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Portada: Hipotipos del foraminífero planctónico *Hendersonia carinata* (Cushman, 1938; Globigerinina, Heterohelicidae), del Santoniense Superior-Campaniense. Microfotografías de Marius Dan Georgescu y Sigal Abramovich.

Cover: Hypotypes of the planktonic foraminifer *Hendersonia carinata* (Cushman, 1938; Globigerinina, Heterohelicidae), from the Upper Santonian-Campanian. Microphotographies by Marius Dan Georgescu and Sigal Abramovich

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Permian palynoflora of the Ainim and Aiduna formations, West Papua

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Resumen

El análisis palinológico, el primero realizado sobre rocas pérmicas de Papúa Occidental (Nueva Guinea occidental), se basa en el análisis de muestras procedentes de seis localidades: tres al norte de la región de Bird's Head (Formación Ainim) y tres al sureste del Central Ranges, en la región de Bird's Body (Formación Aiduna). A pesar del desigual grado de abundancia y preservación, las asociaciones palinológicas obtenidas en ambas localidades evidencian una única y uniforme palinoflora, compuesta mayoritariamente por esporas y granos de polen, y en mucha menor medida por acritarcos, prasinofitas y otros microfósiles de algas. La correlación palinológica entre ambas formaciones corrobora estudios previos basados en la existencia de megaflore. Junto a algunos taxones designados informalmente, la palinoflora descrita contiene 26 especies de esporas incluidas en 21 géneros, 18 especies de polen (principalmente monosacados y bisacados teniados) distribuidas entre 13 géneros y 5 especies de microfitoplancton de pared orgánica. Las nuevas especies de esporas descritas en este trabajo son: *Dictyophyllidites ouyangii*, *Cyclogranisporites rugulogranatus*, *Lophotriletes wagneri*, *Triquirites kaiseri* y *Thymospora miscella*. Junto a éstas, ha sido descrita además una nueva especie de acritarco, *Maculatasporites gravidus*. Teniendo en cuenta tanto el rango estratigráfico como los registros anteriores de las esporas y granos de polen descritos en las formaciones Ainim y Aiduna, es posible obtener una edad comprendida entre fines del Pérmico Temprano y principio del Pérmico Medio (dentro del intervalo Kunguriano-Roadiano). El carácter indudablemente afín a la flora de *Glossopteris* que exhiben tanto las esporas y granos de polen analizados, como la megaflore previamente descrita corrobora la posición de Papúa Occidental en el margen nororiental de Gondwana. En cualquier caso, la presencia, aunque escasa, de ciertas especies de megaflore y palinoflora de clara afinidad Cathaysiana indica la cercanía al norte de este continente. La presencia en particular de esporas de algas de agua dulce en la palinoflora estudiada sugiere un ambiente de depósito de agua dulce o salobre.

Palabras clave: Palinomorfos, Sistemática, Correlación estratigráfica, Fitogeografía, Pérmico, Papúa Occidental

Abstract

This initial palynological analysis of Permian rocks of West Papua (western New Guinea) is based on samples collected from each of six localities: three in the northern Bird's Head region (Ainim Formation) and three, to the southeast, in the Central Ranges of the Bird's Body region (Aiduna Formation). Despite some variations in palynological productivity and preservational quality, it is evident that a single, essentially unified palynoflora – consisting predominantly of spores and pollen grains with much-subordinate acritarchs, prasinophytes, and other algal microfossils – is represented by assemblages yielded by the samples from both formations. This inter-formational correlation corroborates earlier reports of close similarities in respect of plant megafossil content. Apart from some taxa designated informally, the palynoflora comprises 26 species of spores representing 21 genera; 18 species of pollen grains (mainly monosaccates and taeniate bisaccates) distributed among 13 genera; together with five species of organic-walled microphytoplankton. The following spore species are newly established herein: *Dictyophyllidites ouyangii*, *Cyclogranisporites rugulogranatus*, *Lophotriletes wagneri*, *Triquirites kaiseri*, and *Thymospora miscella*; additionally, one new acritarch species, *Maculatasporites gravidus*, is defined. Taking due cognizance of the stratigraphic ranges or occurrences of previously known spore and pollen species, the palynoflora, and hence its hosting Ainim and Aiduna strata, is datable as late Early or early Middle Permian (i.e., within the Kungurian-Roadian).

dian interval). The overall, unmistakably glossopterid (Gondwanan) complexion of both the spore-pollen suite and the associated plant megafossils accords with the palaeogeographic situation of West Papua on the northeastern margin of Gondwana. However, proximity to the Cathaysian landmass to the immediate north is testified by the, albeit minor, presence of certain plant mega- and microfossils of characteristically Cathaysian floral affiliation. A fresh or brackish water depositional environment is indicated, particularly by the nonmarine algal complement of the palynoflora.

Keywords: Palynomorphs, Systematics, Stratigraphic correlation, Phytogeography, Permian, West Papua

1. INTRODUCTION

Palynological floras of Permian age have been investigated from many parts of the world, with particular emphasis on their stratigraphic-correlative and phytogeographic significance (e.g., Hart, 1965b; Anderson, 1977; Kemp *et al.*, 1977; Warrington, 1996; Césari & Gutiérrez, 2001; Playford & Dino, 2005; Traverse, 2007). This applies to Australia's Permian succession, with researches dating back to the 1940s, but not to its northerly near neighbour, the island of New Guinea. Thus the present study represents the first to describe and illustrate the palynological contents of certain New Guinean (specifically West Papuan) Permian strata and to evaluate their chronostratigraphic and palaeofloristic significance. The palaeogeographic situation of New Guinea is generally regarded as the northeastern portion of the Gondwana supercontinent, but with possible links to southeast Asia. Hence the complexion of the present floral assemblage, adduced from the spores-pollen and the plant megafossils, is of potential importance in gauging its affinities with the *Glossopteris* flora of Gondwana on the one hand and with the Cathaysia flora of southeast Asia on the other.

Geographic explanatory notes.- (a) In order to obviate possible geographic confusion, it is noted here that the samples studied herein are from what is now officially termed West Papua. This is the easternmost province of the Republic of Indonesia, and constitutes the western part of the island of New Guinea (the island's eastern part being the independent sovereign nation known as Papua New Guinea); see Figure 1. Previous recent names for West Papua were West Irian and Irian Jaya; prior to October 1962, in the Dutch colonial era, it was termed Netherlands New Guinea. (b) The avian configuration of the island of New Guinea has given rise to the traditional, metaphorical terminology – viz., from west to east, Bird's Head, Bird's Neck, and Bird's Body – that is followed herein and is depicted in Figure 1.

Gondwana vs. Gondwanaland.- Some authors (including G. Playford) favour the term “Gondwana”, others (including J.F. Rigby) are just as staunchly in favour of “Gondwanaland”, to designate the megacontinental landmass that existed in the southern hemisphere during Palaeozoic through mid-Mesozoic times. Several authors (e.g., McLoughlin, 2001, pp. 272-273) have discussed this terminological debacle at some length, presenting the pros and cons of both usages and requiring no reiteration here. Without undue arm-twisting, the present authors have agreed to adopt “Gondwana” consistently in this account.

2. GEOLOGY

The island of New Guinea is divided into three distinct geological provinces (Figure 1, inset map). Of these, the southern represents the northern margin of the Australian Plate, which is separated to the north from the Oceanic (Pacific) Plate by the New Guinea Foldbelt, the collision zone between the plates.

Even on a regional scale, definitive knowledge of the geology of West Papua is sparse. It derives mainly from oil exploration activities (Hermes in Visser & Hermes, 1962) that tended to be concentrated along the northern margin of the Australian Plate (although the existence of the Australian Plate was not recognized at that time). A major attempt at geological mapping was undertaken during 1976-1982 by the Irian Jaya Mapping Project (Pieters *et al.*, 1983) in the western part of the map area (Figure 1). Neither of the journals used for publication was widely disseminated, but the lithostratigraphic units relevant to our study have been tabulated and briefly described by Dow & Sukamto (1984, Table II). More recently, Charlton (2001) has proposed a palaeogeographic reconstruction for the area.

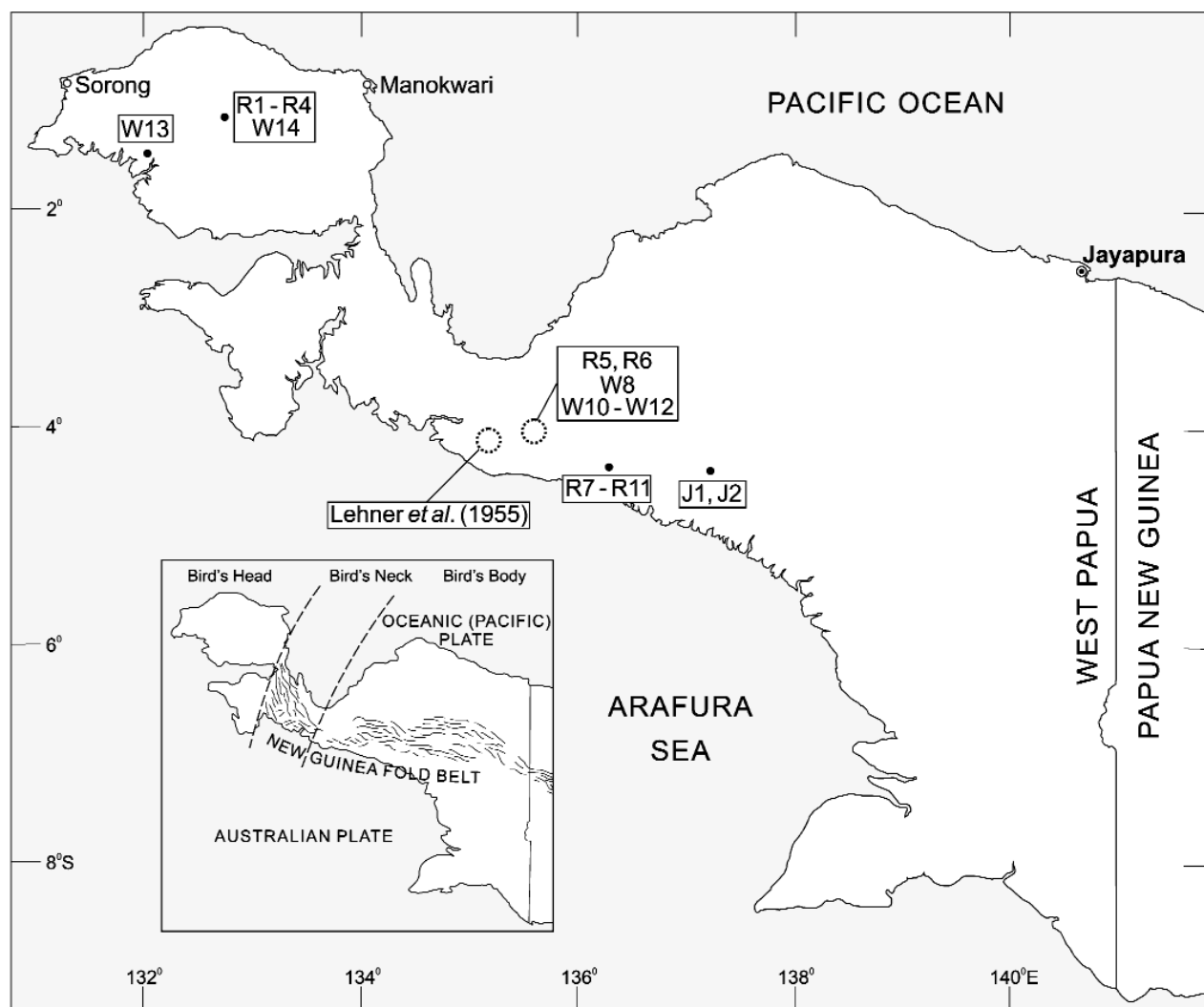


Figure 1. West Papua (excluding neighbouring islands) showing positions of Permian palynological and palaeobotanical collecting localities. More precise locations, listed on Table 1, are measured from the following 1:250,000 sheet-area maps: Taminabuan (Pigram & Sukanta, 1981); Waghete (Pigram & Panggabean, 1982); and Tembagapura (Jongmans, 1940, Text-fig., p. 267). Dots indicate locality positions, but many localities are too close to be plotted separately; broken circles indicate areas containing several localities, including those of Lehner *et al.* (1955). Boundaries of the 1:250,000 sheet areas, omitted for sake of clarity, are as follows: Taminabuan, Lat. 1°–2°S, Long. 131°30′–133°E; Waghete, Lat. 4°–5°S, Long. 133°–134°30′E; and Tembagapura, Lat. 4°–5°S, Long. 134°30′–136°E. Inset map shows major geological and geographic divisions cited in text; modified from Dow & Sukanto (1984, Fig. 8).

The only published base maps differ in detail. The earliest mapping was along the coastline, essentially to assist navigation. Aerial photography was used between 1935 and 1938 in support of petroleum exploration in areas of interest. During and after World War II, reliable aerial photography became available, eventually covering all of West Papua [Irian Jaya]. Maps from the various periods do not agree, particularly in the position of rivers, and most fossil collecting sites were in river valleys.

Geological investigations in West Papua occurred in two distinct phases. The first, associated with oil exploration,

lasted from 1935 to 1960, with a break (1941–1947) during World War II and its immediate aftermath. The work was undertaken by the N.V. Nederlandsche Nieuw Guinee Petroleum Maatschappij, which was owned by a consortium of the Royal Dutch Shell Group, Standard-Vacuum Oil Company, and Far Pacific Investments Company. Full details may be found in the introduction of Visser & Hermes (1962). The consortium produced many reports, which were “submitted to the Department of Mines, Hollandia” [Jayapura]. Because these are unavailable to us, we have made no reference to them except in one case (Lehner *et al.*, 1955, see below). Throughout this

text, spelling and use of names follow that of the particular reference with any alternative spelling provided in square brackets.

Details of the second phase are summarized and supplemented from Pieters *et al.* (1983). During 1976-1982, the Geological Research and Development Bureau, Bandung [Buitenzorg] and the Australian Bureau of Mineral Resources, Canberra (now Geoscience Australia) collaborated in the mapping of an area west of 136°30'E at a scale of 1:250,000. Unfortunately, this program – officially titled the Irian Jaya Mapping Project – was terminated because of factors beyond the control of either organization. Altogether, map sheets, generally as preliminary editions covering the area, were published and were accompanied by open file Geological Data Records. These are available for perusal in Bandung and Canberra. All of the samples upon which the present account is based were collected during this second phase of geological investigation.

No results of any subsequent geological mapping in West Papua have been published. The area is highly inaccessible owing to the exigencies of extreme topographic variation and the dense tropical rainforest cover, virtually unchanged over the past century (e.g., Mackay & Little, 1911). Hence, deficiencies in the mapping and literature cannot currently be alleviated, as it is not feasible to visit the area without the logistics of a major expedition.

Stratigraphic boundaries have not been plotted on our locality map (Figure 1) because any that are figured in the literature are not based on the systematic following of boundaries on the ground nor on examination of aerial photographs. Those boundaries that are marked on published maps do little more than demarcate areas of observed outcrops, as in Visser & Hermes (1962, Enclosures 1, 2). More recent maps do not delineate boundaries for the Permian sediments (e.g., Pigram & Sukanta, 1981; Pigram & Panggabean, 1982). The Tembagapura 1:250,000 sheet was never mapped, but is mentioned in the text because some palaeobotanical occurrences found during the 1930s exploratory period are within its boundaries.

The structural geology of New Guinea is very complex. Dow *et al.* (1984) incorporated the structural elements or provinces of earlier authors (e.g., Visser & Hermes, 1962, Fig. 11-11) as three major conterminous units. The cen-

tral east-west axis included the New Guinea Foldbelt, which is the suture or rift zone immediately north of the Australian Plate and south of the Oceanic (Pacific) Plate. The Foldbelt forms the backbone of the Bird's Body and the Bird's Head. These are separated at the Bird's Neck by the Lengguru [Lenggoeroe] Foldbelt (Dow *et al.*, 1985).

Permian sedimentary rocks (Permo-Carboniferous of some authors) are exposed along the northern edge of the Australian Plate just to the south of and parallel to the New Guinea Foldbelt, and extend southerly beneath younger sediments of the Australian Plate. Outcrops usually occur on the sides of deep river valleys in extremely rugged and densely forested mountainous areas (Robinson *et al.*, 1988, Fig. 1). The Permian strata are mostly marine, with non-marine intercalations toward the top of the succession. The palynological samples of this study were collected exclusively from within these intercalations.

Visser & Hermes (1962, Enclosure 8) plotted a series of stratigraphic columns based on data accrued from field studies and from petroleum exploration boreholes. The columns show plant megafossils occurring only at the top of the Permian sections (Sections D1, Kembelangan 1; G2, Oemar-Poronggo; G6, Otakwa) or over the upper part of the Permian (Section G1, Omba-Aidoena). We identify these sections as being within the Anim or Aidunda formation. A silicified wood horizon was depicted as occurring at the base of the Permian on the Bird's Head in the otherwise completely marine 'A' Member of the Aifam Formation. Prasad (1982) described a typical fossil wood from this horizon.

Based largely on data from the Bird's Head, Hermes (in Visser & Hermes, 1962) defined the Permo-Carboniferous sedimentary sequence as the Aifam Formation, which he divided into the 'A', 'B', and 'C' Members (in ascending order). Pigram & Panggabean (1983; see Table 1 herein) redefined these members, respectively, as follows: Aimau Formation (a lithologically varied non-marine unit of sandstone, mudstone, shale, and conglomerate passing upsection into marine turbidites); Aifat Mudstone, or Aifat Formation of some authors, (shallow marine, carbonaceous, and calcareous mudstone with minor sandy limestone); and Anim Formation (fluvio-lacustrine, carbonaceous, shaly siltstone, with subordinate sandstone and coal). Collectively, these three lithostratigraphic units

constituted the Permian Aifam Group *sensu* Pigram & Panggabean (1983). Their terminology was adopted preemptively by a number of authors (Archbold, 1981a-c; Dickins & Skwarko, 1981; Archbold *et al.*, 1982; Pigram & Sukanta, 1982); also by Glenister *et al.* (1983), Pieters *et al.* (1983), and Dow & Sukamto (1984); and in legends of several 1:250,000 map sheet areas. We give equal status to both publications and open file reports within the text, while identifying open file reports within the References as being unpublished. Whereas Archbold (1981a) and Glenister *et al.* (1983) regarded the formational/group names as “informal”, other authors have used them as if they were formal. We do not include mentions of plant remains in company reports, although these appear in Visser & Hermes (1962) and Rigby (1983). However, the report by Lehner *et al.* (1955) has been included, as their localities have been plotted by the editor on Rigby’s locality map without his knowledge.

Geological mapping continued in the early 1980s in the Bird’s Body region, where Permian strata appear attributable only to the upper part of the Aifam Group. Pigram & Panggabean (1983) expressed uncertainty whether the Permian sediments of the Bird’s Body were precisely equivalent to the Ainim Formation or whether they also included part of the underlying Aifat Mudstone. Accordingly, they defined the Aiduna Formation to include all of the Permian strata of the Bird’s Body (Central Ranges) that are separated by *ca.* 300 km of the Lengguru Foldbelt, which occupies the Bird’s Neck. The Aiduna Formation is a lithologically heterogeneous and predominantly non-marine unit, consisting chiefly of well-bedded lithic sand-

stone, carbonaceous siltstone, conglomerate, and minor coal. No base to the Aiduna was encountered by Pigram & Panggabean (1983), nor were they able to designate a suitable type section. They anticipated that future mapping to the east would facilitate such typification, but the project was terminated before the necessary fieldwork could proceed. In the present account, we use the name Aiduna Formation as it has appeared in publications (Pieters *et al.*, 1983; Dow & Sukamto, 1984; Dow *et al.*, 1985); in legends to 1:250,000 map sheet areas (Enartali by Dow & Hamonangan, 1981; Taminabuan by Pigram & Sukanta, 1981; Waghete by Pigram & Panggabean, 1982); and in open file reports (Pigram & Panggabean, 1983; Dow *et al.*, 1984).

3. PREVIOUS PALAEOONTOLOGICAL STUDIES

Hermes (in Visser & Hermes, 1962) reviewed the very limited biostratigraphic information then available from along the northern margin of what is now known to be the Australian Plate, and provided additional data obtained by the Nederlandsche Nieuw Guinee Petroleum Maatschappij (NNGPM) during petroleum exploration in West Papua. Brachiopods and some other invertebrates were identified using open or questioned nomenclature except for a single rugose coral considered representative of *Amplexus coralloides* Sowerby. These identifications do no more than indicate a late Palaeozoic age. The Visser & Hermes (1962) report was accompanied by numbered Enclosures that appear to have escaped the attention of later authors

Permo-Carboniferous (Hermes in Visser & Hermes, 1962)		Permian (Irian Jaya Mapping Project, 1976–1982)			
Bird's Head			Bird's Body		
Aifam Formation	C Member	**Aifam Group	**Ainim Formation	**Aifam Group	*Aiduna Formation
	B Member		**Aifat Mudstone		-?-?-?-?-?-?
	A Member		**Aimau Formation		

Table 1. Lithostratigraphic unit terminology used for the upper Palaeozoic, Australian Plate, West Papua; based on Pieters *et al.* (1983, Table 5) with minor additions. ** Unit proposed by Pigram & Sukanta (1982); herein accepted as defined. * Unit proposed by Pigram & Panggabean (1983); not formally defined although used in publications and map legends.

other than Rigby (1997, 1998b, 2001). Enclosure 17 ("Photographs of fossils") included plants identified by C.H. Hopping and R.H. Wagner (pp. 2-11); corals identified by H. Dighton Thomas (pp. 12-13); and brachiopods identified by G.E. de Groot (pp. 32-33). The plants have been revised by Rigby (1997, 1998b, 2001). The corals include representatives of the Rugosa (Figs. 11-13, 14b) and Tabulata (Figs. 14a, 15). We consider identification to greater precision to be unwarranted based on the illustrations. The brachiopods (Figs. 39-42) include specimens that appear distinct from any figured by Archbold (1981a, b). The latter author's collections were from the Aifat Mudstone within the Taminabuan map quadrangle of the Bird's Head. The relevant localities are plotted, but unnumbered, on maps in Archbold (1981a) and the Taminabuan 1:250,000 map (Pigram and Sukanta, 1981).

Correlation between the West Papuan [Irian Jayan] brachiopod faunas was discussed by Archbold (1981a) and summarized by Archbold *et al.* (1982). They assessed the age as late Baigendzhinian or early Kungurian, i.e., late Early Permian, based on comparison with faunas from Western Australia, northern Thailand, and along the northern Tethyan shoreline. Fontaine & Gafoer (1989b) pointed out that the brachiopod fauna of West Papua correlates reliably only with faunas of Western Australia and does not show a close relationship to Tethyan faunas.

The only pre-1962 published data concerning non-marine fossils collected by NNGPM are based on plant megafossils obtained from localities J1 and J2 (see Figure 1). These were submitted for identification to W.J. Jongmans (Director, Geological Bureau, Heerlen, Netherlands Limburg); the ensuing report (Jongmans, 1940) is the sole publication dealing with collections made by NNGPM prior to World War II. All other fossil collections appear to have been lost during hostilities. Jongmans (1940) identified species that were predominantly Cathaysian, but with Gondwanan elements which he dated as Permo-Carboniferous. He compared the flora with the extensive Cathaysia flora of Djambi [Jambi] in eastern Sumatra (Jongmans & Gothan, 1935), which did not include any endemic Gondwanan species. A specimen figured by Jongmans (1940, Pl. 3, Figs 9, 9a) as *Taeniopteris cf. taiyuanensis* and reclassified as *Glossopteris skwarkoii* by Rigby (1998b, p. 313; Fig. 21) resembles *G. waginanus* (Rigby, 1966) Rigby, Chandra & Surange, 1988 from the northern

part of the Perth Basin, Western Australia, in having taeniopteroid secondary venation but with rare cross-connections. However, it differs in possessing a series of broader, short areoles along the midrib, which form the base of the taeniopteroid venation covering the leaf blade. No other species of *Glossopteris* from West Papua closely resembles species from Western Australia. A specimen of *Glossopteris*, reported by Mackay & Little (1911, p. 485) from Papua New Guinea (PNG), was suggested by Rigby (1998a, p. 79) to be a misidentification and to have come from Tertiary coal measures based on those authors' description of the locality when plotted on the geological map of PNG. However, because bona fide *Glossopteris* specimens of West Papua occur along the northern margin of the Australian Plate, as does the Mackay & Little collection site, it now appears quite possible that their specimen was correctly identified as *Glossopteris*.

Hopping & Wagner's study (in Visser & Hermes, 1962), mentioned above, named and figured plant megafossils from the northern region of the Australian Plate (localities W1-W14: Figure 1, Table 2). Their taxonomic identifications, albeit unaccompanied by descriptive text, indicated a strong connection with Gondwana (in the form of various *Glossopteris* species), and also with Cathaysia (fern or fern-like fronds). Rigby (1983, 1997, 1998b, 2001) accorded due weight to Hopping & Wagner in his identification of plant megafossils listed in Table 3. In particular, specimens identified by Hopping & Wagner as *Sphenophyllum cf. speciosum* Royle, and as *Trizygia speciosa* Royle by Rigby (2001), are conspecific. This Gondwanan species was originally named *Trizygia speciosa* by Royle (1834, pl. 2, fig. 8; 1840, p. xxix*). Yabe (1922) proposed *Sphenophyllum sino-coreanum* for a Cathaysian species that resembles *T. speciosa*. Both species are common in the Permian of their respective domains. Many later authors have regarded *S. sino-coreanum* as a junior synonym of *T. speciosa*, generally as *S. speciosum*. However, two major reviews of the Cathaysian Sphenophyllales have maintained the species as distinct. Asama (1970) differentiated them on the basis of leaf size, identifying them as *Trizygia speciosa* Royle, 1840 and *T. sino-coreana* (Yabe, 1922) Asama, 1970. Gu & Zhi (1974; evidently unaware of Asama's paper) also segregated what they termed *Sphenophyllum speciosum* (Royle) M'Cllelland, 1850 and *S. sino-coreanum* Yabe, 1922, albeit on the basis of differences in the venation pattern. The generic attribution by

Locality numbers	Sample numbers	1:250,000 sheet area	Name of locality	Geographic coordinates	Formation
J1	P. 2929	Tembagapura	Oetakwa River	4°27'S 137°07'E	(?Aiduna Formation)
J2	KP. 131	Tembagapura	Oetakwa River	4°24'S 137°04'E	(?Aiduna Formation)
R1	79SS7	Taminabuan	79SS7	1°10'S 132°35-40'E	Ainim Formation
R2	79CP201	Taminabuan	79CP201	1°10'S 132°35-40'E	Ainim Formation
R3	79RY188C	Taminabuan	79RY188C	1°10'S 132°35-40'E	Ainim Formation
R4	79RY189A	Taminabuan	79RY189A	1°10'S 132°35-40'E	Ainim Formation
R5	80AG64	Waghete	80AG64	4°03'S 135°04'E	Aiduna Formation
R6	80BH302D	Waghete	Aiduna River	4°01'S 135°37'E	Aiduna Formation
R7	80P201A	Waghete	Uteraupuko River	4°15'S 136°16'E	Aiduna Formation
R8, R9	80P201B 80P201C	Waghete	Uteraupuko River	4°15'S 136°16'E	Aiduna Formation
R10	80P278A	Waghete	Uteraupuko River	4°14'S 136°16'E	Aiduna Formation
R11	80P279A	Waghete	Uteraupuko River	4°15'S 136°16'E	Aiduna Formation
R12	80UH202C	Waghete	Aiduna River	4°02'S 135°38'E	Aiduna Formation
W8	8	Waghete	Aidoena River	4°04'S 135°30'E	(Aiduna Formation)
W10	10	Waghete	Tipoema River	4°05'S 135°25'E	(Aiduna Formation)
W11	11	Waghete	Kenataure River	4°05'S 135°30'E	(Aiduna Formation)
W12	12	Waghete	Upper Aria River	4°05'S 135°15'E	(Aiduna Formation)
W13	13	Taminabuan	Poeragi Well	1°27'S 132°13'E	(Ainim Formation)
W14	14	Taminabuan	Aifat River	1°14'S 132°37'E	(Ainim Formation)

Table 2. Locality data, Permian of West Papua, for sites where plant megafossil species have been identified and figured in publications. Locality numbers are those specified by Rigby (1998b); **bold type** denotes the localities that yielded the palynomorphs reported herein; the other localities either proved barren palynologically (usually because of low grade metamorphism, R series in part, discussed in Rigby, 1997, 1998b) or provided no or insufficient samples for palynological examination (J series, from Jongmans, 1940; and W series, from Hopping & Wagner in Visser & Hermes, 1962). Geographic coordinates were estimated from the published Taminabuan and Waghete 1:250,000 maps; the Tembagapura map has not been published, but relevant data were interpolated from Jongmans (1940, p. 267). Parenthesized formation names are inferred on the basis of the map position of the particular locality. Spelling of names conforms to that used by the original author; alternative spellings are given in the text.

Asama (1970) is endorsed here, as is the species distinction advocated by Gu & Zhi (1974). Accordingly, the West Papuan specimens listed herein (Table 3) as *T. speciosa* are regarded as Gondwanan and as having no convincing relationship with Cathaysian forms attributed to that species.

All literature pertaining to Jambi, including reference to the biostratigraphy, has been reviewed by Fontaine & Gafoer (1989a). The megaflora has been dated as Early Permian. Seemingly coeval faunas have been dated as Middle Permian. The faunas are evidently unrelated to those of Western Australia, but are akin to faunas of Thailand, southern China, and the Tethyan region. Broad features distinguishing these latter faunas from those of West Papua and Western Australia are the lack of species in common, the prolific fusulinid fauna, and the occasional massive coral colonies.

Rigby (1997) examined published figures of species identified by Jongmans (1940) and redetermined most of the

species as belonging to Gondwana-related genera, thereby indicating that the flora was typical of the Gondwanan Permian (not Permo-Carboniferous as previously supposed), and that the putative link with the Cathaysian flora was illusory. However, Rigby (1997) reported the presence of *Gigantonoclea* and *Fascipteris*, both typically Cathaysian. These genera, represented by *G. irianensis* Rigby, 1997 and *F. aidunae* Rigby, 1997, occur in the essentially coeval Ainim and Aiduna formations (Table 3).

Fontaine & Gafoer (1989b) discussed the Middle Permian stratigraphy of Sumatra. In referring to the work of Archbold *et al.* (1982), under the heading "Sumatra-Gondwana relationships during the Permian", they stated (p. 112): "However, we suggest that the palaeontology of Sumatra does not support the geographical proximity of Sumatra and Australia during the Permian except for a small brachiopod fauna (Bolorian-Early Kubergandian in age) found in the Bird's Head region of Irian Jaya which exhibits some similarities with faunas of Thailand and Western Australia (Archbold *et al.*, 1982). We believe that too much empha-

Lithostratigraphic unit	Aiduna Formation	Ainim Formation
Localities (see Table 2 for definitions)	J1 – 2, R5 – 12, W8 – 12	R1 – 4, W13 – 14
* <i>Trizygia speciosa</i> Royle, 1840	✓	
Pecopterid frond sp. A	✓	
Pecopterid frond sp. B	✓	
* fern frond gen. et sp. indet.	✓	✓
<i>Ptychocarpus</i> sp.	✓	
<i>Cladophlebis</i> sp.	✓	
+ <i>Fasciapteris aidunae</i> Rigby, 1997	✓	✓
+ <i>Glossopteris irianensis</i> Rigby, 1997	✓	✓
+ <i>G. jongmansii</i> Rigby, 1998	✓	✓
+ <i>G. skwarkoi</i> Rigby, 1998	✓	✓
+ <i>G. wagneri</i> Rigby, 1998	✓	✓
+ <i>G. sp. cf. G. retifera</i> Feistmantel, 1881	✓	✓
+ <i>G. sp. B</i>	✓	
+ <i>G. sp. C</i>		✓
+ <i>G. sp. E</i>		✓
+ <i>G. sp. F</i>		✓
+ <i>G. sp. H</i>	✓	✓
<i>G. sp. indet.</i>	✓	✓
* <i>Vertebraria indica</i> Royle, 1840	✓	✓
+ <i>Gigantonoclea irianensis</i> Rigby, 1997	✓	
+ <i>Koraua hartonoi</i> Rigby, 1997	✓	

Table 3. Distribution of plant megafossil species identified by Rigby (1997, 1998b) from the Permian of West Papua. * Species known from other parts of Gondwana. + Species endemic to West Papua. **Bold type** indicates species significant for correlating the Aiduna and Ainim formations.

sis has been put on such similarities inasmuch as other fossil groups found in Sumatra (continental flora, marine algae, fusulinids, corals) do not favour such an hypothesis. Moreover, the disjunct distribution of Permian brachiopod genera has already been stressed (Waterhouse, 1967)."

It should be pointed out that the Permian fossils found in West Papua, other than brachiopods and plant megafossils, are limited to a few specimens of corals, goniatites, gastropods, and bivalves, and a single trilobite. Hermes (in Visser and Hermes, 1962) noted, without amplification, that "rare fusulinidae were observed in thin sections from West Vogelkop [West Bird's Head]."

Clearly, the assertion by Archbold *et al.* (1982) that a positive relationship exists with faunas of northern Thailand is difficult to sustain, whereas affinities with faunas of West-

ern Australia appear more cogent. The dating of the West Papuan faunas of the Bird's Head as late Baigendzhinian or early Kungurian (Archbold *et al.*, 1982) remains credible.

Small collections of brachiopods from sites within the Bird's Body were submitted to Archbold (1983). He concluded that the specimens were "often of variable preservation and of low diversity on a locality by locality basis, [hence] are difficult to date with precision."

4. MATERIAL AND METHODS

The six samples comprising the study material – three from each of the Ainim and Aiduna formations (see Table 2) – are all very similar lithologically, consisting of grey to dark

grey, carbonaceous, argillaceous siltstones. Approximately 50 g of each pre-cleaned sample were processed by conventional palynological techniques for the liberation and concentration of palynomorphs. Briefly, these procedures entailed: (a) sample disaggregation into pea-size lumps; (b) sequential immersion in 70% hydrofluoric acid (for removal of silicates) and hot dilute hydrochloric acid (for dissolution of fluorides); (c) brief (ca. 5-10 minutes') oxidation with concentrated nitric acid; and (d) eradication of fine extraneous material, including undissolved mineral matter, via heavy liquid separation. Between each of these steps and following (d), the residues were thoroughly washed to neutrality with distilled water. For each sample, one strew slide was made of its demineralized but unoxidized residue [i.e. immediately following step (b)] and two strew slides of the ultimate residues. These slides were examined in detail by means of an Olympus BH2 binocular microscope (of the Earth Sciences School, The University of Queensland), with attached Leica DFC320 digital camera and complementary image-acquisition computer software (Leica IM50). Also examined and photographed during light microscopy were slides containing singly mounted palynomorphs that had been picked from unmounted final residues (as per Balme, 1957, p. 13). Several of the more productive residues were transferred to absolute ethanol, thus enabling picking of selected palynomorph specimens following the means employed by Playford & Martin (1984, pp. 189-190). These specimens were then examined and images recorded with a scanning electron microscope (FEI Quanta 2000 of the Queensland University of Technology).

5. SYSTEMATIC PALAEOLOGY

The majority of spore, pollen, and organic-walled microphytoplankton species identified in the samples studied are described in detail hereunder. All are designated as morphotaxa in accordance with the precepts of the International Code of Botanical Nomenclature (ICBN; McNeill *et al.*, 2007). The "turmal" suprageneric classification adopted for spores and pollen grains is that inaugurated by Potonié & Kremp (1954) and subsequently modified by them and several other authors (see summary by Playford & Dettmann, 1996, pp. 244-247).

The basionym is cited for previously instituted species, followed where appropriate by either synonyms and binomial re-combinations or simply by reference to synonymy lists provided in existing publications. Certain previously instituted species that have been sufficiently well circumscribed in prior literature are listed without full descriptions, but in such instances supplementary morphological information is included on the basis of specimens observed during the present study. Descriptive morphological terminology for spores and pollen grains follows that employed by such authors as Kremp (1965), Smith & Butterworth (1967), Playford & Dettmann (1996), Traverse (2007), and Punt *et al.* (2007). Morphological terms used in acritarch and algal microfossil descriptions are those defined in the comprehensive glossary of Williams *et al.* (2000). Measurements of equatorial diameters are specified by lowest and highest values, in most cases with intervening bracketed arithmetic mean; e.g., 25 (34) 48 μm . Dimensional terminology applied to bisaccate and bilaterally symmetrical pollen grains accords with Playford & Dino (2002) and most previous authors. Type-species designations are abbreviated thus: OD, original designation; SD, subsequent designation; and M, monotypy.

The appendix incorporates curatorial information pertaining to all figured specimens (Plates 1-8). Permanent repository of the specimens is the Queensland Museum, Brisbane, Australia.

5.1. Spores

- Anteturma PROXIMEGERMINANTES R. Potonié, 1970
- Turma TRILETES Reinsch, 1881 emend. Dettmann, 1963
 - Suprasubturma ACAVATITRILETES Dettmann, 1963
 - Subturma AZONOTRILETES Lubert, 1935 emend.
Dettmann, 1963
 - Infraturma LAEVIGATI Bennie & Kidston, 1886 emend.
R. Potonié, 1956
 - Genus *Calamospora* Schopf, Wilson & Bentall, 1944
 - Type species: *Calamospora hartungiana* Schopf in
Schopf, Wilson & Bentall, 1944 [OD]

Calamospora spp.

Plate 1, Fig. 5

Remarks and previous records.- Indifferently preserved specimens belonging to *Calamospora* Schopf, Wilson & Bentall, 1944 occur uncommonly, though fairly consistently, in the samples studied. Some are at least comparable to *C. microrugosa* Schopf, Wilson & Bentall, 1944, a form that has been recorded by numerous authors from upper Palaeozoic strata worldwide.

Genus *Punctatisporites* Ibrahim, 1933 emend.

R. Potonié & Kremp, 1954

Type species: *Punctatisporites punctatus* (Ibrahim, 1932) Ibrahim, 1933 [OD]

Punctatisporites gretensis Balme & Hennelly, 1956

Plate 1, Figs. 6, 7

1956 *Punctatisporites gretensis* Balme & Hennelly, pp. 245-246; Pl. 2, Figs. 11-13. [1956b]

For further synonymy see Piérart (1974, p. 182).

Remarks and previous records.- This species, featuring relatively thick, laevigate exine, circular-subcircular amb, and equatorial diameter within a range of 51-75 μm , is a rare component of the study samples. It has been recorded extensively from the Permian of Gondwana.

Genus *Leiotriletes* Naumova, 1939 ex Ishchenko, 1952 emend. R. Potonié & Kremp, 1954

Type species: *Leiotriletes sphaerotriangulus* (Loose, 1932) R. Potonié & Kremp, 1955 [SD: R. Potonié & Kremp, 1954, p. 120]

Leiotriletes directus Balme & Hennelly, 1956

Plate 1, Figs. 1, 2

1956 *Leiotriletes directus* Balme & Hennelly, p. 244; Pl. 1, Figs. 1-4; Figs. 1a-f. [1956b]

For further synonymy see Foster (1979, p. 27).

Description.- Spores radial, trilete. Amb subtriangular with acute to broadly rounded apices and \pm straight to slightly convex sides. Laesurae distinct, straight to slightly sinuous, almost attaining equator, accompanied by narrow, elevated lips up to 5 μm high. Exine ca. 0.5-1 μm thick, prone to compressional folding, laevigate to scabrate or very faintly granulate.

Dimensions (6 specimens).- Equatorial diameter 23 (28) 31 μm .

Previous records.- *Leiotriletes directus* Balme & Hennelly, 1956 is known to be widely dispersed through Gondwanan Permian strata. In Australia, it has also been recorded from the Lower Triassic (de Jersey 1970, 1979).

Leiotriletes spp.

Plate 1, Figs. 3, 4

Remarks.- Small, morphologically indistinctive, trilete spores are relatively common in most of the Aiduna samples. These share the following characteristics: concavely triangular amb with rounded apices; equatorial diameter within a range of 22-40 μm ; essentially laevigate exine (apart from minor corrosive effects), ca. 0.5-1.2 μm thick; and simple straight laesurae extending ca. one-third to three-quarters of distance to equator. The specimens appear to constitute a morpho-continuum, combining attributes consonant with those of a number of upper Palaeozoic species, among them *Leiotriletes adnatus* (Kosanke, 1950) R. Potonié & Kremp, 1955, *L. sp. cf. L. adnatus* of Balme (1970), *L. levis* (Kosanke, 1950) R. Potonié & Kremp, 1955, *L. concavus* (Kosanke, 1950) R. Potonié & Kremp, 1955, *Leiotriletes* (spp.) of Bharadwaj (1962) and Singh (1964), and *Cyathidites breviradius* Helby, 1967 [the latter was described originally from the Lower Triassic, but reported subsequently from the Upper Permian by Helby (1973) and de Jersey (1979)]. Because these taxa are not always clearly separable and are of scant stratigraphic import, it is considered preferable here to simply assign the present specimens to *Leiotriletes* without specific designation.

Genus *Dictyophyllidites* Couper, 1958

Type species: *Dictyophyllidites harrisii* Couper, 1958 [OD]

Dictyophyllidites ouyangii Playford sp. nov.

Plate 1, Figs. 8-12

2003 *Dictyophyllidites* sp. of Ouyang Shu, Wang Zhu, Zhan Jia-zhen & Zhou Yu-xing, Pl. 102, Fig. 3. [no description]

Diagnosis.- Spores radial, trilete. Amb subtriangular with rounded apices and \pm straight to concave sides. Laesurae distinct, straight, extending two-thirds to four-fifths of dis-

tance to equator, with distinct or inconspicuous, very narrow lips (individually 1 µm or less wide). Proximal interradial (contact) areas with kytome consisting of 3 thickened exinal ridges 2-3 µm wide, up to ca. 2 µm high, ± parallel laesurae, thus having concavely subtriangular outline; ridges commonly conjoined at or about equatorial radii, thus fully enclosing laesurae, from which they are commonly well separated. Exine 0.7-1.5 µm thick, laevigate or finely sculptured (irregularly scabrate/granulate).

Dimensions (15 specimens).- Equatorial diameter 25 (34) 48 µm.

Holotype.- Sample/slide 80P278A/2, EF O33; Pl. 1, Fig. 8; UQY9367. Subtriangular amb, with near-straight sides and rounded apices; equatorial diameter 32 µm; very narrowly lipped laesurae, ca. three-quarters of spore radius in length; proximal kytome ridges 2 µm wide, continuous around ends of laesurae; exine finely, indistinctly sculptured.

Etymology.- Patronymic for Dr. Ouyang Shu of the Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, People's Republic of China.

Comparison.- *Dictyophyllidites ouyangii* Playford sp. nov. differs from the uppermost Permian-lower Mesozoic species *D. mortonii* (de Jersey, 1959) Playford & Dettmann, 1965 (p. 132; Pl. 12, Figs. 1-3) in its incipient lip development and in the nature of its kytome, the latter being composed of narrower interradial ridges that are well separated from the laesurae and are typically conjoined radially. In contradistinction to the Iraqi Permian species *Iraqispora labrata* Singh, 1964 (described subsequently herein), *D. ouyangii* is unthickened equatorially (acingulate) and its kytome is less strongly developed.

Previous records.- From the Upper Permian Wutonggou and Guodikeng formations of northwestern China (Ouyang Shu *et al.*, 2003, as per above synonymy; Ouyang Shu, email, 27 October 2006).

Infraturma APICULATI Bennie & Kidston, 1886 emend.

R. Potonié, 1956

Subinfraturma GRANULATI Dybová & Jachowicz, 1957

Genus *Cyclogranisporites* R. Potonié & Kremp, 1954

Type species: *Cyclogranisporites leopoldii* (Kremp, 1952)

R. Potonié & Kremp, 1954 [OD]

Cyclogranisporites gondwanensis Bharadwaj &

Salujha, 1964

Plate 5, Fig. 14

1964 *Cyclogranisporites gondwanensis* Bharadwaj & Salujha, p. 192; Pl. 1, Figs. 19-22.

For other synonymy see Foster (1979, p. 32).

Remarks.- A few specimens attributable to *Cyclogranisporites gondwanensis* were encountered in one of the samples studied. In agreement with Bharadwaj & Salujha's (1964) circumscription, the specimens, 22-39 µm in equatorial diameter, feature a comprehensively and uniformly granulate exine (ca. 0.5-0.8 µm thick), together with distinct, essentially simple laesurae extending two-thirds to three-quarters of distance to equator.

Previous records.- Reported widely from the Gondwanan Permian (e.g., Foster, 1979, p. 32).

Cyclogranisporites rugulogranatus Playford sp. nov.

Plate 1, Figs. 15-18

1991 *Cyclogranisporites* sp. A of Backhouse, p. 264; Plate III, 14-19.

Diagnosis.- Spores radial, trilete; amb circular to subcircular. Laesurae commonly indistinct; where observable, simple, straight, length ca. 0.3-0.7 of spore radius. Exine 0.8-1.6 µm thick, characteristically bearing 2 or several large-scale compression folds. Comprehensive, fine exinal sculpture of rounded to ± flat-topped grana and rugulae in varying proportions; a few minute coni may additionally be present; sculptural elements 0.2-1.5 µm apart, up to 1 µm high. Bases of grana notably variable in outline (circular to irregularly polygonal), 0.4-1 µm in diameter. Rugulae mostly unbranched, shape irregular, up to 4.5 µm long, 0.3-2.2 µm wide.

