.A., Almansa, E., Sykes, A.V. & Torres, N.V. 2010. Model based optimization of feeding regimens in aquaculture: Application to the improvement of *Octopus vulgaris* viability in captivity. *Journal of Biotechnology,* 149(3): 209-214.

Houlihan, D.F., Kelly, K. & Boyle, P.R. 1998. Correlates of growth and feeding in laboratory-maintained *Eledone cirrhosa* (Cephalopoda: Octopoda). *Journal of the Marine Biological Association of the United Kingdom*, 78(3): 919-932.

Hoyle, W.E. 1885. Diagnosis of new species of Cephalopoda collected during the cruise of H.M.S. "Challenger" - I. The Octopoda. *Annals and Magazine of Natural History*, (Series 5), 15: 222-236.

Hoyle, W.E. 1886. Report on the Cephalopoda collected by HMS "Challenger" during the years 1873-1876. Report of the Voyage of the "Challenger": Zoology: Vol. XVI, part XLIV: Report on the Cephalopoda: 1-246.

Hoyle, W.E. 1904. V. Reports on the Cephalopoda. *In* Reports on the scientific results of the expedition to the tropical eastern Pacific in charge of Alexander Agassiz, on the U.S. Fish Commission Steamer "*Albatross*" from August, 1899, to March, 1900, Commander Jefferson T. Moser, U.S.N., Commanding. *Bulletin of the Museum of Comparative Zoology*, 43(1): 1-71.

Hoyle, W.E. 1910. Forschungreise im Westlichen und Zentralen Süd-Afrika, Bd IV, 1, p. 261 [*In Denschr. Med.-Naturw. Ges. Jena*, 70 Bd].

Hudelot, C. 2000. *La Systématique des Octobrachia (Mollusca; Cephalopoda): Une Approche Moléculaire*. (Ph.D. dissertation) Paris, France, Muséum National d'Histoire Naturelle. Tome 1. 188 pp., Tome 2. 246 pp.

Huffard, C.L. 2006. Locomotion by *Abdopus aculeatus* (Cephalopoda: Octopodidae): walking the line between primary and secondary defenses. *Journal of Experimental Biology*, 209: 3697-3707.

Huffard, C.L. 2007a. Four new species of shallow water pygmy octopus (Mollusca: Cephalopoda) from the Kingdom of Tonga. *Molluscan Research*, 27(3): 147-170.

Huffard, C.L. 2007b. Ethogram of *Abdopus aculeatus* (d'Orbigny, 1834) (Cephalopoda: Octopodidae): can behavioural characters inform octopodid taxomony and systematics? *Journal of Molluscan Studies*, 73(2): 185-193.

Huffard, C.L. & Godfrey-Smith, P. 2010. Field observations of mating in *Octopus tetricus* Gould, 1852 and *Amphioctopus marginatus* (Taki, 1964) (Cephalopoda: Octopodidae). *Molluscan Research*, 30(2): 81-86.

Huffard, C.L. & Hochberg, F.G. 2005. Description of a new species of the genus *Amphioctopus* (Mollusca: Octopodidae) from the Hawai'ian Islands. *Molluscan Research*, 25(3): 113-128.

Huffard, C.L., Boneka, F. & Full, R.J. 2005. Underwater bipedal locomotion by octopuses in disguise. *Science*, 307(5717): 1927.

Huffard, C.L., Caldwell, R.L. & Boneka, F. 2008a. Mating behavior of *Abdopus aculeatus* (d'Orbigny 1834) (Cephalopoda: Octopodidae) in the wild. *Marine Biology*, 154: 353-362.

Huffard, C.L., Caldwell, R.L. & Boneka, F. 2010a. Male-male and male-female aggression may influence mating associations in wild octopuses (*Abdopus aculeatus*). *Journal of Comparative Psychology*, 124(1): 38-46.

Huffard, C.L., Gentry, B.A. & Gentry, D.W. 2009. Description of the paralarvae of *Wunderpus photogenicus* Hochberg, Norman & Finn, 2006 (Cephalopoda: Octopodidae). *The Raffles Bulletin of Zoology,* 57(1): 109-112.

Huffard, C.L., Saarman, N., Hamilton, H. & Simison, W.B. 2010b. The evolution of conspicuous facultative mimicry in octopuses: an example of secondary adaptation? *Biological Journal of the Linnean Society*, 101(1): 68-77.

Huffard, C.L., Caldwell, R.L., DeLoach, N., Gentry, D.W., Humann, P., MacDonald, B., Moore, B., Ross, R.. Uno, T. & Wong, S. 2008b. Individually unique body color patterns in octopus (*Wunderpus photogenicus*) allow for photoidentification. *PLoS ONE*, 3(11): 1-5.

Hume, F., Hindell, M.A., Pemberton, D. & Gales, R. 2004. Spatial and temporal variation in the diet of a high trophic level predator, the Australian fur seal (*Arctocephalus pusillus doriferus*). *Marine Biology,* 144(3): 407-415.

Humes, A.G. & Voight, J.R. 1997. *Cholidya polypi* (Copepoda: Harpacticoida: Tisbidae), a parasite of deep-sea octopuses in the North Atlantic and northeastern Pacific. *Ophelia*, 46(1): 65-81.

Hunt, J.C. 1999. Laboratory observations of the feeding behavior of the cirrate octopod, *Grimpoteuthis* sp: One use of cirri. *Veliger,* 42(2): 152-156.

Hunter, C.M., Haddon, M., & Sainsbury, K.J. 2005. Use of fishery-dependent data for the evaluation of depensation: case study involving the predation of rock lobster (*Jasus edwardsii*) by octopus (*Octopus maorum*). *New Zealand Journal of Marine and Freshwater Research,* 39: 455-469.

Hvorecny, L.M., Grudowski, J.L., Blakeslee, C.J., Simmons, T.L., Roy, P.R., Brooks, J.A., Hanner, R.M., Beigel, M.E., Karson, M.A., Nichols, R.H., Holm, J.B. & Boal, J.G. 2007. Octopuses (*Octopus bimaculoides*) and cuttlefishes (*Sepia pharaonis, S. officinalis*) can conditionally discriminate. *Animal Cognition*, 10(4): 449-459.

Ibáñez, C.M. 2008. Feeding ecology of *Enteroctopus megalocyathus* (Cephalopoda: Octopodidae) in southern Chile. *Journal of the Marine Biological Association of the United Kingdom*, 88(4): 793-798.

Ibáñez, C.M. & Chong, J. 2008. Feeding ecology of *Enteroctopus megalocyathus* (Cephalopoda: Octopodidae) in southern Chile. *Journal of the Marine Biological Association of the United Kingdom*, 88(4), 793–798.

Ibáñez, C.M., Pardo-Gandarillas, M.C. & George-Nascimento, M. 2005. Microhabitat use by the protozoan parasite *Aggregata patagonica* Sardella, Re & Timi, 2000 (Apicomplexa: Aggregatidae) in his definitive host *Enteroctopus megalocyathus* (Gould, 1852) (Cephalopoda: Octopodidae) in southern Chile. *Revista Chilena De Historia Natural*, 78(3): 441-450.

Ibáñez, C.M., Sepúlveda, R.D. & Chong, J. 2006. A new species of *Benthoctopus* Grimpe, 1921 (Cephalopoda: Octopodidae) from the southeastern Pacific Ocean. *Proceedings of the Biological Society of Washington*, 119(3): 355-364.

Ibáñez, C.M., Sepúlveda, R.D. Guerrero, J. & J. Chong. 2008. Redescription of *Robsonella fontaniana* (Cephalopoda: Octopodidae). *Journal of the Marine Biological Association of the United Kingdom*, 88(3): 617-624.

Ibáñez, C.M., Sepúlveda, R.D., Sanhueza, E., Ruiz, J.F. & Chong, J. 2009. Feeding strategies of *Robsonella fontaniana* (d'Orbigny, 1834) (Cephalopoda: Octopodidae). *Revista de Biologia Marina y Oceanografía*, 44(2): 277-283 [In Spanish].

I.C.Z.N. 1999. *International Code of Zoological Nomenclature*. (The International Trust for Zoological Nomenclature: London). 306 pp.

I.C.Z.N. 1954. Opinion 233, International Code of Zoological Nomenclature. London: The International Trust for Zoological Nomenclature.

I.C.Z.N. 2006. Opinion 2147. International Code of Zoological Nomenclature. London: The International Trust for Zoological Nomenclature.

Iglesias, J., Otero, J.J., Moxica, C., Fuentes, L. & Sánchez, F.J. 2004. The completed life cycle of the octopus (*Octopus vulgaris*, Cuvier) under culture conditions: paralarval rearing using *Artemia* and zoeae, and first data on juvenile growth up to 8 months of age. *Aquaculture International,* 12(4/5): 481-487.

Iglesias, J., Fuentes, L., Sánchez, J., Otero, J.J., Moxica, C. & Lago, M.J. 2006. First feeding of *Octopus vulgaris* Cuvier, 1797 paralarvae using *Artemia*: Effect of prey size, prey density and feeding frequency. *Aquaculture,* 261(2): 817-822.

Iglesias, J., Sánchez, F.J., Bersano, J.G.F., Carrasco, J.F., Dhont, J., Fuentes, L., Linares, F., Muñoz, J.L., Okumura, S., Roo, J., van der Meeren, T., Vidal, E.A.G. & Villanueva, R. 2007. Rearing of *Octopus vulgaris* paralarvae: present status, bottlenecks and trends. *Aquaculture,* 266(1-4): 1-15.

Iribarne, O.O. 1990. Use of shelter by the small Patagonian octopus *Octopus tehuelchus* - availability, selection and effects on fecundity. *Marine Ecology-Progress Series,* 66: 251-258.

Iribarne, O.O. 1991a. Intertidal harvest of the Patagonian octopus, *Octopus tehuelchus* (d'Orbigny). *Fisheries Research,* 12: 375-390.

Iribarne, O.O. 1991b. Life-history and distribution of the small south western Atlantic octopus, *Octopus tehuelchus*. *Journal of Zoology,* 223: 549-565.

Iribarne, O.O. & Fernández, M.E. 1994. Clarification of the taxonomic status of a south western Atlantic octopus. *Malacological Review,* 1994: 115-116.

Iribarne, O.O., Fernández, M.E. & Zucchini, H. 1991. Prey selection by the small Patagonian octopus *Octopus tehuelchus* d'Orbigny. *Journal of Experimental Marine Biology and Ecology,* 148: 271-281.

Iribarne, O.O., Fernández, M.E., Diaz, M. & Clemente, M. 1993. Prey attack by the Patagonian octopus *Octopus tehuelchus* d'Orbigny - an odd pattern. *Veliger,* 36: 199-200.

Isgrove, A. 1909. *Eledone*. *Liverpool Marine Biological Society Committee Memoirs*, 18: 105 pp.

Ishiyama, V., Shiga, B. & Talledo, C. 1999. Biología reproductiva del pulpo *Octopus mimus* (Mollusca: Cephalopoda) de la región de Matarani, Arequipa, Perú. *Revista Peruana de Biología*, 6(1): 110-122.

Itami, K., Izawa, Y., Maeda, S. & Nakay, K. 1963. Notes on the laboratory culture of octopus larvae. *Bulletin of the Japanese Society Scientific Fisheries,* 29(6): 514–520.

Jacoby, C.A., Youngbluth, M.J., Frost, J.R., Flood, P.R. Uiblein, F., Båmstedt, U., Pagès, F. & David Shale. 2009. Vertical distribution, behavior, chemical composition and metabolism of *Stauroteuthis syrtensis* (Octopoda: Cirrata) in the northwest Atlantic. *Aquatic Biology*, 5: 13–22.

Janssen, H.H. 1993. Morphology, egg cocoons, and transmission paths of the Antarctic leech *Glyptonotobdella antarctica* Sawyer and White, 1969 (Hirudinea: Rhynchobdelliformes: Piscicolidae). *Polar Biology*, 13(5): 347-354.

Jereb, P., Allcock, A.L., Lefkaditou, E., Piatkowski, U., Hastie, L.C., and Pierce, G.J. (eds.) 2015. *Cephalopod biology and fisheries in Europe: II. Species Accounts. ICES Cooperative Research Report,* 325: 360 pp.

Johnsen, S. 2001. Hidden in plain sight: the ecology and physiology of organismal transparency. *Biological Bulletin*, 201: 301–318.

Johnsen, S., Balser, E.J., Fisher, E.C. & Widder, E.A. 1999a. Bioluminescence in the deep-sea cirrate octopod *Stauroteuthis syrtensis* Verrill (Mollusca: Cephalopoda). *Biological Bulletin*, 197: 113-114.

Johnsen, S., Balser, E.J., Fisher, E.C. & Widder, E.A. 1999b. Light-emitting suckers in an octopus. *Nature*, 398: 113.

Joll, L.M. 1977. The predation of pot-caught western rock lobster (*Panulirus longipes cygnus*) by octopus. *Western Australian Fisheries and Wildlife Report*, 29: 1-58.

Joll, L.M. 1983. *Octopus tetricus*. *In* P.R. Boyle, ed. *Cephalopod Life Cycles. Volume 1. Species Accounts*. New York, Academic Press. Pp. 325-334.

Jones, A.H. 1956. The paper nautilus. *Bulletin of the Conchology Section of the Auckland Museum,* 12: 20-21.

Jones, E.C. 1963. *Tremoctopus violaceus* uses *Physalia* tentacles as weapons. *Science,* 139: 764-766.

Jorgensen. E.M. 2009. *Field Guide to Squids and Octopods of the Eastern North Pacific and Bering Sea*. Seattle, NOAA Alaska Fisheries Science Center. 100 pp.

Jorgensen, E.M., Strugnell, J.M. & Allcock, A.L. 2010. Description and phylogenetic relationships of a new genus of octopus, *Sasakiopus* (Cephalopoda: Octopodidae), from the Bering Sea, with a redescription of *Sasakiopus salebrosus* (Sasaki, 1920). *Journal of Molluscan Studies*, 76(1): 57-66.

Joubin, L. 1903. Sur quelques Céphalopodes recueillis pendant les dernières campagnes de S.A.S. le *Prince de Monaco* (1901-1902). *Comptes Rendu de Académie des Sciences, Paris* 136: 100-102.

Joubin, L. 1912. Études préliminaires sur les Céphalopodes recueillis au cours des croisières de S.A.S. le *Prince de Monaco*. 2^{e} Note: *Cirroteuthis grimaldii*, nov. sp. *Bulletin de l'Institut Océanographique*, Monaco 226: 1-13.

Joubin, L. 1918. Etudes preliminaires sur les cephalopodes recueillis au cours des croisieres de S.A.S. le Prince de Monaco, 6e Note: *Vitreledonella richardi* Joubin. *Bulletin de l'Institute Oceanographique, Monaco*, 340: 1-40.

Joubin, L. 1920. Cephalopodes provenant des campagnes de la *Princesse-Alice* (1898-1910). *Results des Campagnes Scientifiques Accomplish sur son Yacht par Albert I Prince Souverain de Monaco*, 54: 1-95.

Joubin, L. 1937. Les octopodes de la croisiere du “Dana” 1921-22. *Dana Report*, 11: 1-49.

Jouffre, D. 2002. Are the octopus pots used by the Mauritanian small-scale fishery dangerous for the resource? *Bulletin of Marine Science*, 71(2): 1081-1085.

Juarez, O.E., Rosas, C. & Arena, L. 2010. Heterogenous microsatellites reveal moderate genetic structure in the *Octopus maya* population. *Fisheries Research,* 106: 209-213.

Kamura, S. & Hashimoto, H. 2004. The food habits of four species of triakid sharks, *Triakis scyllium*, *Hemitriakis japanica*, *Mustelus griseus* and *Mustelus manazo*, in the central Seto Inland Sea, Japan. *Fisheries Science,* 70(6): 1019–1035.

Kaneko, N. & Kubodera, T. 2005. A New Species of Shallow Water Octopus, *Octopus laqueus*, (Cephalopoda: Octopodidae) from Okinawa, Japan. *Bulletin of the National Science Museum, Tokyo*, Ser. A, 31(1): 8-15.

Kaneko, N. & Kubodera, T. 2007. A new intertidal octopus species, *Octopus incella* (Cephalopoda: Octopodidae), from Okinawa, southern Japan. *Zootaxa,* (1440): 39-49.

Kaneko, N. & Kubodera, T. 2008. Two new species of pygmy octopuses (Cephalopoda: Octopodidae) from deep water off the Ryukyu Archipelago, southern Japan. *Molluscan Research*, 28(3): 145-157.

Kaneko, N., Oshima, Y. & Ikeda, Y. 2006. Egg brooding behavior and embryonic development of *Octopus laqueus* (Cephalopoda: Octopodidae). *Molluscan Research*, 26(3): 113-117.

Katsanevakis, S. 2006. Seasonal population dynamics of *Octopus vulgaris* in the eastern Mediterranean. *ICES Journal of Marine Science*, 63(1): 151-160.

Katsanevakis, S. & Verriopoulos, G. 2004a. Abundance of *Octopus vulgaris* on soft sediment. *Scientia Marina,* 68(4): 553-560.

Katsanevakis, S. & Verriopoulos, G. 2004b. Den ecology of *Octopus vulgaris* Cuvier, 1797, on soft sediment: availability and types of shelter. *Scientia Marina,* 68(1): 147-157.

Katsanevakis, S. & Verriopoulos, G. 2006a. Seasonal population dynamics of *Octopus vulgaris* in the eastern Mediterranean. *ICES Journal of Marine Science,* 63(1): 151-160.

Katsanevakis, S. & Verriopoulos, G. 2006b. Modelling the effect of temperature on hatching and settlement patterns of meroplanktonic organisms: the case of the octopus. *Scientia Marina,* 70(4): 699-708.

Katugin, O.N., Yavnov, S.V. & Shevtsov, G.A. 2010. [*Atlas of Cephalopod Mollusks of the Far Eastern Seas of Russia*]. Vladivostok, Russia, TINRO-Centre. [In Russian] 136 pp.

Keen, A.M. 1958. *Sea Shells of Tropical West America. Marine Mollusks from Lower California to Columbia*. Stanford, California, Stanford University Press. 626 pp.

Keen, A.M. 1971. *Sea Shells of Tropical West America.* Stanford, California, Stanford University Press. 1064 pp.

Kemp, K.M., Jamieson, A.J., Bagley, P.M., McGrath, H., Bailey, D.M., Collins, M.A. & Priede, I.G. 2006. Consumption of large bathyal food fall, a six month study in the NE Atlantic. *Marine Ecology - Progress Series*, 310: 65-76.

Kier, W.M. & Stella, M.P. 2007. The arrangement and function of octopus arm musculature and connective tissue. *Journal of Morphology*, 268: 831–843.

Kim, D.H. 2008. Optimal economic fishing efforts in Korean common octopus *Octopus minor* trap fishery. *Fisheries Science*, 74(6): 1215-1221.

Kim, D.S. & Kim, J. 2006. Sexual Maturity and Growth Characteristics of *Octopus minor*. *Journal - Korean Fisheries Society*, 39(5): 410-418.

Kim, D.S. & Kim, J.M. 2007. Spawning and Hatching of *Octopus minor*. *Journal - Korean Fisheries Society*, 40(4): 243-247.

Kirk, T.W. 1884. On a new cuttle-fish, *Tremoctopus robsonianus*, obtained by C.H. Robson at Napier. *Transactions and Proceedings of the New Zealand Institute,* 16: 549-550.

Klaich, M.J., Re, M.E. & Pedraza, S.N. 2006. Effect of temperature, sexual maturity and sex on growth, food intake and gross growth efficiency in the “Pulpito” *Octopus tehuelchus* (d’Orbigny, 1834). *Journal of Shellfish Research*, 25(3): 979-986.

