

# MYCOTAXON

Volume 94, pp. 265–292

October–December 2005

## A phylogeny of *Ramariopsis* and allied taxa

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**Abstract**—The phylogenetic relationships of *Ramariopsis* and related taxa were studied through a cladistic analysis of 36 morphological, cytological, and biochemical characters among 23 species in six genera. Two of these genera were directly studied as groups of interest, three as external taxonomic outgroups, and one as operative outgroup. Representatives of *Ramariopsis* sensu Corner formed a monophyletic group, supported by the cyanophilous nature of their basidiospores and derivation of their ornamentation from the tunica. The new combination, *Clavulinopsis antillarum*, is proposed.

**Key words**—*Clavariaceae*, Homobasidiomycetes, spore ultrastructure, outgroup sampling, taxonomy

### Introduction

*Ramariopsis* was described as a subgenus of *Clavaria* by Donk (1933), who selected *Clavaria kunzei* Fr. as the type species; the name refers to its macromorphological similarity to the genus *Ramaria* (Donk 1954). The taxa originally included the type species, *Clavaria angulispora* Pat. & Gaillard, *Clavaria pulchella* Boud., *Clavaria pyxidata* Pers. and *C. subtilis* Pers.

Corner (1950) elevated the taxon to genus level and included several fibulate species with branched, whitish basidiomes, monomitic hyphal systems, and echinulate spores. He retained *Clavaria kunzei* [= *Ramariopsis kunzei* (Fr.) Corner] as the type species, removing three species—*C. angulispora*, *C. pyxidata* and *C. subtilis*—and adding eight more for a total of ten species in the genus. Petersen (1964) added two more species after examining the type specimens of various species of the genus *Clavulinopsis*.

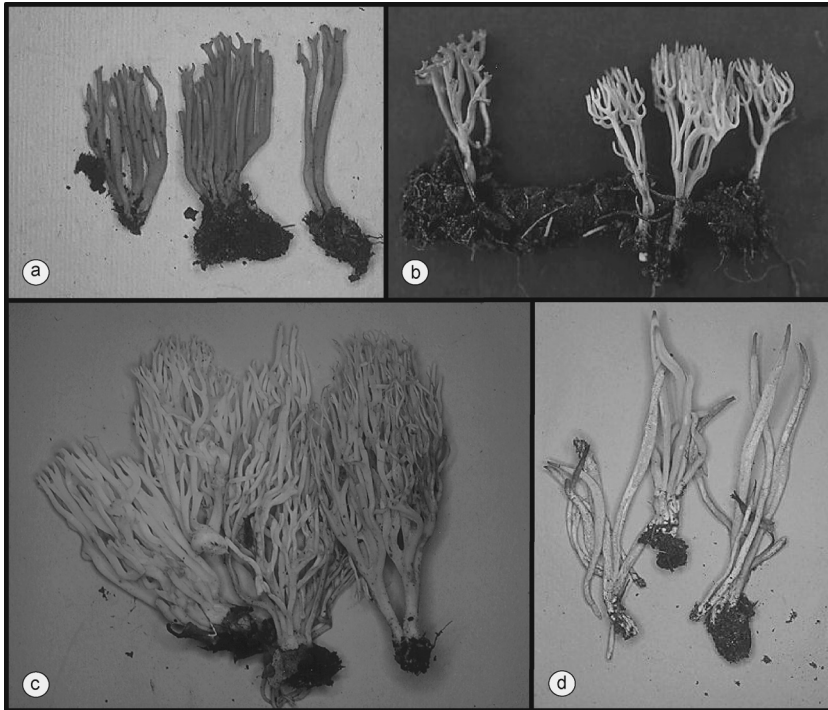
Petersen (1966) emended the original delimitation of the genus, to include taxa with smooth spores and hysterochroic basidiomes. Petersen considered the size of the basidia, the thickness of the spore wall, the composition of the ornamentation—when present—and the pattern of coloration of the basidiomes as the relevant characters for circumscribing the genus. He proposed dividing *Ramariopsis* into two subgenera: *Laevispora*, typified by *Ramariopsis minutula* (Bourdot & Galzin) R.H. Petersen, for species with smooth-spores, and *Ramariopsis*, consisting of species with echinulate spores.

Corner (1970) maintained the original circumscription of the genus, recognizing that it might be an artificial group, closely related to *Scytinopogon* and *Clavulinopsis*. Corner argued that his circumscription conformed to a homogeneous group that was of more utility for fieldwork.

Petersen (1978a) proposed a new delimitation for the genera *Ramariopsis*, *Clavulinopsis*, and *Clavaria* based on the size of the hilar appendix, the type of pigments present in the basidiome and the number of nuclei remaining in the basidium after the formation of spores. He transferred species with globose spores and a conspicuous hilar appendix from *Clavulinopsis* to *Ramariopsis*, and species with elongate spores and a small hilar appendix from *Clavulinopsis* to a new subgenus: *Clavaria* subg. *Clavulinopsis*. He also proposed designating *Clavaria corniculata* Schaeff. [= *Ramariopsis corniculata* (Schaeff.) R.H. Petersen] as the type species of *Ramariopsis*.

Based on Petersen's arguments, *Ramariopsis* should include hysterochroic species with branched or simple basidiomes, with whitish or bright coloration, globose or subglobose and smooth or ornamented spores, and a conspicuous hilar appendix (see Fig. 1). Petersen argued that this circumscription permits a continuum among related species, from smooth-spored species with a large basidiome, to species with a small basidiome and echinulate spores.

There are only a few additional contributions to this polemic. Jülich (1985) transferred all species of *Ramariopsis* to *Clavulinopsis* based on nomenclatural arguments, but this interpretation apparently has not been followed by the majority of taxonomists (Hawksworth et al. 1995, Kirk et al. 2001). Pegler & Young (1985), in an electron microscopy (EM) study of several species of *Ramariopsis*, *Clavulinopsis*, and *Scytinopogon*, described three ultrastructural patterns of spore ornamentation that corresponded with the three genera mentioned before. They also observed that several apparently smooth-spored species, such as *Ramariopsis californica* R.H. Petersen, actually possessed ornamentation. The observed ornamentation was very small and covered by a thin myxosporium, such that the spores appear smooth under a light microscope even at magnifications above 1000x. Pegler & Young (1985) recognized



**Figure 1.** Four species representative of the variation observed in *Ramariopsis* and *Clavulinopsis*. a) *Clavulinopsis corniculata*, b) *Ramariopsis pulchella*, c) *Ramariopsis kunzei* and d) *Clavulinopsis fusiformis*. Photos a: J. Cifuentes, b: A. Estrada-Torres, c: J. Cifuentes, d: J. Cifuentes.

the delimitation proposed by Corner (1950) for *Ramariopsis*, but not the relationship between this genus and *Scytinopogon*.

The genus *Ramariopsis* has been included in the *Clavariaceae* in the majority of the treatments of this family (Donk 1964, Corner 1970, Jülich 1981, Hawksworth et al. 1995), with the exception of Petersen (1978a, 1988a) and Kirk et al. (2001), who placed *Ramariopsis* in *Gomphaceae*.

A phylogenetic study of *Gomphaceae* (Villegas et al. 1999), however, indicates that *Ramariopsis*—at least sensu Corner—should not be considered part of that family. Pine et al. (1999), on the other hand, studied the clavarioid and cantharelloid Homobasidiomycetes, and found that *Clavulinopsis fusiformis* (Sowerby) Corner [= *Ramariopsis fusiformis* (Sowerby) R.H. Petersen] nested within the euagaric clade, forming a monophyletic group with *Clavaria acuta* Sowerby, indicating that *Ramariopsis* subgenus *Laevispora* is related to *Clavaria*, or at least to representatives of *Clavaria* subgenus *Holocoryne*. Additionally results of Larsson et al. (2004) indicate close relationships among *Clavulinopsis helvola* (Pers.) Corner, *Clavaria argillacea* Pers.—*Clavaria* subgenus *Holocoryne*—and *Clavaria fumosa* Pers.—subgenus *Clavaria*—

on a monophyletic group nested in the euagaric clade. This results points to a close relationship between *Clavulinopsis* and at least some part of *Clavaria*.

There are currently only a few works, that have attempted to study the phylogeny of clavarioid and gomphoid macromycetes in general (Pine et al. 1999, Villegas et al. 1999, Humpert et al. 2001), and there is no consensus about the phylogenetic relationships of these taxa.

Given that there is no consensus delimitation for *Ramariopsis*, the number of species in this genus depends on the source consulted (i.e. Jülich 1981, 1985; Hawksworth et al. 1995; Kirk et al. 2001). This number varies from 24 to 45 species, with a distribution that stretches from sub-Arctic regions to the forests of New Zealand (Corner 1950, 1967a, 1970; Thin 1961; Petersen 1968, 1969, 1971a, 1978b, 1979, 1988a, 1989; Pilát 1971; Gómez 1972; García-Sandoval et al. 2002).

The principal objective of the present work is to suggest a more robust delimitation of *Ramariopsis*, based on a phylogenetic analysis of the available information and new morphological characters derived from direct observation of herbarium specimens. The use of morphological characters presents some advantages (see Jenner 2004, Wiens 2004, for an extensive up-to-date review) and for this particular case, these include the possibility of a wide sampling of species because of the availability of herbarium material and the opportunity to directly test the hypothesis of homology for diverse characters considered taxonomically relevant.