Dimensions (77 specimens).- Equatorial diameter 38 (53) 73 µm.

Holotype.- Sample/slide RY189A/28, EF B46/4; Pl. 1, Fig. 16; UQY9374. Subcircular amb modified by peripheral folding, equatorial diameter 72 µm; exine 1.3 µm thick, sculptured comprehensively with irregularly shaped grana and rugulae.

Etymology.- Latin, *rugosus*, wrinkled; *granatus*, grainy; alluding to the composite exine sculpture.

Remarks.- The description and illustrations provided by Backhouse (1991; as per above synonymy) leave little doubt that the specimens described above as *C. rugulogranatus* sp. nov. are conspecific with his *Cyclogranisporites* sp. A. The numerous specimens examined herein exhibit a sculptural gradation linking those featuring almost entirely granulate sculpture to those bearing approximately equal proportions of grana and small rugulae, some of the latter having the appearance of fused grana. Hence, Backhouse's (1991) generic attribution of this species is affirmed. A few specimens show slight development of polumbrate contact areas (e.g., Plate 1, Fig. 15).

Comparison.- *Cyclogranisporites rugulogranatus* differs from the Western Australian Lower Triassic species *Osmundacidites senectus* Balme, 1963 (p. 17; Pl. 4, Figs. 1, 2) in its less-distinct laesurae and, as noted by Backhouse (1991, p. 264), in the detail of its exine sculpture. *Cyclogranisporites arenosus* – described by Mädler (1964, pp. 96-97; Pl. 8, Fig. 11) and Balme (1970, p. 325; Pl. 1, Figs. 10-12) from the Triassic of Germany and Pakistan respectively – is thicker walled and more uniformly sculptured (with grana exclusively) than *C. rugulogranatus* and its laesurae are clearly evident. *Partimtactosporites verrucosus* Anderson, 1977 (p. 31; Appendix 9.3, pp. 80-81; Pl. 76, 1-38), from the South African Permian, superficially resembles *C. rugulogranatus*, but was diagnosed as having verrucate exine and lipped laesurae.

Previous records.- From southwestern Australia's Collie Basin in coal measures of late Early-early Middle Permian age (Backhouse, 1991).

Genus *Granulatisporites* Ibrahim, 1933 emend. R. Potonié & Kremp, 1954

Type species: *Granulatisporites granulatus* Ibrahim, 1933 [vide Schopf, Wilson & Bentall, 1944, p. 33]

Granulatisporites austroamericanus Archangelsky & Gamero, 1979
Plate 1, Figs. 13, 14

1979 *Granulatisporites austroamericanus* Archangelsky & Gamero, pp. 421-422; Pl. I, Fig. 4.

For further synonymy see Playford & Dino (2002, p. 244).

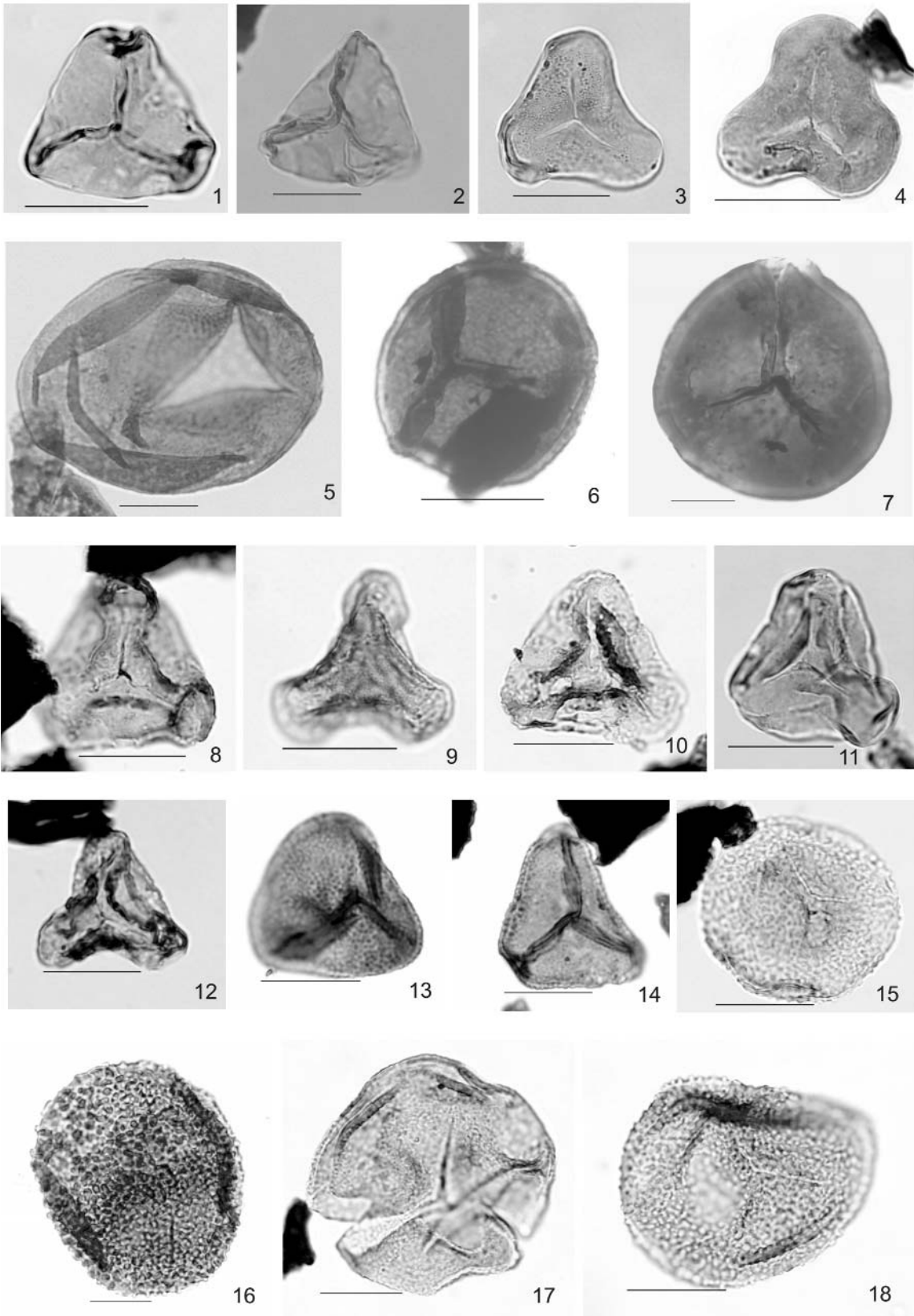
Remarks and comparison.- A few specimens only of *Granulatisporites austroamericanus* Archangelsky & Gamero, 1979 were identified in four of the West Papuan samples. These range in equatorial diameter from 32 µm to 45 µm and show variable lip development and evenly granulate sculpture of the distal and equatorial exine, conforming in these and other respects with the diagnosis furnished by Archangelsky & Gamero (1979) and the detailed description by Playford & Dino (2002). The latter authors (pp. 244, 246) discussed the possible or probable synonymy of *G. austroamericanus* with the Indian Permian species *Microbaculispora tentula* Tiwari, 1965 (pp. 175-176; Pl. 2, Figs. 35-37). Resolution of this question clearly depends on determining the precise nature of the exine sculpture of *M. tentula*; i.e., whether genuinely baculate or granulate.

Granulatisporites trisinus, as originally diagnosed by Balme & Hennelly (1956b, p. 244; Pl. 1, Figs. 5-8) from the Permian of New South Wales, is larger [equatorial diameter 45 (76) 110 µm] and generally thicker walled than *G. austroamericanus*, but has similar, regularly disposed sculptural elements. The two species could be regarded as sculpturally intergradational (cf. Backhouse, 1991, Pl. IV, 7); however, no specimens convincingly attributable to *G. trisinus* have been encountered in the study material.

Previous records.- From Pennsylvanian through Permian (particularly Lower Permian) strata of Gondwana; see Playford & Dino (2002, p. 246).

Plate 1. 1, 2, *Leiotriletes directus* Balme & Hennelly, 1956, median and proximal foci. 3, 4, *Leiotriletes* spp., proximal and median foci. 5, *Calamospira* sp., median focus. 6, 7, *Punctatisporites gretensis* Balme & Hennelly, 1956, median and proximal foci. 8-12, *Dictyophyllidites ouyangii* Playford sp. nov. 8, holotype, proximal view; 9, distal view; 10, proximal view; 11, 12, median foci. 13, 14, *Granulatisporites austroamericanus* Archangelsky & Gamero, 1979, median and proximal foci. 15-18, *Cyclogranisporites rugulogranatus* Playford sp. nov. 15, 18, proximal foci; 16, holotype, median focus; 17, median focus. Scale bars = 20 µm.

Plate 1



Genus *Waltzispora* Staplin, 1960

Type species: *Waltzispora lobophora* (Waltz in Lubert & Waltz, 1938) Staplin, 1960 [OD]

Waltzispora sp. A

Plate 2, Fig. 1

Description.- Spore radial, trilete. Amb trilobate with concave interradian margins and with slight but distinct, shoulder-like, lateral expansions positioned radially. Laesurae distinct, simple, ± straight, length one-half of spore radius. Exine laevigate; 1.2-1.6 µm thick, apart from well-developed polumbra broadly flanking laesurae and with outline ± conforming with amb.

Dimensions (1 specimen).- Equatorial diameter 29 µm.

Comparison.- This form differs from others belonging to this characteristically Carboniferous genus in its morphological combination of short laesurae, unsculptured exine, and proximal polumbra.

Subinfraturma VERRUCATI Dybová & Jachowicz, 1957

Genus *Converrucosisporites* R. Potonié & Kremp, 1954

Type species: *Converrucosisporites triquetrus* (Ibrahim, 1933) R. Potonié & Kremp, 1954 [OD]

Converrucosisporites micronodosus (Balme & Hennelly, 1956) Playford & Dino, 2002

Plate 2, Fig. 2

1956 *Granulatisporites micronodosus* Balme & Hennelly, p. 245; Pl. 1, Figs. 9, 10. [1956b]

2002 *Converrucosisporites micronodosus* (Balme & Hennelly) Playford & Dino, pp. 248, 250; Pl. 3, Figs. 1-8; Text-Fig. 3.

For further synonymy see Playford & Dino (2002, p. 248).

Dimensions (12 specimens).- Equatorial diameter, excluding sculptural projections, 35 (54) 67 µm.

Remarks.- The specimens observed in the West Papuan samples mostly show only minor lip development associated with the laesurae, as in Balme & Hennelly's (1956b) type material; cf. Backhouse (1991, p. 265; Pl. IV, 6).

Previous records.- Known widely from the Permian of

Gondwana: see summary distribution cited in Playford & Dino (2002, p. 250).

Genus *Verrucosisporites* Ibrahim, 1933 emend. Smith & Butterworth, 1967

Type species: *Verrucosisporites verrucosus* (Ibrahim, 1932) Ibrahim, 1933 [OD]

Verrucosisporites andersonii Backhouse, 1988

Plate 2, Figs. 3-5

1977 *Cyclogranisporites verrucosus* Anderson, pars, p. 73; Pl. 72, Figs. 23-56 only.

1988 *Verrucosisporites andersonii* (Anderson) (sic) Backhouse, pp. 55, 57; Fig. 5A-G.

Description.- Spores radial, trilete; amb circular to subcircular or very rounded subtriangular. Laesurae perceptible, straight, extending one-half to two-thirds of distance to equator; simple or with minor lip development. Exine ca. 1 µm thick; sculptured with close-spaced (usually 1 µm or less apart) verrucae and rugulae (1-4 µm in maximum basal dimension, 0.5-1 µm high) and minor grana; sculpture conspicuous distally and proximo-equatorially, commonly less prominent on contact faces.

Dimensions (8 specimens).- Equatorial diameter 41 (55) 62 µm.

Remarks.- Backhouse (1988) provided a more explicit and cohesive definition of Anderson's (1977) species, which had been very broadly characterized and attributed to *Cyclogranisporites*. In view of its predominantly verrucate exinal sculpture, Backhouse (1988) transferred the species to *Verrucosisporites* with the proposal of the epithet *andersonii* as a *nomen novum* [i.e., consequential on the prior establishment of *V. verrucosus* (Ibrahim, 1932) Ibrahim, 1933]. Note that, under ICBN provisions – but contrary to Backhouse (1988) and Stephenson (2004, p. 197) – the *andersonii* epithet, and the binomen *Verrucosisporites andersonii*, are to be attributed exclusively to Backhouse (1988).

Permian spores described by Price (1983, p. 169; Pl. 2, Figs. 8-10) as *Verrucosisporites aspratilis* Playford & Helby, 1968 clearly do not belong to that species, but nor, notwithstanding Backhouse (1988, p. 55), do they appear

assignable to *V. andersonii*. The same applies to *V. basiliscutus* Jones & Truswell, 1992 (p. 161; Fig. 8C, E-H, J-L); cf. Millstead (1999, p. 13), Stephenson (2004, p. 197).

Previous records.- From the Permian of the Karoo Basin, South Africa (Anderson, 1977; Millstead, 1999); Collie Basin, Western Australia (Backhouse, 1988, 1991); Dronning Maud Land, Antarctica (Larsson *et al.*, 1990; Lindström, 1994, 1995b); and Argentina (Vergel, 1998). Some other authentic Gondwanan Permian occurrences of *V. andersonii* were cited by Anderson (1977, p. 73) and Stephenson (2004, p. 197).

Subinfraturma NODATI Dybová & Jachowicz, 1957
Genus *Anapiculatisporites* R. Potonié & Kremp, 1954
Type species: *Anapiculatisporites isselburgensis*
R. Potonié & Kremp, 1954 [OD]

Discussion.- See Playford (1971, p. 16), Jansonius & Hills (1980, card 3835), and McGregor & Camfield (1982, p. 14).

Anapiculatisporites sp. A
Plate 2, Fig. 6

Description.- Spores radial, trilete. Amb subtriangular with convex to \pm straight sides and obtusely or acutely rounded apices. Laesurae distinct, extending at least four-fifths of distance to equatorial margin, commonly almost attaining the latter; flanked by lips up to 4.5 μm high and 2-3 μm in overall width, tapering towards equator. Exine thick (ca. 3-4 μm), with laevigate proximal and spinose distal surfaces. Spinae 3-6 μm long (where intact), tapering rapidly from expanded (bulbous) bases \pm circular in plan view and 1-4 μm in diameter. Spinae distributed irregularly (ca. 1.5-7 μm apart), projecting equatorially.

Dimensions (9 specimens).- Equatorial diameter, excluding sculptural projections, 49 (56) 72 μm .

Remarks and comparison.- The best-preserved specimen is that illustrated by Plate 2, Figure 6. Other specimens encountered show varying effects of degradation, whereby the slender distal extensions of the spinae are partly or entirely lost through decapitation and/or the lip development is subdued.

This form somewhat resembles two species known from

the Permian of Gondwana; viz., *Brevitriletes cornutus* (Balme & Hennelly, 1956) Backhouse, 1991 (pp. 261, 263; Pl. III, 4-6) and "*Acanthotriletes*" *apiculatus* Bose & Maheshwari, 1968 (p. 25; Pl. 4, Figs. 10-12; Text-Fig. 3). *Anapiculatisporites* sp. A differs from the former species mainly in its appreciably larger size, and from both species in having well-defined, lipped laesurae and in bearing more irregularly distributed and distally tenuous spinae (e.g., cf. Beri *et al.*, 2006, p. 233; Figs. 4F, 5B, C, P).

Insufficiency of adequately preserved specimens disallows the formal establishment of this distinctive form as a new species.

Genus *Apiculatasporites* R. Potonié & Kremp, 1956
Type species: *Apiculatasporites spinulistratus* (Loose, 1932) Ibrahim, 1933 [OD]

Discussion.- This genus is adopted in the sense advocated by McGregor & Camfield (1982, p. 18) and Hashemi & Playford (2005, p. 339).

Apiculatasporites sp. A
Plate 2, Figs. 7, 8

1991 *Apiculatisporis* sp. A of Backhouse, p. 261; Pl. III, 1-3.

Description.- Spores radial, trilete. Amb circular or sub-circular. Simple straight laesurae one-half to two-thirds of spore radius in length. Exine 1 μm or less in thickness, sculptured comprehensively with minute, discrete apiculate elements (coni, spinae) up to ca. 1 μm in height, basal diameter, and basal separation.

Dimensions (3 specimens).- Equatorial diameter 24, 27, 31 μm .

Remarks.- The three specimens encountered, even augmented by those few reported by Backhouse (1991; see above synonymy), are considered insufficient for this species to be designated formally.

Previous records.- From the Lower Permian (single bore-hole sample) of the Collie Basin, Western Australia (Backhouse, 1991).

Genus *Lophotriletes* Naumova, 1939 ex R. Potonié & Kremp, 1954

Type species: *Lophotriletes gibbosus* (Ibrahim, 1933) R. Potonié & Kremp, 1955 [SD; Potonié & Kremp, 1954, p. 129]

Lophotriletes novicus Singh, 1964
Plate 2, Figs. 9-12

1964 *Lophotriletes novicus* Singh, p. 247; Pl. 44, Figs. 24, 25.

Description.- Spores radial, trilete. Amb subtriangular; apices broadly rounded; sides concave or, less commonly, almost straight. Laesurae distinct, simple, straight, two-thirds to four-fifths of spore radius in length. Exine 0.8-1.4 µm thick; distally and equatorially bearing ± irregularly distributed coni, ca. 0.4-1.9 µm high, with circular to somewhat irregular bases 0.4-1.5 µm in diameter and up to 5 µm apart. Sculpture tending to be sparser and less conspicuous proximally. In some specimens, exine slightly thickened in proximal polar area.

Dimensions (43 specimens).- Equatorial diameter 23 (28) 35 µm.

Remarks and comparison.- As discussed in Playford *et al.* (1982, pp. 11-12), *Lophotriletes novicus* Singh, 1964 and the Lower to Middle Triassic species *L. bauhinae* de Jersey & Hamilton, 1967 (pp. 7-8; Pl. 3, Figs. 3, 5, 7-9) are morphologically similar, to the extent that some authors had considered them conspecific. However, in terms of the differentiating criteria suggested by Playford *et al.* (1982), and with reference to Singh's (1964) diagnosis and, particularly, Balme's (1970, pp. 322, 324; Pl. 1, Figs. 6-9) description of *L. novicus*, the present specimens are clearly assignable to the latter species.

Several species described from upper Palaeozoic strata resemble *L. novicus*, among them *L. varius* Zhou Yu-xing in Ouyang Shu *et al.* (2003, pp. 194, 482-483; Pl. 6, Figs. 7-10, 12, 13; Text-fig. 7.2). However, the latter species (from China) is generally larger, with laevigate proximal exine that is "somewhat thickened along two sides of tectum." Some of the South African (Karoo Basin) specimens figured by Anderson (1977, Pls. 37-40) as "*Acanthotriletes* (various forms)" appear referable to *L. novicus*. The Italian Pennsylvanian species *L. aduncus*, described by Pittau (in Pittau *et al.*, 2008, pp. 152-153; Pl. 1, Figs. 16, 17), differs from *L. novicus* in bearing "tapering bacula" on its distal surface.

Previous records.- *Lophotriletes novicus* has been reported fairly widely from Permian strata; e.g., Iraq (Singh, 1964), Pakistan (Balme, 1970), Australia (Helby, 1973; Foster, 1979; Gilby & Foster, 1988), New Zealand (Campbell *et al.*, 2001), South Africa (Millstead, 1999), Antarctica (Farabee *et al.*, 1991), and Russia (Sennikov & Golubev, 2006), and also from the Australian Triassic (e.g., de Jersey, 1972; Helby, 1973, Dolby & Balme, 1976). However, at least some of the Triassic occurrences are likely to be representative of *L. bauhinae*, as described and illustrated in, for instance, de Jersey & Hamilton (1967), Playford *et al.* (1982), and Backhouse & Balme (2002).

Lophotriletes wagneri Playford sp. nov.
Plate 2, Figs. 13-16

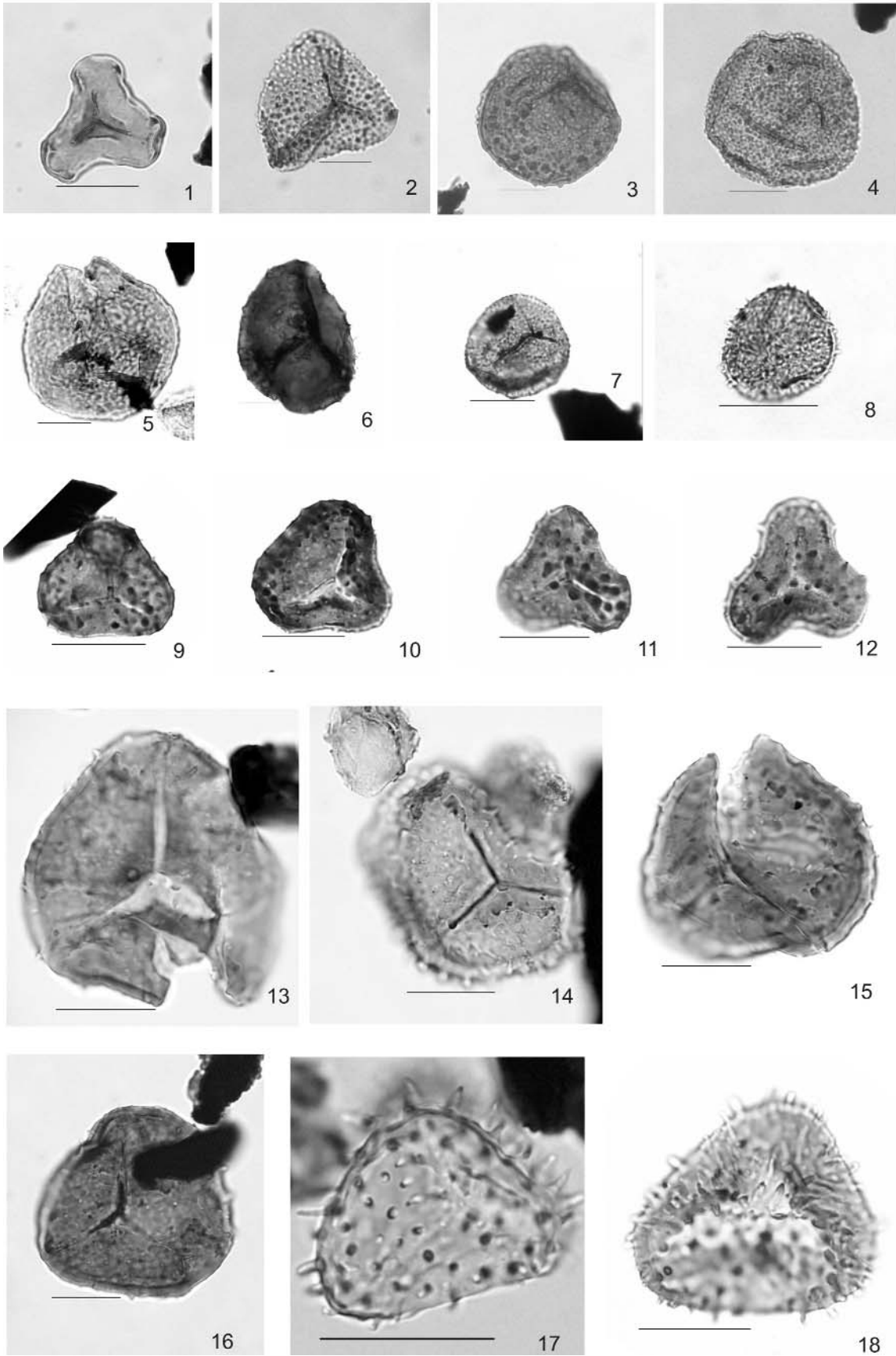
Diagnosis.- Spores radial, trilete; amb subtriangular, with rounded apices and convex to almost straight sides. Laesurae distinct, simple, straight, extending at least three-quarters of distance to equator, commonly almost attaining the latter. Exine relatively thick (2.5-4 µm); distal surface and proximo-equatorial region bearing discrete, ± heterogeneous, apiculate elements consisting predominantly of both broad and narrowly based coni, infrequently spinae. Sculptural elements ca. 0.5-3.5 µm high (acutely pointed tips frequently broken); bases circular, 0.5-3 µm in diameter, up to 5 µm apart. Contact areas (not well delineated) with much-reduced sculpture.

Dimensions (12 specimens).- Equatorial diameter 50 (56) 66 µm.

Holotype.- Sample/slide RY189A/3, EF U10/1; Pl. 2, Fig. 16; UQY9394. Subtriangular amb with convex to almost straight sides and rounded apices; equatorial diameter 60 µm; laesurae ca. three-quarters of spore radius in length, two terminally bifurcant; exine 4 µm thick; apiculate elements (0.5-2.5 µm high and broad basally; 1.5-5 µm

Plate 2. 1, *Waltzispora* sp. A, proximal focus. 2, *Converrucosisporites micronodosus* (Balme & Hennelly, 1956) Playford & Dino, 2002, proximal focus. 3-5, *Verrucosisporites andersonii* Backhouse, 1988; 3, 4, near-proximal foci; 5, median focus. 6, *Anapiculatisporites* sp. A, median focus. 7, 8, *Apiculatasporites* sp. A, proximal and distal foci. 9-12, *Lophotriletes novicus* Singh, 1964; 9, 10, median foci; 11, 12, distal foci. 13-16, *Lophotriletes wagneri* Playford sp. nov. 13, median focus; 14, proximal focus; 15, median-distal focus; 16, holotype, proximal focus. 17, 18, *Horriditriletes filiformis* (Balme & Hennelly, 1956) Backhouse, 1991, distal foci. Scale bars = 20 µm.

Plate 2



apart) borne distally and proximo-equatorially; contact areas with very sparse, diminutive sculpture.

Etymology.- Patronymic for Dr. Roberto H. Wagner, of Centro Paleobotánico, Jardín Botánico de Córdoba, Spain, in recognition of his distinguished contributions to knowledge of Palaeozoic floras.

Remarks and comparison.- Because this species has fundamentally conate sculpture, it is attributed to *Lophotriletes* Naumova, 1939 ex R. Potonié & Kremp, 1954 (pp. 129-130) rather than to *Brevitriletes* Bharadwaj & Srivastava, 1969 (p. 224), which is characterized by spinose sculpture. The thick exine and fairly sharp size differentiation among the apiculate sculptural elements suffice to distinguish *Lophotriletes wagneri* Playford sp. nov. from previously described species.

Subinfraturma BACULATI Dybová & Jachowicz, 1957
Genus *Horriditriletes* Bharadwaj & Salujha, 1964
Type species: *Horriditriletes curvibaculosus* Bharadwaj & Salujha, 1964 [OD]

Discussion.- See Foster (1979, p. 38).

Horriditriletes filiformis (Balme & Hennelly, 1956)
Backhouse, 1991
Plate 2, Figs. 17, 18

1956 *Apiculatisporites filiformis* Balme & Hennelly, p. 247; Pl. 2, Figs. 22, 23. [1956b]

1965 *Acanthotriletes filiformis* (Balme & Hennelly) Tiwari, p. 173; Pl. 1, Figs. 19, 20.

1965 *Apiculatisporis filiformis* (Balme & Hennelly) Pant & Srivastava, p. 472; Pl. 1, Fig. 21.

1991 *Horriditriletes filiformis* (Balme & Hennelly) Backhouse, p. 259; Pl. II, 10-13.

Description.- Spores radial, trilete. Amb subtriangular to subcircular. Laesurae perceptible to distinct, simple or slightly lipped, extending to or nearly to equator. Exine 0.5-1 µm thick; sculptured distally and proximo-equatorially with discrete, narrowly elongate elements of spinose to baculate form having typically blunted (acutely to obtusely rounded or ± truncate) apices. Sculptural elements

2-5 µm long, up to 1.2 µm broad basally, disposed regularly or irregularly 1-5 µm apart. Contact areas with sparse, diminished sculpture.

Dimensions (25 specimens).- Equatorial diameter, excluding sculptural projections, 23 (34) 47 µm.

Remarks.- Of previous generic attributions of this species, that of Backhouse (1991) is adopted here because of the baculate-cum-spinose form of the sculptural projections. The latter are variably distributed among specimens (i.e., densely to sparsely distributed).

Previous records.- Reported widely from the Gondwanan Permian (e.g., Foster, 1979, p. 34). In the Collie Basin (southwestern Australia), Backhouse (1991, Fig. 11) documented the introduction of this species at about the middle of his *Dulhuntyispora granulata* Zone (?Kungurian) and its continuation to the top of his sampled section (*D. parvithola* Zone; ?Ufimian).

Horriditriletes ramosus (Balme & Hennelly, 1956)
Bharadwaj & Salujha, 1964
Plate 3, Figs. 1, 2

Selected synonymy:

1956 *Acanthotriletes ramosus* Balme & Hennelly, p. 249; Pl. 3, Figs. 39-41. [1956b]

1960 *Neoraistrickia ramosus* (Balme & Hennelly) Hart, pp. 3-4; Pl. 3, Fig. 39.

1964 *Horriditriletes ramosus* (Balme & Hennelly) Bharadwaj & Salujha, p. 193.

1968 *Horriditriletes* sp. of Bose & Maheshwari, p. 27; Pl. 5, Fig. 9 only.

1977 *Raistrickia ramosa* (Balme & Hennelly) Rigby & Hekel, p. 14; Pl. 3, Figs. 2, 3, 5, 8, 9.

Description.- Spores radial, trilete. Amb subtriangular; apices rounded; sides variably concave to almost straight or slightly convex. Laesurae distinct or indistinct, extending at least three-quarters of distance to equator, with or without low, narrow lips individually up to 2 µm wide. Exine 0.5-1.3 µm thick, bearing diverse sculpture of bac-

ula (commonly slightly expanded distally) together with subordinate spinae and rare verrucae. Sculptural elements 1-4.5 μm in basal diameter, 2-7 μm high, 1-5 μm apart; developed mainly distally and equatorially; reduced in size and numbers proximally, particularly on contact areas.

Dimensions (11 specimens).- Equatorial diameter, excluding sculptural projections, 29 (35) 42 μm .

Previous records.- Many Permian occurrences of this species have been documented from various parts of Gondwana (e.g., Foster, 1979, p. 34; and subsequent authors).

Infraturma MURORNATI R. Potonié & Kremp, 1954
Genus *Dictyotriletes* Naumova, 1939 emend. R. Potonié & Kremp, 1954

Type species: *Dictyotriletes bireticulatus* (Ibrahim, 1933)
R. Potonié & Kremp, 1955 [SD; Potonié & Kremp, 1955, pp. 106, 107]

Dictyotriletes sp. A of Backhouse, 1991

Plate 3, Figs. 3, 5

1991 *Dictyotriletes* sp. A of Backhouse, p. 273; Pl. VIII, 5, 6.

Remarks.- The few specimens encountered exhibit the following features that are morphologically compatible with Backhouse's (1991) informally named species: subtriangular amb (with rounded apices and straight to convex sides); laesurae (slightly lipped) extending at least three-quarters of distance to equator; exine ca. 1.2 μm thick; distal reticulum imperfectum with low, narrow muri enclosing polygonal lumina (1-4 μm in maximum diameter); equatorial diameter 35, 41 μm (2 specimens measured).

Previous records.- From Permian strata of the Collie Basin, southwestern Australia: viz., *Dulhuntyispora granulata* Zone through *Protohaploxylinus rugatus* Zone (?Kun-gurian-Roadian; Backhouse, 1991).

Dictyotriletes sp. cf. *D. aules* Rigby in Rigby & Hekel, 1977

Plate 3, Figs. 4a, b

cf. 1977 *Dictyotriletes aules* Rigby in Rigby & Hekel, p. 15; Pl. 6, Fig. 8.

For additional synonymy (i.e., of *D. aules* per se), see Rigby & Hekel (1977, p. 15).

Description.- Spores radial, trilete. Amb roundly subtriangular. Laesurae straight to curved, extending to equator; accompanied by lips individually 1-1.5 μm wide. Exine ca. 1.5 μm thick; proximally laevigate; distally bearing reticulum perfectum. Muri ca. 0.5 μm high, 0.5-1.2 μm wide away from intersections; enclosing subcircular, \pm square, or polygonal lumina 1.5-9 μm in maximum dimension.

Dimensions (2 specimens).- Equatorial diameter 37, 39 μm .

Comparison.- The above specimens are identical in all morphological respects with *Dictyotriletes aules* Rigby (in Rigby & Hekel, 1977) with the exception of equatorial diameter: previous authors [Rigby & Hekel (1977), together with Segroves (1970), Foster (1979), de Jersey (1979), and Backhouse (1991)] have reported specimens within the range of 50-80 μm . Hence, a "cf." identification is adopted here.

Vergel's (1998, Pl. II, Fig. 4) Argentinian specimen seems a somewhat dubious identification of *D. aules*, mainly because of its apparently weakly trilete character.

Previous records.- *Dictyotriletes aules* is known per se from Australian and Indian Permian strata, as documented by authors cited above. In particular, Backhouse (1991, pp. 250, 256; Fig. 11) regarded it as a stratigraphically useful species, because of its fairly consistent introduction in the Collie Basin at or just below his *Microbaculispora villosa* Zone (~Baigendzhinian/late Artinskian) and extending to the sampled top (?Ufimian/Roadian) of the basin's succession. A similar range is indicated for the Perth Basin (Segroves, 1970); in the Bowen Basin and in India, the species extends into the Upper Permian (Rigby & Hekel, 1977). Raine (in Campbell *et al.*, 2001) recorded a single specimen either compared to (p. 490) or positively identified with (p. 500) *D. aules* in a New Zealand sample dated palynologically as close to the Early-Middle Triassic boundary, and he commented that the species "has been

recorded only rarely from Early-Middle Triassic sediments."

Subturma ZONOTRILETES Waltz, 1935
Infraturma AURICULATI Schopf, 1938 emend.
Dettmann, 1963

Genus *Indospora* Bharadwaj, 1962 emend. de
Jersey, 1968

Type species: *Indospora clara* Bharadwaj, 1962 [OD]

Indospora clara Bharadwaj, 1962
Plate 3, Figs. 7-10

1962 *Indospora clara* Bharadwaj, p. 83; Pl. 3, Figs. 54, 56, 57 [according to plate explanation, p. 105; but Pl. 3, Figs. 54, 55 on p. 83; however, holotype consistently cited as illustrated by Pl. 3, Fig. 54].

For other synonymy see Foster (1979, p. 48).

Dimensions (40 specimens).- Overall equatorial diameter 25 (38) 55 μm .

Remarks.- The species is well represented in three of the samples studied. The specimens exemplify the morphological variations of *Indospora clara* Bharadwaj, 1962 that have been described and illustrated by previous authors. Principal attributes are as follows: subtriangular amb with rounded apices and concave to straight (rarely slightly convex) sides; long, simple laesurae; \pm irregular exinal thickenings (auriculae) protruding at equatorial radii; distal reticulum perfectum or imperfectum with variable numbers of lumina; discrete, commonly prominent, apiculate sculptural elements of diverse form, size, and distribution on distal surface (bacula, spinae, coni, verrucae, grana; sparse to closely spaced).

Previous records.- *Indospora clara* is known from many, but not all, Gondwanan regions whence Permian strata have been studied palynologically, viz., in the Indian subcontinent, Australia, New Zealand, and Antarctica: see Bharadwaj (1962), Balme (1970), Tiwari & Tripathi (1992), Tiwari (1999), Segroves (1970, 1972), Foster (1979), Backhouse (1991), Balme & Backhouse (1993), Campbell *et al.* (2001), Kemp (1973), Kemp *et al.* (1977), and Playford (1990). The species ranges through much of the Permian in these regions, and in eastern Australia it persists into the Lower or lower Middle Triassic (de Jersey, 1968, 1979).

Genus *Triquitrites* Wilson & Coe, 1940 emend. R. Potonié & Kremp, 1954

Type species: *Triquitrites arcuatus* Wilson & Coe, 1940 [SD; Potonié & Kremp, 1954, p. 153]

Triquitrites kaiseri Playford sp. nov.
Plate 3, Fig. 15; Plate 4, Figs. 1a, b, 2

1976 *Triquitrites incisus* auct. non Turnau 1970; Kaiser, p. 118; Pl. 9, Figs. 7, 8a-c, 9.

Diagnosis.- Spores radial, trilete, auriculate (valvate). Amb subtriangular with rounded apices and concave (typically) to almost straight sides. Laesurae distinct, simple, straight, extending close to inner margin of auriculae, with or without slight terminal bifurcation. Exine 0.8-1.3 μm thick interradially; distinctly thickened radially to form 3 auriculae, each 15-22 μm x 2-8 μm ; surface and margin of auriculae irregularly undulant-lobate or almost entire. Distal exine typically bearing scattered, coarse, irregularly shaped thickenings (verrucae, broadly rounded coni, and rugulae; up to 4 μm wide, 6 μm long, and 2 μm high), more conspicuous in radial regions (i.e., near or contiguous with auriculae); proximal exine featureless or sparsely sculptured.

Dimensions (10 specimens).- Overall equatorial diameter 44 (50) 63 μm . Kaiser (1976) stated a size range of 44-55 μm .

Holotype.- Sample/slide RY188C/5, EF N44; Pl. 4, Figs. 1a, b; UQY9407. Subtriangular amb with concave sides and rounded apices; equatorial diameter 50 μm ; laesurae ca. four-fifths of spore radius in length, each with short terminal bifurcation; exine 1 μm thick interradially; undulating auriculae 20 μm x 4-5 μm ; distal exine with coarse, discrete, irregular thickenings, more prominent towards auriculae.

Etymology.- Patronymic for Dr. Helmut Kaiser, who first described this species.

Remarks and comparison.- Although the auriculae of the above specimens are somewhat irregularly developed, they are not fluted or plicate. Hence assignment to *Triquitrites* Wilson & Coe, 1940 emend. R. Potonié & Kremp, 1954, rather than to *Tripartites* Schemel, 1950 (p. 242), is deemed apposite. Apart from auriculate and other exinal

thickenings, both proximal and distal exine are laevigate or scabrate or, where corroded, irregularly punctate. The ten specimens reported here are all well preserved; these, together with those of Kaiser (see below), are considered sufficient for establishment of a new species.

Triquitrites kaiseri sp. nov is judged to be conspecific with *T. incisus* auct. non Turnau, 1970 as reported by Kaiser (1976). It differs from Turnau's (1970, p. 180; Pl. XI, Figs. 2, 5) species, from the Pennsylvanian of the Polish Carpathians, principally in that its amb is characteristically trilobate and in its distal sculptural features. An Iraqi Permian species, *T. iraqiensis* Singh, 1964 (pp. 249-250; Pl. 44, Figs. 31, 32), appears to be generally similar to *T. kaiseri*, but its diameter (based on five specimens) reportedly does not exceed 30 µm. *Triquitrites protensus* Kosanke, 1950 (p. 40; Pl. 8, Fig. 2), from the Pennsylvanian of Illinois, U.S.A., is also smaller than *T. kaiseri*, and is further distinguished from the latter in its thicker exine and interradial arcuate thickenings.

Previous records.- From northwest Shanxi (North China), in late Early-early Middle Permian strata dated as Kungurian-Roadian and bearing the Middle and Upper Cathaysia Flora (Kaiser, 1976).

Infraturma CINGULATI R. Potonié & Klaus, 1954
emend. Dettmann, 1963

Genus *Iraqispora* Singh, 1964

Type species: *Iraqispora labrata* Singh, 1964 [OD, M]

Iraqispora labrata Singh, 1964
Plate 3, Fig. 6

1964 *Iraqispora labrata* Singh, p. 243; Pl. 44, Figs. 7, 8;
Text-fig. 1.

Remarks.- The single, somewhat corroded specimen exhibits the following attributes enabling its identification with *Iraqispora labrata*, as described originally by Singh (1964) and, more explicitly, by Balme (1970, p. 334; Pl. 3, Figs. 9, 10): subtriangular amb with rounded to truncate apices and convex to straight sides; equatorial diameter 41 µm; laesurae extending almost to equator; kytomate interradial thickening in each contact area; cingulum 4-5 µm wide interradially, slightly broadening in radial positions.

Previous records.- From Upper Permian strata of Iraq (Singh, 1964) and Pakistan (Balme, 1970). Also reportedly occurs in the lower Mesozoic of Iran (Vaez-Javadi & Ghavidel-Syooki, 2005) and Germany (Achilles, 1981; Weiss, 1989).

Suprasubturma LAMINATRILETES Smith &
Butterworth, 1967

Subturma ZONOLAMINATRILETES Smith &
Butterworth, 1967

Infraturma CINGULICAVATI Smith & Butterworth, 1967
Genus *Densoisporites* Weyland & Krieger, 1953 emend.
Dettmann, 1963

Type species: *Densoisporites velatus* Weyland & Krieger,
1953 [OD]

Densoisporites solidus Segroves, 1970
Plate 3, Figs. 11, 12

1970 *Densoisporites solidus* Segroves, p. 62; Pl. 5, Figs.
E-H.

Description.- Spores radial, trilete. Amb convexly subtriangular to subcircular. Exine two-layered, cavate, with clearly defined, laevigate intexinal body, 1-1.5 µm thick, having outline (polar view) closely conformable with amb. Thickness of exoexine similar to that of intexine, except at equator when a narrow, ± distinct cingulum is developed; non-cingulate exoexine commonly with spongy appearance. Laesurae distinct, extending almost to equatorial margin; associated with prominent elevated lips individually 1-2 µm wide.

Dimensions (3 specimens).- Overall equatorial diameter 39-53 µm; diameter of intexine, in polar aspect, 24-35 µm.

Remarks.- Backhouse (1991, p. 273) pointed to *Gondisporites regularis*, described by Anderson (1977, p. 28; Pl. 25, Figs. 36-42) from the South African Permian, as a possible junior synonym of *Densoisporites solidus* Segroves, 1970.

Previous records.- Numerous authors, including Segroves (1970), Rigby & Hekel (1977), Foster (1979), Foster *et al.* (1985), Gilby & Foster (1988), and Backhouse (1991, 1993), have encountered this species in Permian (particularly Lower Permian) strata of Western and eastern Aus-

tralia. Other reports are from the Lower Permian of Antarctica (Lindström, 1994, 1995b) and Saudi Arabia (Stephenson & Filatoff, 2000a); and from the Lower-mid Permian of Peru (Doubinger & Marocco, 1981).

Genus *Gondisporites* Bharadwaj, 1962

Type species: *Gondisporites raniganjensis* Bharadwaj, 1962 [OD, M]

Gondisporites imbricatus Segroves, 1970

Plate 4, Figs. 5-7

1970 *Gondisporites imbricatus* Segroves, p. 63; Pl. 8, Figs. A-C.

Description.- Spores radial, trilete, zonate, cavate. Amb convexly subtriangular (with rounded or ± pointed apices) to subcircular. Laesurae extending to zona's inner margin or just beyond; accompanied by ± membranous, elevated lips, individually ca. 2-3 µm wide. Exoexine scabrate overall, sculptured distally with typically discrete, rounded or pointed conical and stubby bacula 0.5-3.5 µm high, 1-3 µm in basal diameter, up to 8 µm apart; relatively narrow, ± membranous zona with or without distal sculpture, width ca. 15% of spore radius. Proximal exoexine (including zona) devoid of apiculate sculpture. Intexinal body laevigate, ca. 0.5 µm thick, well contracted from exoexine; outline (in polar view) ± conformable with amb; diameter ca. one-third to one-half of spore diameter. Both exine layers subject to mainly peripheral compression folding.

Dimensions (25 specimens).- Overall equatorial diameter 53 (77) 106 µm.

Comparison.- *Gondisporites imbricatus* Segroves, 1970 is very similar to the type species *G. raniganjensis* Bharadwaj, 1962, the former being apparently distinguishable in that its apiculate exoexinal sculpture is distally confined. However, Bharadwaj's (1962, p. 85) diagnosis and description of *G. raniganjensis* are somewhat ambiguous with regard to sculptural distribution and re-study of his type material is necessary to confirm or otherwise whether the sculpture is genuinely comprehensive. If not, *raniganjensis* would, as senior synonym, likely subsume *imbricatus*.

Previous records.- *Gondisporites imbricatus* has been documented from the upper Lower-Upper Permian of the

Perth Basin, Western Australia (Segroves, 1970, 1972). The closely similar *G. raniganjensis*, originally described from the Upper Permian Raniganj stage of India (Bharadwaj, 1962), has been identified subsequently in Lower-Upper Permian strata of South Africa (Anderson, 1977), Australia (Rigby & Hekel, 1977; Backhouse, 1991), and Antarctica (Lindström, 1994, 1996).

Genus *Indotriradites* Tiwari, 1964 emend. Foster, 1979

Type species: *Indotriradites korbaensis* Tiwari, 1964 [OD]; but note that Millsted (1999, pp. 16-17) regarded *I. korbaensis* as a junior synonym of *I. australensis* (Hart, 1963) Millsted, 1999.

Indotriradites niger (Segroves, 1970) Backhouse, 1991

Plate 3, Figs. 13, 14

1970 *Kraeuselisporites niger* Segroves, pp. 66-67; Pl. 9, Figs. C-E.