Klug, C., Korn, D., Richter, U. & Urlichs, M. 2004. The black layer in cephalopods from the German Muschelkalk (Triassic). *Palaeontology*, 47 (6): 1407-1425.

Klug, C., Bruhwiler, T., Korn, D., Schweigert, G., Brayard, A. & Tilsley, J. 2007. Ammonoid Shell Structures of Primary Organic Composition. *Palaeontology*, 50 (6): 1463-1478.

Knudsen, J. 1992. *Tremoctopus violaceus* delle Chiaje, 1830 new to the eastern Mediterranean. Cephalopoda, Octopoda, Tremoctopodidae. *Israel Journal of Zoology,* 12: 1-4.

Knudsen, J. & Roeleveld, M.A.C. 2002. J.T. Reinhadt and V. Prosch (1846): on *Sciadephorus mülleri* (Eschr.) – A translation into English. *Bulletin of Marine Science*, 71(1): 421-447.

Kobayashi, D.R. 1986. Octopus predation on hermit crabs: A test of selectivity. *Marine Biology and Physiology*, 12(2): 125-131.

Kommritz, J.G. 2000. A new species of *Graneledone* (Cephalopoda: Octopodidae) from the Southwest Atlantic Ocean. *Journal of Molluscan Studies*, 66(4): 543-549.

Kondokov, N.N. 1941. Cephalopods of the Far Eastern Seas. *Issled. Dalnevost. Morei,* 1: 216-255. [In Russian].

Kramp, P.L. 1956. Pelagic fauna. *In* A.F. Bruun, S. Greve, H. Mielche & R. Spärk, eds. *The Galathea Deep Sea Expedition 1950-1952*. London, George Allen & Unwin. Pp. 65-86.

Krstulović Šifner, S. & Vrgoč, N. 2009a. Diet and feeding of the musky octopus, *Eledone moschata*, in the northern Adriatic Sea. *Journal of the Marine Biological Association of the United Kingdom*, 89(2): 413-420.

Krstulović Šifner, S. & Vrgoč, N. 2009b. Reproductive cycle and sexual maturation of the musky octopus *Eledone moschata* (Cephalopoda: Octopodidae) in the northern and central Adriatic Sea. *Scientia Marina*, 73(3): 439-447.

Krstulović Šifner, S., Peharda, M., Vrgoč, N., Isajlovic, I., Dadic, V. & Petric, M. 2011. Biodiversity and distribution of cephalopods caught by trawling along the Northern and Central Adriatic Sea. *Cahiers de Biologie Marine*, 52(3): 291-302.

Krstulović Šifner, S., Lefkaditou, E., Ungaro, N., Ceriola, L., Osmani, K., Kavadas, S. & Vrgoč, N. 2005. Composition and distribution of the cephalopod fauna in the eastern Adriatic and eastern Ionian Sea. *Israel Journal of Zoology*, 51(4): 315-330.

Kruta, I., & Landman, N.H. 2008. Injuries on *Nautilus* Jaws: Implications for the Function of Ammonite Aptychi. *Veliger*, 50(3): 241-247.

Kubodera, T. 1992. Distribution and abundance of the early life stages of octopus, *Octopus dofleini* Wülker, 1910 in the North Pacific. *Bulletin of Marine Science*, 49: 235-243 (1991).

Kubodera, T. 2001. Cephalopod fauna in Tosa Bay, western Japan. *National Science Museum Monographs,* 20: 167-197.

Kubodera, T. & Okutani, K. 1986. New and rare cephalopods from the Antarctic waters. *Memoirs of National Institute of Polar Research*, Special Issue No. 44: 129-143.

Kubodera, T. & Okutani, K.. 1994. Eledonine octopods from the Southern Ocean - systematics and distribution. *Antarctic Science*, 6(2): 205-214.

Kubodera, T., Watanabe, H. & Ichii, T. 2007. Feeding habits of the blue shark, *Prionace glauca*, and salmon shark, *Lamna ditropis*, in the transition region of the Western North Pacific. *Reviews in Fish Biology and Fisheries*, 17: 111-124.

Lalas, C. 2009. Estimates of size for the large octopus *Macroctopus maorum* from measures of beaks in prey remains. *New Zealand Journal of Marine and Freshwater Research*, 43(2): 635-642.

Land, M.F. 1992. A note on the elongated eye of the octopus *Vitreledonella richardi*. *Journal of the Marine Biological Association, U.K.*, 72: 89-92.

Landman, N.H., Davis, R.A., Mapes, R.H., Scheel, D., Lauster, A. & Vincent, T.L.S. 2008. Habitat ecology of *Enteroctopus dofleini* from middens and live prey surveys in Prince William Sound, Alaska. *In* N.H. Landman, R.A. Davis & R.H. Mapes, eds. *Cephalopods Present & Past: New Insights & Fresh Perspectives.* Springer, Dordrecht. Pp. 434-458.

Lane, F.W. 1957. *Kingdom of the Octopus: The Life-History of the Cephalopoda*. London, Jarrolds Publishers Ltd. 300 pp.

Lang, M.A. 1997. *Octopus bimaculoides*. *In* M.A. Lang & F.G. Hochberg, eds. *The Fishery and Market Potential of Octopus in California*. Washington, D.C., Smithsonian Institution. (Workshop Proceedings). Pp. 1-9.

Lang, M.A. & Hochberg, F.G. 1997. *The Fishery and Market Potential of Octopus in California*. Washington, D.C., Smithsonian Institution. (Workshop Proceedings). 192 pp.

Laptikhovsky, V.V. 1999. Fecundity and reproductive strategy of three species of octopods from the northwest Bering Sea. *Russian Journal of Marine Biology*, 25: 342-346.

Laptikhovsky, V.V. 2001. Fecundity, egg masses and hatchlings of *Benthoctopus* spp. (Octopodidae) in Falkland waters. *Journal of the Marine Biological Association, United Kingdom* 81: 267-270.

Laptikhovsky, V. & Salman, A. 2003. On reproductive strategies of the epipelagic octopods of the superfamily Argonautoidea (Cephalopoda: Octopoda). *Marine Biology,* 142: 321-326.

Lee, H.J. & Kim, G.B. 2010. Concentration of Heavy Metals in *Octopus minor* in Seosan, Chungnam and Food Safety Assessment. *Hangug Susan Kwahakoeji*, 43(3): 270-276.

Lefkaditou, E. & Papaconstantinou, C. 1995. Distribution, growth and maturity of *Eledone cirrhosa* (Cephalopoda: Octopoda) in the Thracian Sea (eastern Mediterranean). *Rapports et Proces-verbaux des Reunions Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee*, 34: 247.

Lefkaditou, E., Papaconstantinou, C. & Anastasopoulou, K. 1999. Juvenile cephalopods collected in the midwater macroplankton over a trench in the Aegean Sea (Northeastern Mediterranean). *Israel Journal of Zoology,* 45(3): 395-405.

Lefkaditou, E., Peristeraki, P., Bekas, G., Tserpes, G., Politou, C.-Y. & Petrakis, G. 2003. Cephalopods distribution in the southern Aegean Sea. *Mediterranean Marine Science*, 4(1): 79-86.

Lefkaditou, E., Souplet, A., Peristeraki, N., González, M., Kavadas, S., Vidoris, P., Cuccu, D. & Papaconstantinou, C. 2000. Preliminary investigation of factors affecting the spatial distribution and abundance of *Eledone cirrhosa* (Cephalopoda: Octopoda) in the Mediterranean Sea. *Actes de Colloques – IFREMER*, 2000: 208-220.

Leite, T.S. 2007. *Taxonomia, Distribução, Ecologia Alimentar, Pesca e Opções de Manejo de Uma Nova Espécie de Polvo (Octopus insularis: Cephalopoda), no Arquipélago de Fernando de Noronha, Brasil*. Ph.D. dissertation. Rio Grande, Brazil, Fundação Universidade Federal. 59 pp. [In Portugese].

Leite, T.S. 2008. The octopus fishery in the Fernando de Noronha Archipelago, Brazil. *Boletim do Instituto de Pesca*, 34(2): 271-280.

Leite, T.S., Haimovici, M., Molina, W. & K. Warnke. 2008. Morphological and genetic description of *Octopus insularis*, a new cryptic species in the *Octopus vulgaris* complex (Cephalopoda: Octopodidae) from the tropical southwestern Atlantic. *Journal of Molluscan Studies*, 74: 63-74.

Leporati, S.C., Pecl, G.T. & Semmens, J.M. 2007. Cephalopod hatchling growth: the effects of initial size and seasonal temperatures. *Marine Biology*, 151(4): 1375-1383.

Leporati, S.C., Pecl, G.T. & Semmens, J.M. 2008a. Reproductive status of *Octopus pallidus*, and its relationship to age and size. *Marine Biology*, 155: 375-385.

Leporati, S.C., Semmens, J.M. & Pecl, G.T. 2008b. Determining the age and growth of wild octopus using stylet increment analysis. *Marine Ecology Progress Series*, 367: 213-222.

Leporati, S.C., Ziegler, P.E. & Semmens, J.M. 2009. Assessing the stock status of holobenthic octopus fisheries: is catch per unit effort sufficient? *ICES Journal of Marine Science*, 66(3): 478-487.

Levy, Y.A., Haimovici, M. & Conceicao, M. 1988. Genetic evidences for two species to the genus *Eledone* (Cephalopod: Octopodidae) in south Brazil. *Comparative Biochemistry and Physiology*, 90B(2): 275-277.

Leyva-Villarreal, M.M., Osuna-Manoquin, S.A., Ley-Montoya, A.L., Cervantes-Galaviz, F. & Quiñónez-Cruz, J.A. 1987. *Contribucion al Conocimiento Biologico del Pulpo Octopus sp. en la Bahia de Mazatlan, Sinaloa, Mexico*. (Lic. Biol. Pesq. thesis). Mazatlán, Mexico, Universidad Autonoma de Sinaloa. 73 pp.

Liao, J.X. & Lu, C.C. 2009. A new species of *Cistopus* (Cephalopoda: Octopodidae) from Taiwan and morphology of mucous pouches. *Journal of Molluscan Studies*, 75: 269-278.

Liao, Y., Gao, F. & Zhang, J. 2006. The research and aquaculture of octopus, distribution in China. *Journal of Aquaculture,* 2006-5.

Ligas, A., De Ranieri, S. Micheli, D. Reale, B., Sartor, P., Sbrana, M. & Belcari, P. 2010. Analysis of the landings and trawl survey time series from the Tyrrhenian Sea (NW Mediterranean). *Fisheries Research*, 105(1): 46-56.

Lin, G., Huang, J.J., Hu, R. & Song, W. 2008. Preliminary Experiment on Artificial Propagation of *Octopus vulgaris. Journal of Fujian Fisheries,* 2008-03.

Lloret, J. & Lleonart, J. 2002. Recruitment dynamics of eight fishery species in the northwestern Mediterranean Sea. *Scientia Marina*, 66(1): 77-82.

Long, S.M. & Holdway, D.A. 2002. Acute toxicity of crude and dispersed oil to *Octopus pallidus* (Hoyle, 1885) hatchlings. *Water Research,* 36: 2769-2776.

Lopez-González, P.J., Bresciani, J., Huys, R., González, A.F., Guerra, A. & Pascual, S. 2000. Description of *Genesis vulcanoctopusi* gen. et sp nov (Copepoda: Tisbidae) parasitic on a hydrothermal vent octopod and a reinterpretation of the life cycle of cholidyinid harpacticoids. *Cahiers de Biologie Marine*, 41(3): 241-253.

López-Uriarte, E. & Ríos-Jara, E. 2009. Reproductive biology of *Octopus hubbsorum* (Mollusca: Cephalopoda) along the central Mexican Pacific coast. *Bulletin of Marine Science*, 84(1): 109-121.

López-Uriarte, E., Ríos-Jara, E. & González-Rodríguez, M.E. 2010. Diet and feeding habits of *Octopus hubbsorum* Berry, 1953, in the central Mexican Pacific. *The Veliger*, 51(1): 26–42.

López-Uriarte, E., Ríos-Jara, E. & Pérez-Peña, M. 2005. Range extension for *Octopus hubbsorum* (Mollusca: Octopodidae) in the Mexican Pacific. *Bulletin of Marine Science,* 77: 171-175.

Lorois, E.L. 1852. Description d'une nouvelle espèce du genre Argonaute. *Revue et Magazin de Zoologie, Pure et Applique, Series. 2,* 4: 9-10.

Lougovois, V.P., Kolovou, M.K., Savvaidis, I.N. & Kontominas, M.G. 2008. Spoilage potential of ice-stored whole musky octopus (*Eledone moschata*). *International Journal of Food Science & Technology*, 43(7): 1286-1294.

Lourenço, S., Moreno, A. & Pereira, J. 2008. Distribution and Biological revision of *Eledone moschata* (Lamarck, 1978) in south and southwestern Portuguese waters. III Congresso da Ordem dos Biólogos, Lisboa 25 a 27 Fevereiro 2008, Poster, P 13.

Lu, C.C. 2010. A new species of *Opisthoteuthis*, *O. dongshaensis* sp. nov., from the South China Sea (Octopoda: Cirrata: Opisthoteuthidae). *Zoological Studies*, 49(3): 405-420.

Lu, C.C. & Clarke, M.R. 1975a. Vertical distribution of cephalopods at 11ºN, 20ºW in the North Atlantic. *Journal of the Marine Biological Association of the United Kingdom,* 55: 369-389.

Lu, C.C. & Clarke, M.R. 1975b. Vertical distribution of cephalopods at 40ºN, 53ºN and 60ºN at 20ºW in the North Atlantic. *Journal of the Marine Biological Association of the United Kingdom,* 55: 143-163.

Lu, C.C. & Roper, C.F.E. 1979. Cephalopods from deepwater dumpsite 106 (western Atlantic): vertical distribution and seasonal abundance. *Smithsonian Contributions to Zoology,* 288: 1-36.

Lu, C.C. & Stranks, T.N. 1992. *Eledone palari*, a new species of octopus (Cephalopoda: Octopodidae) from Australia. *Bulletin of Marine Science*. 49(1–2): 73–87.

Lu, C.C. & Stranks, T.N. 1994. Synopsis of *Pareledone* and *Megaleledone* species, with description of two new species from east Antarctica (Cephalopoda: Octopodidae). *Memoirs of the Museum of Victoria*, 54: 221-242.

Lu, C. C., Boucher-Rodoni, R., & Tillier, A. 1995. Catalogue of types of recent Cephalopoda in the Muséum National d'Histoire Naturelle de Paris, *Bullétin du Musée Nationale d'Histoire Naturelle de Paris*, 4e ser, 17A (3–4): 307-343.

Lv, G., Wu J., & Chen L. 2007. Research achievements and exploitation prospect of Cephalopoda aquaculture in China. *South China Fisheries Science*, 2007-03.

Lucifora, L.O., Garcia, V.B., Menni, R.C. & Escalante, A.H. 2006. Food habits, selectivity, and foraging modes of the school shark *Galeorhinus galeus*. *Marine Ecology - Progress Series*, 315: 259-270.

Maltagliati, F., Belcari, P., Casu, D., Casu, M., Sartor, P., Vargiu, G. & Castelli, A. 2002. Allozyme genetic variability and gene flow in *Octopus vulgaris* (Cephalopoda, Octopodidae) from the Mediterranean sea. *Bulletin of Marine Science,* 71(1): 473-486.

Mangold, K. 1983a. *Octopus vulgaris*. *In* P.R. Boyle, ed. *Cephalopod Life Cycles. Species Accounts*. Vol. I. London, Academic Press. Pp. 335-365.

Mangold, K. 1983b. *Eledone moschata*. *In* P.R. Boyle, ed. *Cephalopod Life Cycles. Species Accounts*. Vol. I. London, Academic Press. Pp. 387-400.

Mangold, K. 1998. The Octopodinae from the eastern Atlantic Ocean and Mediterranean Sea. *Smithsonian Contributions to Zoology*, 586(2): 521-528.

Mangold, K., Boletzky, S.v. & Froesch, D. 1971. Reproductive biology and embryonic development of *Eledone cirrhosa* (Cephalopoda: Octopoda). *Marine Biology*, 8: 109-117.

Mangold, K.M., Vecchione, M. & Young, R.E. 2010a. Argonautidae Tryon, 1879. *Argonauta* Linnaeus 1758. paper nautilus. Version 03 February 2010 (under construction). http://tolweb.org/Argonauta/20204/2010.02.03 in The Tree of Life Web Project, http://tolweb.org/

Mangold, K.M., Vecchione, M. & Young, R.E. 2010b. Ocythoidae Gray 1849. *Ocythoe tuberculata* Rafinesque, 1814. Version 15 August 2010 (under construction). http://tolweb.org/Ocythoe_tuberculata/20205/2010.08.15 in The Tree of Life Web Project, http://tolweb.org/

Mangold, K.M., Vecchione, M. & Young, R.E. 2010c. Tremoctopodidae Tryon, 1879. *Tremoctopus Chiaie* 1830. Blanket octopus. Version 15 August 2010. http://tolweb.org/Tremoctopus/20202/2010.08.15 in The Tree of Life Web Project, http://tolweb.org/

Mangold-Wirz, K. 1963. Biologie des cephalopodes benthiques et nectonique de la Mer Catalane. *Vie et Milieu,* 13 (Supplement): 285 pp.

Marquez, F. & Ré, M.E. 2009. Morphological and chemical description of the stylets of the red octopus, *Enteroctopus megalocyathus* (Mollusca: Cephalopoda). *Molluscan Research*, 29(1): 27-32.

Martin, P. & Sánchez, P. 1992. Length, distribution and total mortality rate Z of *Merluccius merluccius, Mullus barbatus* and *Eledone cirrhosa* exploited by the trawling fleet in 1982 and 1991 off the Catalan coast (NW Mediterranean). *Rapports et Proces-verbaux des Reunions Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee*, 33: 301 (extended abstract).

Massy, A.L. 1907. Preliminary notice of new and remarkable cephalopods from the south-west coast of Ireland. *Annals and Magazine of Natural History* (Series 7), 20: 374-377.

Massy, A.L. 1924. Note on a new cephalopod, *Cirroteuthis (Cirroteuthopsis) massyae*, Grimpe. *Annals and Magazine of Natural History*, 14: 127-130.

Mather, J.A. 1984. Behaviour and interaction of *Eledone moschata* in the laboratory. *Animal Behaviour*, 33: 1138-1144.

Mather, J.A. 1991a. Foraging, feeding and prey remains in middens of juvenile *Octopus vulgaris* (Mollusca, Cephalopoda). *Journal of Zoology,* 224: 27-39.

Mather, J. A. 1991b. Navigation by spatial memory and use of visual landmarks in octopuses. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology,* 168(4): 491-497.

Mather, J.A. 1994. Home choice and modification by juvenile *Octopus vulgaris* (Mollusca, Cephalopoda) - specialized intelligence and tool use. *Journal of Zoology,* 233: 359-368.

Mather, J.A. & Nixon, M. 1995. *Octopus vulgaris* (Cephalopoda) drills the chelae of crabs in Bermuda. *Journal of Molluscan Studies,* 61: 405-406.

McQuaid, C.D. 1994. Feeding behavior and selection of bivalve prey by *Octopus vulgaris* Cuvier. *Journal of Experimental Marine Biology and Ecology,* 177(2): 187-202.

Messenger, J.B. 1963. Behaviour of young *Octopus briareus* Robson. *Nature*, 197(4873): 1186-1187.

Meyer, W.T. 1906a. Die Anatomie von *Opisthoteuthis depressa* (Ijima und Ikeda). *Zeitschrift für Wissenschaftlich Zoologie*, 85: 183-269.