## Materials and Methods

*Selection of outgroups and taxonomic sampling.* The selection of outgroups was critical for the present study since a reference phylogenetic framework is lacking and an inadequate or insufficient selection of external groups could result in the artificial interpretation of monophyly of the group of interest (Nixon & Carpenter 1993, Hopple & Vilgalys 1999). Selection was based on three criteria: a) a phylogenetic survey of the family *Clavariaceae* sensu lato (results not shown), b) previous phylogenies of the clavarioid Homobasidiomycetes, and c) previous classification proposals that include the genus *Ramariopsis* in some specific family.

The phylogenetic survey was conducted based on diverse delimitations of the family *Clavariaceae* (Donk 1964, Corner 1970, Jülich 1981, Hawksworth et al. 1995). All of the genera included in these proposals were considered, and representatives of the observed variation were selected for study. A matrix of 26 taxa and 30 morphological characters was constructed, and an initial selection of taxonomic outgroups and an operative outgroup was performed based on the strict consensus of the trees obtained from the analysis. The selection of outgroups, especially the operative outgroup, was based partially on the phylogenetic analyses by Hibbett et al. (1997), Pine et al. (1999), Humpert et al. (2001) and Binder & Hibbett (2002). Based on Petersen's (1978a, 1988a) proposals of the phylogenetic affinities of *Ramariopsis*, one additional representative of *Gomphus* was selected to complete the taxonomic outgroups. Sampling of the ingroup was based on Petersen's (1978a) proposed delimitation of *Ramariopsis*, which includes the species considered by Corner (1950). Taxa representative of the observed variation, and with available herbarium specimens, were chosen for analysis.

For a few confusing species [*Clavaria sulcata* (Overeem) R.H. Petersen, *Clavaria vermicularis* Sw., *Clavaria amoena* Zoll. & Moritz and *Clavaria aurantiocinnabarina* Schwein.], assignment of specific epithets and the concepts used to delimit species followed Petersen (1967, 1976, 1979, 1980a, 1988a).

*Analysis of characters and elaboration of the data matrix.* Morphological observations were analyzed and interpreted in the framework of cladistic ontology (Hennig 1966, Farris 1983, de Pinna 1991, De Luna & Mishler 1996). The selection and analysis of characters were based on the variation observed among sampled species, without excluding a priori any sources of information (Poe & Wiens 2000). Hypotheses of homology were elaborated based on the homology criteria proposed by de Pinna (1991), employing similarity, conjunction, independence, variability, and heritability as auxiliary criteria (Patterson 1988, Rieppel 1988, Brower & Schawaroch 1996, Hawkins et al. 1997, Rieppel & Kearney 2002).

Codification of characters followed the criteria proposed by de Pinna (1991) and later additions (Hawkins et al. 1997, Hawkins 2000, Kluge 2003, Grant & Kluge 2004). Characters were not ordered nor polarized a priori to avoid bias in the exploration of tree space (Hauser & Presch 1991). Similarly, no weighting scheme was applied a priori to avoid ad hoc hypotheses that would constrain the results (Farris 1983). Character states were analyzed by directly observing herbarium specimens from distinct collections (see Table 1); these data were complemented by previous descriptions (Coker 1923; Singer 1945, 1986; Corner 1950, 1957, 1966, 1967a, b, 1970; Thin 1961; Petersen 1964, 1965, 1966, 1967a, 1968, 1969, 1971a, b, 1978b, c, d, 1979, 1980b, 1984, 1985, 1988a, b, 1989; Petersen & Olexia 1967, 1969; Bataile 1969; Fiasson et al. 1970; Schild 1971; Kühner 1977; Hubbard & Petersen 1979; Claus 1983; Pegler & Young 1985; Gill & Steglich 1987; Hansen & Knudsen 1997; García-Sandoval et al. 2002; Gill 2003; Bertagnolli & Novello 2004). A matrix of 36 characters (see Appendices 1 and 2) was constructed, that included observations of macro- and micro-morphology, macro- and micro-chemical reactions, and biochemical, cytological, and ultrastructural characters. Information for the homology hypothesis came primarily from direct observation of herbarium specimens and only in few cases were based on previously reported data (see Appendices).

*Tree searches, robustness, and topology test.* A series of heuristic searches were performed with 1,000 replicates in PAUP\* 4.0b10 (Swofford 2002), using TBR, random addition, and MAXTREE set to auto-increase. A branch and bound search was performed using as an upper limit the observed tree length from the heuristic searches, and characters were optimized with the ACCTRAN option.

Interpretation of the change of character states along phylogenies was made in WinClada (Nixon 2002), using one of the most parsimonious trees encountered in the branch and bound search.

Bremer's support (Bremer 1994) was calculated to evaluate the robustness of the observed clades. The analysis was conducted using AutoDecay 4.0 (Eriksson 1999) with 100 heuristic replicates per search, using random addition, MAXTREE set to auto-increase, the ACCTRAN option for optimization, and equally weighted characters. Bootstrap values (Felsenstein 1985) were also calculated using 10,000 replicates sampling all characters, with 10 heuristic searches for each bootstrap replicate, TBR branch rearrangement, and MAXTREE set to 100 trees.

Table 1. List of specimens examined.

Species		Specimens
<i>Clavaria amoena</i>	TO	Corner CLAVARIA-4 (E); Donk 13690 (L)
<i>Clavaria aurantiocinnabarina</i>	TO	Cifuentes 2004-94 (FCME); Corner RSNB-8376 (L); Corner RSNB-8378A (L); Corner ICTA-1501 (E)
<i>Clavaria gibbsiae</i> Ramsb.	TO	Corner 442 (L); Corner 24165 (L); Corner-Singer 24165 (E)
<i>Clavaria sulcata</i>	TO	Hongo 705 (L); Corner s.n. (E); Corner 1676 (E)
<i>Clavaria vermicularis</i>	TO	Brit. Mycol. Soc. 12099 (L); Kotlaba s.n. (L); Corner NG 192 (E); Corner RSS 1439 (E)
<i>Clavaria zollingeri</i> Lév.	TO	Corner s.n. (E); Corner s.n. (E)
<i>Clavariadelphus pistillar</i> (L.) Donk	TO	Meyer 3700 (TENN); Petersen 4920 (TENN)
<i>Clavulinopsis corniculata</i> (Schaeff.) Corner	IG	Piepenbroek & Piepenbroek 876 (L); Mass Geesteranus 14580 (L); Villegas 1144 (FCME); López 782 (ENCB); Aranda-Breceda 4 (FCME); Corner & Thind 206 (E)
<i>Clavulinopsis fusiformis</i>	IG	Guzmán U-482 (XAL); Cooke & Cooke 45644 (XAL); Cooke & Cooke 39815 (XAL); Hongo 764 (L); Villegas 1313 (FCME); Villegas 1305 (FCME); Heredia 371 (XAL); Heredia 371 (XAL); Santillán s.n. (XAL); Guzmán & Ventura 5835 (ENCB); Ventura 13281 (ENCB); Villegas 1438 (FCME)
<i>Clavulinopsis helvola</i>	IG	Bas 6730 (L); Maas Geesteranus 13887 (L)
<i>Clavulinopsis laeticolor</i> (Berk. & M.A. Curtis) R.H. Petersen	IG	Corner 452 (L); Donk 13896 (L); Villegas 1803 (FCME); Hernández 188 (IBUG); Altamirano 628 (TLXM); Villegas 1450 (FCME).
<i>Gomphus clavatus</i> (Pers.) Gray	OO	Petersen 1797 (TENN); Arias-Montes s.n. (FCME)
<i>Gomphus floccosus</i> (Schwein.) Singer	TO	Cifuentes 111 (FCME); Moreno-Fuentes 418 (FCME); Villegas 1109 (FCME); Fajardo s.n. (FCME).
<i>Lactarius indigo</i> (Schwein.) Fr.	TO	Mendoza 9-09-1983 (FCME)
<i>Ramariopsis californica</i>	IG	Petersen 3006 (TENN); Petersen 280109 (TENN)
<i>Ramariopsis crocea</i> (Pers.) Corner	IG	Loerakker s.n. (L); Jalink & Nauta 6384 (L); de Vries s.n. (L)
<i>Ramariopsis kunzei</i>	IG	Bas 5105 (L); Corner RSNB-8291; Petersen 3909 (TENN); Guzmán U-399 (ENCB); Petersen s.n. (TENN); Villegas 1804 (FCME); Pérez-Ramírez 280 (FCME); Rodríguez s.n. (ENCB); Guzmán-Dávalos 2848 (IBUG); Guzmán 22666 (ENCB); Guzmán 6969 (ENCB); Valenzuela 1197 (ENCB); Corner NG-237 (E); Corner NG-229 (E); Ruiz & Herrera 3494 (MEXU)
<i>Ramariopsis pulchella</i> (Boud.) Corner	IG	Corner NG-217 (E); Altamirano 148 (TLXM); Altamirano 157 (TLXM)
<i>Ramariopsis tenuiramosa</i> Corner	IG	Donk 11421 (L); Mass Geesteranus 9576 (L); Geesink 1504 (L); Corner NG-124 (E)
<i>Scytinopogon dealbatus</i> (Berk.) Corner	TO	Corner s.n. (E)
<i>Scytinopogon echinosporus</i> (Berk. & Broome) Corner	TO	Corner 1517 (E)
<i>Scytinopogon robustus</i> (Rick) Corner	TO	Cifuentes 676 (FCME); Cifuentes 2004-26 (FCME)
<i>Scytinopogon pallescens</i> (Bres.) Singer	TO	Martínez-C. s.n. (ENCB)

Herbaria: E = Royal Botanic Garden, Edinburgh, Scotland, United Kingdom; ENCB = Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México; FCME = Facultad de Ciencias, UNAM, México; IBUG = Instituto de Botánica, Universidad de Guadalajara, México; L = National Herbarium Nederland, Leiden University Branch, Netherlands; MEXU = Instituto de Biología, UNAM, México; TENN = University of Tennessee, Knoxville, EUA; TLXM = Centro de Investigación en Ciencias Biológicas, Universidad Autónoma de Tlaxcala, México; XAL = Instituto de Ecología, A.C., Xalapa, México; IG = Ingroup (= group of interest); TO = Taxonomical outgroup; OO = Operative outgroup.