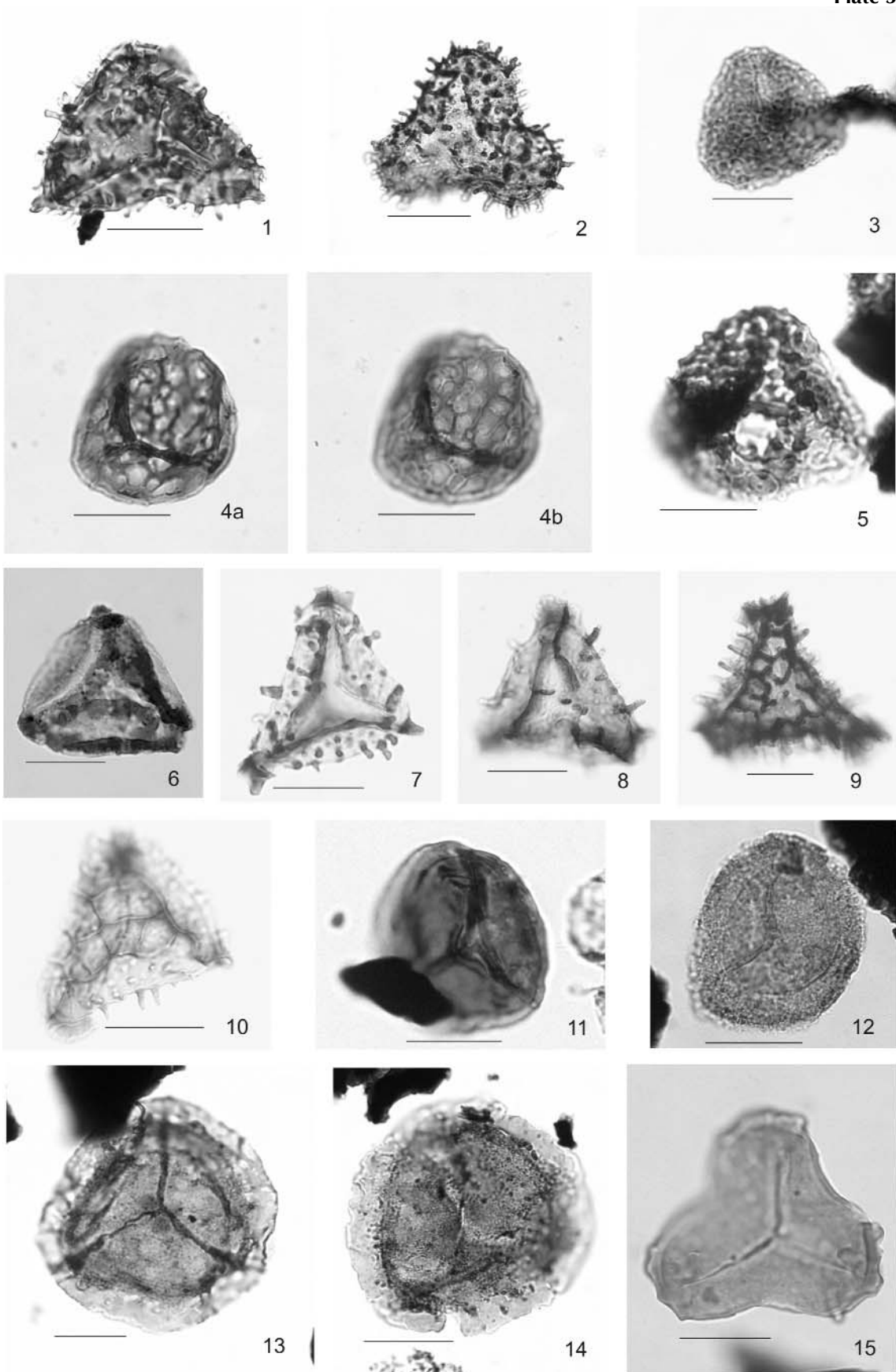
1977 *Perotrilites* sp. cf. *P. niger* (Segroves) Rigby & Hekel, p. 18; Pl. 7, Fig. 10.

1977 *Gondisporites splendens* (auct. non Balme & Hennelly) Anderson, pars, p. 63; Appendix 9.3, p. 30; Pl. 32, Figs. 1-10, 14-17.

1991 *Indotriradites niger* (Segroves) Backhouse, p. 277; Pl. IX, 5-11.

Description.- Spores radial, trilete, zonate, cavate. Amb subcircular to subtriangular with convex sides and rounded or somewhat pointed apices. Laesurae distinct to perceptible, accompanied by narrow, sinuous, elevated lips and extending to thickened inner margin of zona or almost to equator. Distal exoexine commonly microreticulate (possible corrosion effect?), bearing inconspicuous, scattered, small (<2 µm high), apiculate sculptural elements (grana, verrucae, conical), particularly about zona's

Plate 3. 1, 2, *Horriditriletes ramosus* (Balme & Hennelly, 1956) Bharadwaj & Salujha, 1964, proximal and distal foci. 3, 5, *Dictyotriletes* sp. A of Backhouse, 1991, median-distal foci. 4a, b, *Dictyotriletes* sp. cf. *D. aules* Rigby in Rigby & Hekel, 1977, proximal and distal foci. 6, *Iraqispora labrata* Singh, 1964, proximal focus. 7-10, *Indospora clara* Bharadwaj, 1962; 7, proximal focus; 8-10, distal foci. 11, 12, *Densoisporites solidus* Segroves, 1970, proximal and median foci. 13, 14, *Indotriradites niger* (Segroves) Backhouse, 1991, proximal and median foci. 15, *Triquitrites kaiseri* Playford sp. nov., median-proximal focus. Scale bars = 20 µm.



inner margin. Proximal exoexine essentially laevigate. Intexine thin (ca. 0.5 µm thick), laevigate, folded, commonly indistinct, occupying bulk of spore cavity.

Dimensions (14 specimens).- Overall equatorial diameter 44 (54) 65 µm. Zona width ranging from one- to two-thirds of spore radius.

Remarks.- Backhouse (1991, p. 277) suggested a "morphocline" relationship between *Indotriradites niger* (Segroves, 1970) Backhouse, 1991 and *I. splendens* (Balme & Hennelly, 1956) Foster, 1979. However, this has not been observed during the present study; i.e., no specimens clearly identifiable with, or transitional to *I. splendens* have been encountered. Antarctic Permian specimens figured by Lindström (1995b, Pl. VII, 6, Pl. XV, 8; 1996, Pl. 2, Fig. 7) as representatives of *I. niger* are not well preserved, and in any case appear to be misidentifications.

Previous records.- From the upper Lower through Upper Permian of the Perth, Collie, and Bowen basins, Australia (Segroves, 1970, 1972; Backhouse, 1991; Rigby & Hekel, 1977); and of the Karoo Basin, South Africa (Anderson, 1977).

Suprasubturma PSEUDOSACCITRILETES
Richardson, 1965

Infraturma MONOPSEUDOSACCITI Smith &
Butterworth, 1967

Genus *Grandispora* Hoffmeister, Staplin & Malloy, 1955
emend. McGregor, 1973

Type species: *Grandispora spinosa* Hoffmeister, Staplin
& Malloy, 1955 [OD]

Grandispora segrovesii Foster, 1979
Plate 4, Figs. 3, 4

1970 *Grandispora* sp. A of Segroves, pp. 64-65; Pl. 8,
Figs. D, E.

1979 *Grandispora segrovesii* Foster, p. 59; Pl. 18, Figs.
3, 4.

Description.- Spores radial, trilete, cavate. Amb subcircular to convexly subtriangular. Laesurae distinct, narrowly lipped, extending to intexine margin. Intexine laevigate, thin (ca. 0.5 µm), outline ± conformable with equator. Ex-

oexine scabrate, ca. 1 µm thick, sculptured mainly distally and equatorially with discrete, irregularly distributed (1-8 µm apart), pointed coni/spinae 0.5-1.4 µm broad basally, 1-3 µm high.

Dimensions (3 specimens).- Overall equatorial diameter 45, 51, 62 µm; diameter of intexine (polar view) 39, 41, 49 µm.

Previous records.- From Australian Lower-Upper Permian strata (Segroves, 1970, 1972; Foster, 1975, 1979; Foster et al., 1985).

Turma MONOLETES Ibrahim, 1933

Suprasubturma ACAVATOMONOLETES Dettmann, 1963

Subturma AZONOMONOLETES Luber, 1935

Infraturma LAEVIGATOMONOLETI Dybová &
Jachowicz, 1957

Genus *Laevigatosporites* Ibrahim, 1933 emend. Schopf,
Wilson & Bentall, 1944

Type species: *Laevigatosporites vulgaris* (Ibrahim, 1932)
Ibrahim, 1933 [OD]

Laevigatosporites callosus Balme, 1970
Plate 4, Fig. 11

1970 *Laevigatosporites callosus* Balme, p. 346; Pl. 6,
Figs. 16-18.

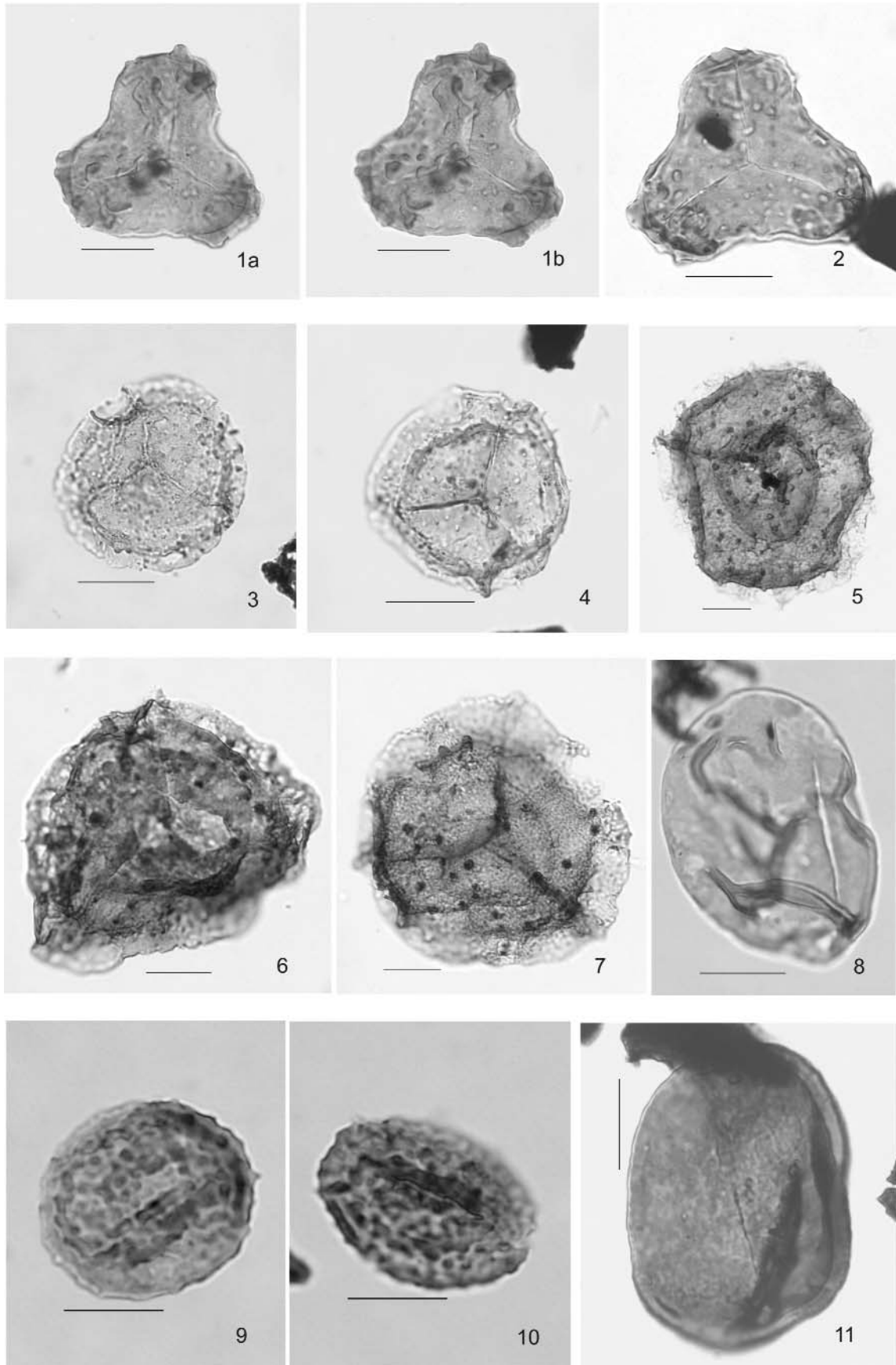
Dimensions (3 specimens).- Equatorial diameter: longitudinal axis 62, 69, 86 µm; transverse axis 48, 55, 75 µm. Exine thickness 2-4 µm.

Previous records.- From the Upper Permian of Pakistan (Balme, 1970).

Laevigatosporites flexus Segroves, 1970
Plate 5, Figs. 11, 12, 15

1970 *Laevigatosporites flexus* Segroves, pp. 69-70; Pl.
11, Figs. C, D.

Plate 4. 1, 2, *Triquitrites kaiseri* Playford sp. nov.; 1a, b, holotype, proximal and distal foci; 2, median focus. 3, 4, *Grandispora segrovesii* Foster, 1979, median and proximal foci. 5-7, *Gondisporites imbricatus* Segroves, 1970, median foci. 8, *Laevigatosporites vulgaris* (Ibrahim, 1932) Ibrahim, 1933, proximo-lateral view. 9, 10, *Tuberculatosporites modicus* Balme & Hennelly, 1956, median and proximal foci. 11, *Laevigatosporites callosus* Balme, 1970, median focus. Scale bars = 20 µm.



Description.- Spores bilateral, monolete; amb oval. Laesura distinct, simple, straight, length two-thirds to three-quarters of spore length. Exine ca. 0.7-1 µm thick, laevigate or scabrate. Distal face convex. Proximal face strongly concave; polar compression thus inducing development of conspicuous transverse exinal folds at ends of spore.

Dimensions (9 specimens).- Equatorial diameter: longitudinal axis 33 (40) 51 µm; transverse axis 25 (30) 40 µm.

Remarks.- In agreement with Segroves (1970, p. 70), but not with Backhouse (1991, p. 282), *Laevigatosporites flexus* Segroves, 1970 is considered distinguishable from *L. vulgaris* (see below) because of its twin transverse folds that are consequential, through compression, on the concavity of its proximal face.

Previous records.- From Australian strata ranging through the Permian (Segroves, 1970; Balme & Backhouse, 1993; Foster, 1979); and from the upper Lower Permian of Bangladesh (Lui Yan-zhe *et al.*, 1998).

Laevigatosporites vulgaris (Ibrahim, 1932) Ibrahim, 1933
Plate 4, Fig. 8

1933 *Laevigatosporites vulgaris* (Ibrahim) Ibrahim, p. 39; Pl. 2, Fig. 16.

1956 *Laevigatosporites vulgaris* forma *colliensis* Balme & Hennelly, pp. 55-56; Pl. 1, Figs. 1-5. [1956a]

1968 *Laevigatosporites colliensis* (Balme & Hennelly) Venkatachala & Kar, p. 66; Pl. 2, Figs. 45-50. [1968a]

For further synonymy see Helby (1966, p. 668), Foster (1979, p. 61), and Playford *et al.* (2008, p. 112).

Dimensions (12 specimens).- Equatorial diameter: longitudinal axis 39 (50) 69 µm; transverse axis 24 (33) 50 µm. Exine thickness ca. 0.4-0.7 µm.

Previous records.- This simple, laevigate, monolete form has been widely recorded globally from Pennsylvanian-Permian strata.

Infraturma SCULPTATOMONOLETI Dybová & Jachowicz, 1957

Genus *Schweitzerisporites* Kaiser, 1976

Type species: *Schweitzerisporites maculatus* Kaiser, 1976 [OD, M]

Discussion.- For the present, and following Playford & Dino (2000a, pp. 22-23), this genus is provisionally segregated from *Striatosporites* Bhardwaj, 1954 emend. Playford & Dino, 2000 (see below), although there could well be grounds for merging the two genera, as per tentative suggestion by Foster (1979, p. 64).

Schweitzerisporites maculatus Kaiser, 1976
Plate 5, Fig. 13

1976 *Schweitzerisporites maculatus* Kaiser, p. 134; Pl. 14, Figs. 1-5.

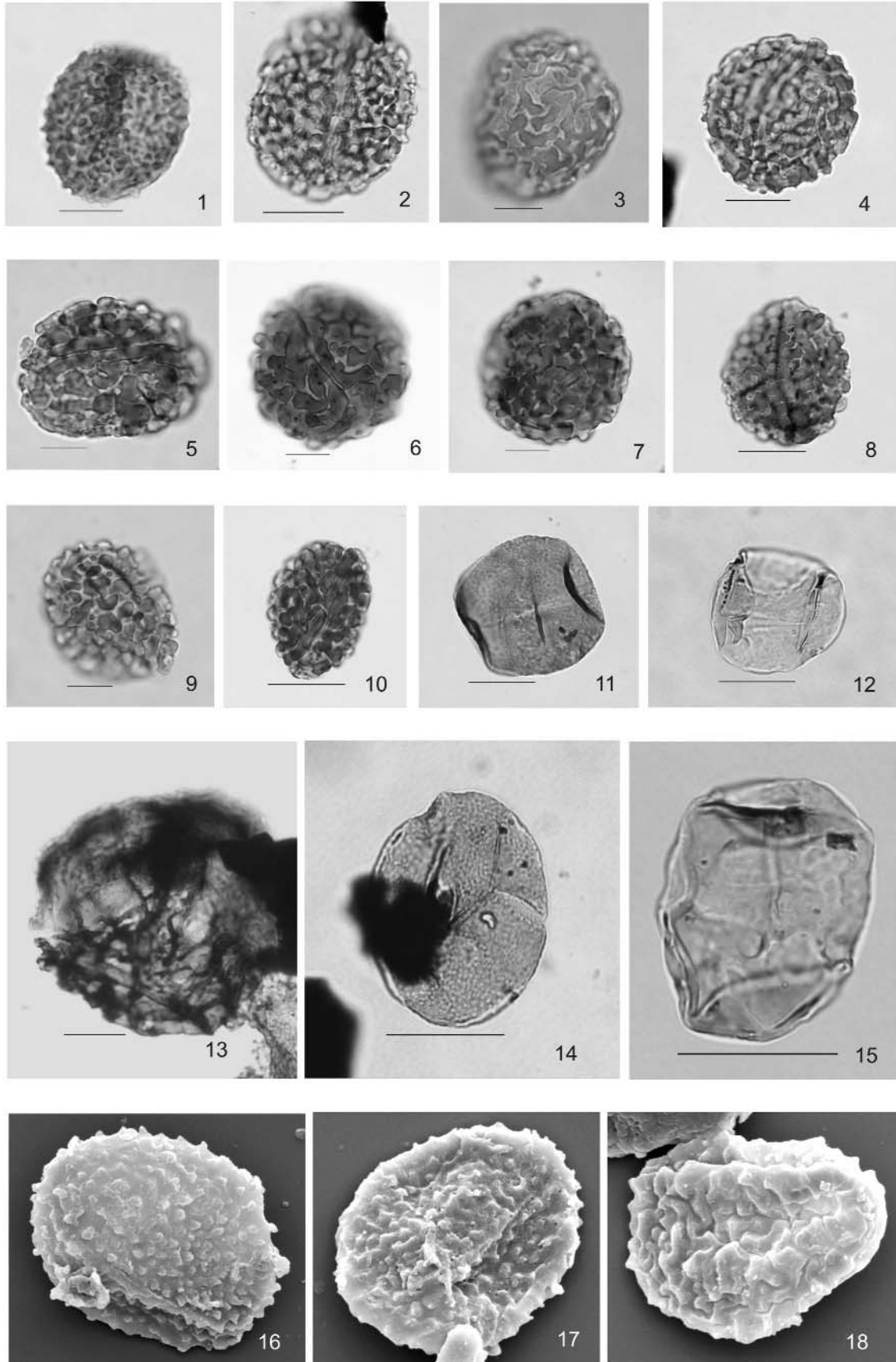
Description.- Spores monolete, broadly ovaloid. Laesura straight, narrowly lipped, length ca. 70 µm. Exine 2-layered; very thin intexine mainly appressed to thicker, coarsely reticulate exoexine. Muri ± straight, ca. 0.8-1.2 µm wide, up to 1.8 µm high; enclosing ± square to polygonal lumina 19-34 µm in maximum dimension, showing no tendency toward longitudinal elongation.

Dimensions (2 specimens).- Diameter 82, 96 µm.

Comparison and remarks.- As intimated by Kaiser (1976, p. 134), two spores reported briefly by Jardiné (1974) from the Permian of Gabon (West Africa) are closely comparable to his *Schweitzerisporites maculatus*; viz., "Spore monolète no. 1" and "Sporomorphe no. 1" of Jardiné (1974, p. 80; Pl. I, 1, 2, and Pl. I, 3, respectively). Of these, the former appears the more likely to prove conspecific with *S. maculatus*.

Doubinger & Marocco (1981, p. 1092) cited this species as "*C.* (= *Schweitzerisporites*) *maculatus* (Kaiser) Foster"; however, Foster (1979) did not formally (or informally)

Plate 5. 1, 16, 17, *Tuberculatosporites modicus* Balme & Hennelly, 1956; 1, median focus; 16, equatorial aspect (x2000); 17, proximal surface (x2000). 2-10, 18, *Thymospora miscella* Playford sp. nov.; 2, holotype, proximal focus; 3, 7, distal foci; 4, 8, median foci; 5, 6, 10, proximal foci; 9, distal-lateral view; 18, equatorial aspect (x1600). 11, 12, 15, *Laevigatosporites flexus* Segroves, 1970, median foci. 13, *Schweitzerisporites maculatus* Kaiser, 1976, equatorial aspect. 14, *Cyclogranisporites gondwanensis* Bharadwaj & Salujha, 1964, proximal-median focus. Scale bars = 20 µm (Figs. 10-15); 10 µm (Figs. 1-9).



propose the binomial combination (i.e., of *maculatus* with *Columinisporites*).

Previous records.- From northwest Shanxi (North China), in late Early-early Middle Permian rocks dated as Kun-gurian-Roadian and bearing the Middle and Upper Cathaysia Flora (Kaiser, 1976).

Genus *Striatosporites* Bhardwaj, 1954
emend. Playford & Dino, 2000

1954 *Striatosporites* Bhardwaj, p. 516.

1964 *Columinisporites* Peppers, pp. 15-16.

1979 *Perocanoidospora* Ouyang Shu & Lu Li-chang in Ouyang Shu, p. 5.

2000 *Striatosporites* Bhardwaj 1954 emend. Playford & Dino, p. 22. [2000a]

Type species: *Striatosporites major* Bhardwaj, 1954
[OD, M]

See Playford & Dino (2000a, pp. 22-23) for generic emen-dation, discussion, and comparison.

Striatosporites heyleri (Doubinger, 1968) Playford & Dino, 2000
Plate 6, Figs. 1-6

1968 *Columinisporites heyleri* Doubinger, p. 6; Pl. IV, Figs. 1-5.

1973 *Columinisporites heyleri* Doubinger emend. Alpern & Doubinger, p. 93; Pl. XXI, Figs. 4-10; Pl. XXII, Figs. 1, 2.

1993 *Columnisporites* (sic) *heyleri* Doubinger emend. Alpern & Doubinger 1973; Backhouse, Fig. 4, p. 126.

2000 *Striatosporites heyleri* (Doubinger) Playford & Dino, pp. 23-24; Pl. 7, Figs. 6-16. [2000a]

2006 *Columinisporites* of Jha, Pl. II, 11. [no description]

For additional synonymy see Playford & Dino (2000a, p. 23).

Remarks.- The West Papuan specimens assigned to this species are common in several of the present samples. They exemplify the range of morphological features detailed in Playford & Dino's (2000a) diagnostic emendation of *Striatosporites heyleri* (Doubinger, 1968). These features include bi-layered exine stratification; the highly distinctive (murornate-reticulate) exoexinal sculptural pattern; and various stages in the divestment of the exoexine as a result of degradation. The latter process, in extreme cases, produces intexinal, *Laevigatosporites*-like, monolete relics, as noted by Balme (1995, pp. 123, 126), confirmed by Playford & Dino (2000a, p. 23; Pl. 7, Figs. 9-11), and illustrated in the present account (Plate 6, Figure 6).

Dimensions (58 specimens).- Equatorial diameter: longitu-dinal axis 44 (79) 112 µm; transverse axis 32 (57) 80 µm.

Previous records.- Widely distributed geographically (Gondwana, China, Euramerica) and geochronologically (Westphalian through Permian): e.g., Doubinger & Marocco (1981, p. 1092), Playford & Dino (2000a, p. 24).

Genus *Thymospora* Wilson & Venkatachala, 1963
emend. Alpern & Doubinger, 1973

Type species: *Thymospora thiessenii* (Kosanke, 1950)
Wilson & Venkatachala, 1963 [OD]

Thymospora miscella Playford sp. nov.
Plate 5, Figs. 2-10, 18

Diagnosis.- Spores bilaterally (commonly) or ± radially symmetrical; monolete (commonly) or asymmetrically trilete or dilete. Amb oval-elliptical to circular; periphery undulant; proximal face ± planar, distal face convex. Laesura(e) distinct to perceptible, reaching to or nearly to equatorial margin; commonly flanked continuously or discontinuously by lips (up to 4 µm wide individually) result-ing from fusion or congregation of sculptural elements. Exine ca. 1.5-2.5 µm thick, comprehensively sculptured with smooth, irregularly shaped elements comprising ± sinuous rugulae together with normally subordinate verru-cae and rare grana; elements, commonly 0.5-3 µm apart, delimiting irregular, negative reticulum imperfectum. Rugulae and verrucae rounded or flat-topped, 1-3 µm high, 1.5-4 µm wide; rugulae freely terminating or branch-ing, up to 11 µm long. Proximal sculpture generally some-what less prominent than distal.

Dimensions (46 specimens).- Maximum equatorial diameter 31 (35) 40 μm .

Holotype.- Sample/slide 79SS7/2, EF P11; Pl. 5, Fig. 2; UQY9431. Amb broadly oval; length 36 μm , maximum width 30 μm ; monolete; laesura extending to equator; irregularly shaped rugulae-verrucae and fewer grana borne comprehensively, but generally coarser and closer spaced distally; laesura attaining equatorial periphery, bordered \pm continuously by lip-forming rugulae (mostly) and verrucae.

Etymology.- Latin, *miscellus*, mixed.

Remarks and comparison.- Chief morphological variables exhibited by specimens of *Thymospora miscella* Playford sp. nov. are amb shape, haptotypic character, and relative proportions of the sculptural element types (rugulae and verrucae, with the former commonly predominating).

Two previously described species warrant comparison with *T. miscella*; viz., *T. opaqua* Singh, 1964 (pp. 252, 254; Pl. 45, Figs. 9-11) from the Permian of Iraq, and *Poly-podiisporites mutabilis* Balme, 1970 (p. 347; Pl. 6, Figs. 7-9) from the Upper Permian of Pakistan. Whereas *T. opaqua* is consistently monolete and verrucate, *T. miscella* possesses a variable (monolete-dilete-trilete) tetrad mark and its sculpture is rugulo-verrucate; furthermore, it is mostly appreciably larger than *T. opaqua*. Compared to *P. mutabilis*, *T. miscella* features coarser sculpture, longer and lipped laesura(e), and a more variable amb.

Genus *Tuberculatosporites* Imgrund, 1952, 1960 ex
R. Potonié & Kremp, 1954

Type species: *Tuberculatosporites anicystoides* Imgrund,
1952, 1960 [OD]

Tuberculatosporites modicus Balme & Hennelly, 1956
Plate 4, Figs. 9, 10; Plate 5, Figs. 1, 16, 17

1956 *Tuberculatosporites modicus* Balme & Hennelly, p.
56; Pl. 1, Figs. 10-13. [1956a]

Description.- Spores bilateral, monolete; amb oval or, less commonly, near-circular. Laesura distinct to perceptible, straight, extending at least 0.7 of distance to equator; commonly accompanied by narrow, lip-like fold(s). Exine 0.5-1 μm thick, comprehensively sculptured with small coni

and verrucae, normally discrete, 0.5-2 μm in basal diameter, 0.5-2 μm high, up to 2.5 μm apart.

Dimensions (22 specimens).- Equatorial diameter: longitudinal axis 17 (22) 29 μm ; transverse axis 14 (18) 25 μm .

Previous records.- From Lower-Upper Permian sediments of the Collie and Perth basins, Western Australia (Balme & Hennelly, 1956a; Segroves, 1970, 1972; Balme & Backhouse, 1993) and the Bowen Basin, Queensland (Rigby & Hekel, 1977). Also listed by Stephenson & Filatoff (2000b) as a component of Upper Permian assemblages of Saudi Arabia.

5.2. Pollen grains

Anteturma VARIEGERMINANTES R. Potonié, 1970
Turma SACCITES Erdtman, 1947

Subturma MONOSACCITES Chitaley, 1951 emend. R.
Potonié & Kremp, 1954

Infraturma VESICULOMONORADITI Pant, 1954
Genus *Potonieisporites* Bhardwaj, 1954 emend. Bhardwaj,
1964

Type species: *Potonieisporites novicus* Bhardwaj, 1954
[OD, M]

Potonieisporites balmei (Hart, 1960) Segroves, 1969
Plate 6, Fig. 7

1960 *Vestigisporites balmei* Hart, p. 14; Pl. 2, Figs. 21,
22.

1969 *Potonieisporites balmei* (Hart) Segroves, pp. 179-
180; Pl. 1, Figs. A-C.

Dimensions (6 specimens, in polar aspect).- Overall breadth 80-125 μm ; overall length 62-103 μm . Corpus breadth 48-79 μm ; corpus length 46-72 μm .

Remarks.- Although indifferently preserved, the few specimens encountered herein appear clearly assignable to this species.

Previous records.- From the Lower Permian of Tanzania (Hart, 1960) and the Perth and Collie basins, Western Australia, with a possible extension into the Upper Permian

(Segroves, 1969, 1972; Backhouse, 1991; Balme & Backhouse, 1993).

Infraturma TRILETESACCITI Leschik, 1956
Genus *Cannanoropollis* R. Potonié & Sah, 1960

For synonymy see Foster (1975, p. 139).

Type species: *Cannanoropollis janakii* R. Potonié & Sah, 1960 [OD]

Discussion.- See Playford & Dino (2002, pp. 264, 266).

Cannanoropollis janakii R. Potonié & Sah, 1960
Plate 6, Fig. 8

1960 *Cannanoropollis janakii* R. Potonié & Sah, pp. 127-128; Pl. 2, Figs. 15, 16.

non 2000 *Cannanoropollis janakii* Potonié & Sah; Azcuy & di Pasquo, p. 118; Pl. 1, Figs. 1, 2; Text-fig. 4A.

For other synonymy see Playford & Dino (2000b, p. 92).

Dimensions (8 specimens in polar aspect).- Overall equatorial diameter 79 (104) 129 µm. Corpus diameter 53 (71) 91 µm. Width of saccus (± variable on individual specimens) 12 (18) 24 µm.

Previous records.- Potonié & Sah (1960) diagnosed this species on the basis of monosaccate grains of probable Permian age preserved in Tertiary lignitic strata of coastal India. Numerous subsequent reports, all evidently *in situ*, are from the Gondwanan upper Palaeozoic (principally Permian).

Genus *Plicatipollenites* Lele, 1964

Type species: *Plicatipollenites malabarensis* (R. Potonié & Sah, 1960) Foster, 1975 [OD as *P. indicus* Lele, 1964 = junior synonym of *P. malabarensis* (*vide* Foster, 1975, p. 142)]

Plicatipollenites gondwanensis (Balme & Hennelly, 1956) Lele, 1964
Plate 6, Fig. 9

1956 *Nuskoisporites gondwanensis* Balme & Hennelly, pars, p. 253; Pl. 7, Figs. 66, 67. [1956b]

1964 *Plicatipollenites gondwanensis* (Balme & Hennelly) Lele, pp. 154-156; Pl. 2, Fig. 11; Text-figs. 4a-c, 12b.

For additional synonymy see Foster (1979, p. 68), Césari (1984, p. 93), and Gutiérrez (1993, p. 171).

Dimensions (2 specimens in polar view).- Overall equatorial diameter 140, 208 µm. Corpus diameter 92, 110 µm. Width of saccus 24, 46 µm. Width of corpus fold 12, 19 µm.

Previous records.- Reported widely in Gondwanan upper Palaeozoic (principally Permian) strata (e.g., Foster, 1979, p. 68; Azcuy & di Pasquo, 2000, p. 119).

Infraturma STRIASACCITI Bharadwaj, 1962

Genus *Striomonosaccites* Bharadwaj, 1962

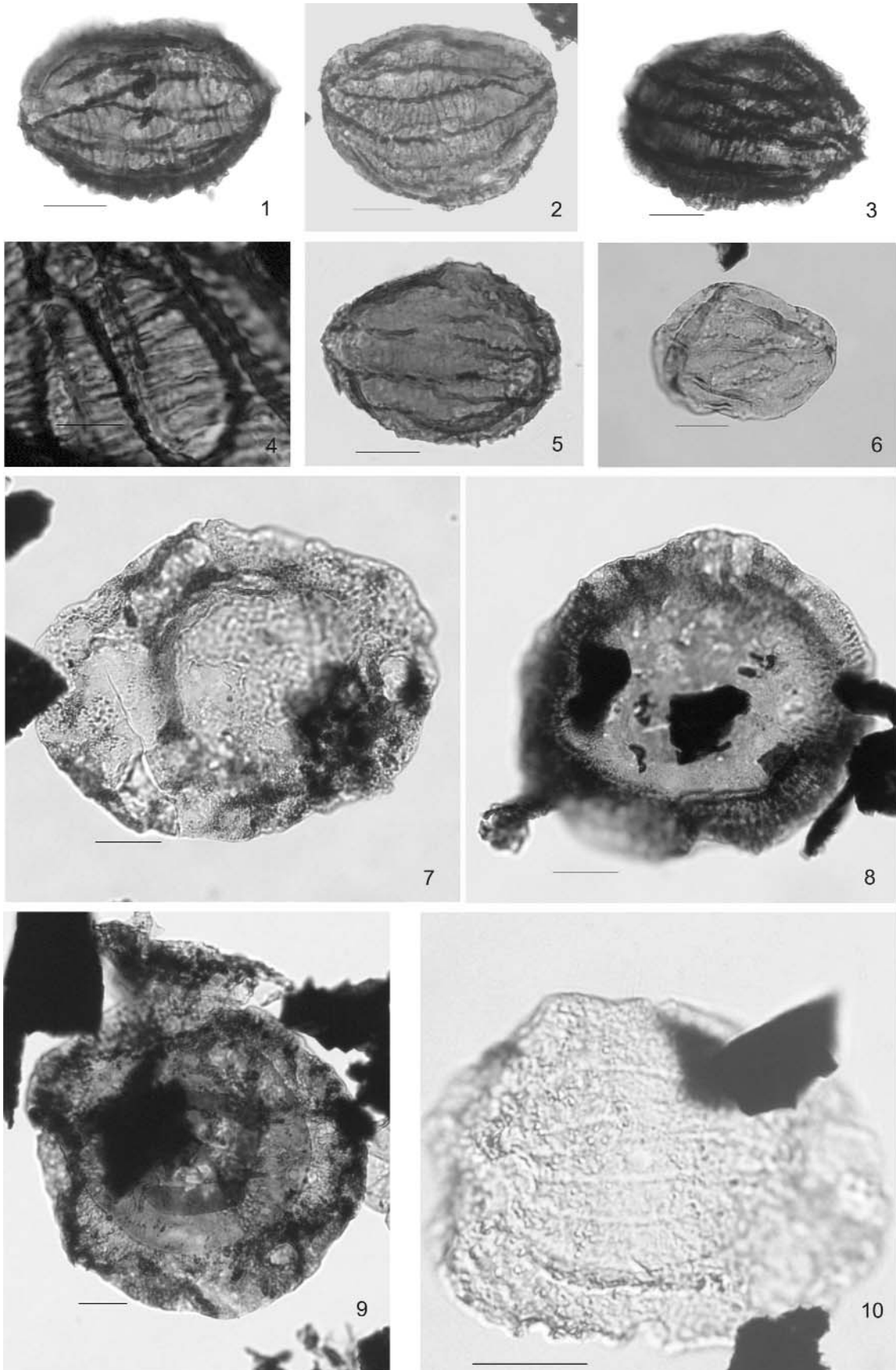
Type species: *Striomonosaccites ovatus* Bharadwaj, 1962 [OD; M]

Discussion. – The well-illustrated and illuminating account by Lindström *et al.* (1997) of the pollen contents of permineralized glossopterid sporangia from the Permian of Antarctica provides a somewhat chastening reality check vis-à-vis the precepts of conventional dispersed-pollen taxonomy. They reported the *in situ* presence of pollen grains, conforming to *Striomonosaccites* Bharadwaj, 1962 and *Crustaesporites* Leschik, 1956 and regarded as aberrancies, in quantitatively subordinate association with grains conforming to two other dispersed morphogenera (*Protohaploxpinus* Samoilovich, 1953 emend. Morbey, 1975 and *Striatopodocarpites* Zoricheva & Sedova ex Sedova, 1956 emend. Hart, 1964).

Striomonosaccites sp. A

Plate 6, Fig. 10

Plate 6. 1-6, *Striatosporites heyleri* (Doubling, 1968) Playford & Dino, 2000; 1, 3, median focus; 2, proximo-lateral view; 4, exoexinal sculptural detail; 5, showing imperfectly preserved exoexinal sculpture of degraded specimen, median focus; 6, laevigate intexinal body devoid of exoexine but showing monolete suture, proximal focus. 7, *Potoniisporites balmei* (Hart, 1960) Segroves, 1969, median focus. 8, *Cannanoropollis janakii* R. Potonié & Sah, 1960, median focus. 9, *Plicatipollenites gondwanensis* (Balme & Hennelly, 1956) Lele, 1964, median focus. 10, *Striomonosaccites* sp. A, proximal focus. Scale bars = 20 µm (Figs. 1-3, 5-10); 10 µm (Fig. 4).



Description.- Pollen grain bilateral, monosaccate, taeniate; amb transversely elongate-oval. Corpus transversely oval (polar view), exine very thin (<0.7 µm thick); one face bearing 6 continuous transverse taeniae, each up to 9.5 µm wide, narrowing to corpus margin, separated by very narrow clefts. Saccus with irregular margin and folding; intrareticulum absent or not preserved.

Dimensions (1 specimen, in polar view).- Overall breadth 79 µm; overall length 61 µm. Corpus breadth 51 µm; corpus length 39 µm.

Comparison.- The single, poorly preserved specimen, though clearly assignable to *Striomonosaccites* Bharadwaj, 1962, bears no obvious resemblance to known species of the genus.

Subturma DISACCITES Cookson, 1947

Genus *Alisporites* Daugherty, 1941 emend. Jansonius, 1971

Type species: *Alisporites opii* Daugherty, 1941 [M]

Alisporites spp.

Plate 8, Fig. 7

Remarks.- The rare presence of generally small to medium-sized, bisaccate, non-taeniate pollen grains, conforming with *Alisporites* Daugherty, 1941 emend. Jansonius, 1971 (p. 355), was noted in several samples. For reasons of indifferent preservation and the consequential absence of definitive morphological criteria, it is both prudent and expedient, as in Backhouse (1991, p. 287), to designate these grains collectively as *Alisporites* spp. While the genus is a typical component of post-Palaeozoic palynofloras, it has been reported by numerous authors from Permian strata; e.g., Segroves (1969), Balme (1970, as *Falcisporites*), Foster (1979), Backhouse (1991), Lindström (1996), and Balarino & Gutiérrez (2006).

Genus *Platysaccus* Naumova, 1939 ex R. Potonié & Klaus, 1954

Type species: *Platysaccus papilionis* R. Potonié & Klaus, 1954 [SD: R. Potonié & Klaus, 1954, p. 539]

Platysaccus leschikii Hart, 1960

Plate 7, Fig. 4

1955 *Lueckisporites fusus* Balme & Hennelly, pars, p. 92; Pl. 1, Fig. 6.

1960 *Platysaccus leschiki* Hart, pp. 11-12; Pl. 3, Figs. 37, 38.

For other synonymy see Foster (1979, p. 78).

Remarks.- The single specimen encountered is, in common with those recorded from the Bowen Basin (Queensland, Australia; Foster, 1979), appreciably smaller than, but otherwise morphologically compatible with specimens diagnosed by Hart (1960) as *Platysaccus leschikii*.

Dimensions (1 specimen, in polar view).- Overall breadth 61 µm. Corpus breadth 26 µm; corpus length 36 µm. Saccus breadth 31 µm; saccus length 47 µm.

Previous records.- From the Permian of Tanzania (Hart, 1960), Australia (e.g., Foster, 1979; Balme & Backhouse, 1993), and Antarctica (Lindström, 1994, 1995b).

Genus *Vitreisporites* Leschik, 1955 emend. Jansonius, 1962

Type species: *Vitreisporites pallidus* (Reissinger, 1950) Nilsson, 1958 [OD, as *V. signatus* Leschik, 1955]

Vitreisporites pallidus (Reissinger, 1950) Nilsson, 1958
Plate 7, Fig. 1

For synonymy see Balme (1970, p. 382).

Dimensions (7 specimens, in polar view).- Overall breadth 24 (33) 39 µm. Corpus breadth 11 (14) 20 µm; corpus length 21 (23) 25 µm. Saccus breadth 9 (11) 13 µm; saccus length 19 (22) 26 µm.

Previous records.- This small, morphologically simple bisaccate species, known extensively from the Mesozoic, has been reported from Permian rocks by such authors as Balme (1970), Foster (1979), Farabee *et al.* (1991), Lindström (1996), and Ouyang Shu *et al.* (2003).

Infraturma STRIATITI Pant, 1954

Genus *Distriatites* Bharadwaj, 1962

Type species: *Distriatites bilateris* Bharadwaj, 1962 [OD]

Distriatites insolitus Bharadwaj & Salujha, 1964
Plate 7, Fig. 3

1964 *Distriatites insolitus* Bharadwaj & Salujha, p. 211; Pl. 12, Figs. 157, 158.

non 2003 *Distriatites insolitus* Bharadwaj & Salujha, 1964; Stephenson, Osterloff & Filatoff, Pl. 5, Fig. 9. [no description]

For additional synonymy see Foster (1979, p. 81).

Remarks.- Despite their generally poor preservation, a few specimens encountered could reliably be assigned to *Distriatites insolitus* Bharadwaj & Salujha, 1964, taking into account the extended size ranges stated by Balme (1970, p. 381) and Foster (1979, p. 81). The single specimen figured by Stephenson *et al.* (2003; see above synonymy), from the ?Upper Permian of Oman, is evidently misidentified and is likely attributable to *D. dettmanniae* (Segroves, 1969, p. 204; Pl. 11, Figs. D-G) Foster, 1979 (p. 82; Pl. 28, Figs. 10, 11).

Dimensions (2 specimens).- Overall breadth 77, 81 μm . Corpus breadth 43, 57 μm ; corpus length 48, 51 μm . Saccus breadth 24, 29 μm ; saccus length 38, 48 μm .

Previous records.- From the Raniganj stage (Upper Permian) of India (Bharadwaj & Salujha, 1964, 1965); Lower Permian of Pakistan (Balme, 1970) and Libya (Loboziak & Clayton, 1988); Upper Permian-Lower Triassic of Australia (records cited by Foster, 1979, p. 81); and Middle-Upper Permian of Arabia (Stephenson & Filatoff, 2000b; Stephenson, 2006).

Genus *Protohaploxylinus* Samoilovich, 1953 emend. Morbey, 1975

Type species: *Protohaploxylinus latissimus* (Luber in Luber & Waltz, 1941) Samoilovich, 1953 [OD]

Discussion. - See discussions of *Striomonosaccites* (above) and *Striatopodocarpites* (below).

Protohaploxylinus amplus (Balme & Hennelly, 1955)
Hart, 1964
Plate 7, Fig. 7

1955 *Lueckisporites amplus* Balme & Hennelly, pars, p. 93; Pl. 3, Figs. 24-27 (?non Fig. 28).

1964 *Protohaploxylinus amplus* (Balme & Hennelly) Hart, pp. 1179-1180; Text-fig. 10.

For additional synonymy see Foster (1979, p. 86).

Remarks.- The haploxylinoid or slightly diploxylinoid form is characteristic of these grains, as is the transversely \pm oval to rectangular corpus with cappa modified by seven-10, essentially unbranched taeniae of variable width (3-11 μm).

Dimensions (6 specimens, in polar view).- Overall breadth 71-110 μm . Corpus breadth 34-52 μm ; corpus length 37-70 μm . Saccus breadth 21-46 μm ; saccus length 39-80 μm .

Comparison.- The difficulty of establishing clear distinction between *Protohaploxylinus amplus* (Balme & Hennelly, 1955) Hart, 1964 and *P. goraiensis* (R. Potonié and Lele, 1961) Hart, 1964 has been highlighted by Millstead (1999, p. 26), who foreshadowed the need to re-investigate type specimens of both species in order to resolve the problem. The present specimens seem more appropriately attributable to *P. amplus*.

Previous records.- Numerous reports indicate extensive dissemination of this species through Gondwanan Permian successions.

Protohaploxylinus limpidus (Balme & Hennelly, 1955)
Balme & Playford, 1967
Plate 7, Figs. 5, 6

1955 *Lueckisporites limpidus* Balme & Hennelly, pars, p. 94; Pl. 3, Figs. 29-32; Pl. 4, Figs. 34, 35 (non Fig. 33).

1967 *Protohaploxylinus limpidus* (Balme & Hennelly) Balme & Playford, p. 185; Pl. 1, Fig. 15.