Meyer, W.T. 1906b. Über den männlichen Geschlechtsapparat von *Opisthoteuthis depressa* (Ijima und Ikeda). *Zoologischer Anzeiger*, 29: 758-760.

Meynier, L., Mackenzie, D.D.S., Duignan, P.J., Chilvers, B.L. & Morel, P.C.H. 2009. Variability in the diet of New Zealand sea lion (*Phocarctos hookeri*) at the Auckland Islands, New Zealand. *Marine Mammal Science*, 25(2): 302-326.

Michels, J., Robertson, J.D. & Young. J.Z. 1987. Can conditioned aversive tactile stimuli affect extinction of visual responses in octopus? *Marine Behaviour and Physiology*, 13(1): 1-11.

Miliou, H., Fintikaki, M., Kountouris, T. & Verriopoulos, G. 2005. Combined effects of temperature and body weight on growth and protein utilization of the common octopus, *Octopus vulgaris*. *Aquaculture,* 249(1-4): 245-256.

Millard de Montrion, C. 1981. La fécondation chez les céphalopodes, avec références particulières a *Loligo vulgaris, Eledone moschata*. Rapport de stage B.E.A. (Biologie du developpement). Univ. P. et M. Curie, Paris, 6, 23 pp.

Miramand, P. & Bentley, D. 1992. Concentration and distribution of heavy metals in tissues of two cephalopods, *Eledone cirrhosa* and *Sepia officinalis* from the French coast of the English Channel. *Marine Biology*, 114: 407-414.

Miske, V. & Kirchhauser, J. 2006. First record of brooding and early life cycle stages in *Wunderpus photogenicus* Hochberg, Norman, and Finn, 2006 (Cephalopoda: Octopodidae). *Molluscan Research*, 26(3): 169-171.

Moolenbeek, R.G. 2008. The genus *Argonauta* (Cephalopoda: Argonautidae) as figured in Rumphius, 1739 and listed in the Portland Catalogue, 1786. *Miscellanea Malacologica,* 3: 25-30.

Moore, J.A., Vecchione, M., Collette, B.B., Gibbons, R. & Hartel, K.E. 2004. Selected fauna of Bear Seamount (New England Seamount chain), and the presence of "natural invader" species. *Archive of Fishery and Marine Research,* 51: 241-250.

Morales, E. 1955. Contribución al conocimiento de la biología de *Eledone aldrovandi* (Rafin.). *Investigacion Pesquera*, 1: 31-57.

Morales, E. 1958. Sobre la morfologia del aparato genital de *Eledone aldrovandi* (Raf.) = *Eledone cirrhosa* (Lamarck). *Commission Internationale pour l'exploration scientifique de la mer Méditerranée, Rapports et Procès-Verbaux des Réunions, (Nouvelle Série)*, 14: 389-394.

Morales, E. 1959. Sobre la presencia de *Opisthoteuthis agassizii* Verrill, en el Mediterraneo. *Investigacion Pesquera*, 15: 113-123.

Moreira, A. A., Tomás, A. R. G. & Hilsdorf, A. W. S. 2011. Evidence for genetic differentiation of *Octopus vulgaris* (Mollusca, Cephalopoda) fishery populations from the southern coast of Brazil as revealed by microsatellites. *Journal of Experimental Marine Biology and Ecology,* 407(1): 34-40.

Moreno, A., Santos, A., Piatkowski, U., Santos, A. M. P. & Cabral, H. 2009. Distribution of cephalopod paralarvae in relation to the regional oceanography of the western Iberia. *Journal of Plankton Research,* 31(1): 73-91.

Moriyasu, M. 1981. Biologie des pêches de céphalopodes benthiques. Application aux Elédones, *Eledone cirrhosa* (Lam., 1798) (Cephalopoda: Octopoda) du Golfe du Lion. Thèse Doctorat, 3ème cycle, Université des Sciences et Techniques du Languedoc, Montpellier, France. 225 pp.

Moriyasu, M. 1983. Étude biométrique de la croissance d'*Eledone cirrhosa* (Lam., 1798) (Cephalopoda, Octopoda) du Golfe du Lion. *Oceanologie Acta,* 6: 35-41.

Moriyasu, M. 1988. Analyse de la maturation sexuelle d'*Eledone cirrhosa* (Cephalopoda: Octopoda) du Golfe du Lion. *Aquatic Living Resources*, 1: 59-65.

Moriyasu, M. & Benhalima, K. 1993. Morphological and morphometrical observations on the mantle stylet of *Eledone cirrhosa* (Lamarck, 1798) (Cephalopoda: Octopoda). *Venus*, 52(2): 149-154.

Morrison, R.L. 1944. *Notes on Octopus*. *Minutes Conchological Club Southern California*, 3l: 2-3.

Mottet, M.G. 1975. The fishery biology of *Octopus dofleini* (Wülker). *Seattle, Washington Department of Fisheries, Technical Report*, 16: 1-39.

Mouche, F., Boisset, N., Lamy, J., Zal, F. & Lamy, J.N. 1999. Structural comparison of cephalopod hemocyanins: Phylogenetic significance. *Journal of Structural Biology*, 127(3): 199-212.

Murphy, J.M., Balguerias, E., Key, L.N. & Boyle, P.R. 2002. Microsatellite DNA markers discriminate between two *Octopus vulgaris* (Cephalopoda: Octopoda) fisheries along the northwest African coast. *Bulletin of Marine Science*, 71(1): 545-553.

Muus, B. 2002. The *Bathypolypus-Benthoctopus* problem of the North Atlantic (Octopodidae, Cephalopoda). *Malacologia*, 44(2): 175-222.

Naef, A. 1923, Cephalopoda. Part II. *Fauna and Flora of the Gulf of Naples*, Monograph No. 35, 1(1) part 2: 313-917.

Nagai, T., Nagamori, K., Yamashita, E. & Suzuki, N. 2002. Collagen of octopus *Callistoctopus arakawai* arm. *International Journal of Food Science and Technology*, 37: 285-289.

Narvarte, M. 2006. Comparison of Tehuelche octopus (*Octopus tehuelchus*) abundance between an open-access fishing ground and a marine protected area: evidence from a direct development species. *Fisheries Research*, 79(1-2): 112-119.

Narvarte, M. 2007. Artisanal mollusk fisheries in San Matias Gulf (Patagonia, Argentina): an appraisal of the factors contributing to unsustainability. *Fisheries Research*, 87(1): 68-76.

Nateewathana, A. 1997. The octopod fauna (Cephalopoda: Octopoda) of the Andaman Sea, Thailand. *Phuket Marine Biological Center Special Publication*, 17(2): 407-452.

Nateewathana, A. & Norman, M.D. 1999. On three new species of ocellate octopuses (Cephalopoda: Octopoda) from Thai waters. *Phuket Marine Biological Center Special Publication*, 19(2): 445-462.

Navarro, J.C. & Villanueva, R. 2003. The fatty acid composition of *Octopus vulgaris* paralarvae reared with live and inert food: deviation from their natural fatty acid profile. *Aquaculture,* 219(1-4): 613-631.

Nesis, K.N. 1975a. [Cephalopods of the American Mediterranean Sea]. *Trudy Inst. Oceanol. Akad. Nauk. SSSR*, 100: 259-288. [In Russian]

Nesis, K.N. 1977. The biology of paper nautiluses, *Argonauta boettgeri* and *A. hians* (Cephalopoda, Octopoda), in the western Pacific and the seas of the East Indian Archipelago. *Zoologicheskii Zhurnal,* 56: 1004-1013.

Nesis, K.N. 1978. Comparison of cephalopod faunas along the coasts of Central America. *Malacological Review*, 11(1/2): 127-128.

Nesis, K. N. 1982/87. Abridged key to the cephalopod mollusks of the world's ocean. 385+ii pp. Light and Food Industry Publishing House, Moscow. (In Russian.). Translated into English by B. S. Levitov, ed. by L. A. Burgess (1987), Cephalopods of the world. T. F. H. Publications, Neptune City, NJ, 351 pp.

Nesis, K.N.1988. Cephalopods of the north polar ocean and it seas. Pages 115–136 *in* A. I. Kafanov, ed. *Fauna and distribution of mollusks: North Pacific and Polar Basin. Vladivostok, Far Eastern Scientific Center*, Acad. Sci. U.S.S.R. Pp. 115-136. [In Russian].

Nesis, K. N. 1991. Cephalopods of the Benguela upwelling off Namibia. *Bulletin of Marine Science,* 49(1-2): 199-215.

Nesis, K.N. 1999. The duration of egg incubation in high latitude and deep-water cephalopods: estimation and ecological consequences. *Biologiya Morya (Vladivostok),* 25: 499-506 [In Russian]

Nesis, K.N. 2001. West-Arctic and East-Arctic distributional ranges of cephalopods. *Sarsia*, 86(1): 1-11.

Nesis, K.N. & Nikitina, I.V. 1991. Larvae of a benthic octopus, *Euaxoctopus panamensis* (Cephalopoda, Octopodidae) in the plankton of the open waters of eastern Pacific. *Zoologichesky Zhurnal,* 70: 30-35.

Nishimura, S. 1968. A preliminary list of the pelagic Cephalopoda from the Japan Sea. *Publications of the Seto Marine Biological Laboratory*, 16(1): 71-83.

Nixon, M. 1979. Hole-boring in shells by *Octopus vulgaris* Cuvier in the Mediterranean. *Malacologia,* 18(1-2): 431-443.

Nixon, M. 1987. Cephalopod diets. *In* P.R. Boyle, ed. *Cephalopod Life Cycles. Volume II. Comparative Reviews*. London, Academic Press. Pp. 201-209.

Nixon, M. 1991. A note on the eggs of *Benthoctopus piscatorum* (Cephalopoda, Octopoda). *Journal of Zoology*, 223: 499-500.

Nixon, M. & Boyle, P.R. 1982. Hole-drilling in crustaceans by *Eledone cirrhosa* (Mollusca, Cephalopoda). *Journal of Zoology, London*, 196: 439-444.

Nixon, M. & Maconnachie, E. 1988. Drilling by *Octopus vulgaris* (Mollusca, Cephalopoda) in the Mediterranean. *Journal of Zoology,* 216: 687-716.

Nixon, M. & Mangold, K. 1996. The early life of *Octopus vulgaris* (Cephalopoda: Octopodidae) in the plankton and at settlement: a change in lifestyle. *Journal of Zoology, London,* 239: 301-327.

Nixon, M & Young, J.Z. 2003. *The Brains and Lives of Cephalopods*. New York, Oxford University Press. 392 pp.

Norman, M.D. 1992a. *Octopus cyanea* Gray, 1849 (Mollusca: Cephalopoda) in Australian waters: description, distribution and taxonomy. *Bulletin of Marine Science*, 49(1-2): 20-38 (1991).

Norman, M.D. 1992b. *Ameloctopus litoralis* gen. & sp. nov. (Cephalopoda: Octopodidae), a new shallow-water octopus from tropical Australian waters. *Invertebrate Taxonomy*, 6: 567-582.

Norman, M.D. 1992c. *Systematics and Biogeography of the Shallow-Water Octopuses (Cephalopoda: Octopodinae) of the Great Barrier Reef, Australia*. (Ph.D. dissertation) Melbourne, Australia, University of Melbourne. Volume I. 281 pp., Volume II. 13 pls. + 76 figs.

Norman, M.D. 1993a. Four new species of the *Octopus macropus* group (Cephalopoda: Octopodidae) from the Great Barrier Reef Australia. *Memoirs of the Museum of Victoria*, 53(2): 267-308.

Norman, M.D. 1993b. Ocellate octopuses (Cephalopoda: Octopodidae) of the Great Barrier Reef, Australia: description of two new species and redescription of *Octopus polyzenia* Gray, 1849. *Memoirs of Museum of Victoria,* 53(2): 309-344.

Norman, M.D. 1993c. *Octopus ornatus* Gould, 1852 (Cephalopoda: Octopodidae) in Australian waters: morphology, distribution and life history. *Proceedings of the Biological Society of Washington*, 106(4): 645-660.

Norman, M.D. 1998. Family Octopodidae, benthic octopuses. *In* K.E. Carpenter & V.H. Niem, eds. *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 2. Cephalopods, Crustaceans, Holothurians and Sharks,* pp. 800-826. Rome, FAO.

Norman, M.D. 2000. *Cephalopods: A World Guide*. Frankfurt, Germany, IKAN Publishing. 320 pp.

Norman, M.D. & Finn, J.K. 2001. Revision of the *Octopus horridus* species group with description of two member species from the Great Barrier Reef, Australia. *Invertebrate Taxonomy*, 15: 13-35.

Norman, M.D. & Hochberg, F.G. 1994. Shallow-water octopuses (Cephalopoda: Octopodidae) of Hong Kong territorial waters. *In* B. Morton, ed. *The Malacofauna of Hong Kong and Southern China III*. Proceedings of the Third International Workshop on the Malacofauna of Hong Kong and southern China. Hong Kong, Hong Kong University Press. Pp. 141-160.

Norman, M.D. & Hochberg, F.G. 2005a. The current state of octopus taxonomy. Proceedings of the International Workshop and Symposium of Cephalopod International Advisory Council, Phuket, 2003. *Phuket Marine Biological Center Special Publication*, 66: 127-154.

Norman, M.D. & Hochberg, F.G. 2005b. The “Mimic Octopus” (*Thaumoctopus mimicus* n. gen. et sp.), a new octopus from the tropical Indo-West Pacific (Cephalopoda: Octopodidae). *Molluscan Research,* 25(2): 57-70.

Norman, M.D. & Kubodera, T. 2006. Taxonomy and biogeography of an Australian subtropical octopus with Japanese affinities. *In* Y. Tomida *et al.*, eds. *Proceedings of the 7th and 8th Symposia on Collection Building and Natural History Studies in Asia and the Pacific Rim*. *National Science Museum Monographs*, 34: 171-189.

Norman, M.D. & Reid, A. 2000. *A guide to squid, cuttlefish and octopuses of Australasia.* CSIRO and Gould League of Victoria, Melbourne, 96 pp.

Norman, M.D. & Sweeney, M.J. 1997. The shallow-water octopuses (Cephalopoda: Octopodinae) of the Philippine Islands. *Invertebrate Taxonomy*, 11: 89-140.

Norman, M.D., Boucher, R. & Hochberg, F.G. 2004a. The sharkclub octopus, *Galeoctopus lateralis*, a new genus and species of deep-water octopus from the western Pacific Ocean (Cephalopoda: Octopodidae). *Journal of Molluscan Studies*, 70: 247-256.

Norman, M.D., Boucher-Rodoni, R. & Hochberg, F.G. 2009. A new genus and two new species of mesobenthic octopuses from Australia and New Caledonia. *Journal of Molluscan Studies,* 75: 323-336.

Norman, M.D., Finn, J.K. & Tregenza, T. 2001. Dynamic mimicry in an Indo-Malayan octopus. *Proceedings of the Royal Society, London, Series B, Biological Sciences*, 268: 1755-1758.

Norman, M.D., Hochberg, F.G. & Boucher-Rodoni, R. 2004b. *Microeledone mangoldi* n. gen. and n. sp., a deep-water pygmy octopus from the Norfolk Ridge, New Caledonia (Cephalopoda: Octopodidae). *Molluscan Research*, 24: 193-209.

Norman, M.D., Hochberg, F.G. & Boucher-Rodoni, R. 2005. A revision of the deep-water octopus genus *Scaeurgus* (Cephalopoda: Octopodidae) with description of three new species from the southwest Pacific Ocean. *Journal of Molluscan Studies,* 71: 319-337.

Norman, M.D., Hochberg, F.G. & Lu, C.C. 1997. Mid-depth octopuses (200-1000 m) of the Banda and Arafura Seas (Cephalopoda: Octopodidae and Alloposidae). *In* A. Crosnier & P. Bouchet, eds. *Resultats des Campagnes MUSORSTOM, Volume 16. Mémoires Museum national d'Histoire naturelle*, 172: 357-383.

Norman, M.D., Paul, D., Finn, J.K. & Tregenza, T. 2002. First encounter with a live male blanket octopus: the world's most sexually size-dimorphic large animal. *New Zealand Journal of Marine and Freshwater Research,* 36: 733-736.

Nottage, J.D. 2007. Cephalopod diversity in commercial fisheries landings of New South Wales, Australia. *Reviews in Fish Biology and Fisheries*, 17(2-3): 271-281.

O'Dor, R.K. & Macalaster, E.G. 1983. *Bathypolypus arcticus*. *In* P.R. Boyle, ed. *Cephalopod Life Cycles. Species Accounts*. Vol. I. London, Academic Press. Pp. 401-410.

Okumura, S., Kurihara, A., Iwamoto, A. & Takeuchi, T. 2005. Improved survival and growth in *Octopus vulgaris* paralarvae by feeding large type *Artemia* and Pacific sandeel, *Ammodytes personatus*: improved survival and growth of common octopus paralarvae. *Aquaculture,* 244(1-4): 147-157.

Okutani, T. 1960. *Argonauta boettgeri* preys on *Cavolina tridentata*. *Venus (The Japanese Journal of Malacology),* 21: 39-41.

Okutani, T. & Kawaguchi, T. 1983. A mass occurrence of *Argonauta argo* (Cephalopoda: Octopoda) along the coast of Shimane prefecture, western Japan Sea. *Venus (The Japanese Journal of Malacology),* 41: 281-290.

Okutani, T. & Osuga, K. 1986. A peculiar nesting behavior of *Ocythoe tuberculata* in the test of a gigantic salp, *Tethys vagina*. *Venus (The Japanese Journal of Malacology),* 45: 67-69.

Okutani, T., Tagawa, M. & Horikawa, H. 1987. *Cephalopods from Continental Shelf and Slope Around Japan*. Tokyo, Japan Fisheries Resource Conservation Association. 194 pp.

Olivares-Paz, A., Zuñiga-Romero, O. & Retamales-Negrete, E. 1994. Escala de madurez sexual de *Octopus* de la I Región, Chile. *Estudios Oceanológicos*, 13: 89-91.

Olivares-Paz, A., Bustos-Obregón, E. Castillo-Alvarez, V. & Zúñiga-Romero, O. 2003. Variaciones del funcionamiento testicular en *Octopus mimus* adultos. *International Journal of Morphology*, 21(4): 315-323.

Olivares-Paz, A., Zamora-Covarrubias, M., Portilla-Reyes, P. & Zúñiga-Romero, O. 2001. Estudio histológico de la ovogénesis y maduración ovárica en *Octopus mimus* (Cephalopoda: Octopodidae) de la II Región de Chile. *Estudios Oceanológicos*, 20: 13-22.

Olivares-Paz, A., Zuñiga-Romero, O., Castro, G., Segura, C. & Sánchez, J. 1996. Bases biológicas para el manejo de *Octopus mimus*: Reproducción y crecimento. *Estudios Oceanológicos*, 15: 61-74.

Oltra, R., Alemany, F., Roig, M. & Mezquita, F. 2005. [Ongrowing of the octopus *Octopus vulgaris* Cuvier, 1797 in floating cages on the Spanish Mediterranean coast of the Levant]. *Boletín. Instituto Español De Oceanografía,* 21(1-4): 187-194.

Oommen, V.P. 1976. A new species of the genus *Opisthoteuthis* Verrill, 1883 (Cephalopoda: Mollusca) from the southwest coast of India. *Journal of the Marine Biological Association of India*, 18: 368-374.

Oosthuizen, A. 2004. Economic feasibility of an experimental octopus fishery in South Africa. *South African Journal of Science*, 100(11-12): 595-602.