These parameters were selected to allow for a large number of bootstrap replicates and a reasonably accurate search procedure for each replicate (as opposed to the “fast bootstrap” option), thus avoiding the underestimation of clade support (DeBry & Olmstead 2000; Mort et al. 2000).

Templeton's topology test (Templeton 1983) was used to evaluate differences between the observed phylogenetic hypothesis and that of Petersen (1978a), employing a two-tailed Wilcoxon's signed rank test following Templeton (1983). To conduct the test, a branch and bound search was performed constraining monophyly of the representatives of *Ramariopsis* sensu Petersen. To select a subgroup of equally parsimonious trees for topology testing, a second branch and bound search was conducted using ACCTRAN to optimize characters and successive weighting (Farris 1969) following Carpenter (1988, 1994), using the RI to calculate reweighting. Each of the most parsimonious trees thus encountered was compared with each of the most parsimonious trees from the branch and bound search with successive weights (see above) using the Templeton test implemented in PAUP\*b10 (Swofford 2002), and the results were compared to tables of critical values of T for the Wilcoxon test.

Diverse methods exist to evaluate the stability of a phylogeny with respect to the inclusion/exclusion of taxa (see Grant & Kluge 2003 for an extensive review). The present study assessed the impact of taxonomic outgroups sampling with a selective inclusion/exclusion of those taxa, followed with branch and bound searches of all of the combinations of taxonomic outgroups: *Clavaria*, *Clavariadelphus*, *Gomphus*, *Lactarius*, and *Scytinopogon*.

## Results

Twenty-three species were chosen for analysis based on the criteria employed for outgroup selection, taxonomic sampling, and character analysis (Table 1). The branch and bound search resulted in 12 trees of 80 steps in length (CI = 0.4875, RI = 0.7153, RC = 0.3487). The strict consensus of these (see Fig. 2) shows *Ramariopsis* sensu Corner (1950, 1970) as a monophyletic group.

This group forms a monophyletic clade with the representatives of *Scytinopogon*. Bootstrap analysis indicated a generally low level of support across the observed clades (see Fig. 2); only the clades containing representatives of *Ramariopsis* Corner, and *Scytinopogon* showed bootstrap support above 50%. Interestingly, there was no significant support for the clade that includes most of the representatives of *Clavaria* sensu Petersen. Bremer support was also relatively low for most of the clades, and the highest values corresponded to the clade of *Scytinopogon*.

During the constrained analysis conducted for topology tests, 1540 equally parsimonious trees of length 85 (CI = 0.4535, RI = 0.6781, RC = 0.3075) were found, five steps longer than those in the unconstrained search.

The application of successive weightings allowed selection of a subset of 8 most parsimonious trees from those found in the original branch and bound search. Application of the topology test, however, did not indicate significant differences between the hypotheses. Comparison of all topologies resulted in no significant values of  $N = 16-14$ ,  $T = 53-39.5$ ,  $P = 0.4545-0.4220$ .

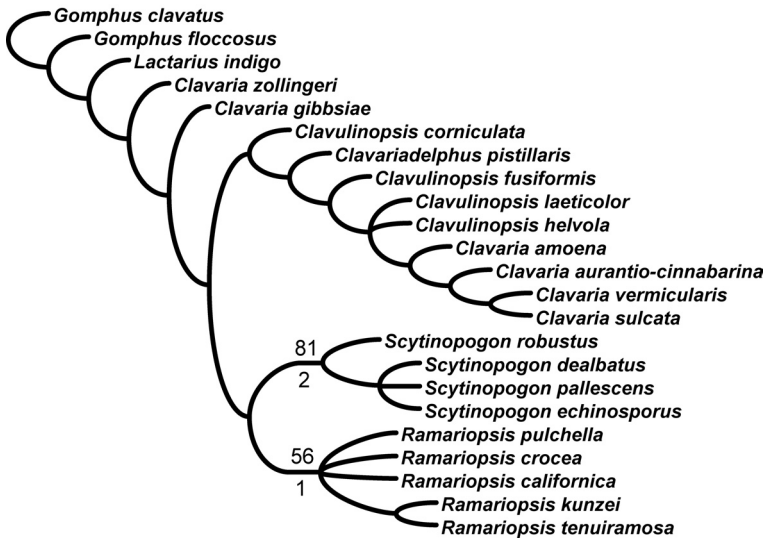


Figure 2. Strict consensus of the 12 trees of 80 steps (CI = 0.4875, RI = 0.7153, RC = 0.3487) found during the branch and bound search. Numbers below branches indicate Bremer support indices, and numbers above branches indicate bootstrap support values.

The combinations of selective inclusion/exclusion tested (not shown) did not modify the monophyly of *Ramariopsis* sensu Corner, but decreased the resolution of the topology.

### Discussion

The phylogenetic analyses performed support the monophyly of *Ramariopsis* sensu Corner (1950), though with moderate bootstrap support (56%). Based on these results, *Ramariopsis* is limited to species with branched basidiomes, echinulate spores, and cyanophilous spore ornamentation derived from the tunica (Pegler & Young 1985).

The ultrastructural composition of the ornamentation is a synapomorphy for the group (see Fig. 3), but a large part of the cladogram was optimized as ambiguous for this character because of the lack of information for several species –e.g. information for any of the species of *Scytinopogon* included is not available. Although Corner did not include *Ramariopsis californica* in his most recent treatment of the genus (Corner 1970), this species exhibits all of the distinctive characters of the genus and the present results support its inclusion in this taxon. On the other hand, Petersen (1978a) included *Clavulinopsis helvola* in *Ramariopsis* [= *Ramariopsis helvola* (Pers.) R.H. Petersen], although this species has simple basidiomes and spores with thick tuberculous ornamentation. Pegler & Young (1985) established that this ornamentation is formed from growth of the corium, whereas ornamentation in *Ramariopsis* is formed via growth of the tunica. The results of the present study support the segregation of *C. helvola* from *Ramariopsis*.



The representatives of *Scytinopogon* form a well-supported group (81% bootstrap support), consistent with the original delimitation of Singer (1945) based on the presence of branched, thelephoroid basidiomes and verrucose spore ornamentation. In our results, *Ramariopsis* sensu Corner forms a monophyletic group with the representatives of *Scytinopogon*. These taxa all have cyanophilous spores with ornamentation partially derived from the tunica, though in *Scytinopogon* the ornamentation also seems to be composed of a thick core of corium (Pegler & Young 1985). It is worth mentioning that most of the species of *Scytinopogon* included in the present analysis have not been studied ultrastructurally—such data exist for only a single species of the genus, whose taxonomic status is in doubt.

The observed relationship between *Ramariopsis* and *Scytinopogon* was first suggested by Corner (1970), but this link should only be considered tentative as the taxonomic sampling of this analysis was designed to resolve a robust delimitation of the genus *Ramariopsis*, and not to identify its sister taxon. Furthermore, the clade *Ramariopsis*+*Scytinopogon* does not show bootstrap support. Thus, without a broader taxonomic sampling designed to establish the affinities of *Ramariopsis* with other taxa, it is preferable to consider these results as preliminary.

One of the principal consequences of this study is that *Ramariopsis* sensu Petersen is a paraphyletic group—i.e. a grade—because it was defined by simplesiomorphic characters. Petersen (1978a) used diverse sources of information for his delimitation, including the absence of carotenoid pigments. Pigment composition has been a frequently-used auxiliary character in fungal systematics (Arpin & Fiasson 1971, Tyler 1971, Gill & Steglich 1987, Frisvad et al. 1998, Gill 2003), but recent studies indicate that phylogenetic patterns inferred in the Homobasidiomycetes based on this type of character are often incongruent with the results obtained using other sources of information (Hibbett & Thorn 2001, Pine et al. 1999).

Nonetheless, the presence of certain types of pigments can be a very useful auxiliary character in studies aimed at generic delimitation (e.g. Feibelman et al. 1997, Weinstein et al. 2002), and the taxonomic relevance of this type of characters should not be completely discarded, but perhaps restricted to use at lower taxonomic levels. In the case of *Ramariopsis*, the delimitation proposed by Petersen (1978a) was based on the absence of carotenoid compounds, without specify the nature of the pigments present and without an explicit reference to a concrete character; the inferred pattern thus cannot be directly confirmed or refuted. In the present study this character was coded as the presence or absence of carotenoid pigments—character 11. (See Appendices for character argumentation.)