For additional synonymy see Balme (1970, p. 362), Foster (1979, p. 89), and Millstead (1999, p. 26).

Remarks and comparison.- The present specimens conform with those described by the original authors, supplemented by more detailed morphological specifications furnished subsequently; e.g., by Segroves (1969, p. 199: Pl. 9, Fig. B), Balme (1970, p. 362; Pl. 10, Figs. 1-3), Foster (1979, pp. 89-90; Pl. 31, Figs. 1-10), and Playford & Dino (2000a, p. 109; Pl. 10, Figs. 1, 2). Criteria that appear to enable *Protohaploxylinus limpidus* (Balme & Hen-

nelly, 1955) Balme & Playford, 1967 to be segregated from *P. amplus* need no reiteration here, having been discussed previously by the authors cited above.

Dimensions (25 specimens, in polar view).- Overall breadth 37 (46) 67 µm. Corpus breadth 19 (27) 40 µm; corpus length 27 (32) 41 µm. Saccus breadth 15 (19) 25 µm; saccus length 19 (30) 38 µm.

Previous records.- *Protohaploxylinus limpidus* is a widely dispersed form in Permian Gondwana palynofloras (Playford & Dino, 2000a). Lindström *et al.* (1997) have described and illustrated well-preserved *P. limpidus*-type pollen grains that reportedly constitute the overwhelming bulk (ca. 96%) of the contents of Antarctic Permian glossopterid sporangia identified as *Arberiella* sp. cf. *A. africana* Pant & Nautiyal, 1960.

Protohaploxylinus rugatus Segroves, 1969
Plate 7, Fig. 2

1969 *Protohaploxylinus rugatus* Segroves, p. 200; Pl. 7, Figs. G, H; Pl. 9, Figs. D-I.

For extended synonymy see Gutiérrez *et al.* (2006, p. 624).

Comparison and remarks.- The few specimens encountered are larger than those originally described by Segroves (1969), but are comparable in size to those reported by, *inter alia*, Gutiérrez *et al.* (2006), who provided an extensive synonymy list for the species.

Dimensions (2 specimens, in polar view).- Overall breadth 50, 53 µm. Corpus breadth 31, 35 µm; corpus length 55, 58 µm. Saccus breadth 14, 15 µm; saccus length 51, 54 µm.

Previous records.- *Protohaploxylinus rugatus* Segroves, 1969 ranges through the Western Australian Lower to Upper Permian according to Balme & Backhouse (1993), although Backhouse (1991, p. 289) indicated its rarity below the Upper Permian. The latter author listed other Australian occurrences of the species, which has also been recorded from many extra-Australian Gondwanan rocks of Permian age; e.g., in South America (Gutiérrez *et al.*, 2006) and Antarctica (Lindström, 1994, 1995a; possibly also Kyle, 1977 and Kyle & Schopf, 1982).

Genus *Striatoabieites* Zoricheva & Sedova ex Sedova, 1956 emend. Hart, 1964

Type species: *Striatoabieites brickii* Sedova, 1956 [SD]

Striatoabieites multistriatus (Balme & Hennelly, 1955) Hart, 1964
Plate 7, Fig. 8

1955 *Lueckisporites multistriatus* Balme & Hennelly, p. 93; Pl. 2, Figs. 16-20.

1964 *Striatoabieites multistriatus* (Balme & Hennelly) Hart, p. 1186; Text-fig. 40.

For further synonymy see Foster (1979, p. 95) and Millstead (1999, pp. 26-27).

Dimensions (8 specimens; polar aspect).- Overall breadth 56-84 µm. Corpus breadth 29-60 µm; corpus length 34-49 µm. Saccus breadth 19-32 µm; saccus length 31-48 µm.

Previous records.- A widely reported component of Gondwanan Permian palynofloras; see, e.g., Anderson (1977, p. 102), Millstead (1999, p. 27), Campbell *et al.* (2001), Playford & Dino (2002, p. 271), and Stephenson *et al.* (2003).

Genus *Striatopodocarpites* Zoricheva & Sedova ex Sedova, 1956 emend. Hart, 1964

Type species: *Striatopodocarpites tojmensis* Sedova, 1956 [SD]

Discussion.- See *Striomonosaccites* (above), and note particularly the suggestion by Lindström *et al.* (1997, p. 679) – based on their detailed analysis of the pollen contents of permineralized glossopterid sporangia (*Arberiella* sp. cf. *A. africana*) – that *Striatopodocarpites* “may represent unexpanded forms of a range of *Protohaploxylinus* species.”

Striatopodocarpites cancellatus (Balme & Hennelly, 1955) Hart, 1965
Plate 7, Fig. 9

1955 *Lueckisporites cancellatus* Balme & Hennelly, pp. 92-93; Pl. 2, Figs. 11-15.

1965 *Striatopodocarpites cancellatus* (Balme & Hennelly) Hart, p. 10. [1965a]

For additional (and extensive) synonymy see Segroves (1969, p. 206), Foster (1979, pp. 96-97), and Millstead (1999, p. 27).

Description.- Pollen grains bisaccate, taeniate, ± distinctly diploxylonoid. Corpus outline near-circular in polar aspect. Cappa divided into 4-8, transverse, mostly continuous (unbranched), ± laevigate taeniae (3-8 µm wide) separated by very narrow clefts. Sacchi >semicircular in polar aspect, intrareticulate in well-preserved specimens.

Dimensions (7 specimens; polar view).- Overall breadth 34-62 µm. Corpus breadth 17-29 µm; corpus length 17-30 µm. Saccus breadth 10-24 µm; saccus length 23-40 µm.

Previous records.- The occurrence of *Striatopodocarpites cancellatus* (Balme & Hennelly, 1955) Hart, 1965 in Permian rocks Gondwana-wide has been documented by such authors as Balme (1970, p. 367), Lindström (1996, p. 41), and Millstead (1999, p. 27). Lindström *et al.* (1997, p. 675) reported that *in situ* glossopterid pollen grains conforming morphologically to *S. cancellatus* comprise some 4% of the pollen contents of the glossopterid sporangia cited above under generic discussion.

Striatopodocarpites fusus (Balme & Hennelly, 1955)
R. Potonié, 1958
Plate 7, Fig. 10

1955 *Lueckisporites fusus* Balme & Hennelly, pars, p. 92; Pl. 1, Figs. 7-10 (non Fig. 6).

1958 *Striatopodocarpites fusus* (Balme & Hennelly) Potonié, p. 54.

For comprehensive synonymy see Balme & Hennelly (1955, p. 92), Foster (1979, p. 97), and Millstead (1999, pp. 27-28).

Remarks and comparison.- *Striatopodocarpites fusus* (Balme & Hennelly, 1955) R. Potonié, 1958 differs from *S. cancellatus* chiefly in being generally larger and more prominently diploxylonoid.

Dimensions (12 specimens; polar view).- Overall breadth 75 (85) 108 µm. Corpus breadth 26 (35) 45 µm; corpus length 31 (37) 48 µm. Saccus breadth 25 (33) 39 µm; saccus length 42 (49) 57 µm.

Previous records.- As for *Striatopodocarpites cancellatus*, with which *S. fusus* is commonly, although not invariably associated.

Turma PLICATES Naumova, 1939 emend. Potonié, 1960
Subturma COSTATES Potonié, 1970
Infraturma COSTATI Jansonius, 1962
Genus *Weylandites* Bharadwaj & Srivastava, 1969
Type species: *Weylandites lucifer* (Bharadwaj & Salujha, 1964) Foster, 1975 [OD, as *W. indicus* Bharadwaj & Srivastava, 1969]

Discussion.- For synonymy and morphological-taxonomic commentaries see Balme (1970, pp. 409-411) and Foster (1979, p. 101).

Weylandites lucifer (Bharadwaj & Salujha, 1964) Foster, 1975
Plate 7, Figs. 13, 14

1964 *Decussatisporites lucifer* Bharadwaj & Salujha, p. 213; Pl. 12, Figs. 169, 171, ?170.

1970 *Paravittatina lucifer* Balme, pp. 411-412; Fig. 14; Pl. 21, Figs. 19-22.

1975 *Weylandites lucifer* (Bharadwaj & Salujha) Foster, p. 153; Pl. 7, Fig. 2.

For extended synonymy see Foster (1979, p. 102) and Gutiérrez *et al.* (2006, p. 626).

Remarks.- A few specimens of *Weylandites lucifer* (Bharadwaj & Salujha, 1964) Foster, 1975 were encountered in one only of the West Papuan samples. These broadly monosulcate, multiply taeniate pollen grains exhibit the characterizing features of the species, viz., sub-circular, roundly subquadrangular, or oval amb; and narrow (<3.5 µm wide), close-spaced, laevigate taeniae extending continuously over both faces of the grain and disposed transversely and longitudinally on the proximal and distal faces respectively. Equatorial diameter (three specimens) ranges from 32 µm to 53 µm.

Previous records.- This species is well known from late Early through Late Permian successions in many Gondwanan regions, and also from Russia; see documentation by Foster (1979), Backhouse (1991), and Lindström

(1996), and, with particular reference to South America, Césari *et al.* (1995), Césari & Gutiérrez (2001), and Gutiérrez *et al.* (2006).

Subturma PRAECOLPATES R. Potonié & Kremp, 1954
Genus *Marsupipollenites* Balme & Hennelly, 1956
emend. Balme, 1970
Type species: *Marsupipollenites triradiatus* Balme & Hennelly, 1956 [OD]

Marsupipollenites striatus (Balme & Hennelly, 1956)
Hart, 1965
Plate 7, Fig. 12

1956 *Marsupipollenites triradiatus* forma *striatus* Balme & Hennelly, p. 61; Pl. 2, Figs. 36, 37. [1956a]

1965 *Marsupipollenites striatus* (Balme & Hennelly)
Hart, p. 104; Fig. 250. [1965b]

For additional synonymy see Archangelsky & Gamero (1979, p. 462) and Foster (1979, p. 104).

Remarks.- The few specimens encountered during this study exhibit the distinctive morphological features of this species, as described and illustrated by such authors as Foster (1979, p. 104; Pl. 37, Figs. 1, 2), Backhouse (1991, p. 295; Pl. XX, 13, 14), and Playford & Dino (2002, pp. 274-275; Pl. 9, Fig. 7).

Dimensions (3 expanded specimens in polar aspect).- Length 32, 38, 46 µm; width 29, 28, 31 µm.

Previous records.- Millsted (1999, p. 19) and Playford & Dino (2002, p. 275) noted that this species is widely dispersed through Permian strata of Gondwana.

Marsupipollenites triradiatus Balme & Hennelly, 1956
Plate 7, Fig. 11

1956 *Marsupipollenites triradiatus* Balme & Hennelly, pp. 60-61; Pl. 2, Figs. 29-35. [1956a]

For additional synonymy see Foster (1979, p. 104).

Dimensions (3 expanded specimens in polar aspect).- Length 39, 40, 43 µm; width 32, 32, 34 µm.

Comparison.- *Marsupipollenites triradiatus* Balme & Hen-

nelly, 1956 differs from *M. striatus* in possessing a non-striate exine.

Previous records.- Numerous Gondwanic Permian reports; see, for example, Balme (1970), Anderson (1977, who included some specimens assignable to *M. striatus* in his concept of "*Vittatina triradiatus*"), Foster (1979), Backhouse (1991), and Millsted (1999).

Subturma MONOCOLPATES Iversen & Troels-Smith, 1950

Genus *Cycadopites* Wodehouse, 1933

Type species: *Cycadopites follicularis* Wilson & Webster, 1946 [SD, M; Wilson & Webster, 1946, pp. 274-275]

Cycadopites cymbatus (Balme & Hennelly, 1956)
Hart, 1965
Plate 7, Fig. 15

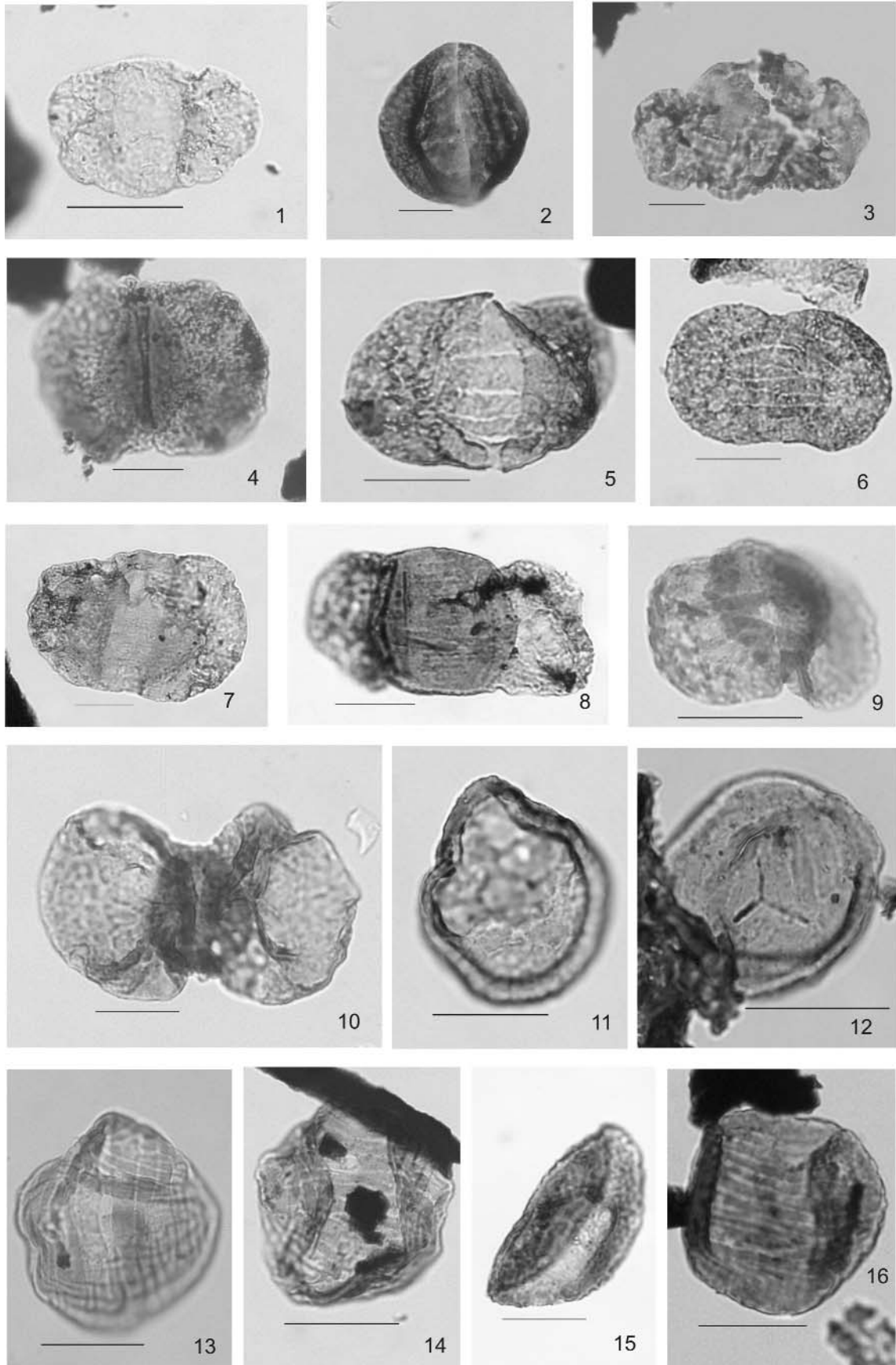
1956 *Entylissa cymbatus* Balme & Hennelly, p. 63; Pl. 3, Figs. 53-56. [1956a]

1961 *Ginkgocycadophytus cymbatus* (Balme & Hennelly) R. Potonié & Lele, pp. 33-34; Pl. 3, Figs. 85-96.

1965 *Cycadopites cymbatus* (Balme & Hennelly) Hart, p. 110; Text-Fig. 265. [1965b]

Description.- Pollen grains monocolpate; amb elongate-oval to fusiform with rounded to ± pointed ends. Distal colpus extending full length of grain, commonly narrowing polewards. Exine 0.8-1.8 µm thick; granulate or almost laevigate.

Plate 7. 1, *Vitreisporites pallidus* (Reissinger, 1950) Nilsson, 1958, median focus. 2, *Protohaploxylinus rugatus* Segroves, 1969, near-distal focus. 3, *Distriatites insolitus* Bharadwaj & Salujha, 1964, median focus. 4, *Platysaccus leschikii* Hart, 1960, near-distal focus. 5, 6, *Protohaploxylinus limpidus* (Balme & Hennelly, 1955) Balme & Playford, 1967, proximal foci. 7, *Protohaploxylinus amplus* (Balme & Hennelly, 1955) Hart, 1964, median focus. 8, *Striatoabieites multistriatus* (Balme & Hennelly, 1955) Hart, 1964, proximal focus. 9, *Striatopodocarpites cancellatus* (Balme & Hennelly, 1955) Hart, 1965, near-proximal focus. 10, *Striatopodocarpites fusus* (Balme & Hennelly, 1955) R. Potonié, 1958, median-distal focus. 11, *Marsupipollenites triradiatus* Balme & Hennelly, 1956, median focus. 12, *Marsupipollenites striatus* (Balme & Hennelly, 1956) Hart, 1965, proximal-median focus. 13, 14, *Weylandites lucifer* (Bharadwaj & Salujha, 1964) Foster, 1975; 13, median focus; 14, distal focus. 15, *Cycadopites cymbatus* (Balme & Hennelly, 1956) Hart, 1965, median focus. 16, *Pakhapites fasciolatus* (Balme & Hennelly, 1956) Hart, 1965, median focus. Scale bars = 20 µm.



Dimensions (7 specimens).- Length 37 (44) 51 μm ; width 26 (30) 38 μm .

Previous records.- This species is well known from the Australian Permian (e.g., Balme & Hennelly, 1956a; Segroves, 1970; Gilby & Foster, 1988; Foster & Waterhouse, 1988; Backhouse, 1991; Balme & Backhouse, 1993) and has also been reported from similar-aged strata elsewhere in Gondwana (Potonié & Lele, 1961; Tiwari, 1965; Anderson, 1977; Lindström, 1996; Stephenson & Osterloff, 2002).

Genus *Pakhapites* Hart, 1965

1965 *Pakhapites* Hart, pp. 104-105. [1965b]

1966 *Fusacolpites* Bose & Kar, pp. 117-118; Fig. 14B.

1968 *Striasulcites* Venkatachala & Kar, p. 164. [1968b]

Type species: *Pakhapites fasciolatus* (Balme & Hennelly, 1956) Hart, 1965

Discussion.- See Playford & Dino (2000b, pp. 114-115; 2002, p. 275).

Pakhapites fasciolatus (Balme & Hennelly, 1956)
Hart, 1965
Plate 7, Fig. 16

1956 *Marsupipollenites fasciolatus* Balme & Hennelly, p. 62; Pl. 3, Figs. 42-45. [1956a]

1962 *Vittatina fasciolata* (Balme & Henn.) emend. Bharadwaj, p. 100; Pl. 5, Fig. 94

1965 *Pakhapites fasciolatus* (Balme & Hennelly) Hart, p. 105; Text-Fig. 252. [1965b]

Description.- Pollen grains monocolpate, taeniate. Amb oval (with \pm weak transverse elongation) to subcircular. Proximal face bearing mostly entire and continuous, laevigate taeniae, transversely disposed, 8-14 in number, and separated by narrow clefts. Distal face with usually broad longitudinal colpus up to 20 μm wide in expanded grains and with irregularly folded margins.

Dimensions.- (6 specimens; polar view). Equatorial diameter 25-36 μm .

Previous records.- From the Lower through Upper Permian of Western Australia (Balme & Hennelly, 1956a; Backhouse, 1991; Balme & Backhouse, 1993) and Queensland (Rigby & Hekel, 1977; de Jersey, 1979); Permian (Microfloral Zones 1-3b) of South Africa (Anderson, 1977); Upper Permian (Raniganj stage) of India (Bharadwaj, 1962); Lower and Upper Permian of Antarctica (Lindström, 1996, p. 43); and Lower Permian of Argentina (Césari *et al.*, 1996; Césari & Gutiérrez, 2001).

5.3. Green algae (chlorophytes, prasinophyte phycmata)

Division CHLOROPHYTA Pascher, 1914

Class CHLOROPHYCEAE Kützing, 1843

Order CHLOROCOCCALES Marchand, 1895 orth. mut.
Pascher, 1915

?Family SCENEDESMACEAE Oltmanns, 1904

Genus *Quadrisporites* Hennelly, 1959 ex R. Potonié & Lele, 1961

1959 *Quadrisporites* Hennelly, nom nud., pp. 364-365.

1961 *Quadrisporites* Hennelly ex R. Potonié & Lele, pp. 25-26.

1966 *Tetraletes* Cramer, pp. 77-78.

Type species: *Quadrisporites horridus* Hennelly, 1959 ex R. Potonié & Lele, 1961 [SD; Potonié & Lele, 1961, p. 25]

Discussion.- Hennelly (1959) regarded *Quadrisporites* as an obligate spore tetrad of vascular plant origin. Subsequently, Backhouse (1991) and Lindström (1994) listed the genus as, respectively, an acritarch and a cryptospore. Brenner & Foster (1994, p. 221; Fig. 4A; Pl. III, 8, 9) described the type species *Q. horridus* as a four-celled coenobium based on its morphological resemblance to the living cruigenioid species *Tetrastrum punctatum* (Schmidle, 1900) Ahlstrom and Tiffany, 1934 of the family Scenedesmaceae. However, they did note that the extant species is markedly smaller than *Q. horridus*. Batten (1996, p. 195) added that the latter is a more durable structure than any of the few living species of *Tetrastrum*, and, on balance, his equivocation about a scenedesmacean affinity for *Quadrisporites* seems justified.

A suggestion by Amenábar *et al.* (2006, p. 352) that the generic diagnosis be expanded to include unsculptured forms, with consequential synonymic suppression of *Disectispora* Tiwari & Navale, 1968 (p. 598), is not endorsed herein.

Quadrisporites horridus Hennelly, 1959 ex
R. Potonié & Lele, 1961
Plate 8, Figs. 1-6

1959 *Quadrisporites horridus* Hennelly, nom. nud.,
pp. 364-365; Pl. 5, Figs. 6, 7.

1961 *Quadrisporites horridus* Hennelly ex R. Potonié
& Lele, p. 26; Pl. 1, Figs. 26-36.

non 2006 *Quadrisporites horridus* Hennelly, 1959 ex Po-
tonié & Lele, 1961; Rubinstein & Toro, Fig. 3,
Specimens 11, 17. [no description]

For other synonymy see Foster (1979, p. 107).

Description.- Organic-walled, composite, tetrad structures, each comprising 4 equal, obligate, originally spherical bodies (cells), sculptured densely with discrete, apiculate elements (spinae/spinulae, bacula, coni, grana) of mostly constant form and dimensions on cells of a given specimen. In some specimens, however, sculptural elements becoming progressively sparser and smaller in regions about cruciform contact zone bordering contiguous cell members. Cell wall thickness ca. 0.8-1.5 µm, difficult to ascertain precisely because of sculptural modification; wall subject to compressional folding.

Dimensions (25 specimens).- Overall diameter 31 (43) 56 µm; diameter of cells 13 (21) 28 µm. Sculptural elements <1-6 µm high, 0.5-1.2 µm in basal diameter, spaced up to 3 µm apart.

Remarks and comparison.- Collectively, although not as individual cells within a given tetrad, the present specimens show an appreciable range of sculptural attributes, mostly conforming to illustrations and descriptions of *Quadrisporites horridus* Hennelly, 1959 ex R. Potonié & Lele, 1961 furnished by such authors as Potonié & Lele (1961), Segroves (1967), Balme (1970), Backhouse (1991), and Balme & Backhouse (1993). In the study material, the species has been encountered in only one sample, in which it is moderately abundant and well preserved.

Undescribed Lower Silurian specimens from Argentina, referred to *Q. horridus* by Rubinstein & Toro (2006; see above synonymy), are best excluded from that species on sculptural grounds. The listing by Steemans *et al.* (2007, Fig. 2, Appendix) of "*Quadrisporites horridus* Cramer (1966)" (sic), from the Saudi Arabian lowermost Devonian, cannot be confirmed in the absence of descriptive and illustrative documentation.

Previous records.- Reported widely from the Permian of Australia, Africa, Indian subcontinent, and South America (Utting, 1978; Foster, 1979; Doubinger & Marocco, 1981); also from Antarctica (Kyle, 1977; Kyle & Schopf, 1982; Lindström, 1994). Younger (Triassic) occurrences, also exclusively Gondwanan, are uncommon or rare (de Jersey, 1979; Brenner & Foster, 1994).

Class PRASINOPHYCEAE Christensen, 1962

Family CYMATIOSPHAERACEAE Mädlar, 1963

Genus *Cymatiosphaera* O. Wetzel, 1933 ex Deflandre,
1954

Type species: *Cymatiosphaera radiata* O. Wetzel, 1933
[SD; Deflandre, 1954, p. 257]

Cymatiosphaera gondwanensis (Tiwari, 1965)
Backhouse, 1991
Plate 8, Figs. 8, 9

1965 *Maculatasporites gondwanensis* Tiwari, p. 205;
Pl. 8, Figs. 191, 192.

1977 *Mehlisphaeridium gondwanensis* (Tiwari) An-
derson, pars, p. 63; Appendix 9.3, p. 5; Pl. 2,
Figs. 24-34, 44.

non 1985 *Maculatasporites gondwanensis* Tiwari, 1965;
Foster, Palmieri & Fleming, Pl. 1, Fig. 3.

1991 *Cymatiosphaera gondwanensis* (Tiwari) Back-
house, pp. 299, 302; Pl. XXII, 13-15.

Description.- Vesicle originally spherical or subspherical; outline circular or subcircular. Eilyma ca. 1-1.5 µm thick, ± arcuate compression folds; comprehensively reticulate. Muri membranous, ca. 0.5 µm wide and 2 µm high, enclosing polygonal to subcircular lacunae 4-9 µm in maximum diameter. Excystment structure not observed.

Dimensions (6 specimens).- Diameter of vesicle 31 (38) 46 µm.

Previous records.- From the Permian of India (Tiwari, 1965; Sinha, 1969), Africa (Kar & Bose, 1976; Anderson, 1977), Australia (Foster, 1979; Backhouse, 1991), and Antarctica (Lindström, 1994, 1996).

5.4. Acritarchs

Group ACRITARCHA Evitt, 1963

Genus *Maculatasporites* Tiwari, 1964

Type species: *Maculatasporites indicus* Tiwari, 1964
[OD, M]

Maculatasporites gravidus Playford sp. nov.

Plate 8, Figs. 10-14, 18

Diagnosis.- Vesicle originally spherical, outline circular, subcircular or, less commonly, roundly subtriangular. Eilyma 1.5-3 µm thick, bearing comprehensive reticulum perfectum. Muri smooth, mostly 1.5-3 µm wide, but wider (up to 7 µm) at intersections; crests rounded or flat; sides ± straight or slightly expanded distally; height ca. 1-2.5 µm. Lacunae subcircular to irregularly rounded-polygonal, 2-14 µm in maximum dimension.

Dimensions (30 specimens).- Diameter of vesicle 41 (54) 68 µm.

Holotype.- Sample/slide 80P201A/3, EF J28; Pl. 8, Fig. 11; UQY9473. Vesicle circular in outline, diameter 52 µm; eilyma ca. 2.5 µm thick; comprehensively, ± regularly reticulate; smooth muri (mainly 1-1.5 µm wide, up to 5 µm at intersections; 1-2 µm high) enclosing subcircular to roundly polygonal lacunae (3-9 µm in maximum dimension).

Etymology.- Latin, *gravidus*, laden, heavy.

Remarks and comparison.- The numerous specimens of *Maculatasporites gravidus* Playford sp. nov. show appreciable, albeit continuous variation in the degree of coarseness of the reticulum (i.e., the lacunae dimensions: Plate 8, Figs. 10-14), but many specimens individually bear fairly regular reticulation.

The present species is morphologically close to *M. indicus* Tiwari, 1964 (p. 258), from the mid Permian (Barakar stage) of India. However, the reticulation of *M. indicus*, although variable, appears to be mostly finer (lacunae breadth 1-5 µm) than that shown by *M. gravidus*. Closer comparison is impeded by the less-than-satisfactory quality of Tiwari's (1964, Pl. 1, Figs. 11, 12) photomicrographs. Superficial resemblance is evident between *M. gravidus* and a Pennsylvanian species, *M. asperatus*, described from Iowa (U.S.A.) by Ravn (1986, p. 119; Pl. 5, Figs. 1-8). However, the latter has sculptured (conate, granulate) muri rather than the smooth muri exhibited by the present species. Ouyang Shu *et al.* (2003; Pl. 8, Fig. 6) illustrated, as *Convolutispora* sp., a Chinese Upper Permian specimen that appears similar to *M. gravidus*; but, in the absence of a description of the Chinese form, no detailed comparison is feasible.

Genus *Mehlisphaeridium* Segroves, 1967

Type species: *Mehlisphaeridium fibratum* Segroves,
1967 [OD, M]

Mehlisphaeridium regulare Anderson, 1977

Plate 8, Figs. 15-17

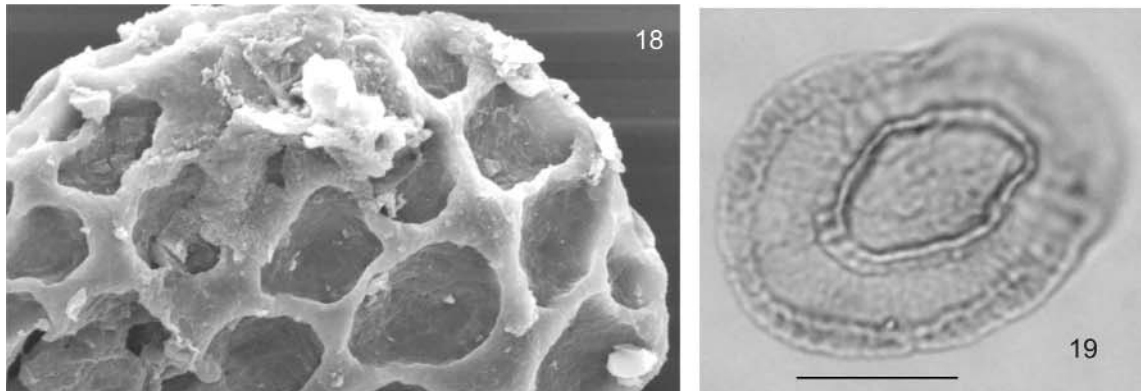
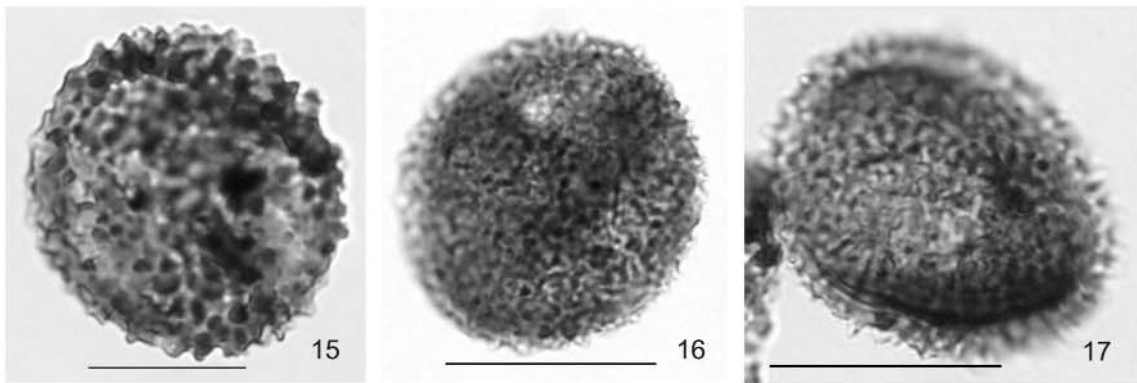
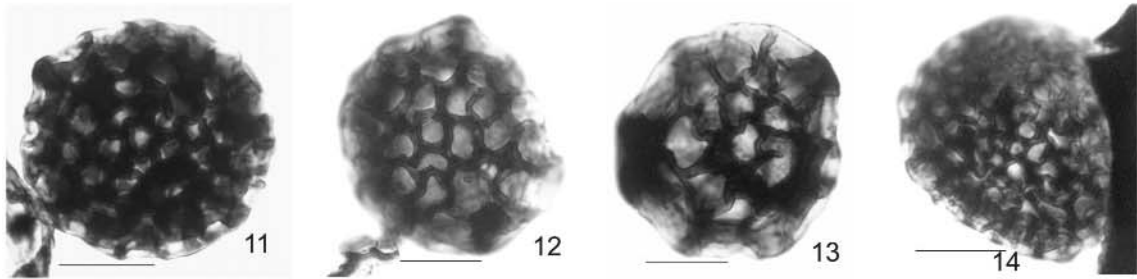
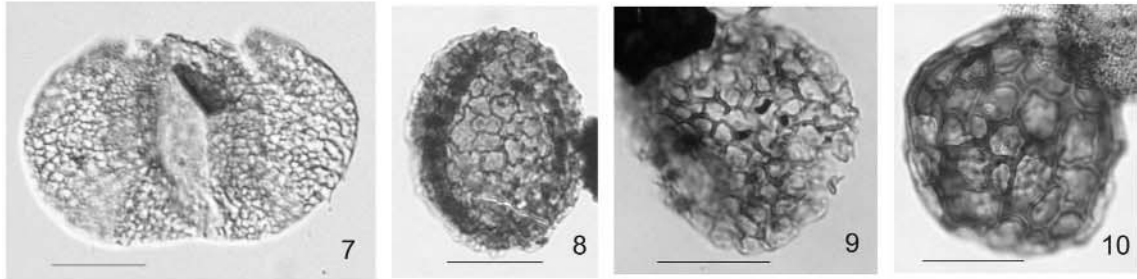
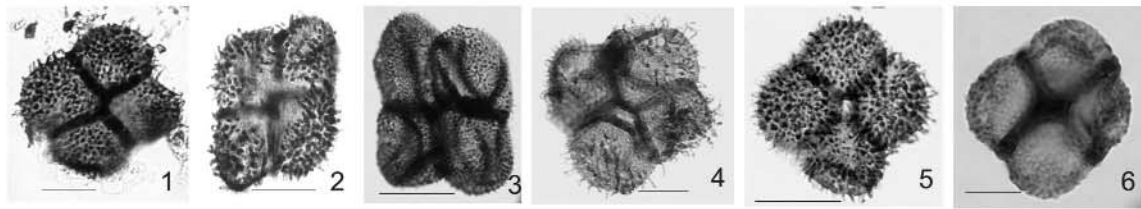
For synonymy see Backhouse (1991, p. 303).

Remarks.- The present specimens concur with Backhouse's (1991) description of *Mehlisphaeridium regulare* Anderson, 1977, some of them (e.g., Plate 8, Fig. 17) having areas devoid of the short apiculate processes that are 1-3 µm long and densely cover the remainder of the eilyma; and one apparently pylomate specimen was encountered (Plate 8, Fig. 16). Vesicle diameter of 10 specimens ranges from 20 µm to 39 µm (mean 30 µm).

Previous records.- *Mehlisphaeridium regulare* is known from the Permian of the Karoo Basin, South Africa (Anderson, 1977) and of Australia (see occurrences cited by Backhouse, 1991, pp. 303-304).

Plate 8. 1-6, *Quadrisporites horridus* Hennelly, 1959 ex R. Potonié & Lele, 1961, note sculptural variation. 7, *Alisporites* sp., median focus. 8, 9, *Cymatiosphaera gondwanensis* (Tiwari, 1965) Backhouse, 1991. 10-14, 18, *Maculatasporites gravidus* Playford sp. nov., note variation in coarseness of reticulum; 11, holotype; 18, x2500. 15-17, *Mehlisphaeridium regulare* Anderson, 1977. 19, *Peltacystia* sp. cf. *P. venosa* Balme & Segroves, 1966. Scale bars = 20 µm (Figs. 1-5, 7-17); 10 µm (Figs. 6, 19).

Plate 8



Genus *Peltacystia* Balme & Segroves, 1966
Type species: *Peltacystia venosa* Balme & Segroves,
1966 [OD]

Peltacystia sp. cf. *P. venosa* Balme & Segroves, 1966
Plate 8, Fig. 19

cf. 1966 *Peltacystia venosa* Balme & Segroves, p. 30; Figs.
3l-o, 4a.

cf. 1977 *Circulisporites venosus* (Balme & Segroves) An-
derson, p. 62; Appendix 9.3, p. 9; Pl. 4, Figs. 1-
15.

Description.- Vesicle (presumably detached hemispheres thereof) circular in outline. Eilyma very thin with 2, low, well-separated concentric ridges: the outer narrow (<0.5 µm wide) with undulant crest and sited ca. 2 µm from periphery; the inner more conspicuous (0.5-1 µm wide), prescribing polar area 12 µm in maximum dimension. Apart the from latter, ± featureless area, surface finely, radially striate.

Dimensions (3 specimens).- Equatorial diameter 24, 25, 30 µm.

Comparison.- Balme & Segroves (1966) established *Peltacystia* to incorporate three new species: *P. venosa* (type), *P. monilis*, and *P. calvitia*. Backhouse (1991, p. 306) stated that these species "form an obvious natural grouping and indeed intergrade morphologically." That view is clearly supported by specimens attributed to *P. venosa* and *Circulisporites venosus* by Balme (1970, Pl. 22, Figs. 3-6) and Anderson (1977, Pl. 4, Figs. 1-15) respectively. The *venosa* epithet is accordingly adopted herein, with the "cf." designation reflecting the fact that the West Papuan specimens are appreciably smaller than those reported hitherto of *P. venosa* (or indeed of *P. monilis* or *P. calvitia*).

Previous records.- *Peltacystia venosa* and intergradational forms have been reported from the Permian, especially Upper Permian, of Western Australia and elsewhere in Gondwana (e.g., Balme & Segroves, 1966; Segroves, 1967; Balme, 1970; Foster, 1975, 1979; Anderson, 1977; Doubinger & Marocco, 1981; Backhouse, 1991; Lindström, 1994, 1996).

6. CONSTITUTION AND STRATIGRAPHIC SIGNIFICANCE OF THE PALYNOFLORA

6.1. General features

From Table 4 it is evident that the six samples representing the Aiduna and Ainim formations contain a preponderance of palynomorph species that are common to both units. Accordingly, a single and fairly diverse palynoflora can be regarded as represented in the study material, notwithstanding some variation in sample-by-sample species occurrences. Generally speaking, the Ainim samples (particularly 79RY188C) yielded the more diverse assemblages. Preservational quality is also variable, but has generally proved adequate for identification purposes.

Spores and pollen grains are the principal palynofloral components, quantitatively as well as qualitatively. The former category includes both trilete and monolete forms, totalling 19 and seven named species respectively and distributed among 21 genera, together with several informally designated taxa. Pollen grains comprise four species of monosaccates (three genera), nine species of taeniate and non-taeniate bisaccates (six genera), and five species of other groups (Plicates, Monocolpates: four genera); additionally, several taxa are designated informally. Organic-walled microphytoplankton are essentially minor constituents, occurring sparingly in four of the samples; four named species (four genera) and one "cf." species are identifiable.

6.2. Correlation and age

A review of the previously documented stratigraphic distribution of palynomorph species identified herein, as documented in the preceding Section 5, provides unequivocal testimony of the Permian age of the subject palynoflora and hence of the sampled portions of the Ainim and Aiduna formations. However, some species, although characteristically Permian, have been recorded as extending into older (Pennsylvanian) or younger (Triassic) rocks and are thus inapplicable to precise age assessment. These include the following: *Leiotriletes directus*, *Granulatisporites austroamericanus*, *Lophotriletes novicus*, *In-*

palynomorph species	formation and sample numbers					
	Ainim Formation			Aiduna Formation		
	79SS7	79RY188C	79RY189A	80P201A	80P278A	80P279A
<i>Calamospora</i> spp.	✓	✓		✓	✓	
<i>Punctatisporites gretensis</i>		✓	✓	✓		
<i>Leiotriletes directus</i>		✓	✓	✓		
<i>Leiotriletes</i> spp.	✓	✓	✓	✓		✓
<i>Dictyophyllidites ouyangii</i>		✓	✓		✓	✓
<i>Cyclogranisporites gondwanensis</i>		✓				
<i>Cyclogranisporites rugulogranatus</i>	✓	✓	✓	✓	✓	✓
<i>Granulatisporites austroamericanus</i>		✓	✓	✓		✓
<i>Waltzispora</i> sp. A		✓				
<i>Converrucosisporites micronodosus</i>	✓	✓	✓		✓	
<i>Verrucosisporites andersonii</i>	✓	✓	✓			
<i>Anapiculatisporites</i> sp. A	✓	✓	✓			
<i>Apiculatasporites</i> sp. A		✓				
<i>Lophotriletes novicus</i>	✓	✓	✓	✓	✓	✓
<i>Lophotriletes wagneri</i>			✓			
<i>Horriditriletes filiformis</i>	✓	✓	✓	✓	✓	✓
<i>Horriditriletes ramosus</i>		✓	✓	✓	✓	
<i>Dictyotriletes</i> sp. A						✓
<i>Dictyotriletes</i> sp. cf. <i>D. aules</i>				✓		
<i>Indospora clara</i>				✓	✓	✓
<i>Triquirites kaiseri</i>		✓				✓
<i>Iraqispora labrata</i>					✓	
<i>Densoisporites solidus</i>		✓				
<i>Gondisporites imbricatus</i>	✓	✓	✓			
<i>Indotriradites niger</i>		✓				
<i>Grandispora segrovesii</i>	✓	✓				
<i>Laevigatosporites callosus</i>			✓			
<i>Laevigatosporites flexus</i>	✓	✓	✓	✓	✓	✓
<i>Laevigatosporites vulgaris</i>	✓		✓	✓		
<i>Schweitzerisporites maculatus</i>		✓	✓			
<i>Striatosporites heyleri</i>	✓	✓	✓		✓	✓
<i>Thymospora miscella</i>	✓	✓	✓	✓		
<i>Tuberculatosporites modicus</i>		✓		✓		
<i>Potonieisporites balmei</i>	✓		✓			
<i>Cannanoropollis janakii</i>	✓		✓			
<i>Plicatipollenites gondwanensis</i>	✓		✓			
<i>Striomonosaccites</i> sp. A			✓			
<i>Alisporites</i> spp.		✓	✓		✓	✓
<i>Platysaccus leschikii</i>		✓				
<i>Vitreisporites pallidus</i>		✓	✓		✓	
<i>Distriatites insolitus</i>			✓		✓	
<i>Protohaploxypinus amplus</i>		✓	✓	✓	✓	✓
<i>Protohaploxypinus limpidus</i>	✓	✓	✓	✓	✓	✓
<i>Protohaploxypinus rugatus</i>				✓		
<i>Striatoabeites multistriatus</i>	✓	✓	✓	✓	✓	
<i>Striatopodocarpites cancellatus</i>		✓	✓	✓		✓
<i>Striatopodocarpites fusus</i>		✓	✓	✓	✓	✓
<i>Weylandites lucifer</i>		✓				
<i>Marsupipollenites striatus</i>		✓	✓			
<i>Marsupipollenites triradiatus</i>	✓		✓			✓
<i>Cycadopites cymbatus</i>		✓				✓
<i>Pakhapites fasciolatus</i>		✓				
<i>Quadrisporites horridus</i>				✓		
<i>Cymatiosphaera gondwanensis</i>		✓			✓	
<i>Maculatasporites gravidus</i>		✓		✓	✓	
<i>Mehlisphaeridium regulare</i>		✓				✓
<i>Peltacystia</i> sp. cf. <i>P. venosa</i>		✓		✓	✓	

Table 4. Checklist of palynomorph species identified in the samples studied.

dospora clara, *Striatosporites heyleri*, *Laevigatosporites vulgaris*, *Vitreisporites pallidus*, and *Quadrisporites horridus*.

Many other species are reportedly confined to but long-ranging through the Permian system; e.g., *Converrucosisporites gondwanensis*, *C. micronodosus*, *Verrucosisporites andersonii*, *Tuberculatosporites modicus*, *Cannanoropolis janakii*, *Plicatipollenites gondwanensis*, *Platysaccus leschikii*, *Protohaploxylinus amplus*, *P. limpidus*, *Striatoabieites multistriatus*, *Striatopodocarpites cancellatus*, *S. fusus*, and *Cymatiosphaera gondwanensis*.