Oosthuizen, A., Jiwaji, M. & Shaw, P. 2004. Genetic analysis of the *Octopus vulgaris* population on the coast of South Africa. *South African Journal of Science,* 100(11-12): 603-607.

Oosthuizen, A. & Smale, M.J. 2003. Population biology of *Octopus vulgaris* on the temperate south-eastern coast of South Africa. *Journal of the Marine Biological Association of the United Kingdom,* 83(3): 535-541.

Opresko, L.K. 1974. *The Early Development of Octopus briareus Robson (Cephalopoda: Octopoda) and the Organogenesis of the Digestive System and its Associated Organs.* (Ph.D. dissertation) Coral Gables, Florida, University of Miami. 155 pp.

Orbigny, A.d' 1826. Tableau methodique de la Classe de Cephalopodes. *Annales des Sciences Naturelles, Paris*, (Ser. 1) 7: 95-169 + 245-314.

Orsi Relini, L. 2009. Notes about colour displays observed in female specimens of *Tremoctopus* and their taxonomic value. *Bollettino Malacologico*, 45: 13-16.

Orsi Relini L., Belluscio A. & Ardizzone G.D. 2004. Tracking the indopacific pelagic octopus *Tremoctopus gracilis* in the Mediterranean. *Rapp. Comm. int. Mer Médit.* 37: 415.

Orsi Relini, L., Mannini, A., Rossi, M. & Fiorentino, F. 2001. Un cefalopode nuovo nella fauna italiana: *Opisthoteuthis agassizii* Verril, 1883 (Octopoda, Cirrata, Opisthoteuthidae). *Biologia Marina Mediterranea*, 8(Part 2): 749-752.

Orsi Relini L., Mannini A., Fiorentino F., Palandri G. & Relini G. 2006. Biology and fishery of *Eledone cirrhosa* in the Ligurian Sea. *Fisheries Research*, 78(1): 72-88.

Ortiz, N. & Ré, M.E. 2011. The eggs and hatchlings of the octopus *Robsonella fontaniana* (Cephalopoda: Octopodidae). *Journal of the Marine Biological Association of the United Kingdom*, 91(3): 705-713.

Ortiz, N., Ré, M.E., Márquez, F. 2006. First description of eggs, hatchlings and hatchling behaviour of *Enteroctopus megalocyathus* (Cephalopoda : Octopodidae). *Journal of Plankton Research*, 28(10): 881-890.

Ortiz, N., Re, M.E., Marquez, F. & Glembocki, N.G. 2011. The reproductive cycle of the red octopus *Enteroctopus megalocyathus* in fishing areas of Northern Patagonian coast. *Fisheries Research*, 110: 217-223.

O'Shea, S. 1999. The marine fauna of New Zealand: Octopoda (Mollusca: Cephalopoda). *National Institute of Water and Atmospheric Research (NIWA) Biodiversity Memoir*, 112. 280 pp.

O'Shea, S. 2004. The giant octopus *Haliphron atlanticus* (Mollusca: Octopoda) in New Zealand waters. *New Zealand Journal of Zoology,* 31: 7-13.

O'Shea, S. & Kubodera, T. 1996. Eggs and larvae of *Graneledone* sp. (Mollusca, Octopoda) from New Zealand. Bulletin of the National Science Museum, Tokyo Series A, 22(3):153-164.

O'Shea, S. **& Lu, C.C.** 2002. A new species of *Luteuthis* (Mollusca: Cephalopoda: Octopoda: Cirrata) from the South China Sea. *Zoological Studies*, 41(2): 119-126.

Osorio, C., Cifuentes, J.A. & Fisher, S.M. 1979. Moluscos marinos de importancia economica en Chile. *Biología Pesquera*, 11: 3-47.

Otero, J., González, Á.F., Sieiro, M.P. & Guerra, Á. 2007. Reproductive cycle and energy allocation of *Octopus vulgaris* in Galician waters, NE Atlantic. *Fisheries Research,* 85(1-2): 122-129.

Otero, J., Álvarez-Salgado, X.A., González, Á.F., Gilcoto, M. & Guerra, Á. 2009. High-frequency coastal upwelling events influence *Octopus vulgaris* larval dynamics on the NW Iberian shelf. *Marine Ecology Progress Series,* 386: 123-132.

Otero, J., Rocha, F., González, Á. F., Gracia, J. & Guerra, Á. 2005. Modelling artisanal coastal fisheries of Galicia (NW Spain) based on data obtained from fishers: the case of *Octopus vulgaris*. *Scientia Marina,* 69(4): 577-585.

Otero, J., Álvarez-Salgado, X.A., González, Á.F., Miranda, A., Groom, S.B., Cabanas, J.M., Casas, G., Wheatley, B. & Guerra, Á. 2008. Bottom-up control of common octopus *Octopus vulgaris* in the Galician upwelling system, northeast Atlantic Ocean. *Marine Ecology Progress Series,* 362: 181-192.

Packard, A. & Hochberg, F.G. 1977. Skin patterning in *Octopus* and other genera. *In* M. Nixon & J.B. Messenger, eds. *The Biology of Cephalopods*. *Symposium of the Zoological Society, London*, No. 138. Pp. 191-231.

Packard, A. & Sanders, G.D. 1971. Body patterns of *Octopus vulgaris* and maturation of the response to disturbance. *Animal Behaviour*, 19: 780-790.

Packard, A. & Wurtz, M. 1994. An octopus, *Ocythoe*, with a swimbladder and triple jets. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences,* 344: 261-275.

Palacio, F.J. 1977. *A study of coastal cephalopods from Brazil with a review of Brazilian zoogeography.* PhD thesis, University of Miami.

Palacio, F.J. 1978. *Vosseledone charrua*: a new Patagonian cephalopod (Octopodidae) with notes on related genera. *Bulletin of Marine Science*, 28(2): 282-296.

Paredes, C., Huamán, P., Cardoso, F., Vivar, R. & Vera, V. 1999. Present state of the knowledge of aquatic mollusks in Peru. *Revista Peruana de Biología,* 6: 5-47.

Paust, B.C. 1988. Fishing for octopus: A guide for commercial fishermen. *Alaska Sea Grant Report*, 88-3. 48pp.

Pearcy, W.G. & Beal, A. 1973. Deep-sea cirromorphs (Cephalopoda) photographed in the Arctic Ocean. *Deep-Sea Research*, 20: 107-108.

Penniket, J.R. & Moon, G.J.H. 1970. *New Zealand Seashells in Colour*. Wellington, New Zealand, A.H. and A.W. Reed. 112 pp.

Pennington, H. 1979. Octopus fishing: Techniques and gear. *Alaska Seas and Coasts*, 7(3): 1-5.

Perales-Raya, C., Bartolome, A., Garcia-Santamaria, M.T., Pascual-Alayon, P. & Almansa, E. 2010. Age estimation obtained from analysis of octopus (*Octopus vulgaris* Cuvier, 1797) beaks: improvements and comparisons. *Fisheries Research,* 106(2): 171-176.

Pereda, S.V., Uriarte, I. & Cabrera, J.C. 2009. Effect of diet and paralarval development on digestive enzyme activity in the cephalopod *Robsonella fontaniana*. *Marine Biology*, 156(10): 2121-2128.

Pereyra, W.T. 1965. New records and observations on the flapjack devilfish, *Opisthoteuthis californiana* Berry. *Pacific Science*, 19: 427-441.

Perez, J.A.A. 1990. Distribuição Reprodução e Alimentação de *Eledone massyae* e *Eledone gaucha* (Cephalopoda: Octopodidae), no Sul do Brasil. Master's thesis, Fundação Universidade do Rio Grande, Rio Grande. 145 pp.

Perez, J.A.A. & Haimovici, M. 1991. Sexual maturation and reproductive cycle of *Eledone massyae*, Voss 1964 (Cephalopoda: Octopodidae) in southern Brazil. *Bulletin of Marine Sciences*, 49(1-2): 270-279.

Perez, J.A.A. & Haimovici, M. 1995. Descriptive ecology of two South American eledonids (Cephalopoda: Octopodidae). *Bulletin of Marine Science*, 56(3): 752-766.

Perez, J.A.A, Haimovici, M. & Cousin, J.C.B. 1990. Sperm storage mechanisms and fertilization in females of two South American eledonids (Cephalopoda: Octopoda). *Malacologia*, 32(1): 147-154.

Perez, J.A.A., Haimovici, M. & Santos, R.A.d. 1997. Observations on the reproductive biology of the octopod *Eledone gaucha* Haimovici, 1988, in southern Brazil. *American Malacological Bulletin*, 14(1): 81-84.

Pérez, M.C., López, D.A., Aguila, K. & González, M.L. 2006. Feeding and growth in captivity of the octopus *Enteroctopus megalocyathus* Gould, 1852. *Aquaculture Research,* 37: 550-555.

Pérez-Losada, M., Guerra, A. & Sanjuan, A. 2002. Allozyme divergence supporting the taxonomic separation of *Octopus mimus* and *Octopus maya* from *Octopus vulgaris* (Cephalopoda: Octopoda). *Bulletin of Marine Science*, 71(2): 653–664.

Perrier, E. & Rochebrune, A.T. de. 1894. Sur octopus nouveau de la basse Californie, habitant les coquilles des Mollusques bivalves. *Comptes Rendus des Seances de l'Academie des Sciences*, 118: 770-773.

Peterson, R.P. 1959. The anatomy and histology of the reproductive systems of *Octopus bimaculoides*. *Journal of Morphology,* 104: 61-87.

Petza, D., Katsanevakis, S., Lykouri, N., Spiliotis, V. & Verriopoulos, G. 2011. Investigation of the potential effect of diet, body mass and maturity on growth and feed performance of common octopus *Octopus vulgaris*: an information theory approach. *Aquaculture Nutrition,* 17(2): E348-E361.

Pham, C.K. & Isidro, E. 2009. Growth and mortality of common octopus (*Octopus vulgaris*) fed a monospecific fish diet. *Journal of Shellfish Research,* 28(3): 617-634.

Phillips, J.B. 1933. Octopi of California. *California Fish & Game*, 21: 20-29.

Piatkowski, U. & Diekmann, R. 2005. A short note on the cephalopods sampled in the Angola Basin during the DIVA-1 expedition. *Organisms Diversity and Evolution*, 5: 227-230.

Pickford, G.E. 1939. A re-examination of the types of *Melanoteuthis lucens* Joubin. *Bulletin de l'Institute Océaonographique, Monaco*, 777: 1-12.

Pickford, G.E. 1945. Le Poulpe Americain: a study of the littoral Octopoda of the Western Atlantic. *Transactions of the Connecticut Academy of Arts and Sciences*, 36: 701-811.

Pickford, G.E. 1946. A review of the littoral Octopoda from central and western Atlantic stations in the collections of the British Museum. *Annals and Magazine of Natural History,* (series 11), 13: 412-429.

Pickford, G.E. 1949a. *Vampyroteuthis infernalis* Chun an archaic dibranchiate cephalopod. II. External anatomy. *Dana Report*, No. 32: 1-132.

Pickford, G.E. 1949b. The distribution of the eggs of *Vampyroteuthis infernalis* Chun. *Journal of Marine Research*, 8(1): 73-83.

Pickford, G.E. 1955. A revision of the Octopodinae in the collections of the British Museum. Part II. A re-examination of the specimens of *Robsonella fontaniana* in the collections of the British Museum. *Bulletin of the British Museum (Natural History) Zoology, London*, 3: 163-167.

Pickford, G.E. & McConnaughey, B.H. 1949. The *Octopus bimaculatus* problem: a study in sibling species. *Bulletin of the Bingham Oceanographic Collection*, 12(4): 1-66.

Piertney, S.B., Hudelot, C., Hochberg, F.G. & Collins, M.A. 2003. Phylogenetic relationships among cirrate octopods (Mollusca: Cephalopoda) resolved using mitochondrial 16S ribosomal DNA sequences. *Molecular Phylogenetics and Evolution*, 27: 348-353.

Pliego-Cárdenas, R., Garcia-Dominguez, F.A., Ceballos-Vazquez, B.P., Villalejo-Fuerte, M. & Arellano-Martinez, M. 2011. Reproductive aspects of *Octopus hubbsorum* (Cephalopoda: Octopodidae) from Espiritu Santo Island, southern Gulf of California, Mexico. *Ciencias Marinas*, 37(1): 23-32.

Pollero, R.J. & Iribarne, O.O. 1988. Biochemical changes during the reproductive cycle of the small Patagonian octopus, *Octopus tehuelchus*, d'Orb. *Comparative Biochemistry and Physiology B-Biochemistry and Molecular Biology,* 90: 317-320.

Portmann, A. 1952. Les bras dorsaux de *Tremoctopus violaceus* delle Chiaje. (Avec deux figures dans le texte). *Revue Suisse de Zoologie,* 59: 288-293.

Quetglas, A., Carbonell, A. & Sánchez, P. 2000. Demersal continental shelf and upper slope cephalopod assemblages from the Balearic Sea (north-western Mediterranean). Biological aspects of some deep-sea species. *Estuarine Coastal and Shelf Science*, 50(6): 739-749.

Quetglas, A., González, M. & Franco, I. 2005. Biology of the upper-slope cephalopod *Octopus salutii* from the western Mediterranean Sea. *Marine Biology,* 146: 1131-1138.

Quetglas, A., Ordines, F. & Valls, M. 2011. What drives seasonal fluctuations of body condition in a semelparous income breeder octopus? *Acta Oecologica*, 37(5): 476-483.

Quetglas, A., González, M., Carbonell, A. & Sánchez, P. 2001. Biology of the deep-sea octopus *Bathypolypus sponsalis* (Cephalopoda: Octopodidae) from the western Mediterranean Sea. *Marine Biology,* 138: 785-792.

Quetglas, A., Ordines, F., González, M. & Franco, I. 2009. Life history of the bathyal octopus *Pteroctopus tetracirrhus* (Mollusca, Cephalopoda) in the Mediterranean Sea*. Deep Sea Research Part I - Oceanographic Research Papers*, 56(8): 1379-1390.

Quetglas, A., Alemany, F., Carbonell, A., Merella, P. & Sánchez, P. 1998. Biology and fishery of *Octopus vulgaris* Cuvier, 1797, caught by trawlers in Mallorca (Balearic Sea, western Mediterranean). *Fisheries Research*, 36(2-3): 237-249.

Rafinesque, C.S. 1840. On the 3 genera of cephalopodes, *Ocythoe*, *Todarus* and *Anisoctus*. *In The Good Book, and Amenities of Nature, or Annals of Historical and Natural Sciences*, Philadelphia. Pp. 63-65.

Rathjen, W.F. 1992. Cephalopod capture methods: an overview. *Bulletin of Marine Science*, 49(1-2): 494-505 (1991).

Rathjen, W.F. & Voss, G.L. 1987. Cephalopod fisheries: a review. *In* P.R. Boyle, ed. *Cephalopod Life Cycles. Volume 2. Comparative Reviews*. London, Academic Press. Pp. 253-275.

Ré, M.E. 1980. Estudio taxonomico de *Enteroctopus megalocyathus* (Gould) (Cephalopoda: Octopoda) con notas sobre su biologia y pesca. *Contribucion Centro Nacional Patagonico Consejo Nacional de Investigaciones Cientificas y Tecnicas*, 52: 1-34.

Ré, M.E. 1984. Maduracion sexual en *Enteroctopus megalocyathus* (Gould) (Cephalopoda: Octopoda). *Contribucion Centro Nacional Patagonico Consejo Nacional de Investigaciones Cientificas y Tecnicas*, 93: 1-28.

Ré, M.E. & Taylor, R. 1981. La pesca de pulpos en Argentina. Artes de captura utilizadas y estadisticas pesqueras hasta 1978. *Contribution Centro Nacional Patagónico* (CONICETI)*,* No. 52: 1-21.

Rees, W.J. 1956. Notes on the European species of *Eledone* with special reference to eggs and larvae. *Bulletin of the British Museum of Natural History*, 3: 283-293.

Reeve, L.A. 1860. Monograph of the genus *Argonauta*. *In* L.A. Reeve, ed. *Conchologia Iconica (illustrations of molluscous animals)*. London, Lovell Reeve. Pls. 1-4.

Reid, M. 1989. Argonauts: ancient mariners in boats of shell. *Australian Natural History*, 22(12): 580-587.

Reinhardt, J.T. & Prosch, V. 1846. Om *Sciadephorus Mulleri* (Eschr.). Copenhagen, Bianco Lunos Bogtrykkeri. 59 pp.

Rigby, P.R. & Sakurai, Y. 2004. Temperature and feeding related growth efficiency of immature octopuses *Enteroctopus dofleini*. *Suisan Zoshoku*, 52(1): 29-36.

Rigby, P.R. & Sakurai, Y. 2005. Multidimensional tracking of giant Pacific octopuses in northern Japan reveals unexpected foraging behaviour. *Marine Technology Society Journal,* 39(1): 64-67.

Robertson, A., Stirling, D., Robillot, C., Llewellyn, L. & Negri, A. 2004. First report of saxitoxin in octopi. *Toxicon*, 44: 765-771.

Robison, B.R. & Young, R.E. 1981. Bioluminescence in pelagic octopods. *Pacific Science*, 35: 39-44.

Robison, B.R., Reisenbichler, K.R., Hunt, J.C. & Haddock, S.H.D. 2004. Light production by the arm tips of the deep-sea cephalopod *Vampyroteuthis infernalis*. *Biological Bulletin,* 205(2): 102-109.

Robson, G.C. 1924. On new species, etc. of Octopoda from South Africa. *Annals and Magazine of Natural History*, Series 9, 13: 202-210.

Robson, G.C. 1929a. *A Monograph of the Recent Cephalopoda. Part I. Octopodinae.* London, British Museum (Natural History). 236 pp.

Robson, G.C. 1929b. *Annals of the Magazine of Natural History*, (10), III: 608.

Robson, G.C. 1929c. On the rare abyssal octopod *Melanoteuthis beebei* (sp. n.): A contribution to the phylogeny of the Octopoda. *Proceedings of the Zoological Society of London*, 1929(3): 469-486.

Robson, G.C. 1930. Cephalopoda: Octopoda. *Discovery Report*, 2: 1-371.

Robson, G.C. 1932. *A Monograph of the Recent Cephalopoda. Part II.* Octopoda*.* London, British Museum (Natural History). 359 pp.

Rocha, F. & Vega, M.A. 2003. Overview of cephalopod fisheries in Chilean waters. *Fisheries Research*, 60(1): 151-159.

Rocha, F., González, A.F., Segonzac, M. & Guerra, A. 2002. Behavioural observations of the cephalopod *Vulcanoctopus hydrothermalis*. *Cahiers de Biologie Marine*, 43(3-4): 299-302.

Rochebrune, A.T. de. 1885. Note sur un nouveau genre de Cephalopodes. *Bulletin de la Societe Philomathique de Paris*, (series 7), 9: 82-85.

Rochebrune, A.T. de. 1895. Note sur les Mollusques recueillis par M. Diguet en Basse-Californie. *Bulletin du Museum d'histoire naturelle*, 1895(2):1-2.

Rochebrune, A.T. de. 1896. Etude sur une form nouvelle du genre *Octopus* nouv. *Archives Museum d'histoire naturelle, Paris*, (ser. 3), 8: 75-86.

Rodaniche, A.F. 1984. Iteroparity in the lesser Pacific striped octopus *Octopus chierchiae* (Jatta, 1889). *Bulletin of Marine Science*, 35(1): 99-104.

Rodhouse, P.G. & Prince, P.A. 1993. Cephalopod prey of the black-browed albatross *Diomedea melanophrys* at South Georgia. *Polar Biology*, 13(6): 373-376.