This character does not show evidence of homoplasy in the present study based on its observed distribution (CI = 1.0), although optimization of the character is not definitive due to the absence of information in several of the considered species (see Fig. 4). Additionally, the distribution of carotenoids in the present study supports the relationship among *Clavaria aurantiocinnabarina*, *C. amoena* and *C. sulcata*, and is congruent with a monophyletic group that includes representatives of *Clavaria* (see Fig. 2). This latter group is consistent with Petersen's (1978a, 1988a) delimitation of *Clavaria*. It is worth mentioning that the aforementioned results regarding *Clavaria* should be

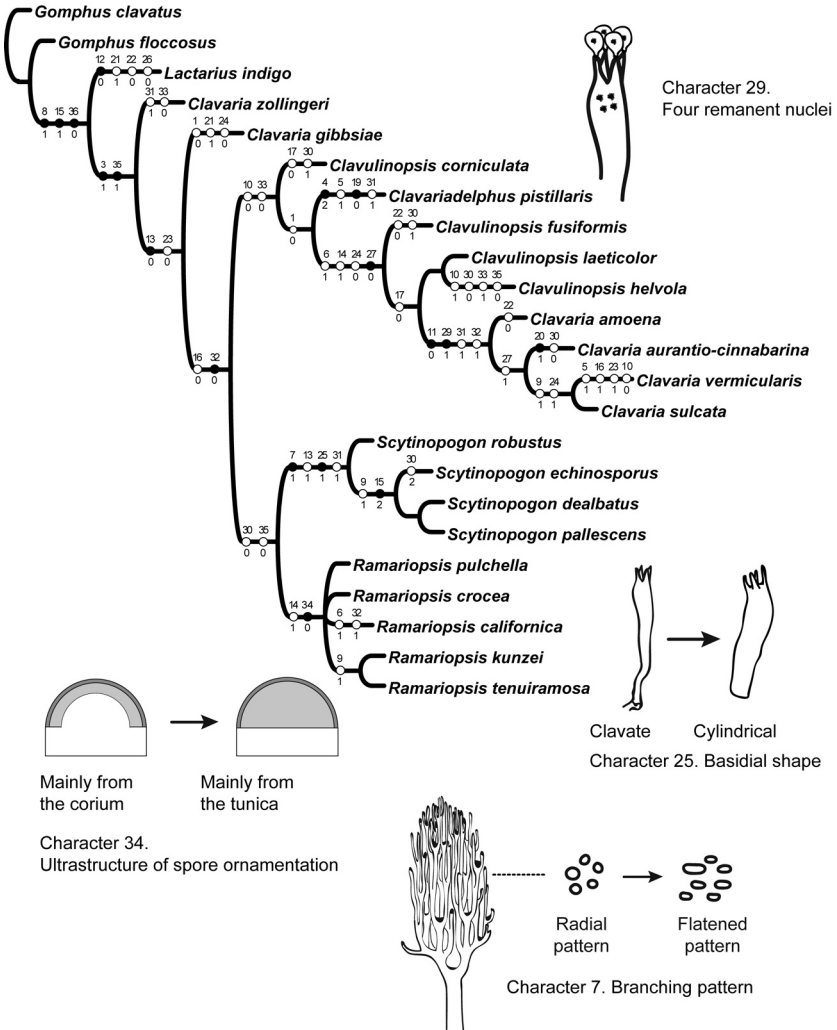


Figure 3. One of the most parsimonious trees encountered during the branch and bound search, showing the character states that can be unambiguously optimized. Numbers above dots indicate the character and numbers below dots the character state. Apomorphic states are shown in black dots and homoplastic states in white dots. Selected character transformations are illustrated close to the branch where change occur (see appendix 1 for character argumentation).

considered as preliminary due to the lack of bootstrap support and the taxonomic sampling of the present study.

Another relevant character used by Petersen (1978a) was the presence of spores with a conspicuous hilar appendix. Several species of *Clavulinopsis* subgenus *Cornicularia*

was transferred by Petersen to *Ramariopsis* based—in addition to the other mentioned character—on the presence of a conspicuous hilar appendix. In this study, this character was included (character 31) and their optimization is depicted in figure 4 (see also Appendices for character argumentation). The present results show it as a simplisiomorphy.

Farris (1991) provided an explicit criterion to recognize paraphyletic groups by tracing the status of the character used to define it; in the case of *Ramariopsis* prominent hilar appendix and absence of carotenoid pigments were used by Petersen in order to define the genus, both characters are plesiomorphic and shared –simplisiomorphic– (see Fig. 4). In the strict sense, the present results show *Ramariopsis* sensu Petersen as a paraphyletic group.

Petersen (1978a) also employed the presence of chiasitic basidia with a post-meiotic mitotic division and four nuclei remaining in the basidia after spore formation as a cytological pattern that supported the delimitation of *Ramariopsis*. Recent phylogenetic studies (Hibbett et al. 1997, Pine et al. 1999) confirm the utility of cytological characters in the delimitation of taxonomic groups among the clavarioid and cantharelloid Homobasidiomycetes, but while the stictic pattern appears phylogenetically informative, the chiasitic condition, which is widely distributed among the Homobasidiomycetes, does not seem to follow a clear phylogenetic pattern (Hibbett & Thorn 2001). As with the presence of carotenoid pigments, the utility of the chiasitic condition in our analyses is noted, though more studies are necessary.

The pattern of four remaining nuclei reported for *Ramariopsis crocea* (Penancier 1961) results from a post-meiotic mitotic division. Post-meiotic mitotic divisions resulting in four nuclei remaining in basidia following spore formation are reported for a diversity of other taxa (Penancier 1961, Duncan & Galbraith 1972, Restivo & Petersen 1976, Kühner 1977, Mueller & Ammirati 1993). Both the meiotic pattern (chiasitic/stictic) and the number of remaining nuclei (see Appendices for discussion and codification) were included as characters in the present study.

All of the species in our study for which data were available present a chiasitic pattern, so it was not informative for addressing our questions. Very possibly this character could have relevance at other hierarchical levels when studying the taxonomic affinities of the genus *Ramariopsis*.

The number of remaining nuclei (character 29 CI = 1.0) did not present a homoplasious distribution, though, similar to the situation for carotenoid pigments, optimization of this character should be considered preliminary since data were not available for all species considered, and this lack of information results in a severely ambiguous optimization (results no shown).

Our finding of a monophyletic group that includes representatives of *Clavulinopsis* and representatives of *Clavaria* is congruent with the results of Pine et al. (1999). However, relationships among *Clavariadelphus pistillaris*, *Clavaria zollingeri* and *C. gibbsiae* are not consistent with previous classifications (see Fig. 2), and *Clavariadelphus* is found in a position incongruent with previous studies (Hibbett et al. 1997, Pine et al. 1999).

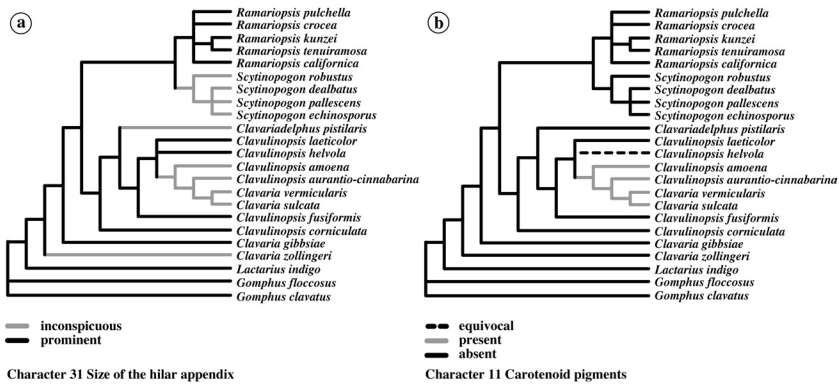


Figure 4. Optimization of two characters used by Petersen (1978a) to define *Ramariopsis*, onto one of the most parsimonious trees. a) Optimization of character 31 showing prominent hilar appendix as a simple simomorphy; b) optimization of character 11 showing the absence of carotenoid pigments as a symplesiomorphy.

The position of *Clavariadelphus pistillaris* could be an artifact, due to the fact that the present sampling of taxonomic outgroups included distantly related groups –e.g. *Gomphus* in the clade Gomphoide-Phalloide sensu Hibbett & Thorn (2001).

To explore this possibility, a branch and bound search was performed excluding *Clavariadelphus*, and the monophyletic group of *Ramariopsis* sensu Corner + *Scytinopogon* obtained in the main analysis was recovered (results not shown).

It has not been possible to clearly elucidate the phylogenetic affinity of *Clavaria zollingeri*. This taxon was included in the analysis of clavarioid and cantharelloid Homobasidiomycetes by Pine et al. (1999), but their results were inconclusive and this species was located outside of any recognized clade in the strict consensus analysis of combined genes. In spite of this, indicated that the current delimitation of *Clavaria* (Corner 1970) –simple or branched basidiomes, monomitic hyphae in the context, clamp connections absent in the context, and present or absent of clamp connections at the base of the basidia– was not a monophyletic group. The results of our study are congruent with those of Pine et al. (1999).