In a more precise biostratigraphic context, the presence of a number of spore-pollen species can, taken together,

assist in the independent dating of the palyniferous strata; these are mainly those species charted in Figure 2. From the reported stratigraphic occurrences of these species – in particular of *Triquitrites kaiseri* (= *T. incisus* auct. non Turnau, 1970 of Kaiser, 1976) and *Schweitzerisporites maculatus* – it becomes clear that the strata are, in all likelihood, of post-Artinskian age and pre-Wordian (= pre-Kazanian) age. In other words, the age or age-range of the subject palynoflora can be bracketed within the Kungurian-Roadian (= Ufimian) interval; i.e., late Early-early Middle Permian. An apparent anomaly is the presence of *Dictyophyllidites ouyangii*. However, the only prior occurrence of that species, formally instituted herein and as depicted in Figure 2, is based on a single figured and undescribed specimen from northwestern China, and con-

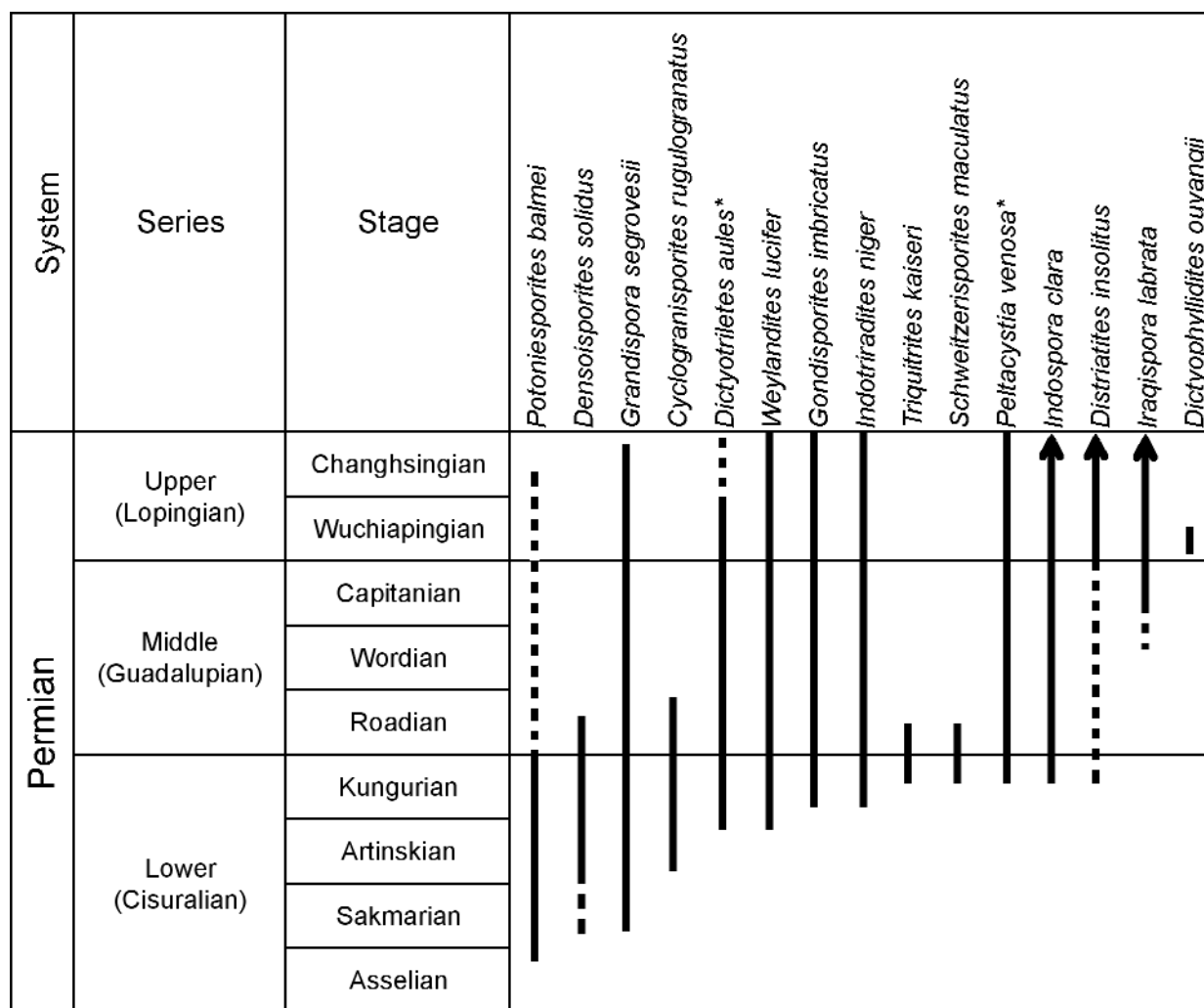


Figure 2. Compilation of stratigraphic ranges of selected species identified in the West Papuan samples based on previously recorded occurrences in Gondwanan strata. Note: (a) see systematics section 5 for sources of data; (b) range calibrations with respect to international stage subdivisions of the Permian system are tentative to varying degree; (c) asterisks denote "cf." identifications in samples of this study.

sequently its stratigraphic range within the Permian can scarcely be adequately assessed.

Within Gondwana, correlation appears closest with the Australian Permian palynofloral sequence, in particular with the upper Stage 4b-lower Stage 5 (APP3-APP4) interval thereof (Kemp *et al.*, 1977; Price, 1983, 1997). However, some critical determinants for defining and subdividing that interval are absent from the sampled Aiduna and Ainim formations. These absentees include most notably species of the highly distinctive trilete scutulate genera *Dulhuntyispora* Potonié, 1956 and *Lopadiospora* Price, 1983. The latter is unrecorded outside Australia, whereas two species of the former, which is likewise characteristic of the Australian Upper Permian, have been reported from South Africa and New Zealand; viz., *D. granulata* Price, 1983 (Anderson 1977; as *D. dulhuntyi* Potonié, 1956) and *D. parvithola* (Balme & Hennelly, 1956) Potonié, 1960 (Raine in Landis *et al.*, 1999, p. 275) respectively.

7. PALAEOBOTANICAL AND PHYTOGEOGRAPHIC SIGNIFICANCE OF THE PALYNOFLORA

Natural relationships of the subject dispersed spore-pollen flora can be inferred, in a fairly generalized manner, principally by reference to Balme's (1995) comprehensive catalogue of the spore and pollen contents of fossilized fructifications.

Taeniate bisaccate pollen grains, which comprise a very conspicuous element of the Aiduna-Ainim palynoflora, are well known from Permian and Triassic assemblages in many parts of the world, and are especially characteristic of Gondwanan Permian strata. Their natural affinities are diverse within the gymnosperms: viz., conifers and pteridosperms (glossopterids, peltasperms, and possibly corytosperms). However, the glossopterids are regarded as the principal parental sources of Permian taeniate bisaccates (Gould & Delevoryas, 1977; Balme, 1995; Lindström *et al.*, 1997). Accordingly, the abundance of taeniate bisaccates in the studied palynoflora, as elsewhere in the Permian of Gondwana, connotes major glossopterid representation in the Aiduna-Ainim terrestrial vegetation.

Trilete and monolete spores – well represented in the palynoflora – evidently derived from a range of spore-producing plants. Especially prominent were ferns, represented by species of such genera as *Dictyophyllidites*, *Cyclogranisporites*, *Verrucosisporites*, *Horriditriletes*, *Triquitrites*, *Densoisporites*, *Gondisporites*, *Laevigatosporites*, and *Thymospora*. Other likely pteridophytic contributors were arthropytes (*Schweitzerisporites*, *Striatosporites*) and lycopodophytes (*Indotriradites*).

Associated with the glossopterids were presumably other seed-bearing gymnospermous plants, including those that produced *Vitreisporites* (caytonialean or peltaspermalean seed ferns); monosaccate pollen grains, including *Potonieisporites*, *Cannanoropollis*, and *Plicatipollenites* (coniferophytes); and *Cycadopites* (cycadophytes).

Apart from the above land-derived components, the palynoflora includes the aquatic green-algal palynomorphs *Quadrisporites* and *Cymatiosphaera*, the former assigned to the Chlorococcales, the latter to the Prasinophyceae. The acritarchs *Maculatasporites*, *Mehlisphaeridium*, and *Peltacystia* are also of likely algal derivation (Balme & Segroves, 1966; Segroves, 1967).

It is pertinent here to review the palynological data in relation to the plant megafossil descriptions and identifications furnished by Rigby (1983, 1997, 1998a, b, 2001), many based on collections from the same localities and strata as those that yielded the palynomorphs documented herein. From Rigby (1998b, 2001; Tables 2, 3 herein) it is clear that close taxonomic coherence exists among the Aiduna and Ainim collections from the various localities shown in Figure 1. Hence a single megaf flora is considered to be represented, not unexpectedly mirroring the commonality, and overwhelmingly Gondwanan complexion, exhibited by the palynomorph assemblages. Rigby (2001) estimated that some 20 megaplant species were identifiable, these being mainly endemic and assignable to *Glossopteris* (11 species). Besides the predominant glossopterids, the flora includes pecopterid fronds (probably of pterophyte affinity), true ferns (*Cladophlebis* sp., *Fasciapteris aidunae* Rigby, 1997), sphenophytes (*Trizygia speciosa* Royle, 1840), and *incertae sedis* gymnosperms (*Gigantonoclea irianensis* Rigby, 1997, *Koraua hartonoi* Rigby, 1997). These floral categories are clearly repre-

sented within the diverse spore-pollen assemblage, although, for ecological and taphonomic reasons, the latter would obviously encompass a much wider spectrum of plants than is represented in the megaplant collections.

The island of New Guinea is traditionally envisaged as situated on the northeastern margin of the Gondwana supercontinent during late Palaeozoic time (e.g., Metcalfe, 1991; McLoughlin, 2001), and, geologically and structurally, as portion of the Australian (or Indian-Australian) Plate. Palaeobotanically and palynologically, this is clearly manifested by its pan-Gondwanan *Glossopteris* flora as reported herein. The distinctiveness of the Permian *Glossopteris* flora from the coeval Cathaysia flora of East Asia has been emphasized by many authors, such as Archangelsky (1986) and Wagner (1993, 2004). Whereas the *Glossopteris* flora is characterized, most conspicuously, by its eponymous leaf morphogenus, the Cathaysia flora is devoid of glossopterids and features a completely different suite of plants, within which the gigantopterids are especially prominent and characteristic (Chandra & Sun Ke-Qin, 1997; Sun Ke-Qin, 2006).

As discussed above, the Aiduna-Ainim megafloora, while unmistakably and predominantly of Gondwanan complexion, does include forms such as *Fasciapteris* Gu & Zhi, 1974 and *Gigantonoclea* Koidzumi emend. Gu & Zhi 1974, both suggestive of a Cathaysian floral input [but note that Charlton (2001, p. 608) incorrectly stated that Rigby (1998b) and other authors found that “the Cathaysian elements ... dominate the flora”]. The palynological flora likewise shows some indication of a Cathaysian element, through its content, albeit minor, of the trilete miospores *Triquitrites kaiseri* and *Dictyophylidites ouyangii* and the monolete form *Schweizerisporites maculatus*, none of which has hitherto been reported outside the Chinese Permian.

The palaeogeographic and palaeoclimatic circumstances of West Papua during Permian time that facilitated intermingling of glossopterid and associated Gondwanan plants with some Cathaysian plants have proven debatable. What seems inescapable is that a postulated wide Tethyan seaway separating the Gondwanan and Cathaysian landmasses at this time would hardly have been conducive to floristic interchange, however limited the latter may have been. Rigby (2001, p. 94), invoking

the Earth Expansion Theory, envisaged that “the Tethys Sea was a narrow, Red Sea-like seaway which had its floor exposed at various times and places allowing migration across its width.” Moreover, Rigby (2001, p. 93), referring to the Ainim/Aiduna content (however subordinate) of the Cathaysian-related species, *Fasciapteris aidunae* and *Gigantonoclea irianensis*, noted that while the former, as a sporophyte, would be capable of dissemination via aerial transportation, the latter, seed-producing plant would scarcely be efficacious in that respect. And Charlton (2001, p. 595) advanced the possibility that, during Permo-Triassic time, a “continental isthmus permitted continuing limited floral and faunal interchange between Gondwanaland and SE Asia until a final separation in the Late Triassic.” While the concept of distinct and generally mutually exclusive floral provinces has long been recognized for the late Palaeozoic (e.g., Chaloner & Lacey, 1973; Archangelsky, 1986; Cúneo, 1996), evidence of so-called “mixed” or transitional floras is not confined to West Papua (see Rigby 1998a, Fig. 3). Thus, other Permian, peripheral-Gondwanan examples include the well-publicized flora of Hazro, southeast Anatolia, Turkey (Wagner, 1982; Archangelsky & Wagner, 1983); together with those reported from Khlong Wang Ang, Thailand (Kon’no, 1963) and from the Arabian Peninsula (Broutin *et al.*, 1995; Fluteau *et al.*, 2001; Berthelin *et al.*, 2003, 2006). Such occurrences led Maheshwari (1992) to speculate on the existence of a Middle through Late Permian “Peri-Gondwanan” region featuring typical *Glossopteris* floral elements intermingling with those characterizing the Cathaysia flora.

8. PALAEOECOLOGICAL AND PALAEOENVIRONMENTAL IMPLICATIONS

The glossopterids, as major elements of the subject flora, are believed to have been opportunistic, well-rooted, deciduous trees that spread progressively over post-glacial pan-Gondwanan Permian landscapes, thriving in well-watered lowland, mire-type settings under conditions of ameliorating temperatures within a high palaeolatitudinal range of some 40°-60°. Associated floristic elements, including a diversity of ferns, arthropytes, seed ferns, and other gymnosperm groups, were also well supported by

such environments, which were clearly in close proximity to the Aiduna-Ainim depositional sites.

Of the hosting formations, the Aiduna has been regarded as the product of nonmarine to shallow marine deposition; and the Ainim to have accumulated under fluvial to lacustrine conditions. The presently sampled strata from both formations certainly lack any palaeontological indications of marine conditions; in fact, quite the reverse, given their preservation of abundant land-derived plant micro- and mega-remains and of sporadic, though persistent, algal aquatic (fresh or brackish water) microphytoplankton.

9. CONCLUSIONS

The palynoflora retrieved from samples of the Ainim and Aiduna formations consists of a diversity of spores and pollen grains with minor contributions from nonmarine algal microphytoplankton. It is of manifestly Gondwanan complexion, thereby substantiating previous inferences as to *Glossopteris* floral affiliations of its megaplant remains. However, both the palynofloral and the megafloreal evidence do point to some minor infiltration by floristic elements from the Cathaysian landmass that lay to the north of the northeastern Gondwana site of West Papua during late Palaeozoic time. Dating of the palyniferous Ainim and Aiduna samples, by reference to previously published stratigraphic ranges of particular spore-pollen species, is added as late Early-early Middle Permian (i.e., Kungurian-Roadian in terms of international age subdivisions of the Permian period). The palaeobotanical and palynological evidence, including particularly the identification of fresh or brackish water algal cyst remains, signifies a nonmarine depositional environment for the sampled strata.

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11. REFERENCES

Note. – In accordance with conventional practice, the bibliographic listing below excludes “taxa-only” references; i.e., those that appear in the text solely as adjuncts to taxonomic names (e.g., *Triquitrites arcuatus* Wilson & Coe, 1940) and without page citations.

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APPENDIX: INVENTORY OF ILLUSTRATED SPECIMENS

Slide locations of individual specimens are specified by coordinates derived from a standard "England Finder" (EF) slide. Specimen catalogue numbers (UQY9360-UQY9480 inclusive) are those of the permanent repository: Queensland Museum, Brisbane, Australia. In left-hand column, type categories are parenthesized thus: Ho, holotype; Pa, paratype; Hy, hypotype.

Palynomorph species	Plate/Fig.	Sample/slide no.	EF	Formation	Catalogue no.
<i>Calamospora</i> sp.	1/5	80P201A/2	G10	Aiduna	UQY9360
<i>Punctatisporites gretensis</i> (Hy)	1/6	79RY188C/k	H19	Ainim	UQY9361
<i>Punctatisporites gretensis</i> (Hy)	1/7	79RY189A/25	G34/2	Ainim	UQY9362
<i>Leiotriletes directus</i> (Hy)	1/1	79RY189A/22	O32/3	Ainim	UQY9363
<i>Leiotriletes directus</i> (Hy)	1/2	79RY188C/3	E21	Ainim	UQY9364
<i>Leiotriletes</i> sp.	1/3	79RY189A/2	U42	Ainim	UQY9365
<i>Leiotriletes</i> sp.	1/4	80P201A/3	U31/1	Aiduna	UQY9366
<i>Dictyophyllidites ouyangii</i> (Ho)	1/8	80P278A/2	O33	Aiduna	UQY9367
<i>Dictyophyllidites ouyangii</i> (Pa)	1/9	80P278A/k	V19	Aiduna	UQY9368
<i>Dictyophyllidites ouyangii</i> (Pa)	1/10	80P278A/k	R22/4	Aiduna	UQY9369
<i>Dictyophyllidites ouyangii</i> (Pa)	1/11	79RY188C/2	W17/4	Ainim	UQY9370
<i>Dictyophyllidites ouyangii</i> (Pa)	1/12	80P278A/3	G21/4	Aiduna	UQY9371
<i>Cyclogranisporites gondwanensis</i> (Hy)	5/14	79RY188C/k	Q23/4	Ainim	UQY9372
<i>Cyclogranisporites rugulogranatus</i> (Pa)	1/15	79RY188C/2	N9	Ainim	UQY9373
<i>Cyclogranisporites rugulogranatus</i> (Ho)	1/16	79RY189A/28	B46/4	Ainim	UQY9374
<i>Cyclogranisporites rugulogranatus</i> (Pa)	1/17	79SS7/2	V33/1	Ainim	UQY9375
<i>Cyclogranisporites rugulogranatus</i> (Pa)	1/18	79RY189A/k	Y20/1	Ainim	UQY9376
<i>Granulatisporites austroamericanus</i> (Hy)	1/13	80P201A/2	Q48/3	Aiduna	UQY9377
<i>Granulatisporites austroamericanus</i> (Hy)	1/14	79RY188C/k	G21/4	Ainim	UQY9378
<i>Waltzisporea</i> sp. A	2/1	79RY188C/k	P11/1	Ainim	UQY9379
<i>Converrucosisporites micronodosus</i> (Hy)	2/2	79RY189A/2	J39/2	Ainim	UQY9380
<i>Verrucosisporites andersonii</i> (Hy)	2/3	79RY188C/3	N19/2	Ainim	UQY9381
<i>Verrucosisporites andersonii</i> (Hy)	2/4	79RY188C/3	F25	Ainim	UQY9382
<i>Verrucosisporites andersonii</i> (Hy)	2/5	79RY189A/2	U10/4	Ainim	UQY9383
<i>Anapiculatisporites</i> sp. A	2/6	79RY189A/7	L38	Ainim	UQY9384
<i>Apiculatasporites</i> sp. A	2/7	79RY188C/k	R24/2	Ainim	UQY9385
<i>Apiculatasporites</i> sp. A	2/8	79RY188C/2	C12	Ainim	UQY9386
<i>Lophotriletes novicus</i> (Hy)	2/9	80P201A/3	T33	Aiduna	UQY9387
<i>Lophotriletes novicus</i> (Hy)	2/10	80P201A/3	V35/1	Aiduna	UQY9388
<i>Lophotriletes novicus</i> (Hy)	2/11	80P201A/8	H44/1	Aiduna	UQY9389
<i>Lophotriletes novicus</i> (Hy)	2/12	80P201A/2	U12/4	Aiduna	UQY9390
<i>Lophotriletes wagneri</i> (Pa)	2/13	79RY189A/2	S30	Ainim	UQY9391
<i>Lophotriletes wagneri</i> (Pa)	2/14	79RY189A/2	V13	Ainim	UQY9392
<i>Lophotriletes wagneri</i> (Pa)	2/15	79RY189A/2	O46/2	Ainim	UQY9393
<i>Lophotriletes wagneri</i> (Ho)	2/16	79RY189A/3	U10/1	Ainim	UQY9394
<i>Horriditriletes filiformis</i> (Hy)	2/17	79SS7/3	K14/4	Ainim	UQY9395
<i>Horriditriletes filiformis</i> (Hy)	2/18	79RY189A/16	K41	Ainim	UQY9396
<i>Horriditriletes ramosus</i> (Hy)	3/1	79RY188C/k	U16	Ainim	UQY9397
<i>Horriditriletes ramosus</i> (Hy)	3/2	80P201A/11	L43/3	Aiduna	UQY9398
<i>Dictyotriletes</i> sp. A	3/3	80P279A/k	V26/2	Aiduna	UQY9399
<i>Dictyotriletes</i> sp. A	3/5	80P279A/2	W33/4	Aiduna	UQY9400
<i>Dictyotriletes</i> sp. cf. <i>D. aules</i>	3/4a, b	80P201A/2	W17	Aiduna	UQY9401
<i>Indospora clara</i> (Hy)	3/7	80P201A/2	Q18/3	Aiduna	UQY9402

Palynomorph species	Plate/Fig.	Sample/slide no.	EF	Formation	Catalogue no.
<i>Indospora clara</i> (Hy)	3/8	80P201A/2	Q17	Aiduna	UQY9403
<i>Indospora clara</i> (Hy)	3/9	80P201A/7	H46	Aiduna	UQY9404
<i>Indospora clara</i> (Hy)	3/10	80P201A/2	H20/4	Aiduna	UQY9405
<i>Triquitrites kaiseri</i> (Pa)	3/15	79RY188C/3	J31	Ainim	UQY9406
<i>Triquitrites kaiseri</i> (Ho)	4/1a, b	79RY188C/5	N44	Ainim	UQY9407
<i>Triquitrites kaiseri</i> (Pa)	4/2	79RY188C/3	P34/1	Ainim	UQY9408
<i>Iraqispora labrata</i> (Hy)	3/6	80P278A/2	G40	Aiduna	UQY9409
<i>Densoisporites solidus</i> (Hy)	3/11	79RY188C/3	E16/3	Ainim	UQY9410
<i>Densoisporites solidus</i> (Hy)	3/12	79RY188C/3	P32	Ainim	UQY9411
<i>Gondisporites imbricatus</i> (Hy)	4/5	79RY189A/17	J42	Ainim	UQY9412
<i>Gondisporites imbricatus</i> (Hy)	4/6	79RY189A/28	L44/3	Ainim	UQY9413
<i>Gondisporites imbricatus</i> (Hy)	4/7	79RY189A/34	M37	Ainim	UQY9414
<i>Indotriradites niger</i> (Hy)	3/13	79RY188C/k	O24	Ainim	UQY9415
<i>Indotriradites niger</i> (Hy)	3/14	79RY188C/k	J17/3	Ainim	UQY9416
<i>Grandispora segrovesii</i> (Hy)	4/3	79RY188C/2	G21	Ainim	UQY9417
<i>Grandispora segrovesii</i> (Hy)	4/4	79RY188C/2	R16/2	Ainim	UQY9418
<i>Laevigatosporites callosus</i> (Hy)	4/11	79RY189A/k	P18/4	Ainim	UQY9419
<i>Laevigatosporites flexus</i> (Hy)	5/11	80P201A/2	B38/3	Aiduna	UQY9420
<i>Laevigatosporites flexus</i> (Hy)	5/12	79RY189A/3	P35/4	Ainim	UQY9421
<i>Laevigatosporites flexus</i> (Hy)	5/15	79RY189A/2	S29/4	Ainim	UQY9422
<i>Laevigatosporites vulgaris</i> (Hy)	4/8	79RY189A/2	G35/4	Ainim	UQY9423
<i>Schweitzerisporites maculatus</i> (Hy)	5/13	79RY189A/k	U15	Ainim	UQY9424
<i>Striatosporites heyleri</i> (Hy)	6/1	79RY188C/3	V25/4	Ainim	UQY9425
<i>Striatosporites heyleri</i> (Hy)	6/2	79RY188C/3	G19/3	Ainim	UQY9426
<i>Striatosporites heyleri</i> (Hy)	6/3	79RY189A/2	B29	Ainim	UQY9427
<i>Striatosporites heyleri</i> (Hy)	6/4	79SS7/2	S13/2	Ainim	UQY9428
<i>Striatosporites heyleri</i> (Hy)	6/5	79RY188C/6	N38/3	Ainim	UQY9429
<i>Striatosporites heyleri</i> (Hy)	6/6	79RY189A/3	F15	Ainim	UQY9430
<i>Thymospora miscella</i> (Ho)	5/2	79SS7/2	P11	Ainim	UQY9431
<i>Thymospora miscella</i> (Pa)	5/3	79RY189A/3	F15/3	Ainim	UQY9432
<i>Thymospora miscella</i> (Pa)	5/4	79SS7/2	T36	Ainim	UQY9433
<i>Thymospora miscella</i> (Pa)	5/5	79RY188C/3	S41	Ainim	UQY9434
<i>Thymospora miscella</i> (Pa)	5/6	79RY188C/k	E25/2	Ainim	UQY9435
<i>Thymospora miscella</i> (Pa)	5/7	79RY188C/k	E24	Ainim	UQY9436
<i>Thymospora miscella</i> (Pa)	5/8	79RY188C/k	K16	Ainim	UQY9437
<i>Thymospora miscella</i> (Pa)	5/9	79SS7/2	Q45	Ainim	UQY9438
<i>Thymospora miscella</i> (Pa)	5/10	79RY189A/11	N38	Ainim	UQY9439
<i>Thymospora miscella</i>	5/18	80P201A		Aiduna	
<i>Tuberculatosporites modicus</i> (Hy)	4/9	80P201A/2	E45/4	Aiduna	UQY9440
<i>Tuberculatosporites modicus</i> (Hy)	4/10	80P201A/2	M10/2	Aiduna	UQY9441
<i>Tuberculatosporites modicus</i> (Hy)	5/1	80P201A/2	K10/2	Aiduna	UQY9442
<i>Tuberculatosporites modicus</i>	5/16	80P201A		Aiduna	
<i>Tuberculatosporites modicus</i>	5/17	80P201A		Aiduna	
<i>Potonieisporites balmei</i> (Hy)	6/7	79RY189A/3	F45	Ainim	UQY9443
<i>Cannanoropollis janakii</i> (Hy)	6/8	79SS7/2	H41/2	Ainim	UQY9444
<i>Plicatipollenites gondwanensis</i> (Hy)	6/9	79RY189A/2	M12/3	Ainim	UQY9445
<i>Striomonosaccites</i> sp. A	6/10	79RY189A/3	C45/4	Ainim	UQY9446
<i>Alisporites</i> sp.	8/7	79RY189A/15	Q40/1	Ainim	UQY9447
<i>Platysaccus leschikii</i> (Hy)	7/4	79RY188C/3	R34	Ainim	UQY9448
<i>Vitreisporites pallidus</i> (Hy)	7/1	79RY188C/k	K10/3	Ainim	UQY9449
<i>Distriatites insolitus</i> (Hy)	7/3	80P278A/3	H40/2	Aiduna	UQY9450
<i>Protohaploxypinus amplus</i> (Hy)	7/7	79RY189A/k	J13/2	Ainim	UQY9451

Palynomorph species	Plate/Fig.	Sample/slide no.	EF	Formation	Catalogue no.
<i>Protohaploxypinus limpidus</i> (Hy)	7/5	80P201A/3	S41/3	Aiduna	UQY9452
<i>Protohaploxypinus limpidus</i> (Hy)	7/6	80P201A/2	E31	Aiduna	UQY9453
<i>Protohaploxypinus rugatus</i> (Hy)	7/2	80P201A/9	M45/3	Aiduna	UQY9454
<i>Striatoabieites multistriatus</i> (Hy)	7/8	79RY189A/3	Z21	Ainim	UQY9455
<i>Striatopodocarpites cancellatus</i> (Hy)	7/9	80P201A/2	Q21/1	Aiduna	UQY9456
<i>Striatopodocarpites fusus</i> (Hy)	7/10	79RY189A/31	T39/1	Ainim	UQY9457
<i>Weylandites lucifer</i> (Hy)	7/13	79RY188C/12	K37	Ainim	UQY9458
<i>Weylandites lucifer</i> (Hy)	7/14	79RY188C/2	O36	Ainim	UQY9459
<i>Marsupipollenites striatus</i> (Hy)	7/12	79RY188C/2	N29/2	Ainim	UQY9460
<i>Marsupipollenites triradiatus</i> (Hy)	7/11	79RY189A/3	J44/4	Ainim	UQY9461
<i>Cycadopites cymbatus</i> (Hy)	7/15	80P279A/2	U42	Aiduna	UQY9462
<i>Pakhapites fasciolatus</i> (Hy)	7/16	79RY188C/k	Q25	Ainim	UQY9463
<i>Quadrisporites horridus</i> (Hy)	8/1	80P201A/2	Y10/2	Aiduna	UQY9464
<i>Quadrisporites horridus</i> (Hy)	8/2	80P201A/3	M9/4	Aiduna	UQY9465
<i>Quadrisporites horridus</i> (Hy)	8/3	80P201A/2	U35/1	Aiduna	UQY9466
<i>Quadrisporites horridus</i> (Hy)	8/4	80P201A/2	D27/3	Aiduna	UQY9467
<i>Quadrisporites horridus</i> (Hy)	8/5	80P201A/3	L14	Aiduna	UQY9468
<i>Quadrisporites horridus</i> (Hy)	8/6	80P201A/3	D12	Aiduna	UQY9469
<i>Cymatiosphaera gondwanensis</i> (Hy)	8/8	80P278A/2	G32	Aiduna	UQY9470
<i>Cymatiosphaera gondwanensis</i> (Hy)	8/9	79RY188C/k	J16/4	Ainim	UQY9471
<i>Maculatasporites gravidus</i> (Pa)	8/10	80P201A/2	Q35/3	Aiduna	UQY9472
<i>Maculatasporites gravidus</i> (Ho)	8/11	80P201A/3	J28	Aiduna	UQY9473
<i>Maculatasporites gravidus</i> (Pa)	8/12	80P201A/3	Y38/1	Aiduna	UQY9474
<i>Maculatasporites gravidus</i> (Pa)	8/13	80P201A/2	L31/3	Aiduna	UQY9475
<i>Maculatasporites gravidus</i> (Pa)	8/14	80P201A/2	N34	Aiduna	UQY9476
<i>Maculatasporites gravidus</i>	8/18	80P201A		Aiduna	
<i>Mehlisphaeridium regulare</i> (Hy)	8/15	80P279A/2	H20	Aiduna	UQY9477
<i>Mehlisphaeridium regulare</i> (Hy)	8/16	80P279A/3	O45/2	Aiduna	UQY9478
<i>Mehlisphaeridium regulare</i> (Hy)	8/17	80P279A/2	H28/3	Aiduna	UQY9479
<i>Peltacystia</i> sp. cf. <i>P. venosa</i>	8/19	80P201A/3	J34/3	Aiduna	UQY9480

Pennsylvanian (Upper Carboniferous) Kloedenelloidea ostracodes from the Appalachian Basin

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Resumen

Se han registrado distintas especies de Ostrácodos asignables a géneros incluidos en la Subclase Kloedenelloidea Ulrich y Bassler, 1908, (Moore, 1961) en lutitas de edad Pensilvaniense procedentes de 33 localidades de la cuenca los Apalaches. La abundancia de los géneros *Oliganinus* Geis, 1932 y *Sansabella* Roundy, 1926 es indicativa de un ambiente costero. En este trabajo se describen por primera vez las especies *Oliganinus parallelus*, *Sansabella matheri*, *S. tumida*, y *S. exulta*, así como el género *Kendrickia* y la especie *K. asketos*.

Palabras clave: Ostracoda, Kloedenelloidea, Pensilvaniense, Carbonífero Superior, Cuenca de los Apalaches

Abstract

Ostracodes representing genera included in the Kloedenelloidea Ulrich & Bassler, 1908, (Moore, 1961) were found in Pennsylvanian shales at 33 localities in the Appalachian basin. The genera *Oliganinus* Geis, 1932, and *Sansabella* Roundy, 1926, are abundantly present indicating a near shore environment. New taxa include, *Oliganinus parallelus*, *Sansabella matheri*, *S. tumida*, *S. exulta*, and the genus and species *Kendrickia asketos*.

Keywords: Ostracoda, Kloedenelloidea, Pennsylvanian, Upper Carboniferous, Appalachian basin

Palynology and paleoenvironment of the Jurassic lacustrine Cañadón Asfalto Formation at Cañadón Lahuincó locality, Chubut Province, Central Patagonia, Argentina

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Resumen

En el contexto de la extensión jurásica del Gondwana sudoccidental, los materiales de la Formación Cañadón Asfalto rellenaron cuencas de semigraben ubicadas en el área central de la provincia de Chubut. Los principales afloramientos estudiados se encuentran en el valle medio del Río Chubut, donde alternan volcanitas y depósitos bioquímicos, piroclásticos y epiclásticos. En este trabajo se presenta un estudio palinológico y palinofacial de las pelitas gris oscuras de la parte inferior de esta Formación en la localidad Cañadón Lahuincó del Depocentro Cerro Cóndor. La abundancia de materia orgánica amorfa (60-90%) en todas las muestras palinológicas estudiadas es característica de condiciones de fondo. El material obtenido corresponde en su mayor parte a palinomorfos destruidos que incluyen microplancton y *Botryococcus*. Los fitoclastos opacos que escasos, consisten en materia equidimensional no estructurada de color negro. La presencia de *Botryococcus* indica niveles lacustres someros y, probablemente, condiciones de salinidad. Procesos diagenéticos como son la degradación, corrosión y ausencia de pirita en todas las muestras indican que las condiciones del fondo lacustre fueron mayormente aeróbicas. En el conjunto de los granos de polen, los de las Cheirolepidiaceae dominan el espectro polínico (hasta 80% de *Classopollis* spp.), junto con los de las Araucariaceae (hasta un 20 %). Los altos porcentajes de Cheirolepidiaceae que fueron termófilas, y Araucariaceae que ocuparon ambientes relativamente húmedos, caracterizan el paleoambiente como cálido y húmedo. Asimismo la presencia de esporas de briofitos (*Nevesisporites* cf. *radiatus*) y granos de polen de pteridospermas (*Alisporites similis*) sugieren condiciones de humedad, al menos local, para la parte inferior de la Formación. La distribución estratigráfica de los palinomorfos indica una edad jurásica media (del Bajociense al Bathoniense temprano).

Palabras clave: Palinología, Paleoambiente, Jurásico, Formación Cañadón Asfalto, Patagonia Central, Argentina

Abstract

In the context of the Jurassic extension of southwestern Gondwana, the Cañadón Asfalto Formation filled the semigrabens located in the central area of the Chubut province. The principal outcrops are in the middle Chubut river valley, where volcanites, biochemical, pyroclastic and epiclastic deposits alternate. The palynologic and palynofacial study of dark gray pelites of the lower part of the Cañadón Asfalto Formation at the Cañadón Lahuincó locality, Cerro Cóndor Depocenter, is presented. The abundance of amorphous organic matter (60-90%) in all the palynologic samples studied is characteristic of stagnant bottom conditions. The material mostly corresponds to destroyed palynomorphs, including microplancton and *Botryococcus*. The scarce opaque phytoclasts consist of black, equidimensional, structureless material. The presence of *Botryococcus* indicates shallow lake levels and probably saline conditions. Diagenetic processes such as degradation, corrosion and the absence of pyrite in all the samples indicate that bottom conditions were mostly aerobic. The Cheirolepidiaceae dominate the spectrum (up to 80% of *Classopollis* spp.), associated with Araucariaceae (up to 20%). Warm and relatively humid climatic conditions are indicated by these high percentages of the thermophilic Cheirolepidiaceae, together with the Araucariaceae that grow under relatively humid conditions. Also, the presence of Bryophyta (*Nevesisporites* cf. *radiatus*) and pteridosperms (*Alisporites similis*) suggest probable local humid conditions for the lower part of the Formation. The stratigraphic range of the palynomorphs indicates a Middle Jurassic (Bajocian to early Bathonian) age for the lower part of the Cañadón Asfalto Formation at the Cañadón Lahuincó locality.

Keywords: Palynology, Paleoenvironment, Jurassic, Cañadón Asfalto Formation, Central Patagonia, Argentina

1. GEOLOGIC SETTING AND SEDIMENTARY ENVIRONMENT

The Cañadón Asfalto Formation is a major Jurassic lithostratigraphic unit of Extra-Andean Patagonia and includes one of the most important accumulations of organic-rich pelites of this region (Flores, 1948; Feruglio, 1949). It is typically exposed in the middle valley of the Chubut River and neighbouring areas, between Paso de Indios and Paso del Sapo (Fig. 1). The outcrops are principally in the eastern part of the geologic map 1:200.000, number 44d: Colan Conhué of the Argentinian Geological Survey; the northeastern part of map 45c: Pampa de Agnia, the western part of map 44e: Valle General Racedo (at the Sierra de los Pichinianos) and near Gastre and GanGan (Map 42d: Gastre), 4369-III: Paso de Indios (Silva Nieto, 2005) and 4369-27: Cerro Condor, scale 1:100.000 (Fig. 2).

The type area was considered in a concise synthesis of the Somuncura Massif stratigraphy (Northpatagonian Massif) by Stipanovic *et al.* (1968). Tasch and Volkheimer (1970) contributed to the biostratigraphy, paleoecology and paleoclimatology of the Cañadón Asfalto Formation, and Turner (1983) presented a geologic map (1:200.000) of the area, which was complemented by the adjacent geologic maps of the Argentinian Geological Survey (Servicio Geológico Nacional) by Nullo (1983) and Proserpio (1987). Cortiñas (1993) defined the Somuncurá-Cañadón Asfalto Basin, its limits and the evolutionary cycles of its sedimentary filling. An updated detailed geologic mapping (1:100.000) and description of the study area is that of Silva Nieto *et al.* (2002). Gallego and Cabaleri (2005) performed additional studies on conchostracans of the Cañadón Asfalto Formation. Salani (2007) obtained a radiometric dating (K/Ar, of total rock) of 170.9 + 4.4 Ma

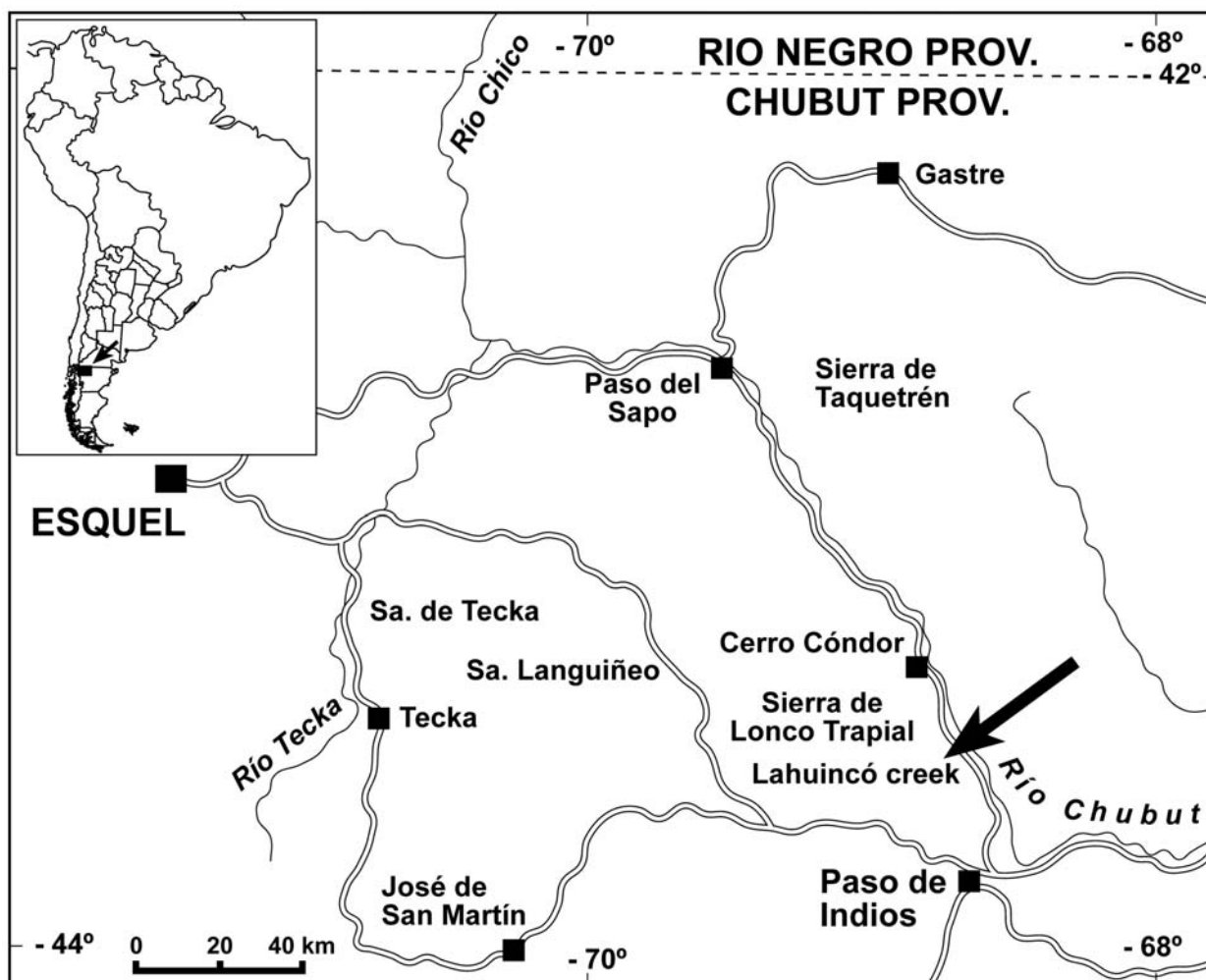


Figure 1. Location map. South America and central Patagonia with the Chubut River valley.

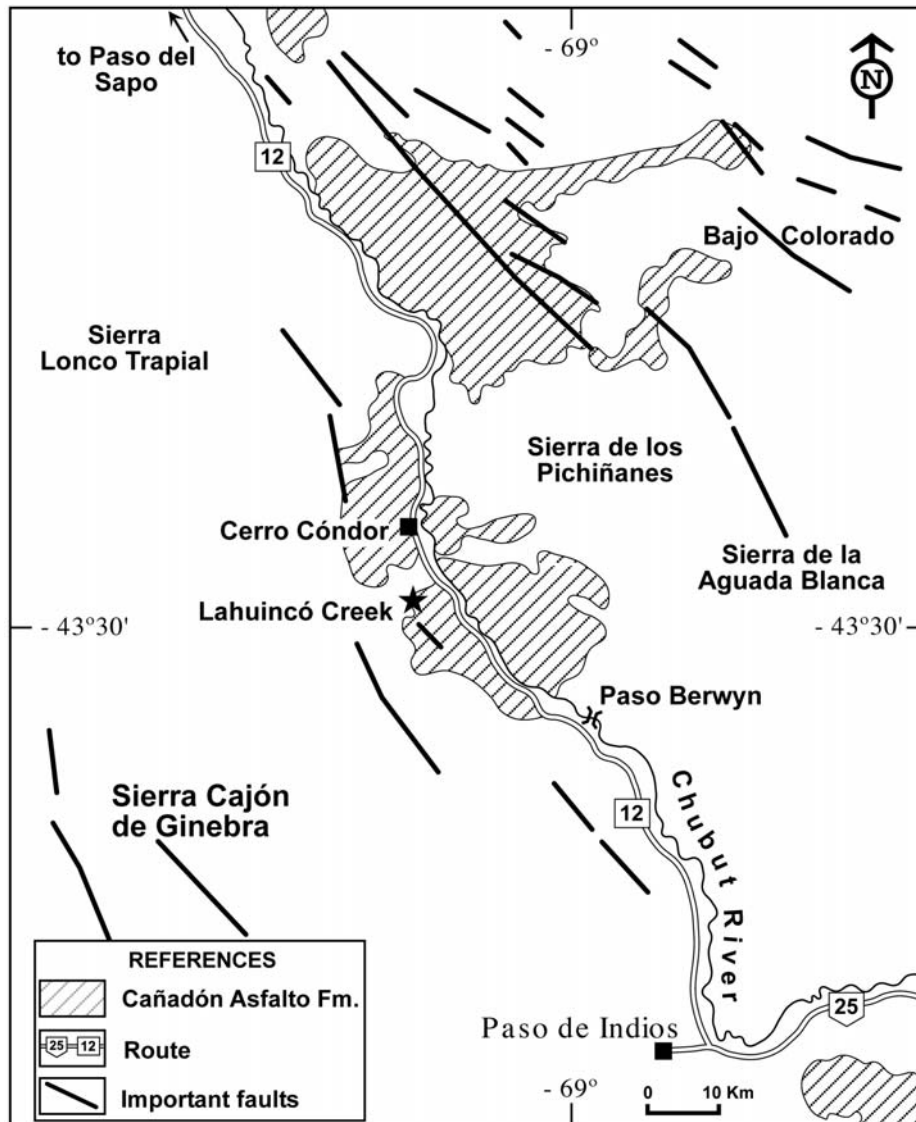


Figure 2. Distribution of outcrops of the Cañadón Asfalto Formation and of important faults. Area of the middle Chubut River valley. The Cañadón Lahuincó is located in the center of the figure.

(Aalenian-Bajocian) of magmatic facies outcropping at Cañadón Los Loros (near Puesto Almada).

The generalized extension which affected the Gondwana Continent since the Triassic, originated the thinning of the lithospheric crust (Cortiñas, 1993). In the Middle Chubut River area, cuneiform basins developed, limited by normal and listric profound faults. The basement, migmatites, foliated granitoids and granitoids of the Mamil Choique Formation (Ravazzoli and Sesana, 1977, Fig. 3) was fragmented, with rotated and basculated blocks, showing evidences of extensional (transtensional?) phases with superimposed compressional (transpressive?) faults, which have formed centers of deposition constituted by the clas-

sic hemigrabens (Figari *et al.*, 1996). The age of the igneous–metamorphic basement is object of controversy, due to the absence of stratigraphic relations which would allow a more precise determination. Several authors assign to the Mamil Choique/Cushamen Formation a large spectrum of radiometric ages, obtained from the Ordovician to the early Mesozoic (Dalla Salda *et al.*, 1999; López de Luchi *et al.*, 1999; Varela *et al.*, 1999).