Rodriguez, C., Carrasco, J.F., Arronte, J.C. & Rodriguez, M. 2006. Common octopus (*Octopus vulgaris* Cuvier, 1797) juvenile in floating cages. *Aquaculture*, 254(1-4): 293-300.

Rodríguez-Rúa, A., Pozuelo, I., Prado, M.A., Gómez, M.J. & Bruzón, M.A. 2005. The gametogenic cycle of *Octopus vulgaris* (Mollusca: Cephalopoda) as observed on the Atlantic coast of Andalusia (south of Spain). *Marine Biology,* 147(4): 927-933.

Roeleveld, M.A.C., Lipiński, M.R., Augustyn, C.J. & Stewart, B.A. 1992. The distribution and abundance of cephalopods on the continental slope of the eastern South Atlantic. *South African Journal of Marine Science*, 12: 739-752.

Roper, C.F.E. 1977. Comparative captures of pelagic cephalopods by midwater trawls. *Symposia of the Zoological Society of London,* 38: 61-87.

Roper, C.F.E. 1997. Experimental octopus fisheries: two case studies. *In* M.A. Lang & F.G. Hochberg, eds. *The Fishery and Market Potential of Octopus in California*. Washington, D.C., Smithsonian Institution. (Workshop Proceedings). Pp. 157-168.

Roper, C.F.E. & Brundage, W.L. 1972. Cirrate octopods with associated deep-sea organisms: new biological data based on deep benthic photographs (Cephalopoda). *Smithsonian Contributions to Zoology*, 121: 1-46.

Roper, C.F.E. & Hochberg, F.G. 1988. Behaviour and systematics of cephalopods from Lizard Island, Australia, based on colour and body patterns. *Malacologia*, 29(1): 153-93.

Roper, C.F.E. & Mangold, K. 1992. *Octopus schultzei* (Hoyle, 1910): a redescription with designation of *Aphrodoctopus* new genus (Cephalopoda: Octopodinae). *Bulletin of Marine Science,* 49(1-2): 57-72 (1991).

Roper, C.F.E. & Sweeney, M.J. 1976. The pelagic octopod *Ocythoe tuberculata* Rafinesque, 1814. *Bulletin of the American Malacological Union,* 1975: 21-28.

Roper, C.F.E. & Young, R.E. 1975. Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology,* 209: 1-51.

Roper, C.F.E., Sweeney, M.J. & Hochberg, F.G. 1995. Cefalopodos. *In* W. Fischer, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter & V.H. Niem, eds. *Guía FAO para la Identificación de Especies para los Fines de la Pesca. Pacífico Centro-Oriental. Volume I. Plantas e Invertebrados* FAO, Rome. Pp. 305-353.

Roper, C.F.E., Sweeney, M.J. & Nauen, C.E. 1984. *FAO Species Catalogue. Volume 3. Cephalopods of the World: An Annotated and Illustrated Catalogue of Species of Interest to Fisheries*. FAO Fisheries Synopsis (125) 3: 1-277. FAO, Rome.

Rosa, R. & Seibel, B.A. 2010. Voyage of the argonauts in the pelagic realm: physiological and behavioural ecology of the rare paper nautilus, *Argonauta nouryi*. *ICES Journal of Marine Science*, 67: 1494-1500.

Rosa, R., Costa, P.R. & Nunes, M.L. 2004. Effect of sexual maturation on the tissue biochemical composition of *Octopus vulgaris* and *O. defilippi* (Mollusca: Cephalopoda). *Marine Biology*, 145(3): 563-574.

Rosa, R., Pereira, J. & Moreno, A. 2009. Bathymetric range, density and reproductive biology of the deep-sea cirrate octopus *Opisthoteuthis calypso* in the Portuguese continental slope. *Journal of the Marine Biological Association of the United Kingdom*, 89(1): 131–134.

Rossi, A., Pellegrini, D., Belcari, P. & Barghigiani, C. 1993. Mercury in *Eledone cirrhosa* from the northern Tyrrhenian Sea: contents and relations with life cycle. *Marine Pollution Bulletin*, 26(12): 683-686.

Roura, Á., González, Á.F., Pascual, S. & Guerra, Á. 2010a. A molecular approach to identifying the prey of cephalopod paralarvae. *ICES Journal of Marine Science,* 67(7): 1408-1412.

Roura, Á., Guerra, Á., González, Á.F & Pascual, S. 2009. Sperm ultrastructural features of the bathyal octopod *Graneledone gonzalezi*. *Vie et Milieu - Life And Environmentgy*, 59(3-4): 301-305.

Roura, Á., Guerra, Á., González, Á.F & Pascual, S. 2010b. Sperm Ultrastructure in *Bathypolypus bairdii* and *B. sponsalis* (Cephalopoda: Octopoda). *Journal of Morphology*, 271: 143–151

Roura, Á., Guerra, Á., González, Á.F & Pascual, S. 2010c**.** Sperm ultrastructure of the hydrothermal vent octopod *Vulcanoctopus hydrothermalis*. *Journal of Morphology*, 271(8): 932-936.

Runham, N.W., Bailey, C.J., Carr, M., Evans, C.A. & Malham, S. 1997. Hole drilling in crab and gastropod shells by *Eledone cirrhosa* (Lamarck, 1798). *Scientia Marina*, 61(2): 67-76.

SAGARPA. 2004. *Anuario Estadístico de Pesca Año 2004*. Secretaria de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación. México, D.F. 266 pp.

Sakaguchi, H. 2006. Studies on the population biology of *Octopus vulgaris* in the eastern Iyo-nada of the Seto Inland Sea, Japan. *Bulletin of the Ehime Prefectural Fisheries Experimental Station*, 12: 25-94.

Sakaguchi, H., Hamano T. & Nakazano A. 1999a. Occurrence of planktonic juveniles of *Octopus vulgaris* in Eastern Iyo-Nada of the Seto Inland Sea, Japan. *Bulletin of the Japanese Society of Fisheries Oceanography,* 63(4): 181-187.

Sakaguchi, H., Hamano, T. & Nakazono, A. 1999b. Relationship between incubation days and rearing temperature of *Octopus vulgaris* eggs. *Bulletin of the Japanese Society of Fisheries Oceanography,* 63(4): 188-191.

Sakaguchi, H., Hamano, T. & Nakazono A. 2000. Population structure of *Octopus vulgaris* estimated from catch size Composition in Northeastern Iyo-Nada of the Seto Inland Sea, Japan. *Bulletin of the Japanese Society of Fisheries Oceanography,* 64(4): 224-234.

Sakaguchi, H., Hamano, T. & Nakazono, A. 2002. Growth of *Octopus vulgaris* in the Northeastern Iyo-Nada of the Seto Inland Sea, Japan. *Bulletin of the Japanese Society of Fisheries Oceanography,* 66(1): 11-15.

Salcedo-Vargas, M.A. & Jaime-Rivera, M. 1999. The octopod *Euaxoctopus panamensis* (Octopodidae: Cephalopoda) in Mexican waters. *Revista de Biologia Tropical*, 47(4): 1139.

Salman, A., Bilecenoglu, M. & Guçlusoy, H. 2001. Stomach contents of two Mediterranean monk seals (*Monachus monachus*) from the Aegean Sea, Turkey. *Journal of the Marine Biological Association of the United Kingdom*, 81(4): 719-720.

Salman, A. & Katagan, T. 1999. Distribution and abundance of the octopods *Eledone cirrhosa* (Lamarck, 1798) and *Eledone moschata* (Lamarck, 1799) (Cephalopoda: Octopoda) in the Aegean Sea. *Turkish Journal of Zoology*, 23(2): 695-702.

Salman, A., Katagan, T. & Boletzky, S.v. 1999. New cephalopod molluscs in the eastern Mediterranean: Previously unnoted species or recent migrants? *Vie et Milieu,* 49: 11-17.

Salman, A., Katagan, T. & Gucu, A.C. 2000. The distribution and fishing of two Mediterranean *Eledone* spp. (Octopoda: Cephalopoda) in the Aegean Sea. *Turkish Journal of Zoology*, 24(2): 165-172.

Salman, A., Laptikhovsky, V.V. & Katagan, T. 2005. Fertility of Indo-Pacific *Octopus kagoshimensis* (Cephalopoda, Octopodidae) males and females in the eastern Mediterranean Sea. *Zoologichesky Zhurnal,* 84: 269-271.

Sánchez, P. 1981. Régime alimentaire d'*Eledone cirrosa* (Lamarck, 1798) (Mollusca, Cephalopoda) dans la mer Catalane. *Rapports et Proces-verbaux des Reunions, Commission internationale pour l'exploration scientifique de la Mer Mediterranée*, 25(5): 209-212.

Sánchez, P. 2003. Cephalopods from off the Pacific coast of Mexico: Biological aspects of the most abundant species. *Scientia Marina*, 67(1): 81-90.

Sánchez, P. 2004. Modelling catch, effort and price in a juvenile *Eledone cirrhosa* fishery over a 10-year period. *Fisheries Research*, 68(1-3): 319-327.

Sánchez, P. & Alvarez, J.A. 1988. *Scaeurgus unicirrhus* (Orbigny, 1840) (Cephalopoda, Octopodidae) - 1st record from the Southeast Atlantic. *South African Journal of Marine Science,* 7: 69-74.

Sánchez, P., Fedi, E. & Belcari, P. 1990. Etude comparative de la relation taille poids de *Eledone cirrhosa* des Mers Catalane et Tyrrhenienne Septentrionale. *Rapports et Proces-verbaux des Reunions, Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee*, 32, 1: 243.

Sánchez, P. & Guerra, A. 1989. A new species of cirrate octopod *Opisthoteuthis vossi* from the southeast Atlantic (Cephalopoda: Octopoda). *Bulletin of Marine Science*, 44: 1159-1165.

Sánchez, P. & Obarti, R. 1993. The biology and fishery of *Octopus vulgaris* caught with clay pots on the Spanish Mediterranean coast. *In* T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Fisheries Biology*. Tokyo, Tokai University Press. Pp. 477-487.

Sánchez, P., Maynou, F. & Demestre, M. 2004. Modelling catch, effort and price in a juvenile *Eledone cirrhosa* fishery over a 10-year period. *Fisheries Research*, 68(1-3): 319-327.

Santos, M.B., Pierce, G.J., Herman, J., López, A., Guerra, A., Mente, E. & Clarke, M.R. 2001a. Feeding ecology of Cuvier's beaked whale (*Ziphus cavirostris*): a review with new information on the diet of this species. *Journal of the Marine Biological Association of the United Kingdom*, 81: 687-694.

Santos, M.B., Pierce, G.J., Smeenk, C., Addink, M.J., Kinze, C.C., Tougaard, S. & Herman, J. 2001b. Stomach contents of northern bottlenose whales *Hyperoodon ampullatus* stranded in the North Sea. *Journal of the Marine Biological Association of the United Kingdom*, 81: 143-150.

Santos, M.B., Pierce, G.J., Boyle, P.R., Reid, R.J., Ross, H.M., Patterson, I.A.P., Kinze, C.C., Tougaard, S., Lick, R., Piatkowski, U. & Hernandez-Garcia, V. 1999. Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990-1996. *Marine Ecology - Progress Series*, 183: 281-294.

Sardella, N.H. & Ré, M.E. 1996. Parasites of the digestive tract in octopuses (Mollusca: Cephalopoda) from Argentinean waters. *Revista de Malacologia Medica & Aplicada*, 8(1): 22 [Abstract – Proceedings of the Fourth International Malacological Congress].

Sardella, N.H., Ré, M.E. & Timi, J.T. 2000. Two new *Aggregata* species (Apicomplexa: Aggregatidae) infecting *Octopus tehuelchus* and *Enteroctopus megalocyathus* (Mollusca: Octopodidae) in Patagonia, Argentina. *Journal of Parasitology*, 86(5): 1107-1113.

Sasaki, M. 1920. Report of Cephalopoda collected during 1906 by the U.S.B.F. Steamer 'Albatross' in the N.W. Pacific. *Proceedings of the U.S. National Museum*, 57: 163-203.

Sasaki, M. 1929. A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. *Journal of the College of Agriculture, Hokkaido Imperial University*, 20(Supplement). 357 pp.

Sato, T. & Hatanaka, H. 1983. Stock assessment of Japanese distant-water fisheries for cephalopods. *In* Advances in Assessment of World Cephalopod Resources. *FAO Fisheries Technical Paper*, 231: 145-180.

Sauer, W.H.H., Potts, W., Raberinary, D., Anderson, J. & Sylvio Perrine, M.J. 2011. Assessment of current data for the octopus resource in Rodrigues, western Indian Ocean. *African Journal of Marine Science*, 33(1): 181-187.

Scheel, D. 2002. Characteristics of habitats used by *Enteroctopus dofleini* in Prince William Sound and Cook Inlet, Alaska. *Marine Ecology*, 23(3): 185-206.

Scheel, D., Lauster, A. & Vincent, T.L.S. 2007. Habitat ecology of *Enteroctopus dofleini* from middens and live prey surveys in Prince William Sound, Alaska. *In* N.H. Landman, R.A. Davis & R.H. Mapes, eds. *Cephalopods Present and Past: New Insights and Fresh Perspectives*, New York, Springer. Pp. 434-458.

Seibel, B.A. & Childress, J.J. 2000. Metabolism of benthic octopods (Cephalopoda) as a function of habitat depth and oxygen concentration. *Deep-Sea Research Part I - Oceanographic Research Papers*, 47(7): 1247-1260.

Seibel, B.A., Thuesen, E.V. & Childress, J.J. 1998. Flight of the vampire: ontogenetic gait-transition in *Vampyroteuthis infernalis* (Cephalopoda: Vampyromorpha). *Journal of Experimental Biology*, 201: 2413-2424.

Seibel, B.A., Thuesen, E.V., Childress, J.J. & Gordezky, L.A. 1997. Decline in pelagic cephalopod metabolism with habitat depth reflects differences in locomotory efficiency. *Biological Bulletin*, 192: 262-278.

Seixas, P., Rey-Méndez, M., Valente, L.M.P. & Otero, A. 2008. Producing juvenile *Artemia* as prey for *Octopus vulgaris* paralarvae with different microalgal species of controlled biochemical composition. *Aquaculture,* 283(1-4): 83-91.

Seixas, P., Rey-Méndez, M., Valente, L.M.P. & Otero, A. 2010a. High DHA content in *Artemia* is ineffective to improve *Octopus vulgaris* paralarvae rearing. *Aquaculture,* 300(1-4): 156-162.

Seixas, P., Otero, A., Valente, L.M.P., Dias, J. & Rey-Méndez, M. 2010b. Growth and fatty acid composition of *Octopus vulgaris* paralarvae fed with enriched *Artemia* or co-fed with an inert diet. *Aquaculture International,* 18(6): 1121-1135.

Sellheim, K. 2006. A comparative analysis of *Paroctopus digueti* populations in the Golfo de California. *The Festivus*, 38(6): 63-70.

Şen, H. 2007. Food preference of *Eledone moschata* Lamarck, 1799 (Cephalopoda: Octopodidae) in captive conditions. *International Journal of Natural & Engineering Sciences*, 1(2): 29-31.

Şen, H. & Akyol, O. 2011. A preliminary study on feeding preference of the musky octopus, *Eledone moschata*, (Cephalopoda: Octopodidae) in Izmir Bay, Aegean Sea. *Journal of Fisheries Sciences.com*, 5(2): 141-145.

Şen, H. & Tanrikul, T.T. 2009. Efficacy of 2-phenoxyethanol as an anaesthetic for the musky octopus, *Eledone moschata* (Lamarck 1799), (Cephalopoda: Octopodidae). *Turkish Journal of Veterinary and Animal Sciences*, 33(6): 463-467.

Sheumack, D.D., Howden, M.E.H. & Spence, I. 1984. Occurrence of a tetrodotoxin-like compound in the eggs of the venomous blue-ringed octopus (*Hapalochlaena maculosa*). *Toxicon,* 22: 811-812.

Shimizu, T. 1983. The study on the octopus (*Octopus vulgaris* Cuvier) resource in the Tokyo bay [Japan], 1: Fluctuation of resource based on catch data. *Bulletin of the Kanagawa Prefectural Fisheries Experiment Station,* 5, 35-40.

Silva, L., Ramos, F. & Sobrino, I. 2004. Reproductive biology of *Eledone moschata* (Cephalopoda: Octopodidae) in the Gulf of Cadiz (south-western Spain, ICES Division IXa). *Journal of the Marine Biological Association of the United Kingdom,* 84: 1221-1226.

Silva, L., Gil, J. & Sobrino, I. 2002a. Definition of fleet components in the Spanish artisanal fishery of the Gulf of Cádiz (SW Spain ICES division IXa). *Fisheries Research,* 59(1-2): 117-128.

Silva, L., Sobrino, I. & Ramos, F. 2002b. Reproductive biology of the common octopus, *Octopus vulgaris* Cuvier, 1797 (Cephalopoda: Octopodidae) in the Gulf of Cádiz (SW Spain). *Bulletin of Marine Science,* 71(2): 837-850.

Sinn, D.L. 2008. Patterns of activity cycles in juvenile California two-spot octopuses (*Octopus bimaculoides*). *American Malacological Bulletin*, 24(1): 65-69.

Sinn, D.L., Penin, N.A., Mather, J.A. & Anderson, R.C. 2001. Early temperamental traits in an octopus *(Octopus bimaculoides). Journal of Comparative Psychology*, 115(4): 351-364.

Smale, M.J. & Buchan, P.R. 1981. Biology of *Octopus vulgaris* off the east coast of South Africa. *Marine Biology*, 65(1): 1-12.

Smale, M.J., Clarke, M.R., Klages, N.T.W. & Roeleveld, M.A.C. 1993. Octopod beak identification - resolution at a regional level (Cephalopoda, Octopoda: southern Africa). South African *Journal of Marine Science*, 13: 269-293.

Smith, C.D. 1999*. Population Biology and Ecology of Octopuses of the South-Western Cape: A Study Towards the Establishment of a Small-Scale Octopus Fishery.* Master's thesis. University of Cape Town, Cape Town, South Africa. 111 pp.

Smith, C.D. 2003. Diet of *Octopus vulgaris* in False Bay, South Africa. *Marine Biology,* 143(6): 1127-1133.

Smith, C.D. & Griffiths, C.L. 2002. Aspects of the population biology of *Octopus vulgaris* in False Bay, South Africa. *South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap,* 24: 185-192.

Smith, P.J.S & Boyle, P.R. 1983. The Cardiac Innervation of *Eledone cirrhosa* (Lamarck) (Mollusca: Cephalopoda). Philosophical Transaction of the Royal Society of London, Series B, 300(1101): 493-511.

Sobrino, I., Juarez, A., Rey, J., Romero, Z. & Baro, J. 2011. Description of the clay pot fishery in the Gulf of Cádiz (SW Spain) for *Octopus vulgaris*: selectivity and exploitation pattern. *Fisheries Research,* 108(2-3): 283-290.

Sola-Simarra, L. Gil de. 1992. Resultados de las campanas de prospeccion qesquera de la especie *Eledone cirrhosa* en la plataforma continental del NO mediterraneo espanol. *Informes Téchnicos, Instituto Espanol de Oceanographia*, 140: 1-103.

Solís-Ramírez, M. 1997. *Octopus maya*: biology and fishery in Mexico. *In* M.A. Lang & F.G. Hochberg, eds. *The Fishery and Market Potential of Octopus in California*. Washington, D.C., Smithsonian Institution. (Workshop Proceedings). Pp. 105-113.

Söller, R., Warnke, K., Saint-Paul, U. & Blohm, D. 2000. Sequence divergence of mitochondrial DNA indicates cryptic biodiversity in *Octopus vulgaris* and supports the taxonomic distinctiveness of *Octopus mimus* (Cephalopoda: Octopodidae). *Marine Biology,* 136(1): 29-35.