*Clavaria gibbsiae* in the present results is located next to *C. zollingeri*, out of any large clade –e.g. *Clavaria* sensu Petersen or *Ramariopsis* sensu Corner. This species is traditionally included in *Clavaria* subgenus *Holocoryne* (Corner 1970, Petersen 1988a). We could expect a relationship between *Clavulinopsis* and representatives of *Clavaria* based on previous results (Pine et al. 1999, Larsson et al. 2004), but these studies also indicate that *Clavaria* is not a monophyletic group (Pine et al. 1999). Our results are congruent with these previous studies and show a core group that includes part of *Clavaria* and all the included representatives of *Clavulinopsis*. These results should be considered as preliminary due to the lack of bootstrap support for this group and the taxonomic sampling of the present study.

One important result from the present study is the proposal of nomenclatural changes in *Ramariopsis*. At the present time, phylogenies seem to be divorced from classifications since few phylogenetic hypotheses are used as the foundation for newer classifications. This may result in the undesirable situation in which robust phylogenetic papers have little impact on the daily practice of taxonomists (for a broader discussion on this issue see Wheeler 2004, Franz 2005). Phylogeneticists are frequently reluctant to introduce changes in the classification due to the nature of the phylogenetic research—e.g. occasionally the relative position of a clade undergoes modifications with the addition of new data. In the present case, we decided to make taxonomical decisions based on our phylogenetic results by introducing changes only when we felt confident to do it.

Our results are robust enough to restrict *Ramariopsis* to species with ornamented spores—which show the characteristic ultrastructural pattern. The only problem arises when we try to identify the species that meet those requirements since in some species spore ornamentation is difficult to see. There are cases in which some taxa originally described with smooth spores are demonstrated to have ornamented spores—one example of this is *Ramariopsis californica* R.H. Petersen (Pegler & Joung 1985). For this reason, and until we have more information—e.g. SEM and TEM studies of the spores—we avoid proposing new combinations for species with smooth spores originally described in *Ramariopsis* (see Appendix 3). We only recommend the use of combinations previously proposed, that are congruent with our results (see Appendix 3). The only exception is *Ramariopsis antillarum* (Pat.) R.H. Petersen. This taxon was originally described as *Clavaria fusiformis* var. *antillarum* Pat.; subsequently, Petersen (1988a) proposed to raise it to species rank based on the differences in the ontogenetic patterns of the basidiomes between yet the species and the variety. We concur with Petersen's proposal, yet we consider that the correct placement for this species is in *Clavulinopsis* based on the presence of simple club basidiomes and globose, smooth spores. Our current knowledge of this species leads us to propose the combination

***Clavulinopsis antillarum* (Pat.) García-Sandoval & Cifuentes, comb. nov.**

Basionym: *Clavulinopsis fusiformis* var. *antillarum* Pat., in Duss, Enum. Methodique des champignons recueilles a la Guadeloupe a la Martinique (Lons-le-Saunier): 14 (1903).

We have included a checklist of available species names for *Ramariopsis* and their correct combinations according to the present results (see appendix 3). The list is divided in three parts: a) species confidently placed in *Ramariopsis* sensu stricto; b) taxa once included in *Ramariopsis* that do not belong to *Ramariopsis* according to our results and available information; and c) species originally described in *Ramariopsis* that need further examination before a new combination be proposed. We think that this checklist provides practical applications, avoiding the proposal of unjustifiable new combinations that may result in unstable nomenclatural changes.

Two combinations are excluded from the list:

a) *Ramariopsis bizzozeriana* (Sacc.) Schild. (= *Clavaria bizzozeriana* Sacc.). *C. bizzozeriana* was recognized as a taxonomic synonym of *Ramariopsis pulchella* by Corner (1950); later the combination *Ramariopsis bizzozeriana* was incorrectly preferred over *Ramariopsis pulchella* by Schild (1972). This last combination should not be used

because *C. bizzoeriana* is currently considered a taxonomic synonym of *R. pulchella* (for details see Corner 1950, Petersen 1978b).

b) *Ramariopsis lentofragilis* (= *Clavaria lentofragilis* Atk.). Corner (1950 p. 640) considered *Clavaria lentofragilis* Atk. a taxonomic synonym of *Ramariopsis kunzei*, although he kept doubts. In his description of *Ramariopsis lentofragilis* f. *propera* (Bourdot) R.H. Petersen, Petersen (1969 p. 550) used the combination *Ramariopsis lentofragilis* without making any reference to the authority of the combination. In a subsequent article Petersen (1978a p.669) acknowledged Corner as the author of the combination. However, *Ramariopsis lentofragilis* was not considered by Corner (1950, 1970), who only referred to the species as a taxonomic synonym of *R. kunzei*. Whether *C. lentofragilis* is a synonym of *R. kunzei* or not is a matter that needs further investigation. For that reason we prefer to exclude that possible combination from the checklist.

In conclusion, the present study indicates that the delimitation of *Ramariopsis* proposed by Corner (1950, 1970) is robust, given currently available data. Although the topological comparisons did not find significant differences between this hypothesis and that proposed by Petersen (1978a), our analysis indicates that *Ramariopsis* sensu Corner represents a more parsimonious hypothesis (five steps shorter), in accordance with ultrastructural data on spore ornamentation and patterns of cyanophilous reaction in the spores. Additionally, the test of sensitivity of the taxonomic sampling indicated that the results obtained were not an artifact of taxon selection and are stable across various resamplings of the data. Relationships among taxa outside of the clade *Ramariopsis* sensu Corner should be taken as tentative, given that the sampling of the present study was designed for other objectives. Recently Dentinger & McLaughlin (2005) addressed the relationships of *Clavariaceae* and *Pterulaceae*; in their sampling they included representatives of *Ramariopsis* sensu Petersen and *Clavaria* sensu Petersen. Their results agree with our study and show *Ramariopsis* sensu Petersen as a paraphyletic group while also showing support for a clade congruent with *Clavaria* subgenus *Clavulinopsis*. In our results, we also find a clade congruent with the mentioned subgenus of *Clavaria*, but with non-bootstrap support. Future studies addressing *Clavariaceae* question are needed, but current findings (e.g. Dentinger & McLaughlin 2005) provide important insights about this questions.

### Acknowledgments

The authors wish to thank Dr. Gregory Mueller of the Field Museum of Chicago and Dra. Laura Guzmán-Dávalos, from Universidad de Guadalajara for peer-review of this manuscript. Also we thank Dr. David S. Hibbett of Clark University in Massachusetts for revision and commentary on a preliminary version of this manuscript; Dr. Ronald H. Petersen of the University of Tennessee for comments and suggestions on a previous version of this work presented at the 2004 Annual Meeting of the Mycological Society of America; Bryn C. Dentinger, of the University of Minnesota, for sharing a copy of their poster presented at the 2005 Annual MSA Meeting; the curators of the herbaria E, ENCB, IBUG, L, MEXU, TENN, TLXM, XAL, especially Dr. Ronald H. Petersen for the facilities and specimens offered, Dr. Roy Watling (E) for the facilities offered for the revision of the collection of Dr. E.J.H. Corner, Dr. Machiel Noordeloos (L) and Evelyn Turnbull (E) for their help during visits to their herbaria. Funds for the present work were provided by CONACYT 34313-V, and DGAPA IN 209605-3. R. G.-S. would also like to thank support from the Programa de Becas Nacionales de Posgrado UNAM. The authors would like to note that conclusions presented in this work are not necessarily those of colleagues that commented earlier versions of this work.

## Appendix 1. Characters and character states.

### Morphological characters of the basidiome

1.- *Simple clavate basidiome*. This type of basidiome corresponds to what Petersen (1988a) defined as clavarioid –holobasidiomycetes, in simple erect columns– excluding the branched forms which show a distinct ontogenetic pattern as described by Corner (1950). This includes intergradations from simple clavate forms to those with some amount of apical branching (bifurcated towards the apex). Within this general pattern are several ontogenetic variants (Corner 1950, Cléménçon et al. 2004) that could be phylogenetically informative, but to date there are too few data to recognize discrete patterns; in the present study only the general pattern was considered. States: 0: present, 1: absent.

2.- *Profusely branched basidiomes*. This character corresponds to what Petersen (1988a) described as clavarioid (see character 1), but is confined to the branched forms, since this corresponds to an ontogenetic pattern distinct from the simple forms (Corner 1950). A basidiome was considered profusely branched when it exhibited three or more levels of branching coming from the middle or below the middle of the basidiome. States: 0: present, 1: absent.

3.- *Basidiome pileate-stipitate*. Corner (1966) defines the pileus as an apical expansion developed from a diageotropic growth that generates fan or umbrella shaped forms. This differs from the cantharelloids in the configuration of the hymenophore and the absence of a thickened hymenium. In the present study any basidiome exhibiting a pileus sensu Corner (1966) and a stipe sensu Kirk et al. (2001) was considered as pileate-stipitate, independent of the conformation of the hymenophore. States: 0: present, 1: absent.

4.- *Form of the hymenophore*. For the present study the hymenophore was defined following Cléménçon et al. (2004) as the portion of the context that supports the hymenium –the layer of basidia, basidiospores, and sterile elements– in contrast to the proposal of Kirk et al. (2001), who considered the hymenophore the structure which supports spores –e.g. a basidiome. In the present study the hymenophore was considered to exhibit variation in form independent of that of the basidiome, and as such is an independent character (Mickevich 1982, Mickevich and Limpscomb 1991, Limpscomb 1992, Mabee 1993, O’Keefe & Wagner 2001) –against Cléménçon et al. (2004) see character three– for example a smooth hymenophore can be present in a simple, clavate, or corticioid basidiome. The recognized states correspond in the case of gills to the description of Singer (1986), for a hymenophore in folds to Corner (1966) in cantharelloid fungi, for a smooth hymenophore to Cléménçon et al. (2004), and for a wrinkled hymenophore to the description of some species of *Clavariadelphus* by Corner (1950) though with a lesser grade of organization. States 0: gills, 1: folds, 2: wrinkles, 3: smooth.