The Middle Jurassic volcano-sedimentary filling is disposed unconformably over the igneous–metamorphic basement, beginning with the effusive cycle of the Lonco Trapial Formation (Lesta and Ferello, 1972). The extrusions are located on the regional lineaments, within an exten-

Cenozoic	Qy	Holocene	Quaternary (Basalts, alluvial, colluvial and piedmont deposits)		
		Pleistocene			
	Neogene	Miocene		El Mirador Fm (Basalts)	
		Paleogene	Oligocene		Collón Curá Fm (Tuffs, paleosoils) Sarmiento Group (Tuffs)
	Eocene		El Buitre Fm / La Primavera Fm (Alkaline basalts)		
	Paleocene		Huitrera Fm (Tuffs and ignimbrites)		
	Mesozoic	Cretaceous	Upper/Late	Maastrichtian	Lefipán Fm (Tidal claystones, siltstones, fine fossiliferous sandstones and fine conglomerates)
				Campanian	Paso del Sapo Fm (Fluvial conglomerates, sandstones and shales)
				Santonian	Chubut Group (Fluvial conglomerates, sandstones, shales, tuffs and tuffites)
				Coniacian	
Turonian					
Cenomanian					
Albian					
Lower/Early			Aptian	Cañadón Calcáreo Fm (Lacustrine / palustrine, shales and fluvial sandstones)	
			Barremian		
			Hauterivian		
		Valanginian			
		Berriasian			
Jurassic		Upper/Late	Tithonian	Cañadón Asfalto Fm (Lacustrine limestones, shales, evaporites, sandstones, tuffs and basalts)	
			Kimmeridgian		
			Oxfordian		
	Middle	Callovian			
		Bathonian			
		Bajocian	Lonco Trapial Fm (Mesosilicic volcanites)		
		Aalenian			
Lower / Early	Las Leoneras Fm (Lacustrine siltstones, shales, sandstones and tuffs)				
Pz	Ordovician - Silurian ?		Mamil Choique Fm (Granite, Migmatite)		

Figure 3. Stratigraphic setting of the middle Chubut River area, central northern Patagonia.

sional-transensional regime (Aragón *et al.*, 2000). These lineaments could respond to old tectonic directions of the basement, which controlled the formation of transcurrent faults and the course of the middle Chubut River. The volcanic facies are characterized by andesites, andesitic breccias and dacitic tuffs, andesitic tuffs and volcanic agglomerates. The sedimentary facies are characterized by conglomerates, conglomeratic sandstones and fine to coarse-grained, greenish-gray sandstones (Lizuain and Silva Nieto, 2005). Different authors agree to assign a Middle Jurassic age to this unit (Stipanovich and Bonetti,

1969; Lesta *et al.*, 1980; Franchi and Page, 1980). At the Sierra de Lonco Trapial locality, Silva Nieto (2005), obtained a radiometric age (K/Ar) of 173 MY.

During the Middle Jurassic and Oxfordian, in the Cerro Cóndor area existed strike-slip basins or pull apart basins (Silva Nieto *et al.*, 2002). The lacustrine systems of the Cañadón Asfalto Formation developed in these basins, constituted by an important volcano-sedimentary association and representing one of the most important records of continental Jurassic in South America. At the Cañadón

Lahuincó locality (Fig. 4), the facies association of the lower half of the outcropping section (up to 147.5 m above the base) suggests a littoral lacustrine paleoenvironment, which consists of an extensive supralittoral and eulittoral zone (Cabaleri and Armella, 1999, 2005).

The Supralittoral Facies are represented by 1) Mudstones with thin microbialite lamination: this facies is constituted by dark clotty micrite, rich in organic matter, and with fenestral fabric; and 2) Mudstones composed of clotty micrite with mudcracks and anhydrite-filled fenestrae and desicc-

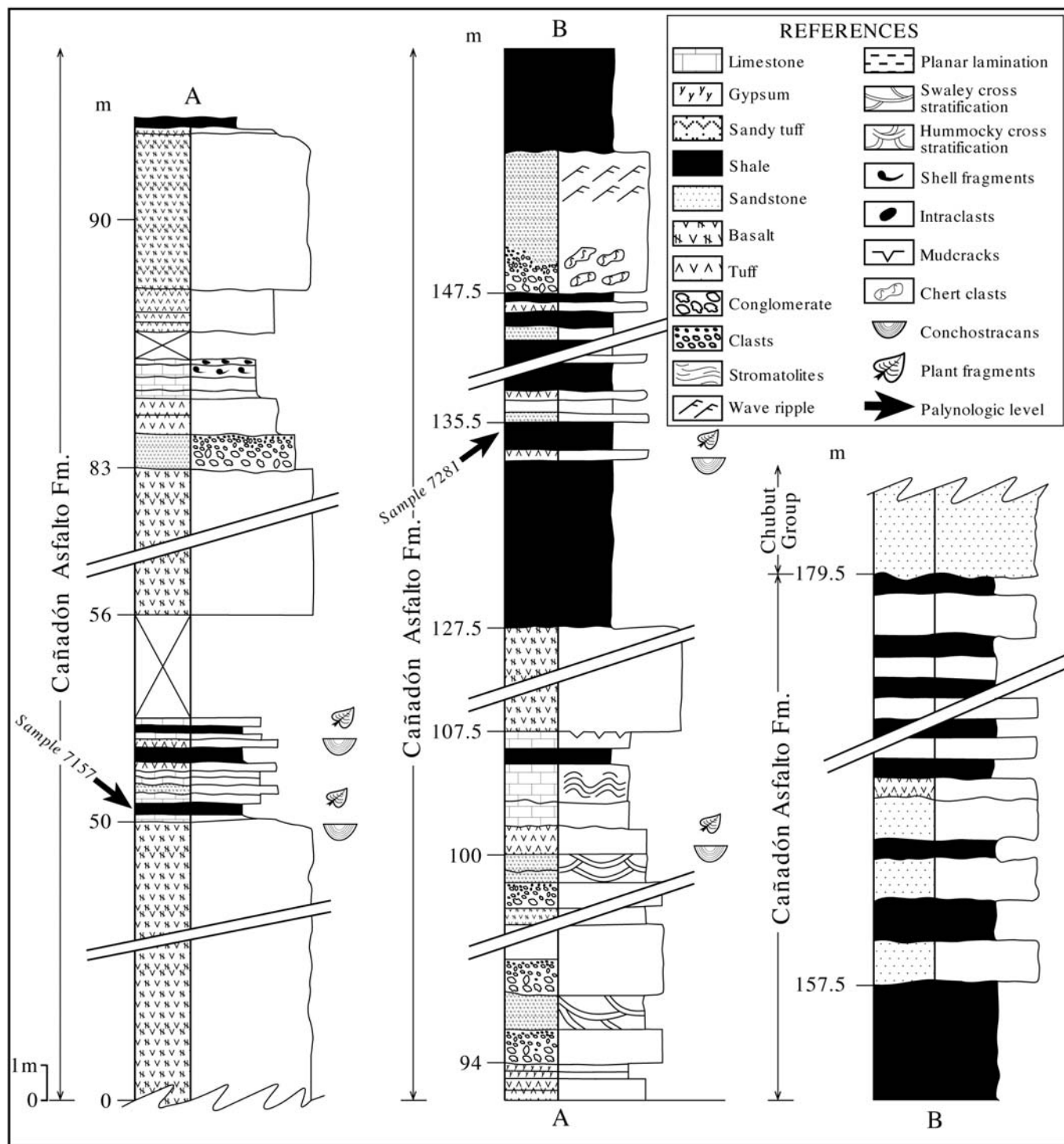


Figure 4. Stratigraphic column of the Cañadón Asfalto Formation at Cañadón Lahuincó. Stratigraphic location of the palynologically fertile samples.

cation breccias: these facies are interbedded with black pelites and fluvio-deltaic deposits. The supralittoral subenvironment covers an extensive area and is characterized by palustrine facies constituted by calcareous mud deposits formed under stagnant water conditions. The features indicate the existence of climatic changes alternating with humid periods, with discharge of materials brought by ephemeral rivers, and extremely arid periods with sulphate precipitation.

On the other side, the Eulittoral Facies are constituted by 3) Microbialite peloidal mudstones/wackestones, with fenestral fabric, algae, conchostracans, bivalves (Martinez *et al.*, 2007), and ostracod remains; and 4) Intraclastic floatstones, poorly sorted, with a grain-supported fabric. The eulittoral zone is adjacent to the supralittoral zone and associated with weak currents and mudcracks. The middle-upper part of the profile (147.5 to 179.5 m above the base) is mainly siliciclastic, with predominance of black pelites, fine massive and laminated tuffs, fine grained sandstones with horizontal lamination and current-ripple marks, medium to coarse calcareous sandstones with trough cross-stratification, fine to medium tuffaceous sandstones with horizontal lamination and matrix-supported conglomerates with subrounded to rounded clasts of fine massive and laminated tuffs and calcareous siltstones with abundant conchostracans.

During the Cretaceous (Barremian-Campanian) new extensive forces produced the fracturing, basculating and rotation of blocks, together with the reactivation of pre-existing faults (Figari and Courtade, 1993), initiating a new subsidence of the basement, regulating the deposition of the Chubut Group, with an angular unconformity over the Cañadón Asfalto Formation. The facies of these basin filling correspond to prograding fluvial cycles of the Los Adobes Formation (Barremian, Codignotto *et al.*, 1979). The posterior thermal subsidence and a pyroclastic cycle of large areal extension correspond to the Cerro Barcino Formation (Aptian to Campanian?, Codignotto *et al.*, 1979).

In the Paleogene initiated a new period of more active convergence between the plates of Nazca and South America, reflected by an intensive explosive volcanism of arc, genetically associated with subduction (Silva Nieto *et al.*, 2002). The calc-alkaline volcanism produced large

volumes of pyroclastic rocks, which filled a pre-existing relief during the Eocene-Oligocene (Sarmiento Group, Simpson, 1941). Simultaneously seated gabbroids, basalts and alkaline basanites, were generated at high depths, outside the magmatic arc (Primavera Formation, Alric, 1996).

During the upper Oligocene-basal Miocene, and as a consequence of the Andean Movements, intensive compressive forces with thrust faulting and folding of the previous tensional structures occurred and the tectonic inversion of the region initiated. In the late Miocene, the region was affected by tensional forces that favored a deep fracturing and the effusion of alkaline basaltic lavas (El Mirador Formation, Volkheimer, 1964). During the Plio-Pleistocene the compressive forces continued, the accommodation of the basement blocks and the re-activation of old fractures which controlled the location of the Chubut River valley, conditioning the modern morphology of the sierras of Lonco Trapial and Pichiñanes. Due to a general uplift of the area, the preexisting longitudinal depressions were enhanced and the Quaternary and Recent sediments began to deposit in their interior.

2. MATERIALS AND METHODS

Fieldwork included sedimentologic and palynologic sampling. Sedimentary facies and facies association were identified in order to define the paleoenvironment and subenvironments. A detailed stratigraphic section was measured at the Cañadón Lahuincó locality (Fig. 4). A detailed palynologic sampling was carried out throughout the whole section.

In the Paleopalynologic Laboratory (IANIGLA, Mendoza), the physical and chemical extraction of more than 30 samples of pelites from the lower part of the Cañadón Asfalto Formation was done by A. Moschetti. Standard palynologic extraction techniques (Volkheimer and Melendi, 1976), involve treatment with hydrochloric and hydrofluoric acids. For the organic matter study, no oxidation by nitric acid was performed, because it affects the fluorescence of the hydrogen-rich particles.

The slides were systematically examined in normal transmitted and incident blue light microscopy, in order to de-

termine the palynofacies (Combaz, 1964). Observation of the slides in blue light fluorescence was an extra help in classifying the nature of unoxidized, thermally immature to mature material and source hydrocarbons. Comparative observations were based in a standard magnification (e.g. a 20X objective).

3. PALYNOFACIES ANALYSIS

A palynofacies is “a body of sediment containing a distinctive assemblage of palynologic organic matter, thought to reflect a specific set of environmental conditions, or to be associated with a characteristic range of hydrocarbon-generating potential”. In addition, palynofacies analysis is

“the palynologic study of depositional environments and hydrocarbon source rock potential based upon the total assemblage of particulate organic matter” (Tyson, 1995). Each sedimentary facies is characterized through its palynologic organic matter content (amorphous organic matter, phytoclasts (translucent and opaque), and palynomorphs) recognized in transmitted white light and incident blue fluorescent light. Organic matter is transported similarly to detritus grains; thus, the results of a particulate organic matter study should correlate with the results of a sedimentary study.

At Cañadón Lahuincó, the amorphous organic matter (60 %, 80-90 %, Fig. 5), consists predominantly of granular to membranaceous amorphous material in samples: 7159,

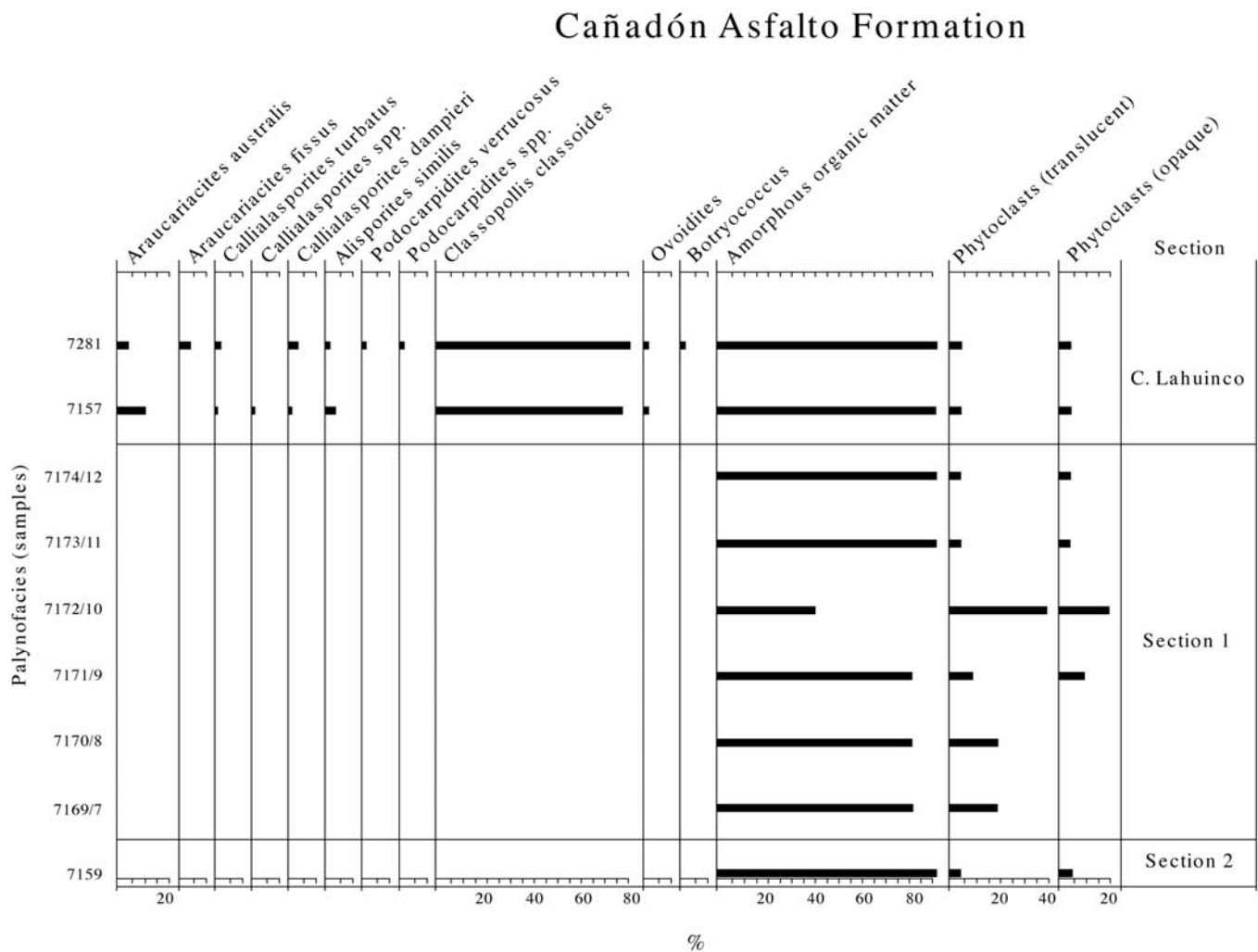


Figure 5. Frequency distributions of palynomorphs and different kinds of organic matter (Palynofacies) in nine samples of dark gray pelites from the lower part of the Cañadón Asfalto Formation, outcropping at Cañadón Lahuincó and nearby areas. Middle Chubut River area. Central Patagonia. Note that palynomorphs have only been observed at Cañadón Lahuincó, while in the other areas studied only unfigured organic matter (amorphous matter, translucent phytoclasts and opaque phytoclasts) have been observed.

7169/7, 7171/9, 7172/10, 7173/11, 7174/12, 7157, and 7281. In sample 7170 the finely dispersed amorphous dominate. The level of fluorescence exhibited by the amorphous organic matter is mostly weak and brown to yellow in color, corresponding to destroyed palynomorphs (Plate 1.7, 1.8). In some cases it is grey to green (samples 7159, 7157) indicating the presence of organic walled paleomicroplankton and *Botryococcus*. Prolonged oxidation of organic matter lowers the hydrogen content and decreases both autofluorescence and source rock potential, prior to its complete destruction (Livingstone and Melack, 1984). Degraded colonies of *Botryococcus* are presumed to reflect differing degrees of microbial degradation in anoxic depositional and early diagenetic conditions, coupled in some cases with thermal alteration (Batten and Grenfell, 1996).

Scarce opaque phytoclasts consist of black, equidimensional, structureless material. Only in sample 7172, they

reach 40 %. The high proportion of phytoclasts is characteristic of environments in which traction predominates over decantation, probably associated with fluvial input (Martinez *et al.* 2005). Taking into account the palynofacies associations and following Del Papa *et al.* (2002), they probably correspond to lacustrine to interdistributary bay environments. The presence of *Botryococcus* indicates falling lake levels and probably more saline conditions.

4. TAXONOMIC LIST OF IDENTIFIED SPECIES

The taxonomic list (Fig. 6) is the result of an extensive sampling throughout the outcropping section. Nevertheless, most samples were palynologically sterile, due to the intensive and repeated volcanic activity during the deposition of the Formation. Only two levels, at 51 m and 135.5

Taxa	Botanical affinity
Spores	
<i>Baculatisporites comaumensis</i> (Cookson) Potonié 1956	Osmundaceae
<i>Dictyophyllidites</i> sp. (Plate 1.5-6)	Pteridophyta
<i>Nevesisporites cf. radiatus</i> (Chlonova) Srivastava, 1972 (Plate 1.4)	Bryophyta
cf. <i>Rugulatisporites</i> sp. (Plate 4.2)	Pteridophyta
Pollen	
<i>Alisporites similis</i> (Balme) Dettmann, 1963 (Plate 2.2)	Caytoniaceae
<i>Alisporites</i> sp.	Caytoniaceae
<i>Araucariacites australis</i> Cookson, 1947 (Plate 2.4)	Araucariaceae
<i>Araucariacites fissus</i> Reiser and Williams, 1969 (Plate 2.6)	Araucariaceae
<i>Callialasporites dampieri</i> (Balme) Dev, 1969 (Plate 3.9-10)	Araucariaceae
<i>Callialasporites microvelatus</i> Schulz 1967	Araucariaceae
<i>Callialasporites turbatus</i> (Balme)Schulz, 1967 (Plate 3.5)	Araucariaceae
<i>Cerebropollenites macroverrucosus</i> (Thiergart) Schulz 1967	Taxodiaceae?
<i>Classopollis classoides</i> (Pflug) Pocock and Jansonius, 1961 (Plate 1.5-6)	Cheirolepidiaceae
<i>Classopollis intrareticulatus</i> Volkheimer 1972	Cheirolepidiaceae
<i>Classopollis simplex</i> (Danzé, Corsin and Laveine) Reiser and Williams 1969	Cheirolepidiaceae
<i>Exesipollenites</i> sp.	Cheirolepidiaceae
<i>Perinopollenites elatoides</i> Couper, 1958 (Plate 2.5)	Taxodiaceae
<i>Phrixipollenites</i> sp. (Plate 3.1)	Podocarpaceae
<i>Podocarpidites verrucosus</i> Volkheimer, 1972	Podocarpaceae
<i>Podocarpidites</i> sp.	Podocarpaceae
<i>Microcachryidites castellanosii</i> Menéndez, 1968 (Plate 2.1)	Podocarpaceae
Algae	
<i>Botryococcus</i> sp. (Botryococcaceae) (Plate 1.2, 4.4-6)	Chlorococcales
<i>Ovoidites</i> spp. (Plate 1.1, 3.3-4, 4.1)	Zygnemataceae
<i>Leiosphaeridia</i> sp.	Prasinophyceae

Figure 6. Taxonomic list of identified species at the Cañadón Lahuincó locality.

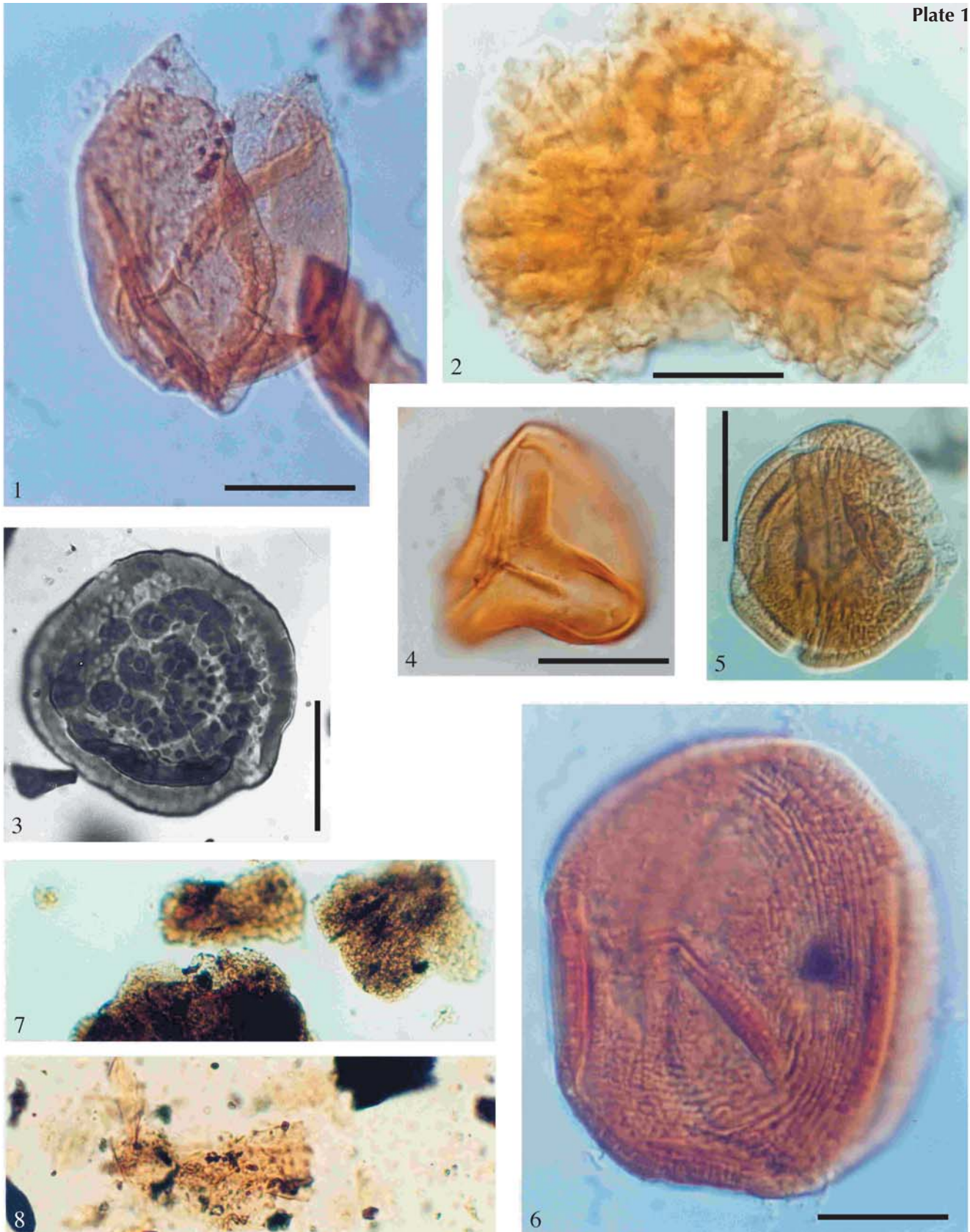


Plate 1. 1. *Ovoidites* sp. (psilate *Spirogyra*-like spore). Sample 7281; 2. *Botryococcus* sp. Sample 7281; 3. *Nevesisporites* cf. *radiatus* (Chlonova) Srivastava. 1972. Sample 7281; 4. *Dictyophyllidites* sp. Sample 7281; 5-6. *Classopollis classoides* (Pflug) Pocock and Jansonius 1951. Sample 7281; 7. Amorphous organic matter, granulese, probably produced by alteration of palynomorphs (exines), tissues (cuticles) and algae (*Botryococcus*), Sample 7169; 8. Organic matter: amorphous, membranaceous and fibrous. Opaque phytoclasts of variable size, mainly present as tablets, Sample 7172. Bars in all figures equal 20 μ m.

m above the outcropping base of the Formation, yielded palynomorph assemblages.

5. COMPARISON OF THE PALYNOFLORA WITH PREVIOUS PALYNOLOGIC AND MACROFLORISTIC RECORDS

An unpublished report of Pöthe de Baldis (1974) about the first palynofloristic assemblage found in carbonaceous shales of the Cañadón Asfalto Formation, in the area of the geologic map 1:200.000: Hoja 45c, Pampa de Agnia, provides a list of the following taxa cited by Nullo and Proserpio (1975):

- Araucariacites australis* Cookson, 1947
- Araucariacites pergranulatus* Volkheimer, 1968
- Classopollis classoides* (Pflug) Pocock and Jansonius, 1961
- Classopollis intrareticulatus* Volkheimer, 1972
- Gliscopollis* sp.
- Alisporites* cf. *robustus* Nilsson, 1958
- Podocarpidites* cf. *ellipticus* Cookson, 1947
- Inaperturopollenites* cf. *indicus* Srivastava, 1966
- Inaperturopollenites microgranulatus* Volkheimer, 1972
- Cyathidites minor* Couper, 1953
- Inaperturopollenites* cf. *turbatus* Balme, 1957

Volkheimer *et al.* (2001) presented an abstract on the palynology and paleoenvironment of the lacustrine Cañadón Asfalto Formation at the 34th Annual Meeting of the American Association of Stratigraphic Palynologists, San Antonio, Texas. They gave a palynofacial characterization of the Formation, mention the environmental significance of *Botryococcus*, the abundance of the thermophilic Cheirolepidiaceae (*Classopollis* spp.) and the presence of Bryophyta (*Nevesisporites* cf. *radiatus*) and pteridosperms (*Alisporites similis*).

A fossil flora collected by Flores in Cañadón Lahuincó, in the lower part of the Cañadón Asfalto Formation, was identified by Frenguelli (1949) and erroneously cited by this author in all later publications as "Flora of Cañadón Asfalto". It contains the following species:

- Sphenopteris patagonica* Halle, 1913
- Sphenopteris hallei* Frenguelli, 1943

- Scleropteris* cf. *furcata* Halle, 1913
- Cladophlebis grahami* Frenguelli, 1947
- Pagiophyllum divaricatum* (Bunbury) Seward, 1894
- Pagiophyllum feistmanteli* Halle, 1913
- Araucarites cutchensis* Feistmantel, 1876
- Arthrotaxis ungeri* (Halle) Florin, 1913
- Elatocladus conferta* (Oldham and Morris) Halle, 1913
- Elatocladus jabalpurensis* (Feistmantel) Sahni, 1928
- Equisetites approximatus* Halle, 1913

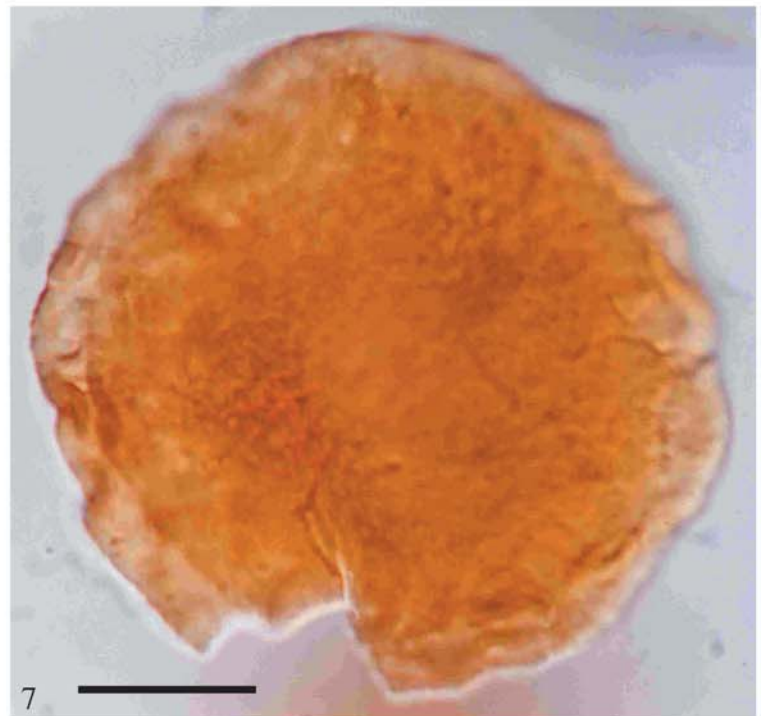
Further information on the Jurassic flora of the middle Chubut river area is given by Cortés and Baldoni (1984). Baldoni (1990) mentions additional material from the Cañadón Asfalto Formation, from Puesto La Vistosa:

- Cladophlebis oblonga* Halle, 1913
- Gleichenites* cf. *taquetrensis* Herbst and Anzotegui, 1968
- Equisetites* sp.
- Araucarites* sp.

The Late Jurassic "Taquetrén Flora", described by Bonetti (1963, 1965) and complemented by Herbst and Anzotegui (1968) is a time equivalent of the lower part of the Cañadón Calcáreo Formation of Proserpio, 1987). It is composed of:

- Equisetites* sp.
- Cladophlebis denticulata* (Brongniart.) Fontaine, Seward, 1900
- Cladophlebis* cf. *antarctica* Nath, Halle, 1913
- Thaumathopteris* sp.
- Clathropteris obovata* Oishi, 1938
- Sphenopteris nordenskjöldii* Halle, 1913
- Archangelskya furcata* (Halle) Herbst, 1964
- Sagenopteris rhoifolia* Presl emend. Röss, 1993
- Gleichenites taquetrensis* Herbst and Anzotegui, 1968
- Zamites pusillus* Halle, 1913
- Zamites* cf. *gigas* Lindley and Hutton, 1837
- Williamsonia* cf. *gigas* (Lindley and Hutton) Carruthers, 1870

Plate 2. All pictures from sample 7281. 1. *Microcachrydites castellanosi* Menéndez 1968; 2. *Alisporites similis* (Balme) Dettmann 1963; 3. *Callialasporites turbatus* (Balme) Schulz 1967; 4. *Araucariacites australis* Cookson 1947; 5. *Perinopollenites elatoides* Couper 1958; 6. *Araucariacites fissus* Reiser and Williams 1969; 7. *Callialasporites microvelatus* Schulz 1967. Bars in all figures equal 20 μ m.



Pagiophyllum feistmantelii Halle emend. Townrow, 1967
Elatocladus conferta (Oldham and Morris) Halle, 1913
Elatocladus casamiquelensis Herbst and Anzotegui, 1968

Araucarites sp.

?*Feruglioa* sp.

Carpolithus sp.

The palynoflora from Cañadón Lahuincó (Fig. 7) contains one formspecies assigned to the bryophyta (*Nevesisporites* cf. *radiatus*), not represented in the macroflora. The 11 species identified of the macroflora correspond to: the Equisetales (*Equisetites approximatus*), Pteridophyta (*Cladophlebis grahami*, *Sphenopteris patagonica*, *S. hallei*), Pteridosperms (*Scleropteris furcata*), Araucariaceae (*Araucarites cuchensis*, *Pagiophyllum divaricatum*, *P. feistmanteli*), Podocarpaceae (*Elatocladus conferta*, *E. jabalpurenensis*) and Taxodiaceae (*Athrotaxis ungeri*) (Fig. 7).

6. STRATIGRAPHIC RANGE OF PALYNOMORPHS

The taxonomic list of identified species gives an overview of the palynologic assemblage, which is well preserved but with low specific diversity. The trilete spores (Bryophyta and Pteridophyta), the 17 species of gymnospermous pollen grains (Cheirolepidiaceae, Araucari-

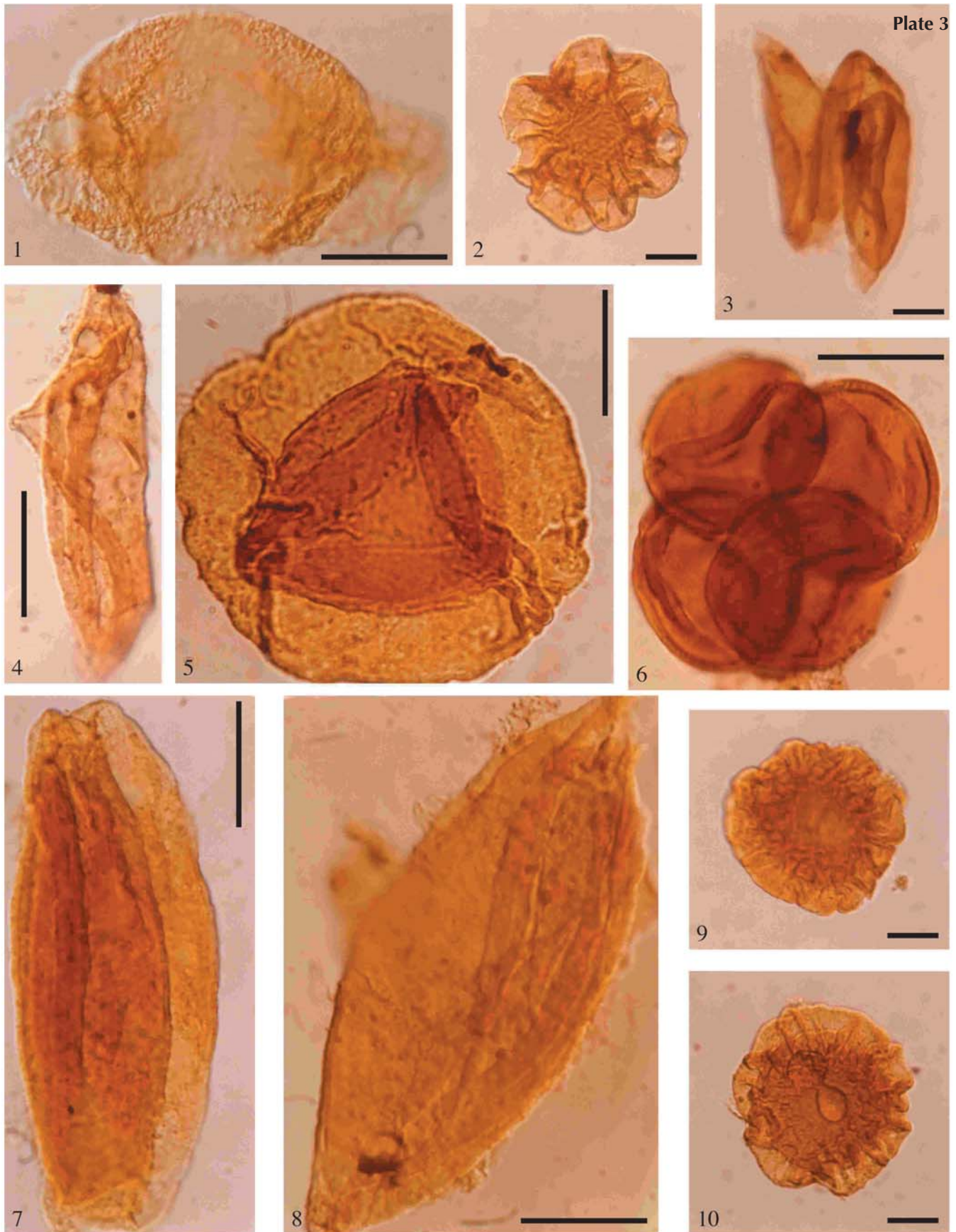
aceae, Podocarpaceae, Taxodiaceae and Caytoniaceae), and the planctonic and non-planctonic green algae present have a wide Mesozoic and Cenozoic stratigraphic range. There are no palynomorph species limited to the Early Jurassic or to the Late Jurassic and /or Early Cretaceous.

An element for establishing the minimum age of the palynologic assemblage is the knowledge of a recently discovered earliest Cretaceous palynoflora in the middle part of the Cañadón Calcáreo Formation at its type locality, where the fluvial and lacustrine/palustrine sediments of the latter unconformably cover, with a basal conglomerate, the mainly carbonatic sequence of the Cañadón Asfalto Formation. The mentioned palynoflora (currently under study by Volkheimer et al., 2008), is characterized by Early Cretaceous elements like *Balmeiopsis limbatus* (Balme) Archangelsky, *Cyclusphaera* cf. *psilata* Volkheimer and Sepúlveda, *Coptospora* sp., and other form species incoming in the Berriasian/Valanginian like *Pilosisporites* cf. *trichopapillosus* (Thiergart) Delcourt and Sprumont and *Trilobosporites* spp.

Plate 3. All pictures from sample 7281. 1. *Phrixipollenites* sp.; 2. *Callialasporites* sp. cf. *C. segmentatus*; 3-4. *Ovoidites* sp. (psilate *Spirogyra*-like spores); 5. *Callialasporites turbatus* (Balme) Schulz 1967; 6. *Classopollis* sp. Tetrade; 7-8. *Ovoidites* sp. (scabrate *Spirogyra*-like spores); 9-10. *Callialasporites* cf. *dampieri* (Balme) Dev 1961. Bars in all figures equal 20 μ m.

Division	Class	Order	Family	Macroflora	Palynoflora
Bryophyta					<i>Nevesisporites</i> cf. <i>radiatus</i>
Tracheophyta	Sphenopsida	Equisetales		<i>Equisetites approximatus</i>	
	Filicopsida	Filicales	Osmundaceae	<i>Cladophlebis grahami</i>	<i>Baculatisporites comaumensis</i> <i>Dictyophyllidites</i> sp., cf. <i>Rugulatisporites</i>
			undifferentiated	<i>Sphenopteris patagonica</i> <i>S. hallei</i>	
	Gymnospermopsida	Coniferales	Pteridosperms	<i>Scleropteris furcata</i>	<i>Alisporites similis</i> <i>Alisporites</i> sp.
			Araucariaceae	<i>Araucarites cuchensis</i> , <i>Pagiophyllum divaricatum</i> , <i>P. feistmanteli</i>	<i>Araucariacites australis</i> , <i>A. fissus</i> , <i>Callialasporites dampieri</i> , <i>C. microvelatus</i> , <i>C. turbatus</i>
			Cheirolepidiaceae		<i>Classopollis classoides</i> , <i>C. intrareticulatus</i> , <i>C.</i> <i>simplex</i> , <i>Exesipollenites</i> sp
			Podocarpaceae	<i>Elatocladus conferta</i> , <i>E. jabalpurenensis</i>	<i>Phrixipollenites</i> sp., <i>Podocarpidites verrucosus</i> , <i>Podocarpidites</i> sp., <i>Microcachrydites</i> <i>castellanosii</i>
			Taxodiaceae	<i>Athrotaxis ungeri</i>	<i>Perinopollenites elatoides</i> <i>Cerebropollenites macroverrucosus</i> (?)

Figure 7. Comparison of the palynoflora of Cañadón Lahuincó with the macrofloristic register of the same locality. For the names of authors of species of the palynoflora see the Taxonomic List of identified species. For authors of the macrofloristic register see chapter 5: Comparison of the palynoflora with previous palynologic and macrofloristic records.



The Jurassic palynoflora of Cañadón Lahuincó is older and clearly different from this Cañadón Calcáreo assemblage, with which it only has in common long ranging forms like *Callialasporites dampieri* (Balme) Dev, *Callialasporites microvelatus* Schulz, *Araucariacites australis* Cookson, *Classopollis classoides* (Pflug) Pocock and Jansonius, and *Podocarpidites verrucosus* Volkheimer. However, the formspecies integrating the assemblage at Cañadón Lahuincó are present in the Middle Jurassic Los Molles Formation of the Neuquén Basin (Martínez *et al.*, 2005) and fit well into the latest early Bajocian to early Bathonian *Microcachryidites castellanosii* Sub-biozone of the same basin (Martínez, 2002).

It is interesting to note that the Jurassic palynoflora described here is a low diversity pioneer flora, installed in a volcanic and lacustrine landscape characterized by intensive and repeated basaltic volcanism with frequent pyroclastic-pumiceous intervals. On the other hand, the local component of the parent plants of the younger Cañadón Calcáreo palynologic assemblage would have grown in an Early Cretaceous deltaic swamp, surrounded by a highly diversified flora of gymnosperms and pteridophytes, which provided, by wind and water transport, the palynomorphs to the sampling locality, previous to the radiation of angiosperms.

7. RECORDS ON VERTEBRATE PALEONTOLOGY

We include this brief review of the vertebrate fauna because it essentially complements the paleoenvironmental and paleobiogeographic framework reflected by the palynologic assemblage. Bonaparte (1979) presented the first record of carnosaurs and sauropod assemblages from the Cañadón Asfalto Formation. The carnosaur *Piatnitzkysaurus floresi* Bonaparte, 1979, related to *Allosaurus*, and the sauropods *Patagosaurus fariasi* Bonaparte, 1979 and *Volkheimeria chubutensis* Bonaparte, 1979 were the first indicators that South America was populated during mid-Jurassic times by carnosaurs and sauropods, and that during the Jurassic a terrestrial faunal interchange between South- and North America and with Africa was possible. A full description of these faunas was given by Bonaparte in 1986. The environmental significance of the big herbiv-

orous sauropods identified by Bonaparte in the lower section of the Cañadón Asfalto Formation, indicating warm conditions and a sufficient disponibility of vegetation, is complementary and corroborates the palynologic and macrofloristic evidence.

Rauhut *et al.* (2002) emphasize that the Cañadón Asfalto Formation, in a large sense, is composed of two sedimentary sequences and found that they are characterized by different dinosaur faunas:

- 1) a lower one, of a probable Middle Jurassic age, with *Volkheimeria*, *Patagosaurus* and the basal tetanuran *Piatnitzkysaurus*. From this sequence proceeds the palynologic assemblage here described.
- 2) a higher one, probably of Kimmeridgian to Tithonian age, with the basal titanosauriform *Tehuelchesaurus* and the recently discovered, short necked sauropod *Brachytrachelopan mesai* Rauhut, Remes, Fechner, Cladera and Puerta, 2005, "with a neck about 40% shorter than other dicraeosaur", and whose ecology may have differed considerably from that of other, long necked sauropods, that obtained food (leafs) from trees. From this second sedimentary sequence proceed also the freshwater fishes from the Cerro Cóndor area (near Puesto Almada and from several new localities near the Chubut river, López-Arbarello, 2004). They are a probable time equivalents of the Cañadón Calcáreo Formation (Rauhut, 2006), being the palaeonisciform *Coccolepis groeberi* Bordas, 1942, *Tharrias feruglioi* Bordas, 1942 and the teleost incertae sedis *Luisiella inexcitata* Bocchino, 1967 the most characteristic forms.

8. COMMUNITIES AND PALEOCLIMATE

The palynomorph assemblage represents (Fig. 8):

- a) a **community of thermophilic cheirolepidiacean conifers**, characterized by the dominance of the pollen genus *Classopollis*. This community inhabited areas near the place of deposition (a lake), as indicated by the high frequency of tetrads and agglomerates of *Classopollis* spp. (Plate 4.3).