Sreeja, V., Bijukumar, A. & Norman, M.D. 2012. First report of *Amphioctopus neglectus* (Nateewathana & Norman, 1999) and *A. rex* (Nateewathana & Norman, 1999) (Mollusca: Cephalopoda) from the Indian coast. *Molluscan Research,* 32(1): 43–49.

Steer, M.A. & Semmens, J.M. 2003. Pulling or drilling, does size or species matter? An experimental study of prey handling in *Octopus dierythraeus* (Norman, 1992). *Journal of Experimental Marine Biology and Ecology,* 290: 165-178.

Stevenson, J.A. 1935. The cephalopods of the Yorkshore coast. *Journal of Conchology*, 20(4): 102-116.

Storelli, M.M. & Marcotrigiano, G.O. 2004. Content of mercury and cadmium in fish (*Thunnus alalunga*) and cephalopods (*Eledone moschata*) from the south-eastern Mediterranean Sea. *Food Additives & Contaminants*, 21(11): 1051-1056.

Storero, L.P., Ocampo-Reinaldo, M., González, R.A. & Narvarte, M.A. 2010. Growth and life span of the small octopus *Octopus tehuelchus* in San Matías Gulf (Patagonia): three decades of study. *Marine Biology*, 157(3): 555-564.

Stoskopf, M.K. & Oppenheim, B.S. 1996. Anatomical features of *Octopus bimaculoides* and *Octopus digueti*. *Zoo and Wildlife Medicine*, 27(1): 1-18.

Stranks, T.N. 1988a. *Systematics of the Family Octopodidae (Mollusca: Cephalopoda) of South-Eastern Australia*. (Master's thesis). University of Melbourne, Melbourne, Australia. 114 pp.

Stranks, T.N. 1988b. Redescription of *Octopus pallidus* (Cephalopoda: Octopodidae) from south-eastern Australia. *Malacologia*, 29(1): 275-287.

Stranks, T.N. 1990. Three new species of *Octopus* (Mollusca: Cephalopoda) from south-eastern Australia. *Memoirs of the Museum of Victoria*, 50(2): 457-465.

Stranks, T.N. 1998. The systematic and nomenclatural status of the Octopodinae described from Australia (Mollusca: Cephalopoda). *In* N.A. Voss, M. Vecchione, R.B. Toll & M.J. Sweeney, eds. *Systematics and Biogeography of Cephalopods. Volume II*. *Smithsonian Contributions to Zoology*, 586:529-547.

Stranks, T.N. & Norman, M.D. 1993. Review of the *Octopus australis* complex (Cephalopoda: Octopodidae) and description of a new species. *Memoirs of the Museum of Victoria (1992),* 53(2): 345-373.

Strugnell, J.M., Allcock, A.L. & Watts, P.C. 2009a. Microsatellite loci from the endemic Southern Ocean octopus *Adelieledone polymorpha* (Robson, 1930). *Molecular Ecology Resources*, 9(3): 1068-1070.

Strugnell, J.M., Allcock, A.L. & Watts, P.C. 2009b. A panel of microsatellite loci from two species of octopus, *Pareledone turqueti* (Joubin, 1905) and *Pareledone charcoti* (Joubin, 1905). *Molecular Ecology Resources*, 9(4): 1239-1242.

Strugnell, J.M., Collins, M.A. & Allcock, A.L. 2008a. Molecular evolutionary relationships of the octopodid genus *Thaumeledone* (Cephalopoda: Octopodidae) from the Southern Ocean. *Antarctic Science*, 20(3): 245-251.

Strugnell, J.M., Norman, M.D., Drummond, A. & Cooper, A. 2004. Neotenous origins for pelagic octopuses. *Current Biology*, 14: R300-R301.

Strugnell, J.M., Voight, J.R., Collins, P.C. & L. Allcock. 2009c. Molecular phylogenetic analysis of a known and a new hydrothermal vent octopod: their relationships with the genus *Benthoctopus* (Cephalopoda: Octopodidae). *Zootaxa,* 2096: 442-459.

Strugnell, J.M., Norman, M.D., Jackson, J., Drummond, A. & Cooper, A. 2005. Molecular phylogeny of coleoid cephalopods (Mollusca: Cephalopoda) using a multigene approach; the effect of data partitioning on resolving phylogenies in a Bayesian framework. *Molecular Phylogenetics and Evolution*, 37(2): 426-441.

Strugnell, J.M., Norman, M.D., Vecchione, M., Guzik, M. & Allcock, A.L. 2013.The ink sac clouds octopod evolutionary history. *Hydrobiologia*. DOI 10.1007/s10750-013-1517-6.

Strugnell, J.M., Rogers, A.D., Prodöhl, P.A., Collins, M.A. & Allcock, A.L. 2008b. The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics*, 24: 1-8.

Strugnell, J.M., Cherel, Y., Cooke, I.R., Gleadall, I.G., Hochberg, F.G., Ibanez, C.M., Jorgensen, E., Laptikhovsky, V.V., Linse, K., Norman, M., Vecchione, M., Voight, J.R. & Allcock, A.L. 2011. The Southern Ocean: Source and sink? *Deep-Sea Research Part II - Topical Studies In Oceanography*, 58(1-2): 196-204.

Sukhsangchan, C. & Nabhitabhat, J. 2007. Embryonic development of muddy paper nautilus, *Argonauta hians* Lightfoot, 1786, from Andaman Sea, Thailand. *Kasetsart Journal (Natural Science),* 41: 531-538.

Sukhsangchan, C., Nabhitabhat, J. & Meksumpun, S. 2008. Notes on the behaviour of the female muddy argonaut, *Argonauta hians* Lightfoot, 1786 in captivity. *Phuket Marine Biology Center Research Bulletin*, 69: 55-59.

Sukhsangchan, C., Meksumpun, S., Nabhitabhata, J. & Segawa, S. 2009. Distribution, biology, and stomach contents of paper nautilus (*Argonauta hians*) in the Andaman Sea. *Science Asia*, 35: 315-319.

Sweeney, M.J. & Roper. C.F.E. 1998. Classification, type localities, and type repositories of recent Cephalopoda. *In* N.A. Voss, M.V. Vecchione, R.B. Toll & M.J. Sweeney, eds. *Systematics and Biogeography of Cephalopods*, Vol. II. Smithsonian Contributions to Zoology, 586: 561–599.

Takeda, R. 1990. The distribution of planktonic juveniles of *Octopus vulgaris* Cuvier in Harima Nada [Japan]. *Suisanzoshoku*, 38(2): 183-190.

Taki, I. 1944. [Studies on the octopus. (2) The sexes and the reproductive organs]. *Venus (The Japanese Journal of Malacology)*, 13: 267-310. [In Japanese].

Taki, I. 1961. On two new eledonid octopods from the Antarctic Sea. *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University*, 3(2): 297-316.

Taki, I. 1962. On species newly added to the fauna of Japanese Cephalopoda. *Dobutsu-Gaku Zasshi* [*Zoologica Magazine Tokyo*], 71: 397-398.

Taki, I. 1963. On four newly known species of Octopoda from Japan. *Journal of the Faculty of Fisheries and Animal Husbandry Hiroshima University*, 5: 57-93.

Takumiya, M., Kobayashi, M., Tsuneki, K. & Furuya H. 2005. Phylogenetic relationships among major species of Japanese coleoid cephalopods (Mollusca: Cephalopoda) using three mitochondrial DNA sequences. *Zoological Science*, 22(2): 147-155.

Talledo, C., Shiga, B. & Ishiyama, V. 1998. Contribución al conocimiento de la biologia del pulpo *Octopus mimus* (Mollusca: Cephalopoda). *Boletín de Lima*, 20(111): 63-72.

Talmadge, R.R. 1967. Notes on cephalopods from northern California. *Veliger*, 10(2): 200-202.

Tanaka, J. 1958. On the stock of *Octopus (Octopus) vulgaris* Lamarck, on the East Coast of Boso Peninsula, Japan. *Bulletin of the Japanese Society Scientific Fisheries,* 24(8): 601-607.

Tarlton, K. & Doak, W. 1968. The paper nautilus. A sad voyage for a rare sailor. *Skin Diver,* November 1968: 36-39, 66.

Teske, P.R., Oosthuizen, A., Papadopoulos, I. & Barker, N.P. 2007. Phylogeographic structure of *Octopus vulgaris* in South Africa revisited: identification of a second lineage near Durban harbour. *Marine Biology,* 151(6): 2119-2122.

Thomas, R.F. 1977. Systematics, distribution and biology of cephalopods of the genus *Tremoctopus* (Octopoda: Tremoctopodidae). *Bulletin of Marine Science,* 27: 353-392.

Thore, S. 1949. Investigations on the “Dana” Octopoda. *Dana Report*, No. 33: 1-85.

Thore, S. 1959. Cephalopoda. *Reports of the Lund University Chile Expeditions 1948-49*, 33: 1-20.

Toll, R.B. 1981. *Benthoctopus oregonae*, a new species of octopod (Mollusca: Cephalopoda) from the southern Caribbean with a redescription of *Benthoctopus januarii* (Hoyle, 1885). *Bulletin of Marine Science*, 31(1): 83-95.

Toll, R.B. 1990. A reaffirmation of the nomenclatural status of *Octopus filosus* Howell, 1868, the senior synonym of *Octopus hummelincki* Adam, 1936. *Nautilus*, 104(1): 26-28.

Toll, R.B. 1998. The systematic and nomenclatural status of the Octopodinae described from the Indian Ocean (excluding Australia) and the Red Sea. *In* N.A. Voss, M. Vecchione, R.B. Toll & M.J. Sweeney, eds. *Systematics and Biogeography of Cephalopods. Volume II*. *Smithsonian Contributions to Zoology*, 586:475-487.

Toll, R.B. & Binger, L.C. 1991. Arm anomalies: cases of supernumerary development and bilateral agenesis of arm pairs in Octopoda (Mollusca, Cephalopoda). *Zoomorphology*, 110(6): 313-316.

Toll, R.B. & Strain, C.H. 1988. Freshwater and terrestrial food organisms as an alternative diet for laboratory culture of cephalopods. *Malacologia*, 29(1): 195-200.

Toll, R.B. & Voss, G.L. 1998. The systematic and nomenclatural status of the Octopodinae described from the West Pacific region. *Smithsonian Contributions to Zoology,* 586: 489–520.

Tollit, D.J. & Thompson, P.M. 1996. Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, 74(6): 1110-1121.

Tranter, D.J. & Augustin, O. 1973. Observations on the life history of the blue-ringed octopus *Hapalochlaena maculosa*. *Marine Biology,* 18: 115-128.

Tsangridis, A., Sánchez, P. & Ioannidou, D. 2002. Exploitation patterns of *Octopus vulgaris* in two Mediterranean areas. *Scientia Marina,* 66(1): 59-68.

Tsuchiya, H., Ikeda, F. & Shimizu, T. 1986. The study on octopus (*Octopus vulgaris* Cuvier) resource in Tokyo bay [Japan], 3: Experiment of marking methods for octopus. *Bulletin of the Kanagawa Prefectural Fisheries Experiment Station*, 7: 45-53.

Tsuchiya, H., Yazawa, K. & Sakunaka, H. 1987. The study on octopus (*Octopus vulgaris* Cuvier) resource in Tokyo bay [Japan], 4: The migration of common octopus with marking. *Bulletin of the Kanagawa Prefectural Fisheries Experiment Station*, 8: 17-26.

Tsuchiya, K., Yamamoto, T. & Abe, H. 2002. *Cephalopods in Japanese waters*, TBS-Britanica Co. Ltd., Tokyo.

Turek, V. 2008. *Boionautilus* gen. nov. from the Silurian of Europe and North Africa (Nautiloidea, Tarphycerida). *Bulletin of Geosciences*, 83 (2): 141-152.

Tursi, A., D’Onghia, G., Lefkatidou, E., Maiorano, P. & Panetta, P. 1995. Population biology of *Eledone cirrhosa* (Mollusca, Cephalopoda) in the north Aegean Sea (eastern Mediterranean Sea). *Vie et Milieu*, 45(2): 139-145.

Tutman, P., Krstulović Šifner, S., Dulčić, J., Pallaoro, A., Gavrilović, A., Jug-Dujaković, J.& Glamuzina, B. 2008. A note on the distribution and biology of *Ocythoe tuberculata* (Cephalopoda: Ocythoidae) in the Adriatic Sea. *Vie et Milieu*, 58(3-4): 215-221.

Uchida, Y., Yoshimura, E. and Kimura, H. 2005. Ecology and stock fluctuation of *Octopus vulgaris* in the Seto Inland Sea coast, Yamaguchi prefecture, *Bulletin of Yamaguchi Prefectural Fisheries Research Center*, 3, 45-54.

Ulas, A., Unsal, S., Lok, A., Duzbastilar, O. & Metin, C. 2002. The studies on artificial reef design for *Octopus vulgaris* (Cuvier, 1797) in Izmir Bay field and tanks observations (Aegean Sea, Turkey). *Biologia Marina Mediterranea,* 9: 188-189.

Undheim, E.A.B., Norman, J.A., Thoen, H.H. & Fry, B.G. 2010a. Identification of Southern Ocean octopod samples using mtCOI. *Compte Rendu Biologique,* 333: 395–404.

Undheim, E.A.B., Georgieva, D.N., Thoen, H.H, Norman, J.A., Mork, J., Betzel, C. & Fry, B.G. 2010b. Venom on ice: First insights into Antarctic octopus venoms. *Toxicon*, 56: 897–913

Uriarte, I., Farias, A., Paschke, K., Navarro, J.C. & Rosas, C. 2011. Observations on feeding and biochemical characteristics to improve larviculture of *Robsonella fontaniana* (Cephalopoda: Octopodidae). *Aquaculture*, 315(1-2): 121-124.

Uriarte, I., Hernandez, J., Dorner, J., Paschke, K., Farias, A., Crovetto, E. & Rosas, C. 2010. Rearing and growth of the octopus *Robsonella fontaniana* (Cephalopoda: Octopodidae) from planktonic hatchlings to benthic juveniles. *The Biological Bulletin,* 218(2): 200-211.

Uriarte, I., Zuniga, O., Olivares, A., Espinoza, V., Cerna, V., Farias, A. & Rosas, C. 2009. Morphometric changes and growth rate during embryonic development of *Robsonella fontaniana*. *Vie et Milieu - Life And Environment*, 59(3-4): 315-323.

Valverde, J.C., Hernández, M.D., Aguado-Giménez, F. & García García, B. 2008. Growth, feed efficiency and condition of common octopus (*Octopus vulgaris*) fed on two formulated moist diets. *Aquaculture,* 275(1-4): 266-273.

Van Heukelem, W.F. 1983a. *Octopus cyanea*. *In* P.R. Boyle, ed. *Cephalopod Life Cycles. Volume 1, Species Accounts*, pp. 267-276. New York, Academic Press. Pp. 267-276.

Van Heukelem, W.F. 1983b. *Octopus maya*. *In* P.R. Boyle, ed. *Cephalopod Life Cycles. Volume 1, Species Accounts*. New York, Academic Press. 311-324.

Vardala-Theodorou, E. 1994. *Tremoctopus violaceus* delle Chiaje, 1830, from Epidaurus Gulf (Aegean Sea, Greece). Contribution to knowledge of its geographical distribution. *Annales Musei Goulandris*, 9: 471-477.

Vargas-Yáñez, M., Moya, F., Garcia-Martinez, M., Rey, J., González, M. & Zunino, P. 2009. Relationships between *Octopus vulgaris* landings and environmental factors in the northern Alboran Sea (southwestern Mediterranean). *Fisheries Research*, 99(3): 159-167.

Vasquez-Rowe, I., Moreira, M.T. & Feijoo, G. 2011. Environmental assessment of frozen common octopus (*Octopus vulgaris*) captured by Spanish fishing vessels in the Mauritanian EEZ. *Marine Policy,* 36: 180-188.

Vaz-Pires, P., Seixas, P. & Barbosa, A. 2004. Aquaculture potential of the common octopus (*Octopus vulgaris* Cuvier, 1797): a review. *Aquaculture,* 238(1-4): 221-238.

Vecchione, M. 1998. Extraordinary abundance of squid paralarvae in the tropical eastern Pacific Ocean during El Niño of 1987. *Fishery Bulletin,* 97: 1025-1030.

Vecchione, M. & Collins, M.A. 2002. Systematics, ecology and biology of cirrate octopods: workshop report. *Bulletin of Marine Science*, 71(1): 79-94.

Vecchione. M. & Pohle, G. 2002. Midwater cephalopods in the western North Atlantic Ocean off Nova Scotia. *Bulletin of Marine Science*, 71: 883-892.

Vecchione, M. & Roper, C.F.E. 1991. Cephalopods observed from submersibles in the western North Atlantic. *Bulletin of Marine Science*, 49: 433-445.

Vecchione, M. & Young, R.E. 1997. Aspects of the functional morphology of cirrate octopods: locomotion and feeding. *Vie et Milieu*, 47(2): 101-110.

Vecchione, M, Allcock, A.L. & Piatkowski, U. 2005. Unusual incirrate octopods from the South Shetland Islands, Antarctica, including *Bathypurpurata profunda*, a newly discovered genus and species of deepwater pygmy octopod. *Phuket Marine Biological Center Research Bulletin,* 66: 109-116.

Vecchione, M., Mangold, K.M. & Young, R.E. 2014. Cirrata Grimpe, 1916. Finned octopods. Version 06 December 2014 (under construction). *http://tolweb.org/Cirrata/20086/2014.12.06 In* The Tree of Life Web Project, http://tolweb.org/

Vecchione, M., Piatkowski, U. & Allcock, A.L. 1998. Biology of the cirrate octopod *Grimpoteuthis glacialis* (Cephalopoda; Opisthoteuthidae) in the South Shetland Islands, Antarctica. *South African Journal of Marine Science*, 20: 421-428.

Vecchione, M., Allcock, A.L., Piatkowski, U. & Strugnell, J. 2009, *Benthoctopus rigbyae*, n. sp., a new species of cephalopod (Octopoda; Incirrata) from near the Antarctic Peninsula. *Malacologia*, 51(1): 13-28.

Vega-Petkovic, M.A. 2007. Description of the female of *Grimpoteuthis bruuni* Voss, 1982. *Gayana*, 71(2): 207.

Veguilla, V. 2009. The exploitation of octopuses in Morocco: conflicts and collective action. *Politique Africaine,* 116: 43-62.

Velasco, F., Olaso, I. & Sánchez, F. 2001. The role of cephalopods as forage for the demersal fish community in the southern Bay of Biscay. *Fisheries Research*, 52: 65-77.

Verrill, A.E. 1879. Notice of recent additions to the marine fauna of the eastern coast of North America, No. 7. *American Journal of Science and Arts*, 18: 468-470.

Verrill, A.E. 1880. Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England. *American Journal of Science*, (Ser. 3), 20(41): 390-403.

Verrill, A.E. 1881. The cephalopods of the northeastern coast of America. Part II. The smaller cephalopods, including the squids and the octopi and other allied forms. *Transactions of the Connecticut Academy of Arts and Sciences,* 5: 259-446.

Verrill, A.E. 1883. No. 5. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and in the Caribbean Sea (1878-79), by the U.S. Coast Survey Steamer “Blake,” Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., Commanding. XXV. Supplementary report on the Blake cephalopods. *Bulletin of the Museum of Comparative Zoology*, 11(5): 105-123.

Verrill, A.E. 1884. Second catalogue of the Mollusca, recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep sea species, with notes on others previously recorded. *Transactions of the Connecticut Academy of Sciences*, 6(1): 139-294.