5.- *Longitudinally sulcate in simple clavate basidiomes*. This character corresponds to the description by Petersen (1988a) and represents those basidiomes that exhibit a furrow or longitudinal fold along the fertile part of the basidiome; it differs from a wrinkled hymenophore in that the furrow or fold is singular. States: 0: present, 1: absent.

6.- *Development of the context at the level of the hymenium*. This character corresponds to the presence or absence of the condition described as fistular or hollow by Kirk et al. (2001), but confined to the context at the level of the hymenium. The portion of the context below the hymenophore and subhymenium can exhibit distinct grades of development with two clearly recognizable states: when it is well developed, the basidiome exhibits a solid aspect in transverse section, but when poorly developed the basidiome appears hollow or fistulate in transverse section. States 0: fistulate, 1: solid.

7.- *Pattern of branching*. Profusely branched basidiomes exhibit different patterns of branching derived from differences in ontogenetic development (Corner 1950). The nomenclature and patterns described by Corner (1950) were followed for the present study. Only two states were observed among the included species in the present analysis. States 0: radial, 1: flattened.

8.- *Mycelial cords*. Aggregates of linear hyphae growing away from the basidiome and visible to the naked eye were considered mycelial cords. Cléménçon et al. (2004) and Boddy (1999) distinguished between mycelial cords and rhizomorphs based on the level of organization and the type of growth of the structure. In the present study no distinctive apical growth was identified, and the observed structures were thus only characterized as mycelial cords in the general sense of Cairney et al. (1991). States: 0: present, 1: absent.

9.- *Mycelium at the base of the stipe*. Basidiomes growing from a patch or pillow of mycelium were considered as exhibiting mycelia at the base of the stipe. The mycelial growth was always conspicuous and found above the substrate; this mycelium covers the base of the stipe and exhibits different types of generative hyphae. Petersen (1988a) described subiculate as a patch of mycelia in the substrate from where the basidiome grows, but Cléménçon et al. (2004) restricted the term subiculate to the thick layer of mycelia from which the corticioid basidiomes develop. We treat the character as equivalent to what Petersen (1988a) denominates subiculate, but since Cléménçon et al. (2004) employed the term in a different manner, the descriptor subiculate is not used in the present study. States: 0: present, 1: absent.

10.- *Reaction of hymenium to iron salts*. The reaction to iron salts is a widely used character in the systematics of clavarioid fungi (Corner 1950; Donk 1964; Petersen 1978a, 1988a). The reagent contains ferric chloride in a 10% aqueous solution (Petersen 1988a), and is applied directly to the hymenium. A positive reaction is recognized by a color change to olive-green or gray-green. This reaction is considered indicative of the presence of the compound pistillarine (Steglich et al. 1984). A positive reaction to this reagent can exhibit other color changes due to the presence of distinct compounds (Gill & Steglich 1987, Singer 1986). In the present study only positive reactions that engendered olive-green or gray-green color changes were considered. Observations were made in dried exemplars. In our experience species with positive reaction in fresh material also react when dry. States 0: positive, 1: negative.

11.- *Carotenoid pigments in the basidiome*. Along with sesquiterpenoids, carotenoids are the only pigments present in the macromycetes derived from the mevalonate pathway (Gill & Steglich 1987, Gill 2003). This character was coded as a nominal variable –sensu Hawkins (2000)– based on the available information for the species considered since other types of coding would require additional data about the specific metabolic pathways generating the compound (e.g. Barkman 2001). States 0: present, 1: absent.

### **Micromorphological characters distinct from the hymenium and the spores**

12.- *Lactiferous hyphae*. This structure corresponds to what Singer (1986) described as lactiferous in the strict sense –hyphae that produce latex. These hyphae can exhibit nuclei and septa and thus correspond to a specialized type of heteroplera sensu Cléménçon et al. (2004). States 0: present, 1: absent.

13.- *Inflated hyphae*. Inflated hyphae are those generative hyphae that exhibit increased growth behind the point of lateral growth, widening and elongating significantly (Corner 1950, Kirk et al. 2001). They are recognizable by having a considerably greater diameter than the rest of the hyphae, and by having constrictions in the zone of the septa; they may or may not have clamp connections. Corner (1950) distinguished two types of monomitic contexts that present inflated hyphae based on the presence of secondary septa and clamps. In the present study this classification was not used, since it mixes two independently varying characters. States: 0: present, 1: absent.

14.- *Crystals in the hyphae of the basal mycelia*. The hyphae of the mycelia at the base of the stipe sometimes present amorphous crystals, similar to those reported in the context of the base of the stipe for *Ramariopsis pulchella* (Petersen 1988a) –5–20µm, hyaline or yellowish, and do not dissolve



in 5% KOH. The crystals are found covering the exterior surface of the hyphae and are not easily removed. States: 0: present, 1: absent.

15.- *Degree of thickening in the hyphal wall.* Thickening of the hyphal wall was considered only in the generative hyphae. The presence of generative hyphae with thickened walls has been a relevant systematic character in several genera (Corner 1966, Pegler 1996). In the present study three qualitative degrees of thickening were recognized due to the difficulty in making precise quantitative measurements. States: 0: none, 1: scarce, 2: conspicuous.

16.- *Simple fibulae.* Simple fibulae –clamp connections, clamp cells– are frequently observed in Basidiomycetes. Clémençon et al. (2004) recognized three types of simple fibulae, of which two were observed in the present study: closed and ring or medallion fibulae. Both types were considered equivalent since there were insufficient elements to determine discrete states, due the continuous variation observed. States: 0: present, 1: absent.

17.- *Geniculate fibulae.* Geniculate fibulae are those that exhibit a marked bend at the point of inflection, giving the appearance of a bent knee. The bend partially deforms the profile of the fibulae, allowing them to be easily differentiated from simple fibulae. These structures correspond to those described in various species of *Clavulinopsis* by Petersen (1968). Geniculate fibulae are not homologous to simple fibulae since both structures are found simultaneously in the same basidiome and are thus independent characters according to the conjunction test (Patterson 1988, Rieppel 1988, De Luna & Mishler 1996, Rieppel & Kearney 2002, Grant & Kluge 2004). States: 0: present, 1: absent.

18.- *H connections.* These connections are structures formed by the union of two parallel hyphae through a third, transverse, hypha. They can be considered functional homologous –biologically homologous following Roth (1988)– to fibulae, but are not phylogenetically homologous sensu de Pinna (1991), since they are both present simultaneously with distinct types of fibulae. They should thus be considered independent characters following the conjunction test (Patterson 1988, Rieppel 1988, De Luna & Mishler 1996, Rieppel & Kearney 2002, Grant & Kluge 2004). States: 0: present, 1: absent.

19.- *Ampulliform fibulae.* This type of fibula is characterized by the presence of a marked widening, giving the appearance of an inflated fibula similar to the inflated hyphae. This corresponds to the description by Petersen (1988a) as a characteristic of *Ramaria* subg. *Lentoramaria* Corner. This type of fibula is not phylogenetically homologous to the other types of fibulae described since it can be found present simultaneously with those other structures and should therefore be considered as an independent character by the conjunction test (Patterson 1988, Rieppel 1988, De Luna & Mishler 1996, Rieppel & Kearney 2002, Grant & Kluge 2004). States: 0: present, 1: absent.

### Hymenial characters

20.- *Subhymenium clearly differentiated.* The subhymenium was considered to be the layer of generative hyphae growing below the hymenium (Kirk et al. 2001) and from which the hymenium forms (Petersen 1988a). Several distinct anatomical patterns of the subhymenium have been described (Clémençon et al. 2004), and in the case of the clavarioid fungi, Petersen (1988a) considered three types. The variation observed in the present study; did not permit differentiation of distinct types of subhymenium; only the conspicuous presence or absence of a subhymenium was considered. States: 0: present, 1: absent.

21.- *Thickening of the hymenium.* Corner (1950) described the thickening of the hymenium as a pattern resulting from the sympodial growth of the hyphae of the subhymenium, generating successive superimposed layers of hymenium, collapsing the preceding basidia. No additional patterns of variation of this type have been described to date, and in the present study no further variation was observed. States: 0: present, 1: absent.

22.- *Cystidia of the hymenium*. Cystidia are sterile hyphal apices, generally with a distinctive form and found in variable locations in the basidiome (Kirk et al. 2001, Cléménçon et al. 2004). The form and anatomic disposition of the cystidia have been used as taxonomic characters, but only the cystidia in the hymenium were considered for the present study, as no other cystidia were observed in the species studied. States: 0: present, 1: absent.

23.- *Fibulate basidia*. Clamp connections on basidia are restricted to the base of the basidia. The presence on the basidia is independent of the presence of fibulae in the rest of the hyphae of the basidiome. As such, it was considered as an independent character. In the case of *Clavaria* subgenus *Holocoryne* the basidia exhibit a fibula described as broadly free (Corner 1950) or bifurcated (Petersen 1988a). States: 0: present, 1: absent.