Plate 3

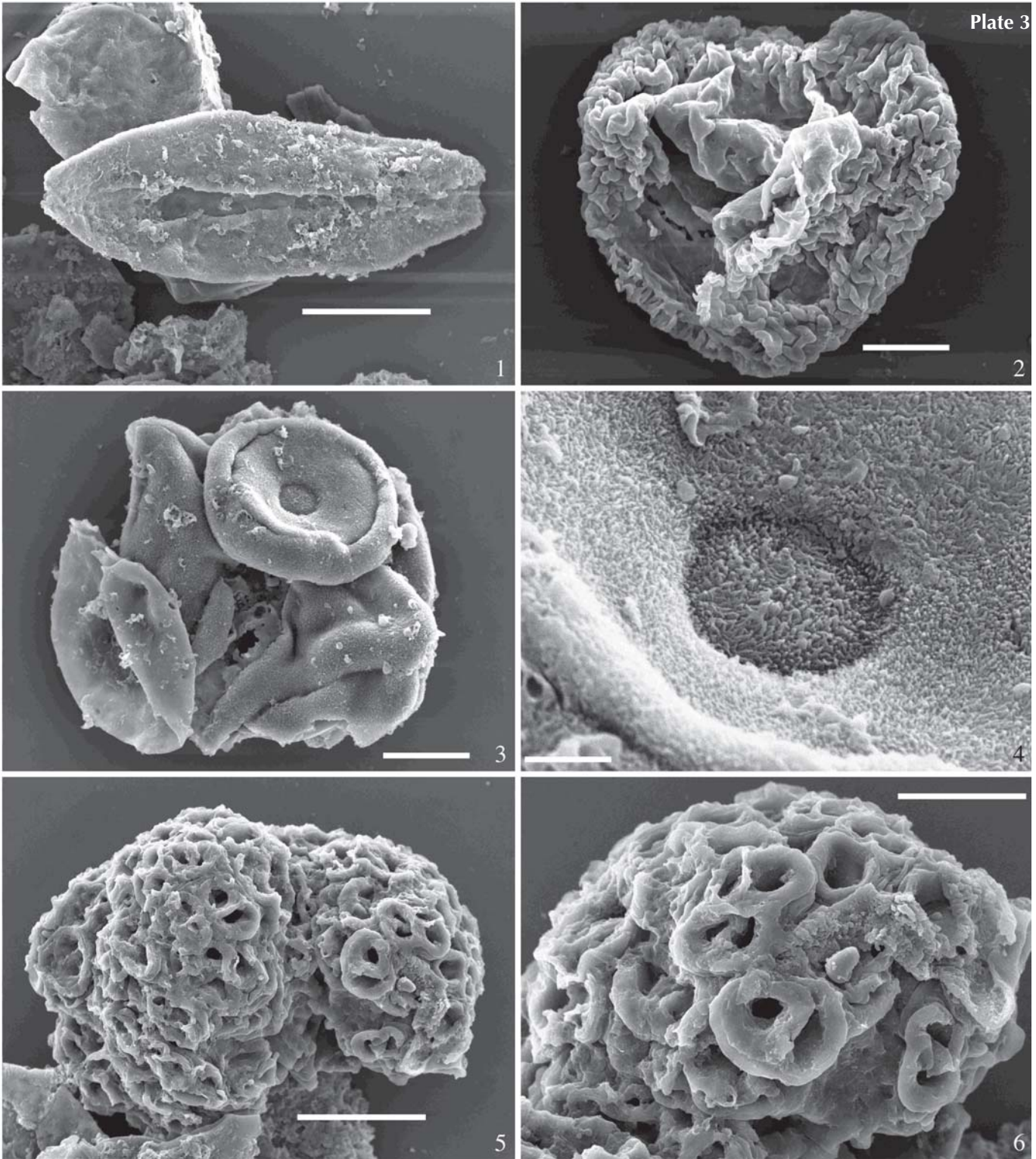


Plate 4. All pictures from sample 7281. 1. *Ovoidites* sp. (psilate *Spirogyra*-like spore); 2. cf. *Rugulatisporites* sp.; 3. Agglomerate of *Classopollis* sp.; 4. Detail of 3: Distal hemisphere of *Classopollis* sp. with pseudopore and detail of hairy micro-ornamentation; 4-5. *Botryococcus* sp. Compound colony; 6. Detail of 5, showing well-defined cups.

- b) a **planctonic community of protocists**, principally composed of colonial chlorococcalean algae of the genus *Botryococcus*, accompanied by rare specimens of prasinophycean algae (*Leiosphaeridia* sp.)
- c) a **hydrophilous community of zygnematacean algae**, represented by *Spirogyra*-like spores (*Ovoidites* spp.). These green algae of non-planctonic lifestyle are often found in slowly flowing waters of the inflow and outflow of ponds and lakes (Zippi, 1998).
- d) a **hydrophilous lowland(?) community of Bryophyta and Pteridophyta**, represented in low proportions and therefore not shown in the distribution chart (Fig. 5). Their spores (*Nevesisporites*, *Dictyophyllidites*, *Baculatisporites*, *Rugulatisporites*) are dispersed by water.
- e) the **Araucariaceae community** could have occupied ecotones associated with lowlands (García *et al.*, 2006.). Some authors related them even with coastal (Abbink, 1998) and/or swampy (Whitaker *et al.*, 1992) communities. The morphologic and structural features of their pollen grains suggest that they are not suitable for transport over large distances or for eolian dispersion (Caccavari, 2003). A special case are the pollen grains of the different formspecies of the genus *Callialasporites*. Their morphology seems better adapted for transport by water than by air. That explains that some early authors considered them as planctonic organisms. From an actualistic point of view, the presence of Araucariacean pollen grains in high proportions could be related to forests of altitude or to relatively lower areas where the transport of pollen was carried out principally by fluvial currents (Martínez *et al.*, 1996), which could be the case of Cañadón Lahuincó.
- f) the **Podocarpaceae community** is thought to have grown on elevated areas. Their anemophilous pollen grains (*Podocarpidites* spp, *Phrixipollenites*, *Microcachryidites*), together with the grains of Caytoniales (*Alisporites similis*) characterize the regional input of palynomorphs into the depositional site.

Climate was the principal factor which regulated the carbonatic sedimentation within the water bodies. The Cañadón Asfalto Formation at Cañadón Lahuincó presents associations of sedimentary facies characteristic for a hy-

drologically closed lacustrine basin, with the input of rivers forming at their mouths small deltaic lobes. During humid seasons (periods of expansion), the water entering the basin flooded the littoral areas and favoured the sedimentation of carbonatic mud with microbialithic levels and black shales characteristic of palustrine environments. The system received the input of fluvial sediments forming beds of conglomerates and sandstones with wave and storm structures.

During dry seasons, the water body contracted and the strong evaporation favoured the precipitation of evaporitic levels and the bottom sediment dried out, originating mud cracks and desiccation breccias. In palustrine environments, paleosoils were formed and in the pools where gypsum-stromatolites were forming. The lower part of the formation was affected by basaltic flows and levels of associated tuffs. The upper part is characterized by intercalations of tuffs, channeled and deltaic sandstones, and conglomerates.

9. CONCLUSIONS

From the palynologic and organopalynologic record, the following paleoenvironmental, paleoclimatic and biostratigraphic conclusions can be drawn:

- a) High abundance of organic matter in all palynologic samples indicates stagnant bottom conditions in the lacustrine bodies.
- b) The algal assemblage, composed of palynomorphs of planctonic (*Botryococcus*) and non-planctonic lifestyle (the *Spirogyra*-like spores of the genus *Ovoidites*) indicates freshwater conditions for the two levels bearing the palynofloras studied. The presence of *Botryococcus* suggests oligotrophic to mesotrophic and euryhaline conditions.
- c) High percentages of pollen of the thermophilic Cheirolepidiaceae indicate warm climate and well drained soils around the lakes. Relatively humid conditions are indicated by the frequency of Araucariacean pollen, transported from nearby elevated areas by wind and water showing the paleovegetation around the lake at Cañadón Lahuincó locality.

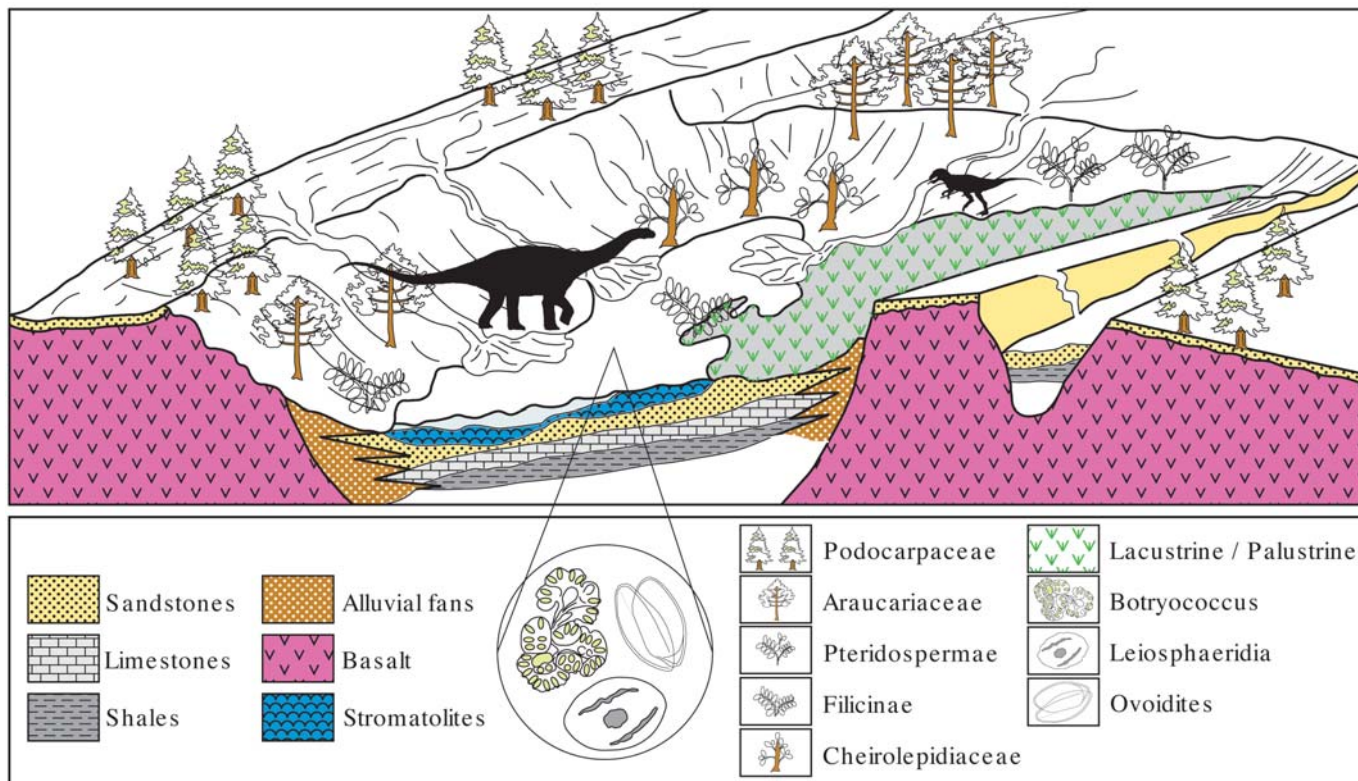


Figure 8. Lower section of the Cañadón Asfalto Formation. Paleovegetation around the lake. Cañadón Lahuincó area, Chubut Province, Argentina. The dinosaur icons correspond to herbivor *Patagosaurus* (centre) and the carnivor *Piatnitzkysaurus* (on the right side).

- d) High percentages of Chlorococcales (*Botryococcus* sp.) are responsible for the presence of abundant bituminous matter in the pelites and palustrine-type limestones of the Cañadón Asfalto Formation.
- e) The age of the palynologic assemblage of the Cañadón Asfalto Formation at Cañadón Lahuincó locality is defined by formspecies integrating the Middle Jurassic (latest early Bajocian to early Bathonian) *Microcachrydites castellanosii* Sub-biozone (Martínez, 2002).
- f) A Middle Jurassic age is also compatible with the age of the overlying earliest Cretaceous palynoflora contained in the middle part of the Cañadón Calcáreo Formation.

From the stratigraphic analysis of the Cañadón Asfalto Formation at Cañadón Lahuincó results a volcano-sedimentary sequence with olivinic basalts and green tuffs at the base, covered by a siliciclastic, lacustrine sequence. The sediments represent short cycles related with periods of contraction and expansion of the paleolake water level.

During expansion, the lake invaded littoral areas, producing black pelites and limestones of palustrine type. In change, during extremely dry intervals, the water body contracted, gypsum precipitated and dissection breccia formed. Such conditions prevailed in the uppermost levels of the Formation, where the sedimentary regime was changing from carbonatic to siliciclastic, with levels indicating deltaic environments and hyperconcentrated deposits.

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Taxonomic revision and phylogenetic classification of the Late Cretaceous (Upper Santonian-Maastrichtian) serial planktonic foraminifera (Family Heterohelicidae Cushman, 1927) with peripheral test wall flexure

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Resumen

Un linaje de foraminíferos planctónicos seriados de edad Santoniense Superior-Maastrichtiense desarrolló una flexión en su pared periférica (Familia Heterohelicidae Cushman, 1927). Este linaje está compuesto por dos géneros, *Hendersonia* nov. gen. y *Paraspiroplecta* n. gen. El género *Hendersonia*, de edad Santoniense Superior-Campaniense, está formado por tres especies biseriales, *H. hendersoni* n. sp., *H. carinata* (Cushman, 1938) y *H. jerseyensis* n. sp. Este linaje muestra el desarrollo gradual de flexión en la pared periférica. El género *Paraspiroplecta* (Campaniense Superior-Maastrichtiense) presenta un enrollamiento inicial planoespiral y la flexión en la pared periférica pobremente desarrollada, probablemente relict. Este género es monoespecífico, formado únicamente por *P. navarroensis* (Loeblich, 1951).

Palabras clave: Foraminífero planctónico, Santoniense-Maastrichtiense, Taxonomía, Nuevo género, Nuevas especies

Abstract

Peripheral test wall flexure is developed in an upper Santonian-Maastrichtian lineage of serial planktonic foraminifera (Family Heterohelicidae Cushman, 1927). This lineage consists of two genera, *Hendersonia* nov. gen. and *Paraspiroplecta* nov. gen. *Hendersonia* (Upper Santonian-Campanian) includes three biserial throughout species, namely *H. hendersoni* nov. sp., *H. carinata* (Cushman, 1938) and *H. jerseyensis* nov. sp. This lineage shows the gradual development of the peripheral test wall flexure. *Paraspiroplecta* (Upper Campanian-Maastrichtian) presents early planispiral coil and weakly developed, probably relict, peripheral test wall flexure. It is monospecific, including only *P. navarroensis* (Loeblich, 1951).

Keywords: Planktonic foraminifera, Santonian-Maastrichtian, Taxonomy, New genera, New species

1. INTRODUCTION

The test morphology of two Cretaceous serial planktonic foraminiferal lineages was re-evaluated in two recent studies (Georgescu, 2007a, 2007b). Georgescu (2007a) demonstrated that the incipient reticulate ornamentation, presence/absence of the supplementary apertures along the central 'zigzag' suture and rate of chamber growth can

be used to separate two distinct species in a late Campanian-Maastrichtian lineage formalized as *Braunella* Georgescu, 2007, namely *B. punctulata* (Cushman, 1938) and *B. brauni* Georgescu, 2007. The earliest 'pseudoguembelinid' planktonic foraminifera of the Turonian were included in a distinct genus, namely *Huberella* Georgescu, 2007, based on the lack of supplementary apertures along the central 'zigzag' suture; the pseudoguembelinid appear-

ance of the tests included in this genus-lineage is apparently given by the chamber backward prolongations, which are attached to the previous chamber in the same row of the biserial stage. These studies showed that certain minute morphological features, which cannot be studied with accuracy with the aid of the classical optical binocular microscope, occur consistently in the stratigraphic record of the taxonomic units described in the past as species. Accordingly, higher accuracy in the study of the morphological features of the heterohelid tests can be achieved by large scale observations based on the scanning electron microscope techniques (SEM and ESEM).

The peripheral structures are relatively poorly developed in the Cretaceous serial planktonic foraminifera (Superfamily Heterohelicacea Cushman, 1927) when compared to other Cretaceous planktonic groups, such as rotaliporids and globotruncanids. Most of them were described by Cushman (1938): *Gümbelina globocarinata*, *G. carinata* and *G. punctulata*. The genus *Gümbelina* Egger, 1899 to which they were originally assigned is not valid, as shown by Montanaro Gallitelli (1957) and Loeblich & Tappan (1961). Accordingly, they were reassigned to *Heterohelix* Ehrenberg, 1843 and this taxonomic status was recognized in the subsequent taxonomic revisions by Pesagno (1967), Masters (1977) and Nederbragt (1991).

Examination of the type material of the three species, together with a vast number of newly collected specimens showed that no true peripheral keel is present in either of them. Accordingly, careful taxonomic revision is necessary in order to clarify their test morphology, phylogenetic relationships and taxonomic status. This begun with the reassignment of *Gümbelina punctulata* to *Braunella* Georgescu, 2007, in which it was designated the type species. Noteworthy, no peripheral structures were developed in the *Braunella punctulata* – *Braunella brauni* Georgescu, 2007 lineage (Georgescu, 2007a).

Herein we propose a taxonomic re-evaluation of *Gümbelina carinata* (Cushman, 1938, p. 18, pl. 3, fig. 10), which is considered the type species of *Hendersonia* nov. gen. This new genus is proposed for an upper Santonian-Campanian lineage consisting of three species: *H. hendersoni* nov. sp. – *H. carinata* – *H. jerseyensis* nov. sp. The peripheral structures of the species in the *Hendersonia* lineage consist of a test wall flexure, contrasting thus to the pe-

ripheral structures of *Gublerina rajagopalani* Govindan, 1972 of the upper Campanian-Maastrichtian in which it consists of thick costae parallel to the test periphery (Govindan, 1972). The well-developed test wall flexure at the test periphery appears a characteristic of this genus-lineage among the planktonic foraminifera with serial chamber arrangement. Vestiges of the peripheral test wall flexure are herein reported in excellently preserved tests with early planispiral coil, originally described as *Heterohelix navarroensis* (Loeblich, 1951). A new genus is proposed to accommodate this species, *Paraspiroplecta* nov. gen. High detail test morphology observations suggests that *Hendersonia* is the ancestor of *Paraspiroplecta*.

2. STUDIED MATERIAL

The material analyzed for this study comes mostly from DSDP/ODP (Deep Sea Drilling Project/Ocean Drilling Program) wells drilled in the Caribbean region and Atlantic Ocean. These include DSDP Site 95 (Gulf of Mexico, Yucatan Shelf), DSDP Site 356 (São Paulo Plateau), DSDP Site 357 (Rio Grande Rise), DSDP Site 511 (Falkland Plateau), ODP Holes 1050C and 1052E (Blake Plateau, western North Atlantic Ocean) and ODP Leg 174AX (New Jersey coastal plain). Additional material was studied from a new core, Mullinax-3 (Mull-3), which was drilled by DOSECC (Drilling, Observation and Sampling of Earth's Continental Crust) at Falls County Brazos River, Texas (Fig. 1). A concise presentation of the occurrences and preservation of the species of *Hendersonia* nov. gen. and *Paraspiroplecta* nov. gen. in these sections investigated during our study is also presented (Fig. 2). Very well preserved specimens of *Gublerina rajagopalani* Govindan, 1972 from the Maastrichtian sediments of the Exmouth Plateau (East Indian Ocean) were studied in order to compare the peripheral structures of this species with those of *Hendersonia* nov. gen. and *Paraspiroplecta* nov. gen. Rich and well preserved material of *Hendersonia carinata* (Cushman, 1938) was studied in the Van Morkhoven Collection (National Museum of Natural History, Washington, D.C.). No precise location of the wells from which this material was collected can be given.

The type specimens of *Hendersonia carinata* (holotype USNM 307940 and paratypes USNM 307938-307939)

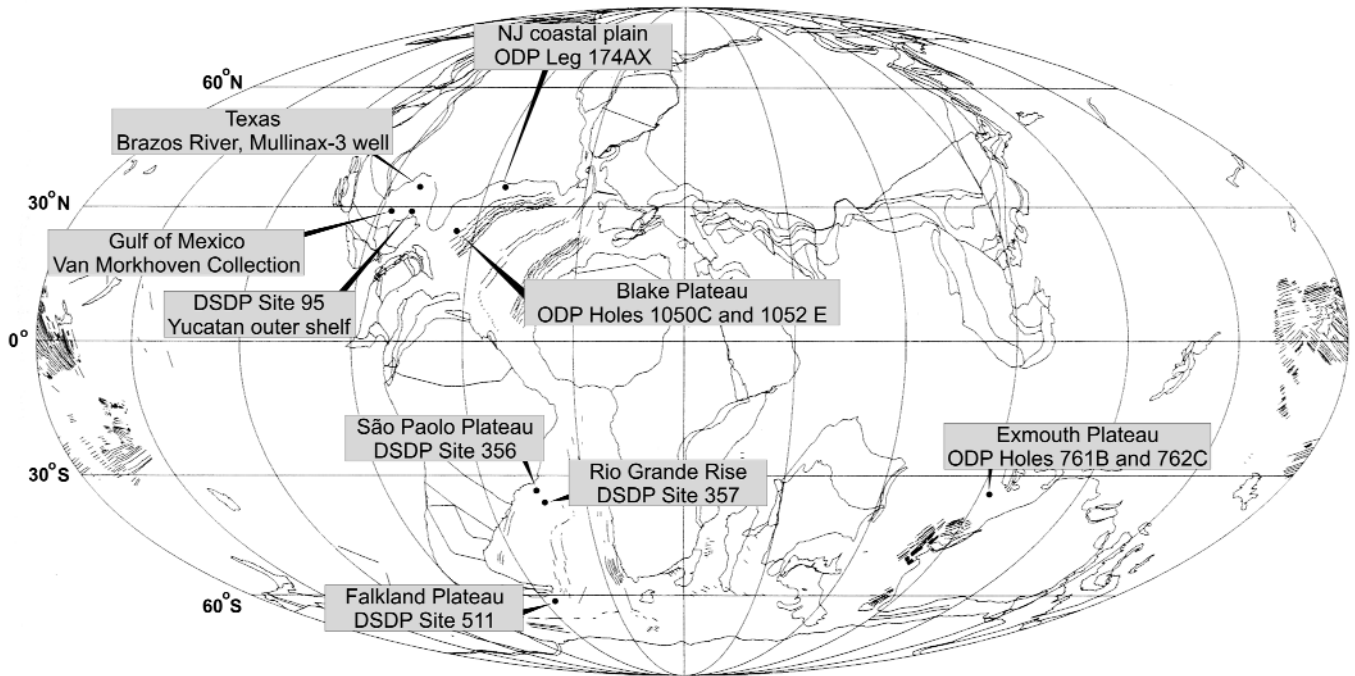


Figure 1. Location of the sites of provenance of the specimens of *Hendersonia* nov. gen. and *Paraspiroplecta* nov. gen., which were used in this study. Base map after Hay *et al.* (1999).

Well	Location	Age	Species	Preservation
3SDP Site 95	Yucatan outer shelf, Gulf of Mexico	Upper Santonian	<i>Hendersonia hendersoni</i> n. sp	Good
3SDP Site 511	Falkland Plateau, South Atlantic Ocean	Upper Campanian	<i>Hendersonia hendersoni</i> nov. sp. (type locality)	Excellent
3SDP Site 356	São Paulo Plateau, South Atlantic Ocean	Upper Santonian	<i>Hendersonia carinata</i> (Cushman, 1938)	Moderate to poor
3SDP Site 357	Rio Grande Rise, South Atlantic Ocean	Upper Santonian	<i>Hendersonia carinata</i> (Cushman, 1938)	Moderate to poor
3D P Leg 174AX	New Jersey coastal plain	Upper Santonian and upper Campanian	<i>Hendersonia carinata</i> (Cushman, 1938)	Excellent
		Lower Campanian	<i>Hendersonia jerseyensis</i> nov. sp. (type locality)	Excellent
		Upper Campanian	<i>Paraspiroplecta navarroensis</i> (Loeblich, 1951)	Excellent
3DP Hole 1050 C	Blake Plateau, Western North Atlantic	Maastrichtian	<i>Paraspiroplecta navarroensis</i> (Loeblich, 1951)	Good
DDP Hole 1052 E	Blake Plateau, Western North Atlantic	Maastrichtian	<i>Paraspiroplecta navarroensis</i> (Loeblich, 1951)	Good

Figure 2. Occurrence and preservation of the species of *Hendersonia* nov. gen. and *Paraspiroplecta* nov. gen. in the Deep Sea Drilling Project/Ocean Drilling Program wells investigated during our study.

and *Heterohelix navarroensis* (holotype USNM 309369 and USNM 309370-309379) were examined in the Cushman Collection at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (Fig. 3). Two other heterohelicid species were described by Cushman (1938) with keels on the lateral sides of the earlier portion of the test: *Gümbelina globocarinata* (ibid., p. 10, pl. 2, figs 4-5) and *G. punctulata* (ibid., p. 13, pl. 2, figs 15-16). Peripheral keels were not observed in the type specimens of *G. globocarinata* (holotype USNM 307952 and paratypes USNM 307953-307954), which were examined in the Cushman Collection (NMNH). The morphological features, taxonomic status and stratigraphic distribution of *Gümbelina punctulata* were recently re-evaluated by Georgescu (2007a) who considered it the type species of *Braunella* Georgescu, 2007. No peripheral keels are present in the type specimens of this species (Cushman Collection, NMNH).

3. SYSTEMATIC TAXONOMY

Higher categories are after Loeblich & Tappan (1987). Species concept follows Georgescu & Huber (2007).

Order FORAMINIFERIDA Eichwald, 1830

Suborder GLOBIGERININA Delage & Hérouard, 1896

Superfamily HETEROHELICACEA Cushman, 1927

Family HETEROHELICIDAE Cushman, 1927

Genus *Hendersonia* nov. gen.

Type species: *Gümbelina carinata* Cushman, 1938, p. 18, pl. 3, fig. 10.

Diagnosis.— Heterohelicidae with test wall flexure on the lateral sides of the test, resulting in carinate appearance.

Description.— Test is biserial throughout. Chambers are globular to subrectangular in lateral view, increasing gradually and moderately in size as added. Sutures are distinct and depressed, straight to slightly oblique to the test axis of growth. Periphery is subacute due to the development of a test wall flexure, which results in the duplication of the test wall in the periphery region. Aperture is arch-shaped, situated at the base of the last formed chamber. Two small and symmetrical periapertural flanges, rimmed or not, border the aperture on the lateral sides. Apical part

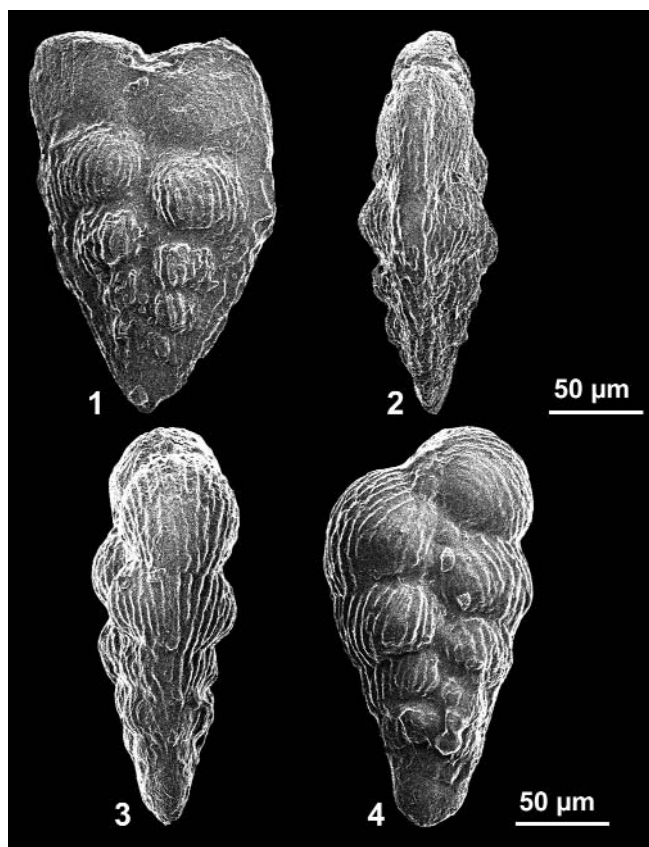


Figure 3. Holotypes of *Hendersonia carinata* (Cushman, 1938) and *Paraspiroplecta navarroensis* (Loeblich, 1951) from the National Museum of Natural History, Washington D.C. 1-2. Holotype of *Hendersonia carinata* (Cushman, 1938) originally described as *Gümbelina carinata* by Cushman (1938, pl. 3, fig. 10) from the lower Taylor Marl of Lamar County, Texas (USA). 3-4. Holotype of *Paraspiroplecta navarroensis* (Loeblich, 1951) originally described as *Heterohelix navarroensis* by Loeblich (1951, pl. 12, figs 1-2) from the Kemp Clay of the Guadalupe County, Texas (USA). The two specimens were figured using the ESEM technique and were previously figured online in the Taxonomic Dictionary of Mesozoic Foraminifera by the Mesozoic Foraminifera Working Group (2006, B.T. Huber – editor).

can be smooth. Pustulose periapertural area is present above the aperture. Chamber surface ornamented with costae, which can be parallel to the periphery, longitudinal or oblique to the test axis of growth. Ornamentation thickenings can be present on the earlier chambers in the proximity of the central 'zigzag' suture. Test wall calcareous, hyaline perforate; pores can be simple, or situated in the center of a crater-like structure in the evolved species.

Remarks.— *Hendersonia* nov. gen. is characterized by the development of the test wall flexure in the periphery area. Another species with peripheral structures of the Upper Cretaceous (upper Campanian-Maastrichtian) is *Gublerina*

rajagopalani Govindan, 1972. It was described by Govindan (1972, p. 170) as having the test periphery "... ornamented with thick, strongly raised, longitudinal costae." Nederbragt (1991) re-evaluated the morphology of this species and considered the "Periphery of early part of test acute to keeled, becoming more rounded in the adult chambers." (Nederbragt, 1991, p. 348). Examination of well preserved material from DSDP Site 356 (São Paulo Plateau, South Atlantic Ocean), DSDP Site 357 (Rio Grande Rise, South Atlantic Ocean) and ODP Holes 761B and 762C (Exmouth Plateau, East Indian Ocean) confirmed the original description by Govindan, the keeled appearance of the earlier portion of the test being given by the development of thick costae. Accordingly, *Gublerina rajagopalani* appears phylogenetically unrelated to any species of *Hendersonia*, in which the subacute test periphery is the result of the development of a test wall flexure.

Species included.— *Gümbelina carinata* Cushman, 1938 (p. 18, pl. 3, fig. 10); *Hendersonia hendersoni* nov. sp.; *Hendersonia jerseyensis* n. sp.

Phylogenetic relationships.— *Hendersonia* nov. gen. evolved from the *Heterohelix planata* (Cushman, 1938)

group of species and is the ancestor of *Paraspiroplecta* nov. gen. (Fig. 4).

Etymology.— Genus named after Dr Charles M. Henderson (University of Calgary) in appreciation for his outstanding contributions in paleontology and biostratigraphy.

Stratigraphic range.— Upper Santonian-Campanian (from the upper part of the *Dicarinella asymetrica* Biozone throughout *Radotruncana calcarata* Biozone).

Geographic distribution.— USA (Texas, Alabama, Mississippi, New Jersey), Africa (Nigeria, Tunisia), Gulf of Mexico (Yucatan outer shelf), South Atlantic Ocean (Falkland Plateau, Rio Grande Rise and São Paulo Plateau).

Hendersonia hendersoni nov. sp.
(Pl. 1, Figs. 1-10)

1982 *Heterohelix planata* (Cushman) – Oláníyí Odébòdé, p. 240, pl. 1, fig. 3, pl. 2, fig. 1 (Santonian-Campanian, Calabar Flank, Nigeria).

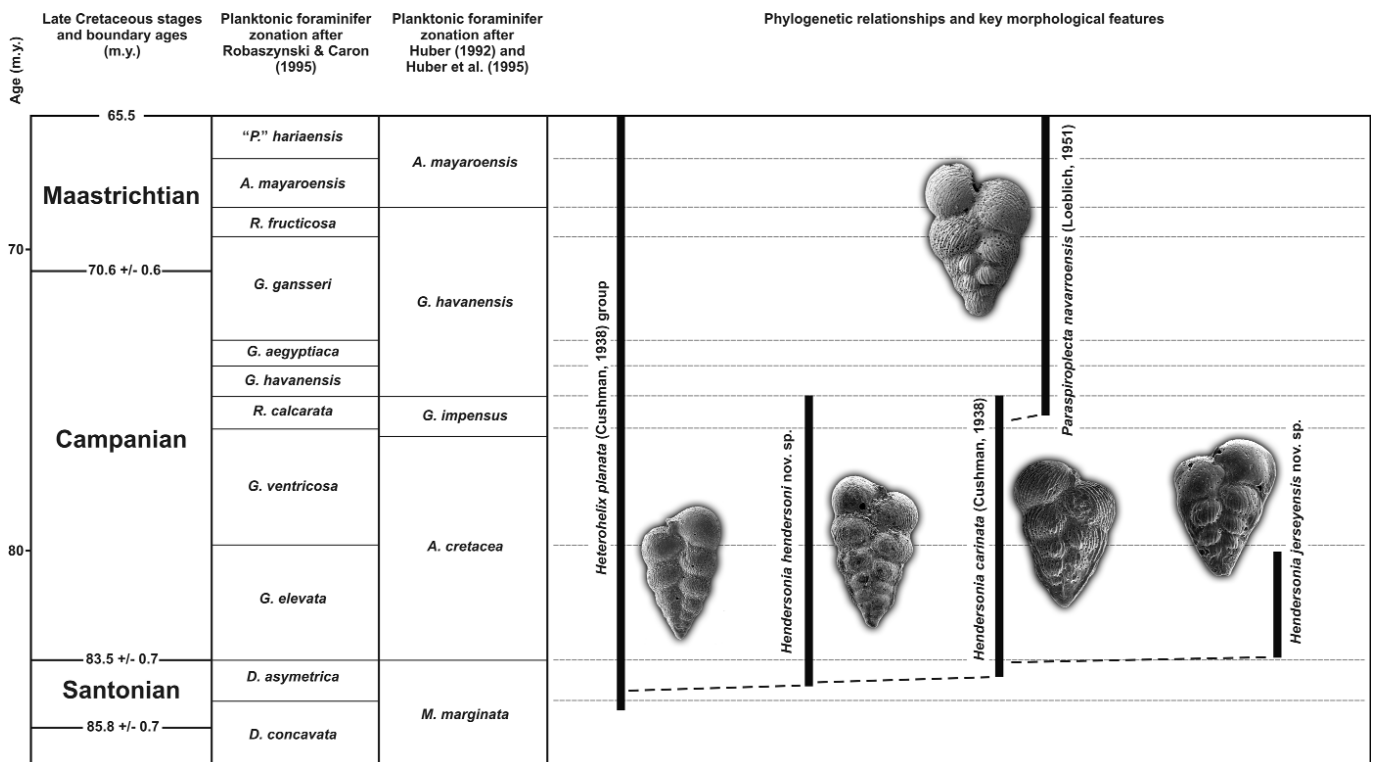


Figure 4. Inferred phylogeny in the *Hendersonia-Paraspiroplecta* lineage. Absolute ages after Gradstein et al. (2004).

1983 *Heterohelix glabrans* (Cushman) – Krasheninnikov & Basov, pl. 12, figs 9-10 (Upper Campanian, DSDP Site 511, Falkland Plateau, South Atlantic Ocean).

1991 *Heterohelix carinata* (Cushman) – Nederbragt, p. 341, pl. 1, fig. 5 only (Lower Campanian, El Kef, Tunisia).

Holotype.– Specimen WKB 010027.

Dimensions of the holotype.– Length: L = 0.263 mm; width: W = 0.150 mm; W/L = 0.570; thickness: T=0.070 mm; T/W = 0.266.

Paratypes.– Five specimens WKB 010028.

Dimensions.– L = 0.240-0.273 mm; W = 0.150-0.196 mm; W/L = 0.570-0.717; T = 0.070-0.091 mm; T/L = 0.266-0.334.

Type locality.– DSDP Site 511, Falkland Plateau (South Atlantic Ocean). Geographic coordinates: 51° 00' S, 47°58' W.

Type level.– Upper Campanian (*Globigerinelloides impensus* Biozone), Sample 79-511-24-5, 21-24 cm. Planktonic foraminiferal zonation after Huber (1992) and Huber et al. (1995).

Material.– Over fifty specimens.

Etymology.– As for the genus.

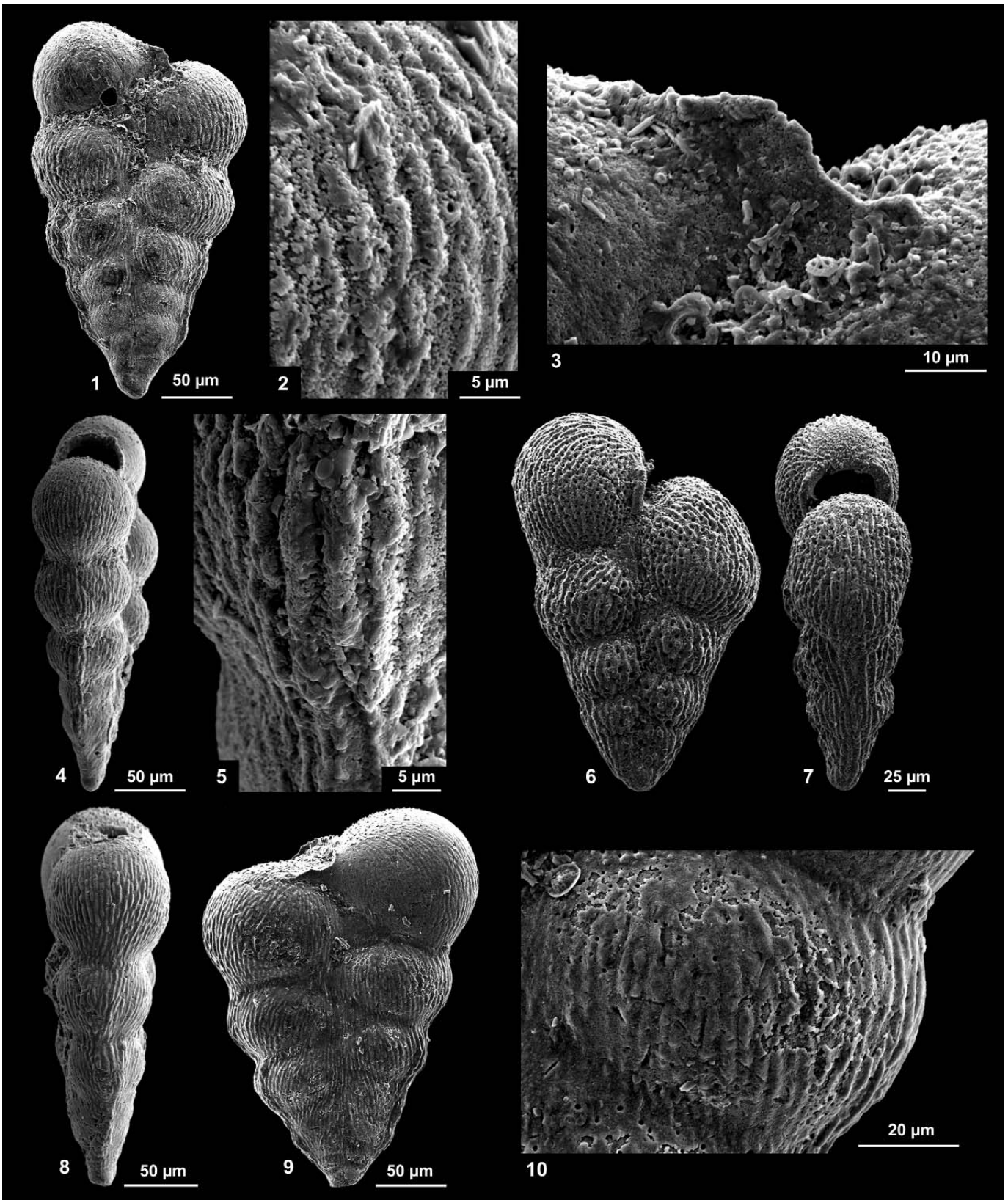
Diagnosis.– Primitive *Hendersonia*, with incipient test wall flexure on the lateral sides of the earlier portion of the test.

Description.– Test biserial throughout. Proloculus is small (8.8-11.0 µm), followed by 12 to 15 chambers that increase gradually, slowly to moderately in size as added. Chambers are globular in lateral view, overlapping at various rates; those of the earlier portion of the test are subrectangular in shape (Pl. 1, Figs 1, 6, 9), excepting the last formed one or two, petaloid. Chambers are subglobular to globular in edge view (Pl. 1, Figs 4, 7, 8), gradually increasing in size as added. Sutures are distinct and depressed, straight and slightly oblique to the test axis of growth. Periphery is subacute in the earlier portion of the

test due to the development of a test wall flexure (Pl. 1, Figs 1, 4, 8, 9); in the absence of the test wall flexure, last-formed chambers present rounded periphery. Aperture is in the shape of a medium-high arch situated at the base of the last formed chamber. Two small, imperforate to microperforate, symmetrical flanges border the aperture; flanges can be simple or rimmed (Pl. 1, Figs 3, 6). Chamber surface is ornamented with costae with variable width (2.3-3.1 µm). The earlier part of the test can be smooth; a periapertural pustulose area is consistently present (Pl. 1, Figs 1, 3, 4, 6, 7-9). Test wall calcitic, hyaline and microperforate to finely perforate; pore size varies between 0.7 and 2.4 µm (Pl. 1, Figs 2, 5, 6, 9).

Remarks.– *Hendersonia hendersoni* nov. sp. consists of two test varieties. The “primitive” variety (Pl. 1, Figs 1-5, 8-10) is dominant at lower latitudes (e.g., South Atlantic Ocean) and presents resemblances with the ancestral species of the *Heterohelix planata* (Cushman, 1938) group in general test appearance, finer costae (3.3 to 3.7 µm) and small pores (0.7-0.9, rarely up to 1,1 µm). The “evolved” variety (Pl. 1, Figs 6-7) is dominant in the tropical waters (e.g., southern USA, Yucatan outer shelf). It presents thicker costae (3.6-4.1 µm) and larger pores (1.0-2.4 µm), resembling by these features the descendant species, *Hendersonia carinata* (Cushman, 1938). The two test varieties record the incipient stage of evolution of the *Hendersonia* and the initiation of the lineage is apparent in the increase in costae width, pore diameter and consistent occurrence of incipient test wall flexure on the lateral sides of the early part of the test, the latter giving the appearance of keeled periphery. *Hendersonia hendersoni* differs from *Heterohelix planata* in having coarser costae, larger pores and incipiently developed test wall flexure on the lateral sides of the earlier parts of the tests. Cushman (1938, p. 10, pl. 2, figs

Plate 1. Specimens of *Hendersonia hendersoni* nov. gen., nov. sp. 1-5. Holotype from the Upper Campanian (*Globigerinelloides impensus* Biozone) of the Falkland Plateau (South Atlantic Ocean), Sample 79-511-24-6, 20-23 cm; note the fine pores (2, 5), rimmed periapertural flange (3) and parallel costae at the test periphery (5). 6-7. Hypotype from the Upper Santonian (*Dicarinella asymetrica* Biozone) of the Yucatan outer shelf (Gulf of Mexico), Sample 10-95-14-1, 99-112 cm; note the weak test wall flexure on the earlier chambers of the test, which is best visible in edge view (7). 8-10. Paratype from the Upper Campanian (*Globigerinelloides impensus* Biozone) of the Falkland Plateau (South Atlantic Ocean), Sample 79-511-24-6, 20-23 cm; note the fine costae (10) and test wall flexure developed on the earlier portion of the test (8, 9).



4-5) described *Gümbelina globocarinata* from the Campanian of Texas (USA). Examination of the type specimens of this species (NMNH, Cushman Collection, Washington, D.C.) showed that according to the test periphery, which is not carinate, and the general test architecture, chamber shape and aperture shape and periapertural structures, it should be included within the *Heterohelix globulosa* (Ehrenberg, 1840) group of species (Fig. 5).

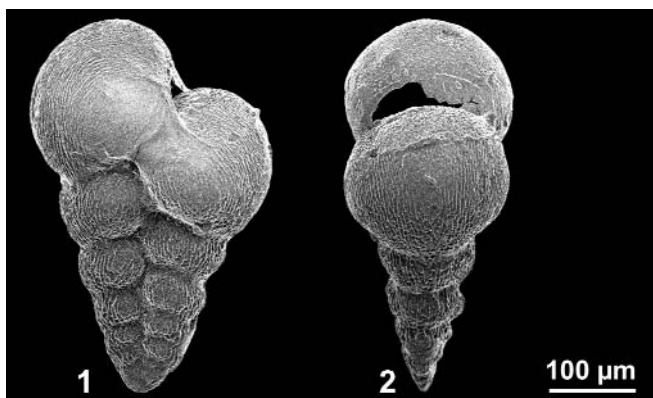


Figure 5. 1-2. Holotype of "*Heterohelix*" *globocarinata* (Cushman, 1938) originally figured as *Gümbelina globocarinata* (Cushman, 1938, p. 10, pl. 2, fig. 4) from the Taylor Marl of the Lamar County, Texas (USA). ESEM illustration previously published online in the Taxonomic Dictionary of Mesozoic Foraminifera by the Mesozoic Foraminifera Working Group (2006, B. T. Huber – editor).

Phylogenetic relationships.– *Hendersonia hendersoni* evolved from a species of the *Heterohelix planata* group; it is the ancestor of *Hendersonia carinata* (Cushman, 1938) (Fig. 4).

Stratigraphic range.– Upper Santonian-Campanian (from the upper part of the *Dicarinella asymetrica* Biozone throughout the *Radotruncana calcarata* Biozone). Planktonic foraminiferal biozonation after Robaszynski & Caron (1995).

Geographic distribution.– Gulf of Mexico (Yucatan outer shelf), western Africa (Nigeria), northern Africa (Tunisia) and South Atlantic Ocean (Falkland Plateau).

Hendersonia carinata (Cushman, 1938) – emended
(Pl. 2, Figs. 1-12, Pl. 3, Figs. 1-2)

1938 *Gümbelina carinata* Cushman, p. 18, pl. 3, fig. 10 (Campanian, Texas, USA).

1946 *Gümbelina carinata* Cushman – Cushman, p. 105, pl. 45, fig. 8 (Santonian-Campanian, Texas, Mississippi, USA).

1957 *Heterohelix carinata* (Cushman) – Montanaro Galitelli, pl. 31, fig. 16 (Santonian-Campanian, southern USA).

1977 *Heterohelix carinata* (Cushman). Masters, 1977, p. 339, pl. 1, figs 4-5 (Santonian Campanian, southern USA).