Verrill, A.E. 1885. Third catalogue of Mollusca, recently added to the Fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. *Transactions of the Connecticut Academy of Arts and Sciences*, 6(2): 395-452.

Verrill, A.E. 1896. The Opisthoteuthidae. A remarkable new family of deep sea Cephalopoda, with remarks on some points in molluscan morphology. *American Journal of Science*, 2: 74-80.

Vidal, É. A. G., Fuentes, L. & da Silva, L. B. 2010a. Defining *Octopus vulgaris* populations: a comparative study of the morphology and chromatophore pattern of paralarvae from Northeastern and Southwestern Atlantic. *Fisheries Research,* 106(2): 199-208.

Vidal, E.A.G., Haimovici, M. & Hackbart, V.C.S. 2010b. Distribution of paralarvae and small juvenile cephalopods in relation to primary production in an upwelling area off southern Brazil. *ICES Journal of Marine Science*, 67: 1346-1352.

Villanueva, R. 1992a. Deep-sea cephalopods of the north-western Mediterranean - indications of up-slope ontogenic migration in 2 bathybenthic species. *Journal of Zoology,* 227: 267-276.

Villanueva, R. 1992b. Continuous spawning in the cirrate octopods *Opisthoteuthis agassizii* and *O. vossi*: features of sexual maturation defining a reproductive strategy in cephalopods. *Marine Biology*, 114: 265-275.

Villanueva, R. 1993. Diet and mandibular growth of *Octopus magnificus* (Cephalopoda). *South African Journal of Marine Science*, 13: 121-126.

Villanueva, R. 2000. Observations on the behaviour of the cirrate octopod *Opisthoteuthis grimaldii* (Mollusca, Cephalopoda). *Journal of the Marine Biological Association of the United Kingdom*, 80: 555-556.

Villanueva, R. & Bustamante, P. 2006. Composition in essential and non-essential elements of early stages of cephalopods and dietary effects on the elemental profiles of *Octopus vulgaris* paralarvae. *Aquaculture,* 261(1): 225-240.

Villanueva, R. & Guerra, A. 1991. Food and prey detection in two deep-sea cephalopods: *Opisthoteuthis agassizii* and *O. vossi* (Octopoda: Cirrata). *Bulletin of Marine Science*, 49: 288-299.

Villanueva, R. & Norman, M.D. 2008. Biology of the planktonic stages of benthic octopuses. *Oceanography and Marine Biology: An Annual Review*, 46: 105-202.

Villanueva, R. & Sánchez, P. 1993. Cephalopods of the Benguela Current off Namibia - new additions and considerations on the genus *Lycoteuthis*. *Journal of Natural History*, 27(1):15-46.

Villanueva, R. & Segonzac, M. 1997. ?*Cirrothauma murrayi* Chun, 1911. *In* D. Desbruyères & M. Segonzac (Eds.). *Handbook of Deep-Sea Hydrothermal Vent Fauna*. IFREMER: Brest, France. Pp. 156.

Villanueva, R., Nozais, C. & Boletzky, S.V. 1997a. Swimming behaviour and food searching in planktonic *Octopus vulgaris* Cuvier from hatching to settlement. *Journal of Experimental Marine Biology and Ecology,* 208(1/2): 169-184.

Villanueva, R., Sánchez, P. & Compagno-Roeleveld, M.A. 1992. *Octopus magnificus* (Cephalopoda: Octopodidae), a new species of large octopod from the southeastern Atlantic. *Bulletin of Marine Science*, 49: 39-56 (1991).

Villanueva, R., Segonzac, M. & Guerra, A. 1997b. Locomotion modes of deep-sea cirrate octopods (Cephalopoda) based on observations from video recordings on the Mid-Atlantic Ridge. *Marine Biology*, 129: 113-122.

Villanueva, R., Collins, M., Sánchez, P. & N. Voss. 2002a. Systematics, distribution and biology of the cirrate octopods of the genus *Opisthoteuthis* (Mollusca, Cephalopoda) in the Atlantic Ocean, with description of two new species. *Bulletin of Marine Science*, 71: 933-985.

Villanueva, R., Koueta, N., Riba, J. & Boucaud-Camou, E. 2002b. Growth and proteolytic activity of *Octopus vulgaris* paralarvae with different food rations during first feeding, using *Artemia nauplii* and compound diets. *Aquaculture,* 205(3-4): 269-286.

Villanueva, R., Escudero, J.M., Deulofeu, R., Bozzano, A. & Casoliva, C. 2009. Vitamin A and E content in early stages of cephalopods and their dietary effects in *Octopus vulgaris* paralarvae. *Aquaculture,* 286(3-4): 277-282.

Villanueva, R., Riba, J., Ruiz-Capillas, C., González, A.V. & Baeta, M. 2004. Amino acid composition of early stages of cephalopods and effect of amino acid dietary treatments on *Octopus vulgaris* paralarvae. *Aquaculture,* 242(1-4): 455-478.

Villegas, P. & Tafur, R. 2000. Aspectos reproductivos del pulpo (*Octopus mimus* Gould, 1895) en el área de Callao durante 1998. *Informe Progresivo, Instituto del Mar Peru (IMARPE)*, 121: 3-15.

Voight, J.R. 1984. Habitat selection, reproduction and sibling species of *Octopus digueti*. *Journal of the Arizona-Nevada Academy of Sciences*, 19: 13-14 [abstract].

Voight, J.R. 1988a. Trans-Panamanian geminate octopods (Mollusca: Octopoda). *Malacologia*, 29(1): 289-294.

Voight, J.R. 1988b. A technique for trapping sandflat octopuses. *American Malacological Bulletin*, 6(1): 45-48.

Voight, J.R. 1988c. Shell use by the Pacific pygmy octopus. *Thatcheria*, 23(3): 1-3.

Voight, J.R. 1990. *Population Biology of Octopus digueti and the Morphology of American Tropical Octopods*. (Ph.D. dissertation). University of Arizona, Tucson, Arizona. 196 pp.

Voight, J.R. 1991a. Ligula length and courtship in *Octopus digueti*: a potential mechanism of mate choice. *Evolution*, 45(7): 1726-1730.

Voight, J.R. 1991b. Enlarged suckers as an indicator of male maturity in Octopus. *Bulletin of Marine Science*, 49(1-2): 98-106.

Voight, J.R. 1992. Movement, injuries and growth of members of a natural population of the Pacific pygmy octopus, *Octopus digueti*. *Journal of Zoology, London*, 228: 247-263.

Voight, J.R. 1993. The arrangement of suckers on octopodid arms as a continuous character. *Malacologia*, 35(2): 351-359.

Voight, J.R. 1995. Sexual dimorphism and niche divergence in a mid-water octopod (Cephalopoda: Bolitaenidae). *Biological Bulletin*, 189: 113-119.

Voight, J.R. 1996. Male reproductive anatomy of *Vitreledonella* (Cephalopoda: Octopoda). *American Malacological Bulletin*, 13(1-2): 61-64.

Voight, J.R. 1997. Cladistic analysis of the octopods based on anatomical characters. *Journal of Molluscan Studies*, 63: 311-325.

Voight, J.R. 2000a. A deep-sea octopus (*Graneledone* cf. *boreopacifica*) as a shell-crushing hydrothermal vent predator. *Journal of Zoology*, 252(3): 335-341.

Voight, J.R. 2000b. The distribution of octopuses of *Graneledone* (Cephalopoda: Octopodidae) in reference to deep-sea features. *Malacologia*, 42(1-2): 63-74.

Voight, J.R. 2001a. The relationship between sperm reservoir and spermatophore length in benthic octopuses (Cephalopoda: Octopodidae). *Journal of the Marine Biological Association of the United Kingdom*, 81(6): 983-986.

Voight, J.R. 2001b. Morphological deformation in preserved specimens of the deep-sea octopus *Graneledone*. *Journal of Molluscan Studies*, 67(1): 95-102.

Voight, J.R. 2005. Hydrothermal vent octopuses of *Vulcanoctopus hydrothermalis*, feed on bathypelagic amphipods of *Halice hesmonectes*. *Journal of the Marine Biological Association of the United Kingdom*, 85: 985-988.

Voight, J.R. 2008. Observations of deep-sea octopodid behavior from undersea vehicles. *American Malacological Bulletin*, 24(1-2): 43-50.

Voight, J.R. & Drazen, J.C. 2004. Hatchlings of the deep-sea octopus *Graneledone boreopacifica* are the largest and most advanced known. *Journal of Molluscan Studies*, 70(4): 400-402.

Voight, J.R. & Feldheim, K.A. 2009. Microsatellite inheritance and multiple paternity in the deep-sea octopus *Graneledone boreopacifica* (Mollusca: Cephalopoda). *Invertebrate Biology*, 128(1): 26-30.

Voight, J.R. & Grehan, A.J. 2000. Egg brooding by deep-sea octopuses in the North Pacific Ocean. *Biological Bulletin*, 198(1): 94-100.

Voss, G.L. 1951a. A first record of the cephalopod *Scaeurgus unicirrhus* from the western Atlantic. *Bulletin of Marine Science of the Gulf and Caribbean*, 1: 64-71.

Voss, G.L. 1951b. Further description of *Octopus burryi* Voss with a note on its distribution. *Bulletin of Marine Science of the Gulf and Caribbean*, 1(3): 231-240.

Voss, G.L. 1955. The Cephalopoda obtained by the Harvard Havana Expedition of the east coast of Cuba in 1938-1939. *Bulletin of Marine Science of the Gulf and Caribbean*, 5: 81-115.

Voss, G.L. 1956. A review of the cephalopods of the Gulf of Mexico. *Bulletin of Marine Science of the Gulf and Caribbean,* 6(2): 85-178.

Voss, G.L. 1957. A first record of *Octopus macropus* Risso from the United States with notes on its behavior, feeding and gonads. *Quarterly Journal of the Florida Academy of Sciences*, 20: 223-232.

Voss, G.L. 1964. A note on some cephalopods from Brazil with a description of a new species of octopod, *Eledone massyae*. *Bulletin of Marine Science of the Gulf and Caribbean*, 14(3): 511-516.

Voss, G.L. 1967. The biology and bathymetric distribution of deep-sea cephalopods. *Studies in Tropical Oceanography,* 5: 511-535.

Voss, G.L. 1968. Octopods from the R/V *Pillsbury* southwestern Caribbean Cruise, 1966, with a description of a new species, *Octopus zonatus*. *Bulletin of Marine Science*, 18(3): 645-659.

Voss, G.L. 1971a. Cephalopods collected by the R/V *John Elliott Pillsbury* in the Gulf of Panama in 1967. *Bulletin of Marine Science,* 21(1): 1-34.

Voss, G.L. 1971b. Shy monster, the octopus. *National Geographic Magazine,* December: 776-799.

Voss, G.L. 1976. Two new species of octopods of the genus *Graneledone* (Mollusca: Cephalopoda) from the Southern Ocean. *Proceedings of the Biological Society of Washington*, 88(42): 447–458.

Voss, G.L. 1979. *Octopus rapanui*, new species, from Easter Island (Cephalopoda: Octopoda). *Proceedings of the Biological Society of Washington*, 92(2): 360-367.

Voss, G.L. 1981. A redescription of *Octopus ornatus* Gould, 1852 (Octopoda: Cephalopoda) and the status of *Callistoctopus* Taki, 1964. *Proceedings of the Biological Society of Washington*, 94(2): 525-534.

Voss, G.L. 1982. *Grimpoteuthis bruuni*, a new species of finned octopod (Octopoda: Cirrata) from the southeastern Pacific. *Bulletin of Marine Science*, 32(2): 426-433.

Voss, G.L. 1985. Octopus fishery information leaflet. Gulf & South Atlantic Fisheries Development Foundation. 11 pp.

Voss, G.L. 1988a. Evolution and phylogenetic relationships of deep-sea octopods (Cirrata and Incirrata). *In* M.R. Clarke & E.R. Trueman, eds. *The Mollusca. Volume 12. Paleontology and Neontology of Cephalopods,* pp. 253-276. New York, Academic Press.

Voss, G.L. 1988b. The biogeography of the deep-sea Octopoda. *Malacologia*, 29(1): 295-307.

Voss, G.L. & Pearcy, W.G. 1990. Deep-water octopods (Mollusca: Cephalopoda) of the northeastern Pacific. *Proceedings of the Californian Academy of Sciences,* 47: 47-94.

Voss, G.L. & Toll, R.B. 1998. The systematics and nomenclatural status of the Octopodinae described from the western Atlantic Ocean. *In* N.A. Voss, M. Vecchione, R.B. Toll & M.J. Sweeney, eds. *Systematics and Biogeography of Cephalopods. Volume II*. *Smithsonian Contributions to Zoology*, 586: 457-474.

Voss, G.L. & Williamson, G.R. 1971. *Cephalopods of Hong Kong*. Hong Kong, Hong Kong Government Press. 138 pp.

Wagner, R.J.L. & Abbott, R.T. 1982. World size records (revision 1). *In Standard Catalog of Shells*. Greenville, South Carolina, American Malacologists, Inc. Pp. 80-001 to 80-030.

Ward, P.D. 1999. Reply by Peter D. Ward. *Journal of Paleontology*, 7: 1217-1218.

Warnke, K., Söller, R., Blohm, D. & Saint-Paul, U. 2000. Rapid differentiation between *Octopus vulgaris* Cuvier (1797) and *Octopus mimus* Gould (1852), using randomly amplified polymorphic DNA. *Journal of Zoological Systematics and Evolutionary Research,* 38(2): 119-122.

Warnke, K., Söller, R., Blohm, D. & Saint-Paul, U. 2002. Assessment of the phylogenetic relationship between *Octopus vulgaris* Cuvier, 1797 and *O. mimus* Gould 1852, using mitochondrial 16s rDNA in combination with morphological characters. *Abhandlungen der Geologischen Bundesanstalt,* 57: 401-405.

Warnke, K., Söller, R., Blohm, D. & Saint-Paul, U. 2004. A new look at geographic and phylogenetic relationships within the species group surrounding *Octopus vulgaris* (Mollusca, Cephalopoda): indications of very wide distribution from mitochondrial DNA sequences. *Journal of Zoology, Systematics and Evolution Research* 42: 306-312.

Warr, D. 1987. *Seashore Biology Notes: A Field Guide to the Common Animals in the Northern Gulf of California Tidepools*. Winter Publishing Co., Tucson, Arizona. 97 pp.

Watson, R. & Pauly, D. 2001. Systematic distortions in world fisheries catch trends. *Nature*, 414: 534-536.

Wells, M.J., O'Dor, R.K., Mangold, K. & Wells, J. 1983. Diurnal changes in activity and metabolic rate in *Octopus vulgaris*. *Marine and Freshwater Behaviour and Physiology,* 9(4): 275-287.

Whitaker, J.D., Delancey, L.B. & Jenkins, J.E. 1991. Aspects of the biology and fishery potential for *Octopus vulgaris* off the coast of South Carolina. *Bulletin of Marine Science,* 49(1-2): 482-493.

Willassen, E. 1986. *Haliphron atlanticus* Steenstrup (Cephalopoda, Octopoda) from the coast of Norway. *Sarsia,* 71: 35-40.

Williams, B. & Caldwell, R.L. 2009. Intra-organismal distribution of tetrodotoxin in two species of blue-ringed octopuses (*Hapalochlaena fasciata* and *H. lunulata*). *Toxicon*, 54(3): 345-353.

Williams, B., Hanifin, C.T., Brodie, E.D., & Caldwell, R.L. 2011. Ontogeny of tetrodotoxin levels in blue-ringed octopuses: maternal investment and apparent independent production in offspring of *Hapalochlaena lunulata*. *Journal of Chemical Ecology,* 37(1): 10-17.

Wolff, M. & Perez, H. 1992. Population dynamics, food consumption and gross conversion efficiency of *Octopus mimus* Gould 1853 (Cephalopoda: Octopoda), from Antofagasta (northern Chile). *International Council for the Exploration of the Sea (ICES), Shellfish Committee Report. C.M: 1992K.29*. 13 pp.

Wolterding, M.R. 1971. *The Rearing and Maintenance of Octopus briareus in the Laboratory, with Aspects of Their Behavior and Biology*. (Master's thesis). Coral Gables, Florida, University of Miami. 120 pp.

Wodinsky, J. 1972. Breeding season of *Octopus vulgaris*. *Marine Biology,* 16(1): 59-63.

Wood, J.B. 2000. *The Natural History of Bathypolypus arcticus (Prosch), a Deep-Sea Octopus*. Ph.D. dissertation. Dalhousie University Halifax, Nova Scotia, Canada. 265 pp.

Wood, J.B., Kenchington, E. & O'Dor, R.K. 1998. Reproduction and embryonic development time of *Bathypolypus arcticus*, a deep-sea octopod (Cephalopoda: Octopoda). *Malacologia*, 39(1-2): 11-19.

Wurtz, M. & Palumbo, F. 1984. Osservazioni sulla distribuzione e riproduzione di *Eledone cirrhosa* (Lam. 1798) (Cephalopoda, Octopoda) in Mar Ligure. *Nova Thalassia*, 6 (Suppl.): 721-723.

Wurtz, M., Matricardi, G. & Belcari, P. 1992. Distribution and abundance of the octopus *Eledone cirrhosa* in the Tyrrhenian Sea, central Mediterranean. *Fisheries Research*, 13(1): 53-66.

Xavier, J.C., Rodhouse, P.G., Purves, M.G., Dawe, T.M., Arata, J. & Pilling, G.M. 2002. Distribution of cephalopods recorded in the diet of the Patagonian toothfish (*Dissostichus eleginoides*) around South Georgia. *Polar Biology*, 25(5): 323-330.

Yagi, N., Ariji, M., Takahara, A. & Senda, Y. 2009. Application of a bioeconomics model to examine sustainability of fishery resources in the global market: the case of octopus resource in Morocco. *Fisheries Science*, 75(1): 43-46.

Yang, Q.-L., Lin, X.-Z., Zheng, X.-D. & Su, Y.-Q. 2009. Genetic Diversity in Populations of *Cistopus* sp. based on the sequences of mitochondrial 16S rRNA and CO I gene fragments. *Oceanologia Et Limnologia Sinica*, 40(5): 646-652.

Yasumuro, H. & Ikeda, Y. 2011. Effects of environmental enrichment on the behavior of the tropical octopus *Callistoctopus aspilosomatis*. *Marine and Freshwater Behaviour and Physiology*, 44:3, 143-157

Yau, C., Allcock, A.L., Daly, H.I. & Collins, M.A. 2002. Distribution of *Pareledone* spp. (Octopodidae: Eledoninae) around South Georgia. *Bulletin of Marine Science*, 71(2): 993-1002.

Yotsu-Yamashita, M. 2007. Distribution of tetrodotoxin in the body of the blue-ringed octopus (*Hapalochlaena maculosa*). *Toxicon*, 49(3): 410-412.

Young, J.Z. 1989. The angular acceleration receptor system of diverse cephalopods. *Philosophical Transactions of the Royal Society, B, Biological Sciences*, 325: 189-237.

Young, J.Z. 1991. Light has many meanings for cephalopods. *Visual Neuroscience*, 7: 1-12.

Young, R.E. 1964. *The Anatomy of the Vampire Squid.* M.Sc. Thesis. University of Southern California. Los Angeles, California, USA, 229 pp.

Young, R.E. 1972a. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. *Smithsonian Contributions to Zoology*, 97: 1-159.

Young, R.E. 1972b. Brooding in a bathypelagic octopus. *Pacific Science*, 26: 400-404.

Young, R.E. 1978. Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. *Fishery Bulletin*, 76: 583-615.

Young, R.E. 1995. Aspects of the natural history of pelagic cephalopods of the Hawaiian mesopelagic-boundary region. *Pacific Science,* 49: 143-155.