24.- *Basidia with refringent contents*. This character refers to basidia with an oily, yellowish, appearance of its content, which is homogeneous and refringent in 10% KOH. It corresponds partially to what Petersen (1988a) described as gloeoplerotic, excluding the foamy appearance. Similarly, it corresponds partially to what Cléménçon et al. (2004) described as oil-producing – resinous content– and to what Singer (1986) describes as oil-producing sensu Fayoid, but without the positive sulfovainillin reaction. States: 0: present, 1: absent.

25.- *Shape of the basidia*. The variation observed during the present study permitted recognition of two forms or general profiles of basidia: cylindrical and clavate. These terms correspond to the definitions of Kirk et al. (2001). States 0: clavate, 1: cylindrical.

26.- *Base of clavate basidia*. Clavate basidia exhibit variation in the size of the base. Variation of the size was coded as an independent character because it refers to a property or feature of an anatomical region particular to clavate basidia and is not homologous with terete basidia (de Pinna 1991, De Luna & Mishler 1996, Rieppel & Kearney 2002, Grant & Kluge 2004). Additionally, this coding reflects the variation observed as it describes properties with independent variation. The size of the basidia exhibits variation logically independent of the form and thus can be coded as an independent character (Hawkins et al. 1997, Hawkins 2000, O’Keefe & Wagner 2001, Rieppel & Kearney 2002). States 0: short, 1: long.

27.- *Geniculate basidia*. These basidia exhibit a point of inflection in the middle part, and thus a marked bend giving the appearance of a flexed knee. This bend conspicuously deforms the profile of the basidia allowing them to be clearly differentiated. This pattern corresponds to that described in various species of *Clavulinopsis* by Petersen (1968). Geniculate basidia do not constitute a pattern or form homologous in the phylogenetic sense (de Pinna, 1991), since both structures are simultaneously present in the same basidiome and thus constitute independent characters by the conjunction test (Patterson 1988, Rieppel 1988, De Luna & Mishler 1996, Rieppel & Kearney 2002, Grant & Kluge 2004). States: 0: present 1: absent.

28.- *Orientation of the achromatic spindle*. Juel (1898) described two basic patterns of orientation of the meiotic spindle of basidia during meiosis: chiasitic –transversal to the principal axis and situated in the apex– and stictic –parallel to the principal axis and situated in the middle. Boidin (1958) recognized an intermediate pattern that he called hemichiasitic; Donk (1964) later qualified this as a homologous variant of the chiasitic form. In the present study only the chiasitic and stictic patterns were considered, given that those are the only patterns reported for the species studied. States: 0: chiasitic, 1: stictic.

29.- *Four remaining nuclei*. After meiosis a third nuclear division sometimes occurs, producing a total of eight nuclei. In some species four of these nuclei disintegrate and are termed remaining nuclei (Penancier 1961). This pattern has been reported for several of the species considered in the present study and corresponds to that described as post-meiotic pattern “A” by Duncan & Galbraith (1972) and to that described by Kühner (1977). The data available for the species considered in

the present study only allowed recognition of the presence of a third division –exhibiting pattern “A”– and the absence of this division (only four nuclei form); this character was thus coded as a nominal variably (Hawkins 2000). States: 0: present, 1: absent.

### Characters of the basidiospores

30.- *Spore form*. The variation observed during the present study allowed the recognition of three spore forms: globose, subglobose, and elongate. States were assigned qualitatively, excluding the deformations produced by ornamentation when present, and correspond to the forms described by Kirk et al. (2001), except for the fusiform and ellipsoid forms, which are considered as elongated spores. States: 0: subglobose, 1: globose, 2: elongate.

31.- *Size of the hilar appendix*. The hilar appendix –also called the apicule, sterigmal appendix or apophysis (Kirk et al. 2001, Cléménçon et al. 2004)– is the small conical or papilla-shaped projection, which is the point of connection between the spore and the sterigma. This structure is involved in the active liberation of the spores (Cléménçon et al. 2004). Based on the observed variation in the species studied, two qualitative states were recognized to describe the size of the appendix. States: 0: prominent, 1: inconspicuous.

32.- *Thickness of the spore wall*. The species considered in the present study do not exhibit significantly thickened spore walls, but some species show a slight thickening. Based on the observed variation two qualitative states were recognized. States: 0: slightly thickened, 1: thin.

33.- *Smooth spores*. Spore ornamentation has been a relevant taxonomic character for *Ramariopsis* (Corner 1950), but several studies have shown that ornamentation can be derived from different layers of the spore wall. Treating the presence of ornamentation as homologous in different taxa could thus fail the test of similarity (Rieppel 1988, Nelson 1994, Rieppel & Kearny 2002). The presence of smooth spores –spores without modifications or deformations in the wall– was observed in preparations mounted in 5% KOH using a bright field light microscope at 1000x magnification. States: 0: present, 1: absent.

34.- *Ultrastructure of spore ornamentation*. The spore wall has been characterized in different studies using different sources of information –light and electron microscopy– that generated different terms to denominate the observed ultrastructural patterns (Cléménçon et al. 2004). It is known that seemingly similar forms can exhibit different ultrastructural patterns (Cléménçon et al., 2004), and as such regarding these forms as homologous sensu de Pinna (1991) would be incorrect by the test of similarity (Rieppel & Kearney 2002, Grant & Kluge 2004). Based on this knowledge, the ultrastructure of the ornamentation was coded instead by the morphological patterns observed. In the present study the nomenclature of Pegler & Young (1985) was used, which also corresponds to the descriptions of Hawksworth et al. (1995). States: 0: tunica, 1: corium.

35.- *Cyanophilous reaction of the spores*. For the present study a cyanophilous reaction was considered positive when the wall of the spore stains with cotton blue, following the nomenclature proposed by Kotlaba & Pouzar (in Donk 1964). During the present study the reagent was prepared dissolving 1.6 g of cotton blue in 10 ml of lactic acid. After adding the reagent, the preparation was heated until boiling and then left to cool for 10 minutes before observations were made. States: 0: positive, 1: negative.

36.- *Pattern of cyanophylly in the spores*. The positive reaction to cotton blue (cyanophylly) exhibits two patterns of coloring: homogeneous or more intense in the ornamentation. States: 0: homogeneous coloring, 1: ornamentation more cyanophilous.

Appendix 2. Data matrix

Table 2. Data matrix for the 23 species and 36 characters.  
 ? = missing data, – = inapplicable data. For description of the characters and character states see Appendix 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
<i>Clavaria amoena</i>	0	1	1	3	0	1	–	1	0	0	0	1	0	1	1	0	0	0	
<i>Clavaria aurantiocimabarina</i>	0	1	1	3	0	1	–	1	0	1	0	1	0	0	1	0	0	0	
<i>Clavaria gibbsiae</i>	0	1	1	3	0	0	–	1	0	1	?	1	0	?	1	1	–	0	
<i>Clavaria sulcata</i>	0	1	1	3	0	1	–	1	1	1	?	1	0	–	1	0	0	0	
<i>Clavaria vermicularis</i>	0	1	1	3	1	1	–	1	1	1	?	1	0	–	1	1	–	0	
<i>Clavaria zollingeri</i>	1	0	1	3	–	0	0	1	0	1	?	1	1	0	1	1	–	0	
<i>Clavariadelphus pistillaris</i>	0	1	1	2	1	0	–	1	0	0	1	1	0	0	1	0	1	0	
<i>Clavulinopsis corniculata</i>	1	0	1	3	–	0	0	1	0	0	1	1	0	0	1	0	0	0	
<i>Clavulinopsis fusiformis</i>	0	1	1	3	0	1	–	1	0	0	1	1	0	1	1	0	1	0	
<i>Clavulinopsis helvola</i>	0	1	1	3	0	1	–	1	0	1	?	1	0	1	1	0	0	?	
<i>Clavulinopsis laeticolor</i>	0	1	1	3	0	1	–	1	0	0	1	1	0	?	1	0	0	0	
<i>Gomphus clavatus</i>	1	1	0	1	–	0	–	0	1	1	1	1	1	1	–	0	0	1	?
<i>Gomphus flocosus</i>	1	1	0	1	–	0	–	0	0	1	?	1	1	0	0	1	–	?	
<i>Lactarius indigo</i>	1	1	0	0	–	0	–	1	1	1	?	0	1	–	1	1	–	1	
<i>Ramariopsis californica</i>	1	0	1	3	–	1	0	1	0	1	?	1	0	1	1	0	1	0	
<i>Ramariopsis crocea</i>	1	0	1	3	–	0	0	1	0	1	1	1	0	1	1	0	1	0	
<i>Ramariopsis kunzei</i>	1	0	1	3	–	0	0	1	1	1	?	1	0	–	1	0	1	0	
<i>Ramariopsis pulchella</i>	1	0	1	3	–	0	0	1	0	1	?	1	0	1	1	0	1	0	
<i>Ramariopsis tenuiramosa</i>	1	0	1	3	–	0	0	1	1	1	?	1	0	–	1	0	1	0	
<i>Scytinopogon dealbatus</i>	1	0	1	3	–	0	1	1	1	1	?	1	1	–	2	0	1	0	
<i>Scytinopogon echinosporus</i>	1	0	1	3	–	0	1	0	1	1	?	1	1	–	2	0	1	0	
<i>Scytinopogon robustus</i>	1	0	1	3	–	0	1	0	0	1	?	1	1	0	1	0	1	0	
<i>Scytinopogon pallescens</i>	1	0	1	3	–	0	1	1	1	1	?	1	1	–	2	0	1	0	