Young, R. E. 2010. Nautiloidea. Nautilidae Blainville 1825. Pearly nautiluses. Version 15 August 2010 (under construction). http://tolweb.org/Nautilidae/19397/2010.08.15 in The Tree of Life Web Project, http://tolweb.org/

Young, R.E. 2013. Alloposidae Verrill 1881. *Haliphron atlanticus* Steenstrup 1861. Version 08 January 2013 (under construction). http://tolweb.org/Haliphron_atlanticus/20200/2013.01.08 in The Tree of Life Web Project, http://tolweb.org/

Young, R.E. 2014. Vampyroteuthidae Thiele, in Chun, 1915. *Vampyroteuthis infernalis* Chun, 1903. The Vampire Squid. Version 06 December 2014. *http://tolweb.org/Vampyroteuthis_infernalis/20084/2014.12.06* in The Tree of Life Web Project, *http://tolweb.org/*.

Young, R.E. & Harman, R.F. 1997. *Octopus cyanea* and *Octopus ornatus*: biology and fisheries in Hawaii. *In* M.A. Lang & F.G. Hochberg, eds. *The Fishery and Market Potential of Octopus in California*. Washington, D.C., Smithsonian Institution. (Workshop Proceedings). Pp. 115-123.

Young, R.E., Vecchione, M. & Donovan, D.T. 1998. The evolution of coleoid cephalopods and their present biodiversity and ecology. *South African Journal of Marine Science*, 20: 393-420.

Zalygalin, V.P. 2009. Morphology of spermatophores of the giant octopus *Enteroctopus dofleini apollyon* (Incirrata, Octopodidae). *Hydrobiological Journal C/C of Gidrobiologicheskii Zhurnal*, 45(5): 35-42.

Zamora, C.M. & Olivares, P.A. 2004. Variaciones bioquímicas e histológicas asociadas al evento reproductivo de la hembra de *Octopus mimus* (Mollusca: Cephalopoda). *International Journal of Morphology*, 22(3): 207-216.

Zeidler, W. 1989. The pelagic octopus *Tremoctopus violaceus* delle Chiaje, 1830, from southern Australian waters. *Veliger,* 32: 166-170.

Zheng X., Lin, X., Lu, C.C. & Ma, R. 2012. A new species of *Cistopus* Gray, 1849 (Cephalopoda: Octopodidae) from the East and South China Seas and phylogenetic analysis based on the mitochondrial COI gene. *Journal of Natural History,* 46(5–6): 358.

Zhong, J., Li, L. & Ning, Y. 2009. A Review on the Bio-characteristics and Reproduction of Octopus. *Journal of Fujian Fisheries*, 2009-04-019.

Zielinski, S. & Sartoris, F.J. 2001. Temperature effects on hemocyanin oxygen binding in an Antarctic cephalopod. *Biological Bulletin*, 200(1): 67-76.

Zumholz, K. & Frandsen, R.P. 2006. New information on the life history of cephalopods off west Greenland. *Polar Biology*, 29: 169–178.

Zuñiga-Romero, O., Olivares-Paz, A. & Ossandón-R., L. 1995. Influencia de la luz en la maduración sexual de hembras de *Octopus mimus*. *Estudios Oceanologicos*, 14: 75-76.

Zylinski, S. 2011. Camouflage and chromatophores in the open ocean: transparency and body patterning in the mesopelagic octopus *Japetella*. *Integrative And Comparative Biology*, 51: E157.

LINKS TO AVAILABLE DATA ONLINE:

Cephalopod International Advisory Council (CIAC):
http://www.abdn.ac.uk/CIAC

Cephalopods at the National Museum of Natural History:
http://invertebrates.si.edu/cephs

FAO FishFinder Web Page:
http://www.fao.org/fishery/fishfinder /en

FAO Statistical Database:
http://faostat.fao.org

GlobeFish (Cephalopods):
http://www.globefish.org/cephalopods-market-reports.html

Smithsonian Institution Research Information System (SIRIS):
http://sirismm.si.edu/siris.cephalopod.htm

Tree of Life (Cephalopods):
http://tolweb.org/cephalopoda

World Register of Marine Species:
http://www.marinespecies.org

6. INDEX OF SCIENTIFIC AND VERNACULAR NAMES

Explanation of the system

Italics:	Valid taxonomic allocation (double entry by genera and species).
‘Italics’:	Provisional taxonomic allocation (double entry by genera and species).
Italics:	Previous taxonomic allocation of species placed under provisional taxonomic allocation (double entry by genera and species).
Italics:	Synonyms, misidentifications, subgenera, subspecies and other combinations (double entry by genera and species).
ROMAN:	Family names.
ROMAN:	Scientific names of divisions, classes, subclasses, orders, suborders and subfamilies.
Roman:	FAO names.
Roman:	Local names.

7. LIST OF COLOUR PLATES

PLATE I

1. ***Abdopus abaculus*** (Roger Munns/SCUBAZOO)
2. ***Abdopus aculeatus*** (Mark Norman)
3. ***Abdopus capricornicus*** (Mark Norman)
4. ***Ameloctopus litoralis*** (Mark Norman)
5. ***Amphioctopus aegina*** (Mark Norman)
6. ***Amphioctopus arenicola*** (Jerry Kane)
7. ***Amphioctopus burryi*** (Roger Steene)
8. ***Amphioctopus exannulatus*** (Mark Norman)

PLATE II

9. ***Amphioctopus fangsiao*** (Hideki Abe)
10. ***Amphioctopus kagoshimensis*** (Julian Finn)
11. ***Amphioctopus marginatus*** (Mark Norman)
12. ***Amphioctopus mototi*** (Mark Norman)
13. ***Amphioctopus siamensis*** (Paul Humann)
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PLATE III

17. ***Callistoctopus alpheus*** (Mark Norman)
18. ***Callistoctopus aspilosomatis*** (Mark Norman)
19. ***Callistoctopus dierythraeus*** (Mark Norman)
20. ***Callistoctopus luteus*** (Roger Steene)
21. ***Callistoctopus macropus*** (Helmut Debelius)
22. ***Callistoctopus ornatus*** (Mark Norman)
23. ***Cistopus chinensis*** (Xiaodong Zheng)
24. ***Cistopus taiwanicus*** (Mark Norman)

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26. ***Eledone moschata*** (Jean Lecomte)
27. ***'Eledone' palari*** (Tom Bowling)
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29. ***Enteroctopus dofleini*** (Fred Bavendam)
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40. ***Octopus bimaculoides*** (Roger Hanlon)

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41. ***Octopus hubbsorum*** (Clay Bryce)
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51. ***‘Octopus’ berrima*** (Julian Finn)
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PLATE VIII

57. ***‘Octopus’ gorgonus*** (Roy Caldwell)
58. ***‘Octopus’ huttoni*** (Peter Batson)
59. ***‘Octopus’ kaurna*** (Julian Finn)
60. ***‘Octopus’ maorum*** (Mark Norman)
61. ***‘Octopus’ minor*** (Ryo Minemizu)
62. ***‘Octopus’ rubescens*** (Howard Hall)
63. ***‘Octopus’ vitiensis*** (Roger Steene)
64. ***Pareledone charcoti*** (Michael Vecchione/ Uwe Piatkowski)

PLATE IX

65. ***Pteroctopus tetracirrhus*** (Oceana Europe)
66. ***Robsonella fontanianus*** (Dirk Schories)
67. ***Scaeurgus unicirrhus*** (Oceana Ranger Expedition)
68. ***Thaumeledone gunteri*** (Inigo Everson)
69. ***Thaumoctopus mimicus*** (Mark Norman)
70. ***Vulcanoctopus hydrothermalis/*** unidentified ***Benthoctopus*** (Rich Lutz)
71. ***Wunderpus photogenicus*** (Alex Kerstitch)
72. ***Amphitretus pelagicus*** (Dick Young)

PLATE X

73. ***Bolitaena pygmaea*** (Dick Young)
74. ***Japetella diaphana*** (Dick Young)
75. ***Vitreledonella richardi*** (David Wrobel)
76. ***Argonauta argo*** (Julian Finn)
77. ***Argonauta hians*** (Koji Nakamura)
78. ***Argonauta nodosus*** (David Paul)
79. ***Haliphron atlanticus*** (Nan Daeschler Hauser)
80. ***Ocythoe tuberculata*** (Uwe Piatkowski)

PLATE XI

81. ***Tremoctopus violaceus*** (Peter Wirtz)
82. ***Tremoctopus gracilis*** female (Julian Finn)
83. ***Tremoctopus gracilis*** male (David Paul)
84. ***Grimpoteuthis*** sp. (Ed McSweeny)
85. ***Opisthoteuthis grimaldii*** (Michael Vecchione)
86. ***Cirroteuthis muelleri*** (NOAA)
87. ***Stauroteuthis syrtensis*** (David Shale)
88. ***Vampyroteuthis infernalis*** (Brad Seibel)

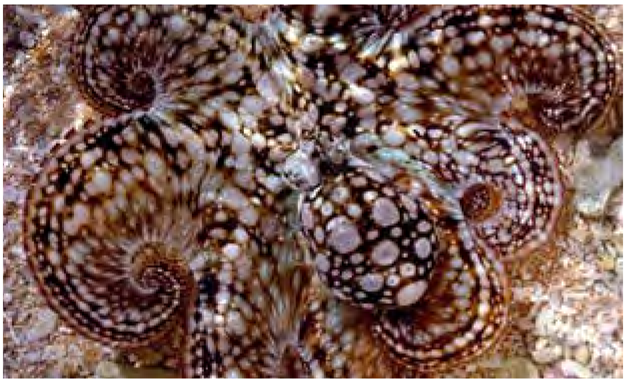
COLOUR PLATES

photo by F.G. Hochberg

PLATE I

1. ***Abdopus abaculus***
(Roger Munns/SCUBAZOO)

2. ***Abdopus aculeatus***
(Mark Norman)



3. ***Abdopus capricornicus***
(Mark Norman)

4. ***Ameloctopus litoralis***
(Mark Norman)

5. ***Amphioctopus aegina***
(Mark Norman)

6. ***Amphioctopus arenicola***
(Jerry Kane)

7. ***Amphioctopus burryi***
(Roger Steene)

8. ***Amphioctopus exannulatus***
(Mark Norman)

PLATE II

9. ***Amphioctopus fangsiao***
(Hideki Abe)

10. ***Amphioctopus kagoshimensis***
(Julian Finn)

11. ***Amphioctopus marginatus***
(Mark Norman)

12. ***Amphioctopus mototi***
(Mark Norman)

13. ***Amphioctopus siamensis***
(Paul Humann)

14. ***Bathypolypus bairdii***
(James Wood)

15. ***Benthoctopus canthylus***
(Neptune Canada)

16. ***Benthoctopus levis***
(Tim Stranks)

PLATE III

17. *Callistoctopus alpheus*
(Mark Norman)

18. *Callistoctopus aspilosomatis*
(Mark Norman)

19. *Callistoctopus dierythraeus*
(Mark Norman)

20. *Callistoctopus luteus*
(Roger Steene)

21. *Callistoctopus macropus*
(Helmut Debelius)

22. *Callistoctopus ornatus*
(Mark Norman)

23. *Cistopus chinensis*
(Xiaodong Zheng)

24. *Cistopus taiwanicus*
(Mark Norman)

PLATE IV

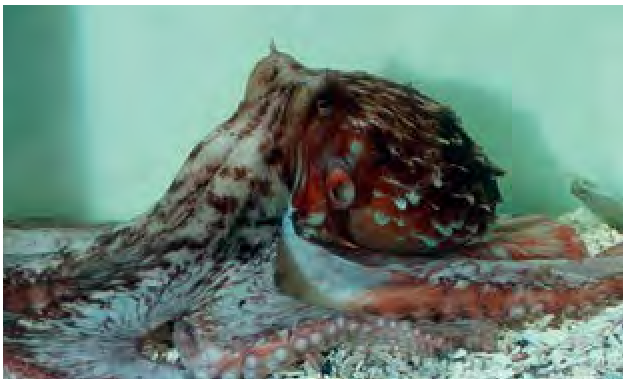
25. *Eledone cirrhosa*
(Jean Lecomte)

26. *Eledone moschata*
(Jean Lecomte)

27. *'Eledone' palari*
(Tom Bowling)

28. *Eledone schultzei*
(Mark Norman)

29. *Enteroctopus dofleini*
(Fred Bavendam)



30. *Enteroctopus magnificus*
(Dane Gerneke)

31. *Enteroctopus megalocyathus*
(Dirk Schories)

32. *Enteroctopus zealandicus*
(Julian Finn)

PLATE V

33. *Graneledone boreopacifica*
(Neptune Canada)

34. *Grimpella thaumastocheir*
(Mark Norman)

35. *Hapalochlaena fasciata*
(Mark Norman)

36. *Hapalochlaena lunulata*
(Roy Caldwell)

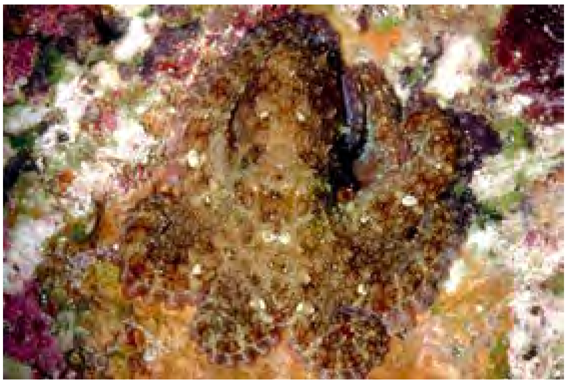
37. *Hapalochlaena maculosa*
(Mark Norman)

38. *Megaleledone setebos*
(Uwe Piatkowski)

39. *Octopus bimaculatus*
(Roger Hanlon)

40. *Octopus bimaculoides*
(Roger Hanlon)

PLATE VI



41. ***Octopus hubbsorum***
(Clay Bryce)

42. ***Octopus maya***
(Roger Hanlon)

43. ***Octopus mimus***
(Jim Black)

44. ***Octopus oculifer***
(Fred Bavendam)

45. ***Octopus tetricus***
(Mark Norman)

46. ***Octopus vulgaris sensu stricto***
(Helmut Debelius)

47. ***Octopus vulgaris*** **type I – Caribbean**
(Roger Steene)

48. ***Octopus vulgaris*** **type III – South Africa**
(Mark Norman)

PLATE VII

49. ***Octopus vulgaris*** **type IV - Japan**
(Hideki Abe)

50. ***'Octopus' australis***
(David Paul)

51. ***'Octopus' berrima***
(Julian Finn)

52. ***'Octopus' briareus***
(Roger Steene)

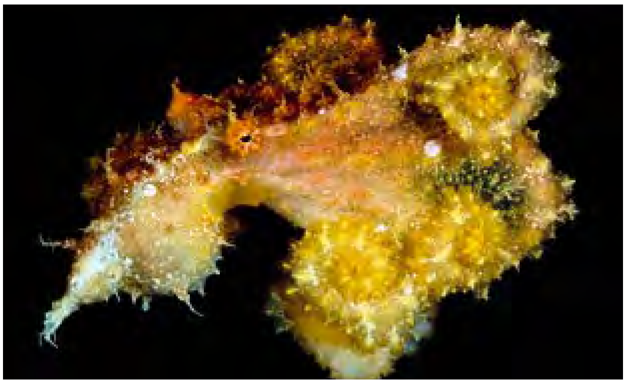
53. ***'Octopus' bunurong***
(Julian Finn)

54. ***'Octopus' californicus***
(Norbert Wu)

55. ***'Octopus' chierchiae***
(Roy Caldwell)

56. ***'Octopus' cyanea***
(Mark Norman)

PLATE VIII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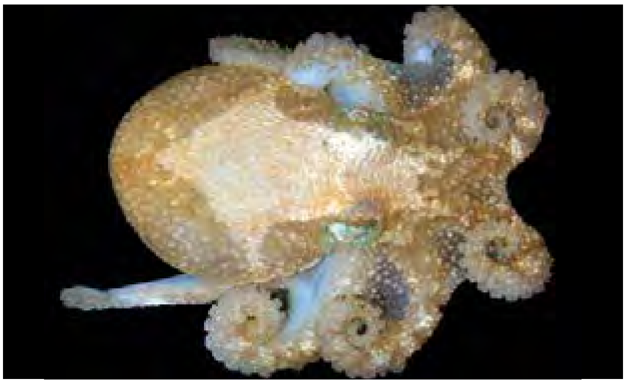
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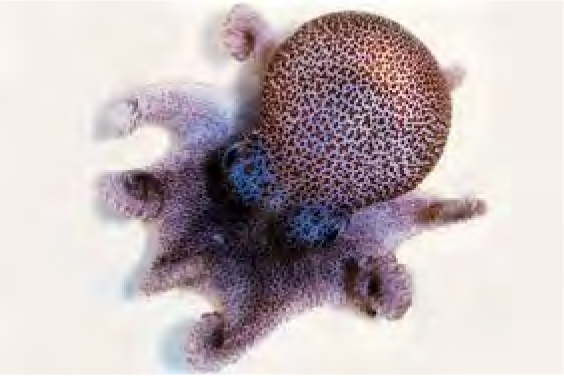

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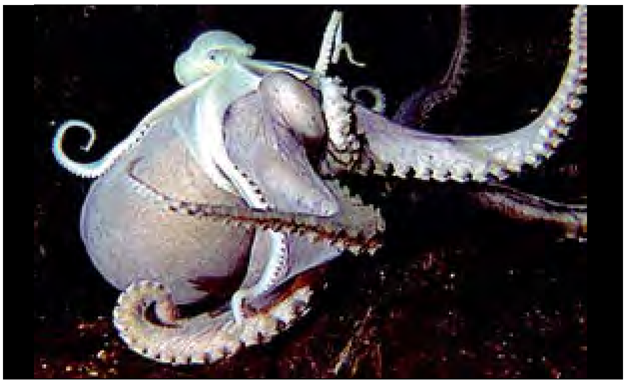

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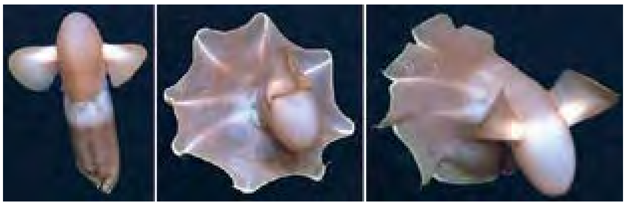

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This is the third volume of the entirely rewritten, revised and updated version of the original FAO Catalogue of Cephalopods of the World (1984). The present Volume is a multiauthored compilation that reviews 13 families, i.e. (in alphabetical order), *Alloposidae, Amphitretidae, Argonautidae, Bolitaenidae, Cirroctopodidae, Cirroteuthidae, Octopodidae, Ocythoidae, Opisthoteuthidae, Stauroteuthidae, Tremoctopodidae, Vampyroteuthidae, Vitreledonellidae*, with 56 genera and the 280 species known and named to the date of the completion of the volume. It provides accounts for all families and genera, as well as illustrated keys. Information under species accounts includes: valid modern systematic name and original citation of the species (or subspecies); synonyms; English, French and Spanish FAO names for the species; illustrations of dorsal aspects of the whole animal (as necessary) and other distinguishing illustrations; field characteristics; diagnostic features; geographic and vertical distribution, including GIS map; size; habitat; biology; interest to fishery; local names when available; a remarks section (as necessary) and literature. The Volume is fully indexed and also includes sections on terminology and measurements, an extensive glossary, an introduction with an updated review of the existing biological knowledge on octopods and Vampire squids (including fisheries information and main catch data for recent years) and a dedicated bibliography.

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