Table 2, continued

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Clavaria amoena</i>	1	0	0	0	0	0	0	1	0	0	1	2	1	1	0	?	1	-
<i>Clavaria aurantiocinnabarina</i>	1	1	0	1	0	0	0	1	1	0	1	0	1	1	0	?	1	-
<i>Clavaria gibbsiae</i>	-	0	1	1	0	0	0	1	1	?	?	2	0	1	1	?	1	-
<i>Clavaria sulcata</i>	1	0	0	1	0	1	0	1	1	?	?	2	1	1	0	?	1	-
<i>Clavaria vermicularis</i>	-	0	0	1	1	1	0	1	1	?	?	2	1	1	0	?	1	-
<i>Clavaria zollingeri</i>	-	0	0	1	1	1	0	1	1	?	?	2	1	1	0	?	1	-
<i>Clavariadelphus pistillaris</i>	0	0	0	1	0	1	0	1	1	0	?	2	1	0	0	?	1	-
<i>Clavuthopsis corniculata</i>	1	0	0	1	0	1	0	1	1	0	0	1	0	0	0	?	1	-
<i>Clavuthopsis fusiformis</i>	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	?	1	-
<i>Clavuthopsis hebola</i>	1	0	0	1	0	0	0	1	0	?	?	0	0	0	1	1	0	0
<i>Clavuthopsis laeticolor</i>	1	0	0	1	0	0	0	1	0	0	0	2	0	0	0	?	1	-
<i>Gomphus clavatus</i>	1	0	0	1	0	1	0	1	1	0	?	2	0	1	1	?	0	1
<i>Gomphus floccosus</i>	-	0	0	1	1	1	0	1	1	?	?	2	0	1	1	?	0	1
<i>Lectarius indigo</i>	-	0	1	0	1	1	0	1	1	?	?	2	0	1	1	?	0	0
<i>Ramariopsis californica</i>	1	0	0	1	0	1	0	0	1	?	?	0	0	1	1	0	0	1
<i>Ramariopsis crocea</i>	1	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1
<i>Ramariopsis kunzei</i>	1	0	0	1	0	1	0	0	1	?	?	0	0	0	1	0	0	1
<i>Ramariopsis pulchella</i>	1	0	0	1	0	1	0	0	1	?	?	0	0	0	1	0	0	1
<i>Ramariopsis tenuiramosa</i>	1	0	0	1	0	1	0	0	1	?	?	0	0	0	1	0	0	1
<i>Scytinopogon dealbatus</i>	1	0	0	1	0	1	1	-	1	?	?	0	1	0	1	?	0	0
<i>Scytinopogon echinosporus</i>	1	0	0	1	0	1	1	-	1	?	?	2	1	0	1	?	0	0
<i>Scytinopogon robustus</i>	1	0	0	1	0	1	1	-	1	?	?	0	1	0	1	?	0	0
<i>Scytinopogon pallescens</i>	1	0	0	1	0	1	1	-	1	?	?	0	1	0	1	?	0	0

### Appendix 3. Checklist of species names.

#### Part 1. Species of *Ramariopsis* sensu stricto

- Ramariopsis asterella* (G.F. Atk.) Corner  
 = *Clavaria asterella* G.F. Atk.
- Ramariopsis avellanea* R.H. Petersen
- Ramariopsis avellaneainversa* R.H. Petersen
- Ramariopsis biformis* (G.F. Atk.) R.H. Petersen  
 = *Clavaria biformis* G.F. Atk.
- Ramariopsis californica* R.H. Petersen
- Ramariopsis cinnamomea* R.H. Petersen
- Ramariopsis cinnamomipes* R.H. Petersen
- Ramariopsis citrina* Schild
- Ramariopsis clavuligera* (R. Heim) Corner  
 = *Clavaria clavuligera* R. Heim
- Ramariopsis costaricensis* L.D. Gómez
- Ramariopsis crocea* (Pers.) Corner  
 = *Clavaria crocea* Pers.
- Ramariopsis curta* (Fr.) Corner  
 = *Clavaria curta* Fr.
- Ramariopsis flavescens* R.H. Petersen
- Ramariopsis hibernica* Corner
- Ramariopsis kunzei* (Fr.) Corner  
 = *Clavaria kunzei* Fr.
- Ramariopsis longipes* R.H. Petersen
- Ramariopsis novahibernica* Corner
- Ramariopsis pulchella* (Boud.) Corner  
 = *Clavaria pulchella* Boud.
- Ramariopsis ramarioides* R.H. Petersen
- Ramariopsis rufipes* (G.F. Atk.) R.H. Petersen  
 = *Clavaria rufipes* G.F. Atk.
- Ramariopsis subarctica* Pilát
- Ramariopsis tenuicula* (Bourdot & Galzin) R.H. Petersen  
 = *Clavaria tenuicula* Bourdot & Galzin
- Ramariopsis tenuiramosa* Corner
- Ramariopsis tortuosa* R.H. Petersen
- Ramariopsis vestitipes* (Peck) Corner  
 = *Clavaria vestitipes* Peck

#### Part 2. Species sometimes placed in *Ramariopsis* that belong in other genera

##### *Clavaria* L.

- Clavaria asperulospora* G.F. Atk.  
 = *Ramariopsis asperulospora* (G.F. Atk.) Corner

##### *Clavulinopsis* Overeem

- Clavulinopsis antillarum* (Pat.) García-Sandoval & Cifuentes, comb. nov.  
 = *Clavaria fusiformis* var. *antillarum* Pat.  
 = *Ramariopsis antillarum* (Pat.) R.H. Petersen
- Clavulinopsis corniculata* (Schaeff.) Corner  
 = *Clavaria corniculata* Schaeff.

- = *Ramariopsis corniculata* (Scaeff.) R.H. Petersen
- Clavulinopsis depokensis* (Overeem) Corner
  - = *Clavaria depokensis* Overeem
  - = *Ramariopsis depokensis* (Overeem) R.H. Petersen
- Clavulinopsis dichotoma* (Godey) Corner
  - = *Clavaria dichotoma* Godey
  - = *Ramariopsis dichotoma* (Godey) R.H. Petersen
- Clavulinopsis fusiformis* (Sowerby) Corner
  - = *Clavaria fusiformis* Sowerby
  - = *Ramariopsis fusiformis* (Sowerby) R.H. Petersen
- Clavulinopsis helvola* (Pers.) Corner
  - = *Clavaria helvola* Pers.
  - = *Ramariopsis helvola* (Pers.) R.H. Petersen
- Clavulinopsis holmskiodii* (Oudem.) Corner
  - = *Clavaria holmskiodii* Oudem.
  - = *Ramariopsis holmskiodii* (Oudem.) R.H. Petersen
- Clavulinopsis laeticolor* (Berk. & M.A. Curtis) R.H. Petersen
  - = *Clavaria laeticolor* Berk. & M.A. Curtis
  - = *Ramariopsis laeticolor* (Berk. & M.A. Curtis) R.H. Petersen
- Clavulinopsis luteo-ochracea* (Cavara) Corner
  - = *Clavaria luteo-ochracea* Cavara
  - = *Ramariopsis luteo-ochracea* (Cavara) R.H. Petersen
- Clavulinopsis luteotenerrima* (Overeem) Corner
  - = *Clavaria luteotenerrima* Overeem
  - = *Ramariopsis luteotenerrima* (Overeem) R.H. Petersen
- Clavulinopsis minutula* (Bourdot & Galzin) Corner
  - = *Clavaria minutula* Bourdot & Galzin
  - = *Ramariopsis minutula* (Bourdot & Galzin) R.H. Petersen
- Clavulinopsis subtilis* (Pers.) Corner
  - = *Clavaria subtilis* Pers.
  - = *Ramariopsis subtilis* (Pers.) R.H. Petersen
- Clavulinopsis umbrinella* (Sacc.) Corner
  - = *Clavaria umbrinella* Sacc.
  - = *Ramariopsis umbrinella* (Sacc.) R.H. Petersen

### **Ramaria Fr.**

- Ramaria lorithamnus* (Berk.) R.H. Petersen
  - = *Clavaria lorithamnus* Berk.
  - = *Ramariopsis lorithamnus* (Berk.) Corner

### **Scytinopogon Singer**

- Scytinopogon dealbatus* (Berk.) Corner
  - = *Clavaria dealbata* Berk.
  - = *Ramariopsis dealbata* (Berk.) R.H. Petersen

### **Part 3. Species initially described in *Ramariopsis* that require further examination**

- Ramariopsis agglutinata* R.H. Petersen
- Ramariopsis alutacea* R.H. Petersen
- Ramariopsis aurantio-olivacea* R.H. Petersen
- Ramariopsis bicolor* R.H. Petersen
- Ramariopsis cremicolor* R.H. Petersen

*Ramariopsis junquillea* R.H. Petersen  
*Ramariopsis lignicola* R.H. Petersen  
*Ramariopsis ovispora* R.H. Petersen  
*Ramariopsis pseudosubtilis* R.H. Petersen  
*Ramariopsis simplex* R.H. Petersen

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