1977 *Heterohelix carinata* Cushman – Petters, pl. 1, figs 4-5 (Upper Santonian-Campanian, New Jersey, USA).

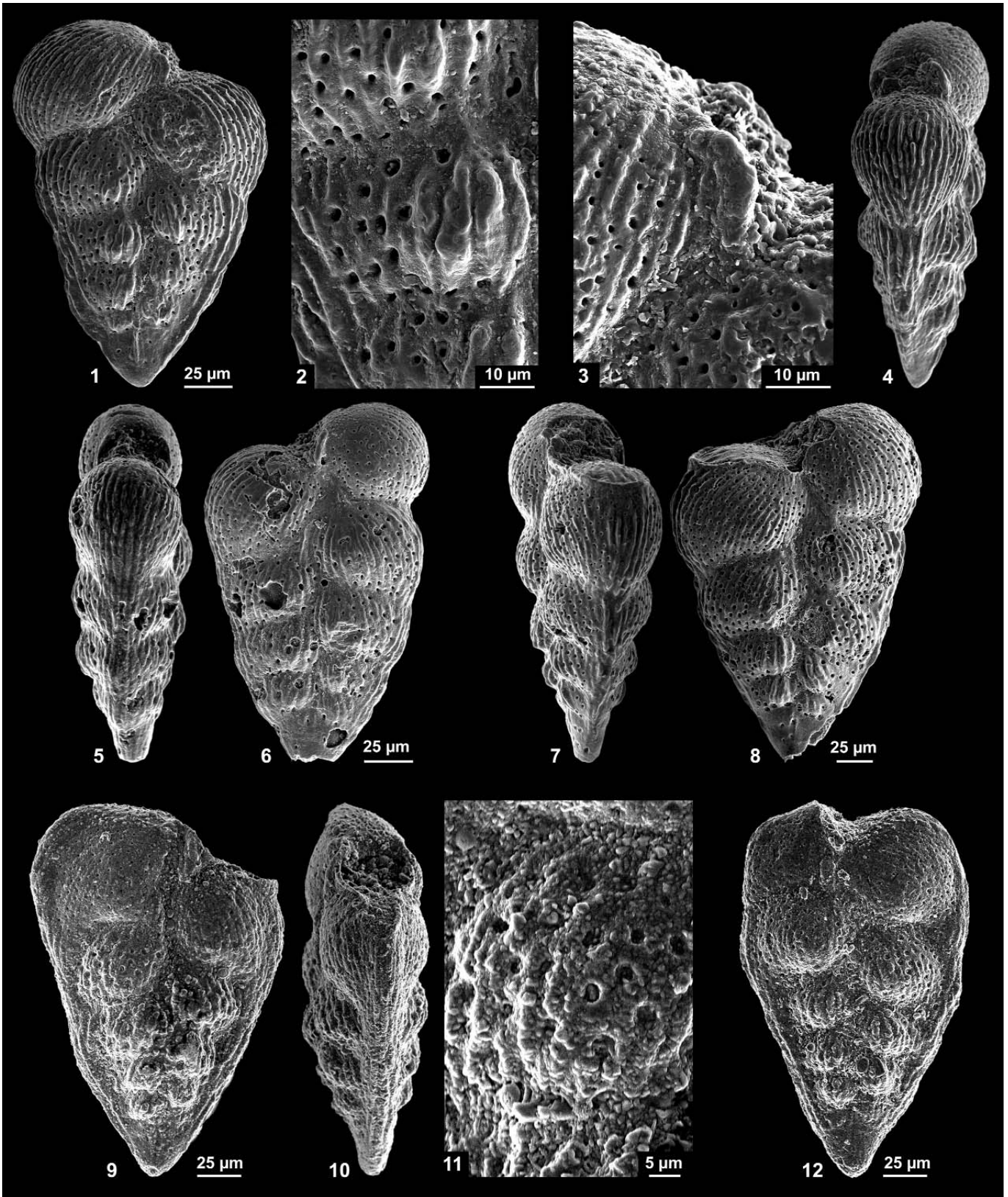
1982 *Heterohelix* sp. 2 – Olányi Odébòdé, p. 244, pl. 3, figs 4-5 (Santonian-Campanian, Calabar Flank, Nigeria).

1991 *Heterohelix carinata* (Cushman) – Nederbragt, p. 341, pl. 1, figs 6-7 only (Santonian-Lower Campanian, Tunisia, Rio Grande Rise, São Paulo Plateau).

2006 *Heterohelix carinata* (Cushman) – Georgescu, fig. 4:1-3 (Upper Santonian-Campanian, New Jersey, USA).

Diagnosis.– *Hendersonia* with well developed test wall flexure, which sometimes forms a rim around the test.

Plate 2. Hypotypes of *Hendersonia carinata* (Cushman, 1938), the type species of *Hendersonia* nov. gen. 1-4. Specimen from the Upper Santonian (*Globotruncana arca* Biozone) of the New Jersey coastal plain subsurface, ODP 174AX at Bass River Site, Sample 505.35-.38 m; note the incipient ornamentation thickenings in the proximity of the central 'zigzag' suture (2) and the small, rimmed periapertural flanges (3). 5-6. Specimen from the Upper Santonian (*Globotruncana arca* Biozone) of the New Jersey coastal plain subsurface, ODP 174AX at Bass River Site, Sample 505.35-.38 m. 7-8. Specimen from the Upper Santonian (*Globotruncana arca* Biozone) of the New Jersey coastal plain subsurface, ODP 174AX at Bass River Site, Sample 505.35-.38 m; note the test wall flexure developed only on the earlier part of the test (7). 9-11. Specimen from the Upper Campanian (*Radotruncana calcarata* Biozone) of the Gulf of Mexico (well for which no precise location can be given) from the Van Morkhoven Collection (NMNH); note the well-developed test wall flexure forming a rim-like structure around the test as seen in lateral view (9). 12. Specimen from the Upper Campanian (*Radotruncana calcarata* Biozone) of the Gulf of Mexico (well for which no precise location can be given) from the Van Morkhoven Collection (NMNH).



Original description.— “Test only slightly longer than broad, much compressed, early portion rapidly tapering; later with the sides nearly parallel, all but the latest chambers keeled; chambers broader than high, increasing somewhat in relative height in the last chambers, only slightly inflated; sutures of the early portion slightly limbate, later ones slightly depressed; wall in the early portion slightly costate, later smooth, finely perforate; aperture low, arched.” (Cushman, 1938, p. 18).

Emended description.— Test biserial throughout, with a small proloculus (6.9 – 10.2 μm), which is followed by 13 to 16 chambers that increase moderately in size as added. Earlier chambers are globular, then subrectangular in lateral view; chambers are consistently subglobular in appearance in edge view (Pl. 2, Figs 4, 5, 7, 10, Pl. 3, Fig. 2). Sutures are distinct and depressed, perpendicular to slightly oblique on the test axis of growth. Periphery is subacute due to a test wall flexure, which results in a carinate appearance (Pl. 2, Figs 4, 5, 7, 10, Pl. 3, Fig. 2). Aperture is a low to medium high arch at the base of the last chamber. Two symmetrically developed rimmed flanges border the aperture on the lateral side; the two flanges are imperforate, rarely microperforate and are not merged in the upper part of the aperture (Pl. 2, Figs 4, 5, Pl. 3, Fig. 2). There is a periapertural pustulose area at the top of the chamber and above the aperture (Pl. 2, Figs 1, 4, 5-8, 9, 12, Pl. 3, Figs 1, 2). The earlier portion of the test, consisting of proloculus and the first two to three chambers can be smooth in some specimens (Pl. 2, Fig. 1). Most of the test is covered with costae with variable orientation, parallel to the periphery in the peripheral region, longitudinal and/or oblique in the central part of the test; the thickness of the costae ranges between 2.9 and 3.5 μm . Some specimens can have thickened costae on the earlier chambers towards the central ‘zigzag’ suture (Pl. 2, Figs 1, 8, Pl. 3, Fig. 1). Test wall is calcitic, hyaline and perforate; pore diameter is between 1.1 and 2.7 μm ; smaller pores are developed commonly over the last formed chamber.

Remarks.— *Hendersonia carinata* (Cushman, 1938) differs from its ancestor, *H. hendersoni* nov. sp., by the development of the test wall flexure at the periphery, which can form a rim-like structure around the test. The emendation proposed is to include the details on the periapertural structures, test ornamentation and porosity.

Phylogenetic relationships.— *Hendersonia carinata* (Cushman, 1938) evolved from *H. hendersoni* nov. sp. It is the ancestor of *H. jerseyensis* n. sp. (Fig. 4).

Stratigraphic range.— Upper Santonian-Campanian (from the upper part of the *Dicarinella asymetrica* Biozone throughout the *Radotruncana calcarata* Biozone). Planktonic foraminiferal biozonation after Robaszynski & Caron (1995).

Geographic distribution.— USA (Texas, New Jersey, Mississippi), western Africa (Nigeria), northern Africa (Tunisia) and South Atlantic Ocean (Rio Grande Rise and São Paulo Plateau).

Hendersonia jerseyensis n. sp.
(Pl. 3, Figs. 3-10)

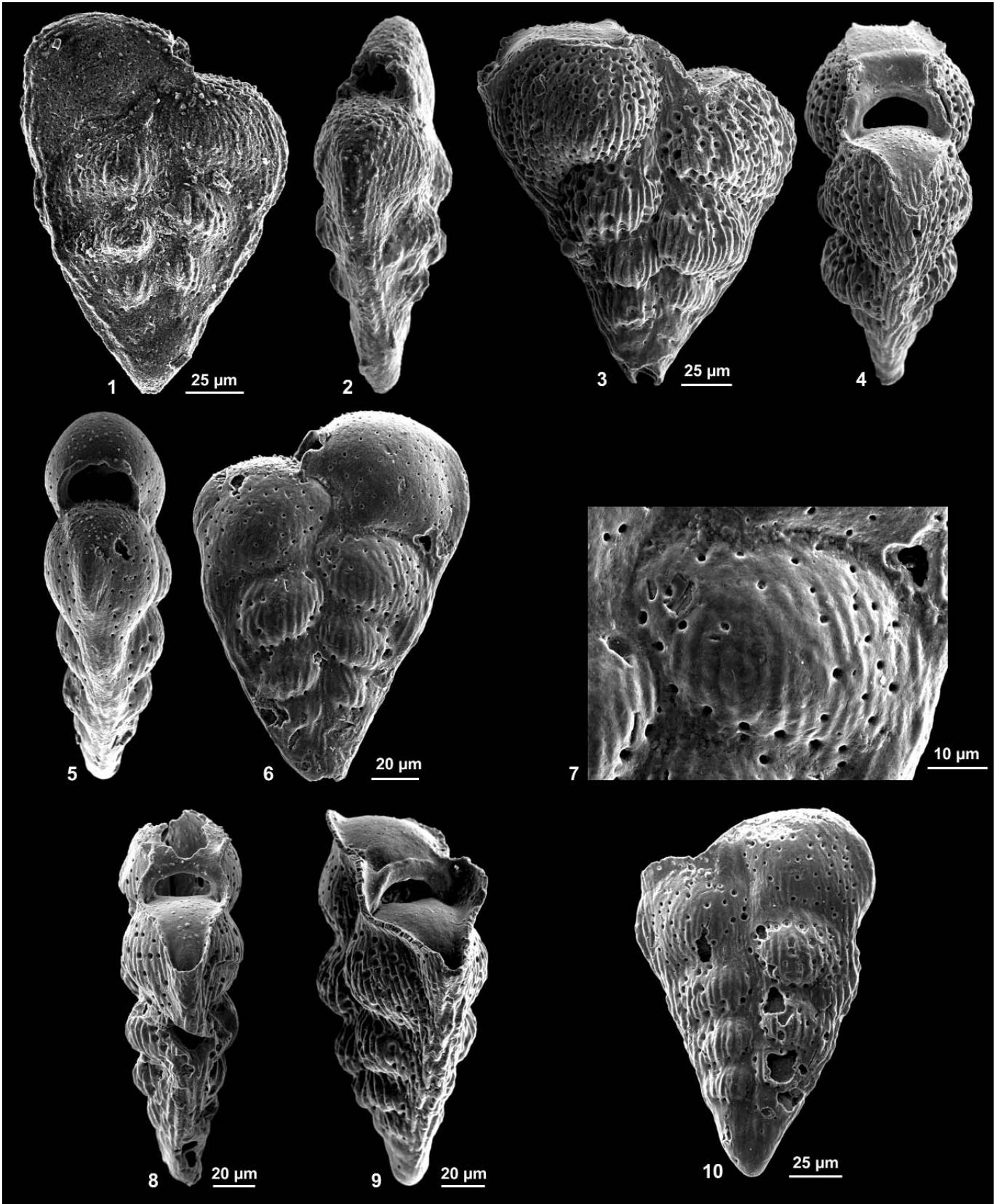
Holotype.— Specimen WKB 010025.

Dimensions of the holotype.— Length: L = 0.162 mm; width: W = 0.119 mm; W/L = 0.735; thickness: T = 0.052 mm; T/L = 0.321.

Paratypes.— Six specimens, WKB 010026.

Dimensions.— L = 0.157-0.225 mm; W = 0.114-0.166 mm; W/L = 0.606-0.841; T = 0.050-0.085 mm; T/L = 0.302-0.467; ranges based on measurements of 12 specimens.

Plate 3. Specimens of *Hendersonia carinata* (Cushman, 1938) and *H. jerseyensis* nov. sp. 1-2. Specimen of *Hendersonia carinata* (Cushman, 1938) from the Upper Campanian (*Radotruncana calcarata* Biozone) of the Gulf of Mexico (well for which no precise location can be given) from the Van Morkhoven Collection (NMNH). 3-4. Paratype of *Hendersonia jerseyensis* nov. gen., nov. sp. from the Lower Campanian (*Globotruncana arca* Biozone) of the New Jersey coastal plain subsurface, ODP 174AX at Bass River Site, Sample 495.30-.33 m; note the pores of the last formed chambers situated in the center of crater-like structures (3). 5-7. Holotype of *Hendersonia jerseyensis* nov. gen., nov. sp. from the Lower Campanian (*Globotruncana arca* Biozone) of the New Jersey coastal plain subsurface, ODP 174AX at Bass River Site, Sample 495.30-.33 m; note the pore distribution with the clear tendency to be aligned to the sutures (7). 8-9. Two poorly preserved paratypes of *Hendersonia jerseyensis* nov. gen., nov. sp. from the Lower Campanian (*Globotruncana arca* Biozone) of the New Jersey coastal plain subsurface, ODP 174AX at Bass River Site, Sample 495.30-.33 m; note the wall flexure, which results in the duplication of the test wall in the peripheral region. 10. Paratype of *Hendersonia jerseyensis* nov. gen., nov. sp. from the Lower Campanian (*Globotruncana arca* Biozone) of the New Jersey coastal plain subsurface, ODP 174AX at Bass River Site, Sample 495.30-.33 m; note that most of the pores on the earlier chambers of the test are aligned to the sutures (10).



Type locality.— ODP Leg 174AX at Bass River Site, New Jersey coastal plain (USA). Geographical coordinates: 39° 36' 42" N and 74° 26' 12 " W.

Type level.— Lower Campanian (upper part of the *Globotruncana arca* Biozone), Sample at 495.30–.33 m. Planktonic foraminiferal zonation after Georgescu (2006).

Material.— Over fifty specimens.

Etymology.— Species named after the state of New Jersey where the type locality is situated.

Diagnosis.— *Hendersonia* with test wall flexure developed on all the chambers of the test, distinct trend of pore alignment in the proximity of the sutures, costae thickenings in the central part of the test, adjacent to the 'zigzag' suture and sometimes with crater-like pores.

Description.— Test is biserial throughout. Proloculus is small (8.1–11.7 µm). There are 12 to 14 globular to subglobular chambers, which increase gradually and moderately in size as added. Earlier chambers are globular in shape, those of the adult portion of the test are subglobular to subrectangular in shape as seen in lateral view (Pl. 3, Figs 3, 6, 10); chamber shape is consistently globular to subglobular in shape in edge view (Pl. 3, Figs 4, 5, 8, 9). Sutures are distinct and depressed, straight to slightly oblique to the test axis of growth. Periphery is subacute due to the development of a test wall flexure, which results in the duplication of the test wall in the chamber periphery region (Pl. 3, Figs 8, 9). The test wall flexure is developed on all the chambers of the test, sometimes forming a rim-like structure around the test (Pl. 3, Figs 1, 2, 5, 6, 10). Aperture is a low to medium high arch at the base of the last chamber. Two short, symmetrically developed flanges, which can be imperforate to microperforate, border the aperture on the two lateral sides (Pl. 3, Figs 4, 6). The oldest portion of the test (apical region) can be smooth in some specimens (Pl. 3, Fig. 9). There is a distinct pustulose periapertural area at the top of the chambers (Pl. 3, Figs 3–6, 8), which can be absent in more or less eroded specimens (Pl. 3, Fig. 9). Most of the test surface is covered with thick costae, which can be linear (Pl. 3, Figs 6, 7, 10) or with undulated sides (Pl. 3, Fig. 3); their thickness range is between 3.1 and 5.3 µm, being thicker on the inner part of the chambers, in the proximity of the central 'zigzag'

suture (Pl. 3, Figs 3, 6, 10). Test wall is calcitic, hyaline and finely perforate; pores can be simple (Pl. 3, Figs 6–8, 10) or situated in the center of a crater-like structure (Fig. 6, Pl. 3, Figs 3–4). Pore diameter ranges between 1.1 and 2.4 µm. There is a distinct trend of pore alignment around the chambers and in the proximity of the sutures on the earlier chambers of the test (Pl. 3, Figs 3, 6, 7, 10).

Remarks.— *Hendersonia jerseyensis* n. sp. differs from *H. hendersoni* nov. sp. by the development of a test wall flexure on all the chambers of the test, thicker costae (3.1–5.3 µm when compared to 2.3–3.1 µm), ornamentation thickenings on in the proximity of the central 'zigzag' suture on the earlier chambers and the trend to develop pore alignment around the chambers on those of the earlier portion of the test. This species differs from *H. carinata* (Cushman, 1938) by the pore alignment trend around the chambers of the early part of the test and the absence of the compressed appearance of the last chamber in edge view. Worth mentioning, the development of pores situated in the central part of a crater-like structure is a characteristic of *Hendersonia jerseyensis* n. sp. among the other species of the genus; the taxonomic significance of these structures was recently demonstrated in the case of the hedbergellid species *Liueella falklandica* Georgescu, 2008 from the Lower Campanian sediments of the Falkland Plateau (Georgescu, 2008).

Phylogenetic relationships.— *Hendersonia jerseyensis* n. sp. evolved from *H. carinata* (Cushman, 1938). Apparently it became extinct leaving no descendants (Fig. 4).

Stratigraphic range.— Lower Campanian (upper part of the *Globotruncana arca* Biozone). Biostratigraphic framework after Georgescu (2006).

Geographic distribution.— USA (New Jersey).

Genus *Paraspiroplecta* nov. gen.

Type species: *Heterohelix navarroensis* Loeblich, 1951, p. 107, pl. 12, figs 1–3.

Diagnosis.— Test with early planispiral coil and weak test wall flexure on the periphery of the earlier portion of the test.

Description.— Test with early planispiral coil and biserial in the adult stage. Earlier chambers are globular, those of the

adult stage subglobular. Periphery slightly subangular with a weak test wall flexure developed mostly on the chambers of the earlier portion of the test. Aperture is a low to medium high arch at the base of the last formed chamber. Two small, symmetrical flanges border the aperture on the lateral sides. Chamber surface is costate and with ornamentation thickenings in the proximity of the 'zigzag' suture on the earlier chambers. Test wall calcitic, hyaline, finely perforate to macroperforate.

Remarks.— *Paraspiroplecta* nov. gen. differs from *Hendersonia* nov. gen. by the presence of the early planispiral coil. *Spiroplecta* Ehrenberg, 1844 presents more globular chambers, which can be best seen in the edge view, and has smaller pores (0.7 to 1.3 μm rather than 1.5-3.2 μm). These suggest that *Spiroplecta* is apparently a descendant from a species of the *Heterohelix globulosa* (Ehrenberg, 1840) group.

Species included.— *Heterohelix navarroensis* Loeblich, p. 107, Pl. 12, Figs. 1-3.

Phylogenetic relationships.— *Paraspiroplecta* nov. gen. evolved from *Hendersonia* nov. gen. It became extinct in the proximity of the Cretaceous/Tertiary boundary leaving no descendants (Fig. 4).

Etymology.— The Greek prefix "para" (= opposed to) is added to the pre-existing serial planktonic foraminiferal genus name *Spiroplecta*.

Stratigraphic range.— Upper Campanian-Maastrichtian (from the *Radotruncana calcarata* Biozone throughout "*Pseudoguembelina*" *hariaensis* Biozone).

Geographic distribution.— USA (Texas, New Jersey), northern Africa (Tunisia), Israel and North Atlantic Ocean (Blake Plateau, Sohm Basin, Gulf of Guinea).

Paraspiroplecta navarroensis (Loeblich, 1951) —
emended
(Pl. 4, Figs. 1-11)

1951 *Heterohelix navarroensis* Loeblich, p. 107, pl. 12, figs 1-3 (Maastrichtian, Texas, USA).

1960 *Heterohelix navarroensis* Loeblich – Olsson, p. 107,

pl. 12, figs 1-3 (Upper Maastrichtian, New Jersey coastal plain, USA).

1967 *Heterohelix navarroensis* Loeblich – Pessagno, p. 261, pl. 89, figs 8-9 (Maastrichtian, Texas, USA).

1973 *Heterohelix navarroensis* Loeblich – Smith & Pessagno, p. 18, pl. 3, figs. 4-7 (Maastrichtian, Texas, USA).

1977 *Heterohelix navarroensis* Loeblich – Petters, pl. 1, fig. 13 (Upper Maastrichtian, New Jersey coastal plain, USA).

1983 *Heterohelix navarroensis* Loeblich – Weiss, p. 44, pl. 1, figs 10-11 (Upper Maastrichtian, Texas, USA and North Atlantic Ocean, Sohm Basin).

1983 *Heterohelix navarroensis* Loeblich – Petters, p. 43, pl. 1, fig. 21 (Maastrichtian, Gulf of Guinea, Atlantic Ocean).

1991 *Heterohelix navarroensis* Loeblich – Nederbragt, p. 344, pl. 3, fig. 5 (Campanian-Maastrichtian, Tunisia, northern Africa).

2006 *Heterohelix navarroensis* Loeblich – Georgescu, fig. 4:13-14 (Upper Campanian, New Jersey coastal plain, USA).

2007 *Heterohelix navarroensis* Loeblich – Yovel, pl. 1, fig. 32 (Upper Maastrichtian, Hor Hahar, Israel).

Diagnosis.— Test with early planispiral coil and weak test wall flexure at periphery.

Original description.— "Test minute and subtriangular in side view, the biserial portion flaring widely from the tiny planispiral coil, periphery broadly rounded; the five to six chambers of the coil are low and not much inflated, the later 6 to 11 biserially arranged chambers increasing rapidly in height so that later ones are inflated and subglobular; sutures distinct, straight, somewhat oblique, depressed; wall calcareous, hyaline, surface faintly striate, finely perforate; aperture a low arch at the inner margin of the final chamber, sometimes with a slight lip." (Loeblich, 1951, p. 107).

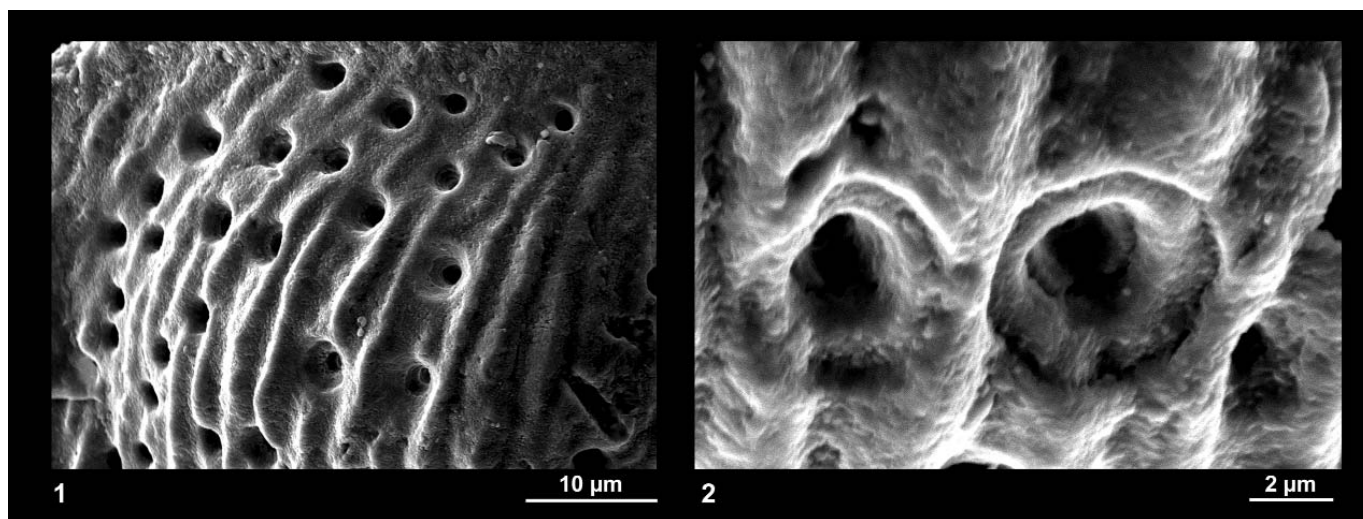


Figure 6. 1-2. The crater-like structures surrounding the pores in two well preserved specimens of *Hendersonia jerseyensis* nov. gen., nov. sp. Paratypes from the Lower Campanian (*Globotruncana arca* Biozone) of the New Jersey coastal plain subsurface, ODP 174AX at Bass River Site, Sample 495.30-.33 m.

Emended description.— Test with early planispiral coil consisting of 4-5 chambers, followed by the adult portion, which presents biserial chamber arrangement. Proloculus is small (8.0- to 9.0 µm). The early planispiral coil, which represents 6 to 14% of the test length, consists of four to six small chambers, which increase gradually in size (Pl. 4, Figs 1, 4, 7-9, 11). The chambers in the biserial portion are subglobular and with subrectangular shape in lateral view due to overlapping. The chambers are subglobular and increase gradually in size in edge view (Pl. 4, Figs 2, 5, 6, 10). Sutures are distinct and depressed, straight to slightly oblique to the test axis of growth. Periphery is slightly subangular on the early portion of the test due to the development of a weak test wall flexure (Pl. 4, Figs 2, 4, 5, 10). Aperture is in the shape of a low to medium high arch at the base of the last formed chamber (Pl. 4, Figs 2, 5, 6). Two small and symmetrically developed periapertural flanges border the aperture on the lateral sides. Earlier part of the test can be smooth in some specimens (Pl. 4, Figs 1, 7, 9, 10). A periapertural pustulose area is developed on top of the chambers and is adjacent to the aperture (Pl. 4, Figs 1, 2, 4-11). Chamber surface is covered with costae, which are parallel to the periphery on the lateral sides of the test and more or less oblique to the axis of growth in the central part. Costae thickness is between 3.3 and 6.7 µm. Ornamentation thickenings are developed in the proximity of the central 'zigzag' suture over the earlier chambers of the test (Pl. 4, Figs 1, 4, 7, 8, 9, 11). Test wall is calcitic, hyaline and perforate, with pore diameter range between 1.5 and 3.2 µm. The pores present a

distinct trend to be aligned to the sutures and around the ornamentation thickenings developed over the earlier part of the test (Pl. 4, Figs 1, 4, 7, 9, 11); they are present over the entire chamber surface and penetrating through the costae in the last formed pair(s) of chambers (Pl. 4, Figs 1-11).

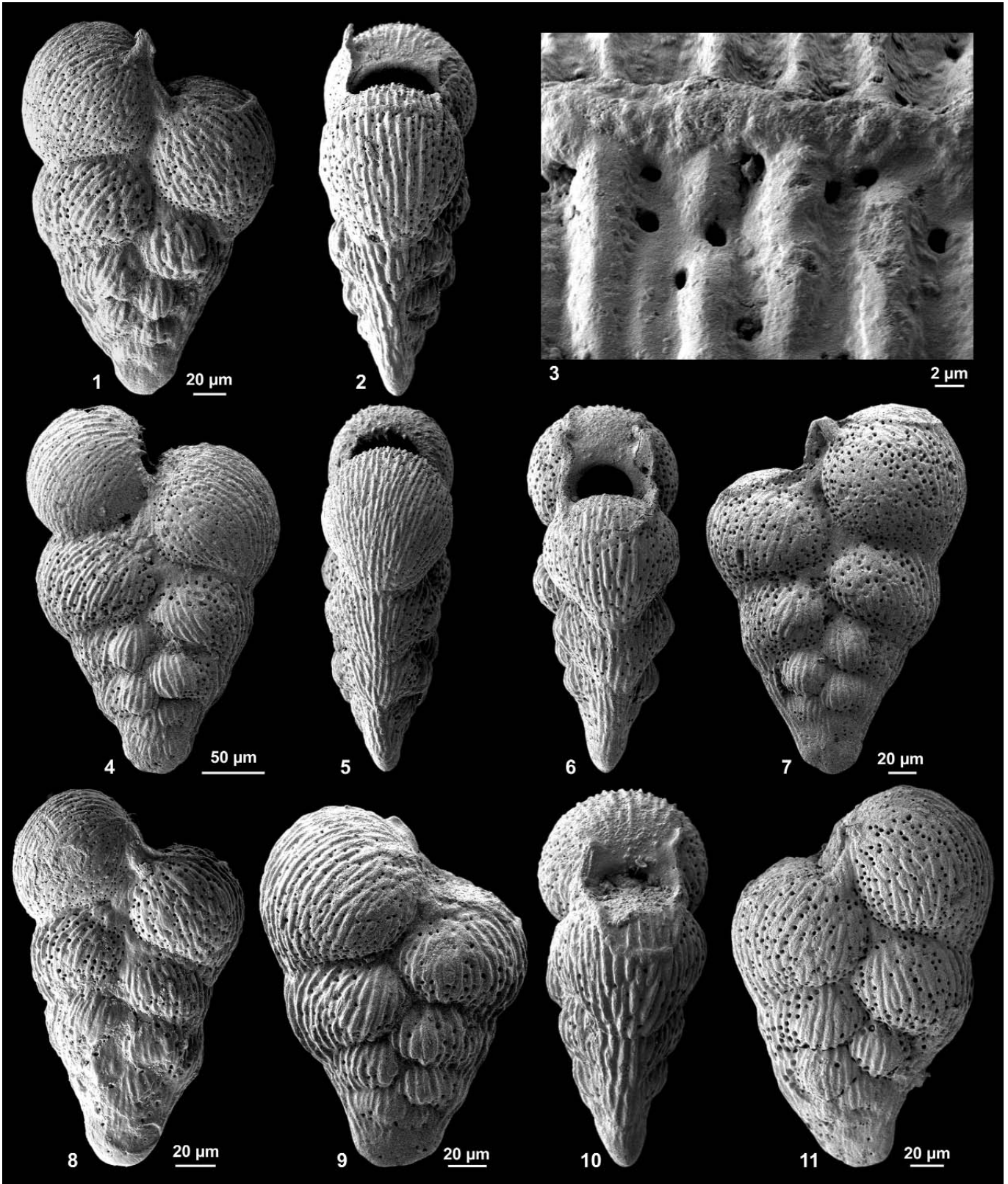
Remarks.— *Paraspiroplecta navarroensis* (Loeblich, 1951) differs from any species of *Hendersonia* nov. by the presence of an early planispiral coil. *Spiroplecta americana* Ehrenberg, 1844 lacks the weak peripheral test wall flexure and ornamentation thickenings on the chambers of the earlier part of the test; it evolved probably from a species of the *Heterohelix globulosa* group and its morphology, taxonomic position and phylogenetic relationships will be the subject of a forthcoming article.

Phylogenetic relationships.— As for the genus.

Stratigraphic range.— Upper Campanian-Maastrichtian (from the *Radotruncana calcarata* Biozone throughout "*Pseudoguembelina*" *hariaensis* Biozone).

Geographic distribution.— USA (Texas, New Jersey), northern Africa (Tunisia), Israel and North Atlantic Ocean (Blake Plateau, Sohm Basin, Gulf of Guinea).

Plate 4. Hypotypes of *Paraspiroplecta navarroensis* (Loeblich, 1951), from the Brazos River. Mullinax-3 well, sample 77, 6-2, 9.79 m. Note the well developed ornamentation thickenings on the central part of the test in the earlier portion (1, 4, 7-9, 11) and the pores that can interrupt the costae (3).



4. DISCUSSION AND CONCLUSIONS

The development of a test wall flexure at the test periphery is documented in a lineage initiated in the upper Santonian (*Dicarinella asymetrica* Biozone) and which became extinct in the Upper Campanian (*Radotruncana calcarata* Biozone). This lineage is formalized as *Hendersonia* nov. gen. and it includes three species: *H. hendersoni* nov. sp., *H. carinata* (Cushman, 1938) and *H. jerseyensis* nov. sp. *Hendersonia carinata* is selected as type species of the newly proposed genus. The main feature, which significantly changes during the evolutionary history of this lineage, is the peripheral test wall flexure. It is incipiently developed in the earliest species of the

genus, *Hendersonia hendersoni*. There is significant variability of the test wall flexure in *H. carinata*, where it can be absent on the last formed one or two chambers of the test to fully developed, resulting in a rim-like structure around the test. The test wall flexure formation and development resulted in the test wall duplication in the peripheral region. This feature is developed on all the chambers of the test in *H. jerseyensis* nov. sp. (Fig. 7).

Distinct evolutionary trends of other features are recorded in the *Hendersonia* lineage, such as: (i) increase in pore size, (ii) increase in costae thickness, (iii) development of ornamentation thickenings on the chambers of the earlier portion of the test in the proximity of the 'zigzag' suture

<i>Hendersonia</i> nov. gen.			<i>Paraspiroplecta</i> nov. gen.
<i>H. hendersoni</i> nov. sp.	<i>H. carinata</i> (Cushman, 1938) 'primitive'	<i>H. jerseyensis</i> nov. sp.	<i>P. navarroensis</i> (Loeblich, 1951)
1. Presence/absence of the early planispiral coil			
No early planispiral coil		Early planispiral coil with 4-5 chambers	
2. Degree of development of the test wall flexure at the test periphery			
Weak and present on the early part of the test	Well-developed excepting for the last 1-2 chambers	Well-developed on all the chambers, resulting in a rim-like structure around the test	Weak and present on the early part of the test (relict?)
3. Costae thickness			
2.3 - 3.1 μm	2.9 - 3.5 μm	3.1 - 5.3 μm	3.3 - 6.7 μm
4. Pore trend to be aligned to the sutures			
No pore alignment		Distinct trend of pore alignment to the sutures	Occasional pore alignment to the sutures
5. Pore type and size			
Simple; D = 0.7 - 2.4 μm	Simple; D = 1.1 - 2.7 μm	Simple or in the middle of a crater-like structure; D = 1.1 - 2.4 μm	Simple; D = 1.5 - 3.2 μm

Figure 7. Diagram presenting the variability of six selected features in the *Hendersonia-Paraspiroplecta* lineage. The development of an early planispiral coil is indicative for the initiation of a distinct genus-lineage (i.e., *Paraspiroplecta*).

and (iv) the trend to develop pores aligned to the sutures, mainly on the earlier chambers (Fig. 7). *Hendersonia jerseyensis* nov. sp. is the only species of this genus, which shows a part of the pores of the chambers from the adult portion of the test in the middle of a crater-like structure. The periapertural structures consisting of small and symmetrically developed rimmed flanges present remarkable stability in the *Hendersonia* lineage. Notably, the periapertural flanges present different porosity than the rest of the test; they are imperforate to microperforate when compared with the test wall, which is finely-perforate to macroperforate.

Paraspiroplecta nov. sp. is characterized by the presence of an early planispiral coil. Excellently preserved material from the Maastrichtian sediments of the Brazos River core, Mullinax-3 (Texas, USA) shows that a weakly developed, most likely relict, test wall flexure is developed on the lateral sides of the early portion of the test. *Paraspiroplecta* is a monospecific genus, including only *P. navarroensis* (Loeblich, 1951). It evolved probably from the tests of *Hendersonia carinata* with test wall flexure developed only on the earlier portion of the test and absent on the last formed one or two chambers and incipient ornamentation thickenings on the early chambers.

The *Hendersonia-Paraspiroplecta* lineage evolved from *Heterohelix planata* (Cushman, 1938) as suggested by the close morphological resemblances between this species, as ancestor, and *Hendersonia hendersoni*, as descendant. The latter is the first species of with test wall flexure on the lateral sides of the earlier portion of the test.

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Présentation des microfossiles extraits par acétolyse dans le Campanien supérieur du Mont Juandechaco (Navarre, Espagne); potentiel chronologique global et vis à vis du stratotype de limite Campanien-Maastrichtien à Tercis (Sud Ouest France)

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Resumen

El afloramiento del Monte Juandechaco en la Navarra española, está caracterizado por calizas o margo-calizas de edad Campaniense superior, datadas a partir de ammonites. La presencia de ammonioideos en este afloramiento permitiendo establecer correlación entre dicho corte y el estratotipo del límite Campaniense-Maastrichtiense situado en Tercis (Landes). Los patrones de evolución del género *Micraster*, que es el equínido más abundante en Navarra, no se pueden comparar con los identificados en el estratotipo porque las especies que se encuentran en sus materiales son distintas y habían evolucionado de manera diferente. La disgregación de los sedimentos con ácido acético concentrado (acetólisis) nos deja observar una gran variedad de microfósiles: pithonellas, osículos de asteroideos, de crinoideos, de ofiúridos, valvas de ostrácodos, conchas de foraminíferos bentónicos y planctónicos, y formas desconocidas denominadas "microproblemática". La disolución con ácido fluorhídrico nos ha permitido obtener quistes de dinoflagelados. Los foraminíferos planctónicos han permitido datar los materiales del afloramiento a partir de la presencia de *Radotruncana calcarata*, que fue observado por primera vez en estas formaciones de plataforma navarra. Los microproblemática de Navarra, con 17 taxones identificados, se pueden comparar a los que se han descubierto recientemente en el estratotipo de Tercis, siendo ésta la primera vez que se han reconocido fuera del estratotipo mencionado. Dichos microproblemática siguen el mismo patrón evolutivo en ambos perfiles constituyendo el instrumento bioestratigráfico más preciso de la sucesión del Campaniense superior. Además, se describe una especie nueva: *Lucernellus* sp. 1, sp. nov. no detectada fuera del corte de Navarra. Los minerales de origen piroclástico encontrados en el estratotipo de Tercis quizás tienen equivalentes en la sucesión de Navarra (biotita, zircón), pero están mezclados con minerales de origen magmático, cuya remodelación no se evidencia. Esta es la razón de que la presencia de algunos microcristales, como los de zircón, pueda ser cuestionable.

Palabras clave: Bioestratigrafía, equínidos, *Micraster*, micropaleontología, foraminíferos, microproblemática, Campaniense, Navarra, España

Résumé

La coupe du Mont Juandechaco, en Navarre espagnole, expose un Campanien supérieur carbonaté daté par ammonites. Un repérage biostratigraphique sur le terrain à l'aide de la macrofaune a conduit à une localisation générale des couches par rapport à la section stratotypique de la limite Campanien-Maastrichtien de Tercis (Landes) grâce à quelques ammonites. Pour les échinides, plus abondants, l'évolution du genre *Micraster* en Navarre n'a pu être comparée à celle du stratotype car les formes sont distinctes et évoluent différemment. La dissociation des sédiments par acétolyse a livré des restes variés: pithonelles, ossicules d'astérides, de crinoïdes, d'ophiures, des ostracodes, des foraminifères benthiques et planctoniques, des microproblematica. L'attaque fluorhydrique a donné des kystes de dinoflagellés. Les foraminifères planctoniques ont permis de réaliser un repérage chronologique relatif grâce à la présence de *Radotruncana calcarata* mise en évidence pour la première fois dans ces formations de plate-forme navarraises. Les microproblematica de Navarre, dont 17 taxons ont été identifiés, sont comparables à ceux nouvellement découverts dans le stratotype de Tercis et ils constituent la première observation de ces restes en dehors des environs immédiats du stratotype landais où ils ont été observés et nommés.

Il est montré que ces microproblematica suivent la même évolution, au même moment que ceux identifiés à Tercis où il a été établi qu'ils constituaient l'outil biostratigraphique le plus précis de la succession du Campanien supérieur. De plus, une nouvelle espèce : *Lucernellus* sp. 1 nov. sp. est décrite mais non nommée. Les minéraux d'origine pyroclastique rencontrés dans le stratotype de Tercis ont peut-être leur équivalent dans la série navarroise (biotite, zircon) mais ils y sont mêlés à des minéraux d'origine magmatique dont le remaniement est si discret qu'ils peuvent jeter un doute sur l'origine des premiers.

Mots clés: Biostratigraphie, échinides, *Micraster*, micropaléontologie, foraminifères, microproblematica, Campanien, Navarre, Espagne

Abstract

The Juandechaco Mount, in Spanish Navarra, is made of upper Campanian ammonite-bearing carbonate deposits. A biostratigraphical relative dating using several specimens of these ammonites found during the field sampling allowed general location of the strata versus the Campanian-Maastrichtian boundary type section of Tercis (Landes). Echinoids are more abundant than ammonites; however, the evolution of the morphology of the genus *Micraster* in Navarra is not similar to that observed in the type section where distinctly different forms characterise the successive Campanian deposits and no correlation could be made using this biostratigraphical tool. The sediments dissociated using acetolysis provided diversified microfaunal remains: pithonellids, ossicles of asteroids, crinoids, and ophiuroids, tests of ostracodes, benthic and planktonic foraminifers, and microproblematica pointing to an external platform facies very similar in the Juandechaco Mount and at Tercis. Hydrofluoric acid dissolution provided dinoflagellate kysts. The planktonic foraminifers allowed a precise relative chronologic dating thanks to the presence of *Radotruncana calcarata* identified for the first time from the Navarrese platform deposits. The Navarrese microproblematica of which 17 taxa were identified in spite of the generally poor preservation of the microfossils, are comparable to those recently discovered at Tercis. This fauna of microproblematica constitute the first observation out of the area of the type section where they were originally observed and named. It is shown that the taxa follow the same morphological evolution in Spain with the same timing compared to the area around Tercis where they provided the most precise biostratigraphical tool within the upper Campanian portion of the section. Pyroclastic minerals surprisingly encountered in the type section at Tercis have probably their equivalent in the Navarrese series (biotite, zircon); however, they are admixed with magmatic minerals of which the marks of reworking are so difficult to identify that the actual volcanic origin of the former might be questioned.

Key words: Biostratigraphy, Echinoids, *Micraster*, micropalaeontology, foraminifers, microproblematica, Campanian, Navarra, Spain.

1. INTRODUCTION

La définition la plus récente des étages du Crétacé terminal (Odin & Lamaurelle, 2001) utilise, comme limite entre le Campanien et le Maastrichtien, le point stratotypique mondial établi à Tercis (SO France). Au cours des recherches destinées à qualifier ce stratotype (Odin, 2001a), des signes d'activité volcanique acide (explosive) ont été observés dans le Campanien supérieur (Odin, 2001b). Pour évaluer la signification de cet événement dans la région pyrénéenne, il convenait de le retrouver régionalement et, donc, de repérer précisément son niveau dans le temps. C'est ainsi que des études micropaléontologiques ont été entreprises sur une dizaine de sections situées dans le Sud-Ouest de la France et au Nord de l'Espagne, dans un paléo-bassin qui comprenait, en son centre, des dépôts profonds de type flysch et, sur ses bordures nord et sud, des dépôts de plate-forme ainsi qu'il a été décrit pour le bassin aturien (Laurent *et al.*, 2001, Fig. 1).

Du côté espagnol, la micropaléontologie du faciès flysch a fait l'objet d'études pour les foraminifères (Herm, 1965; Arz & Molina, 2002). Cependant, trouver des traces de volcanisme explosif sous la forme de minéraux pyroclastiques microscopiques dans des flyschs restait problématique du fait de la rapidité de la sédimentation qui dilue les apports volcaniques ponctuels. Les recherches se sont ainsi adressées au faciès de plate-forme. Du côté français, les affleurements étudiés se groupent aux environs de Dax. Du côté espagnol, la stratigraphie des faciès de plate-forme se fonde le plus souvent sur la macrofaune, en particulier sur les ammonites (Küchler *et al.*, 2001). Les connaissances sont moins bien établies pour ce qui est de la microfaune en général et des foraminifères en particulier si l'on s'en réfère à la carte géologique. Au centre de la carte au 1/50.000 de Garralda, en Navarre, le Santonien (C24 dolomitique) supporte l'unité C26m qui, sur le terrain, se révèle ne pas être du flysch mais un faciès de plate-forme comparable à celui de Tercis avec sa pétro-

graphie carbonatée, la présence très commune d'échinides et celle, plus rare, d'ammonites et d'inocérames. Carbayo Olivares *et al.* (1978) notent dans la notice de cette carte « *Al no encontrar una microfauna determinativa de edad Campaniense hemos optado por ceñir este tramo al Maastrichtiense* ». Par suite, l'ensemble des niveaux de faciès plate-forme affleurant dans les environs d'Imiscoz est attribué au Maastrichtien.

Küchler (2000) indique la présence de foraminifères planctoniques campaniens en Navarre (*Globotruncana elevata* puis *Globotruncana ventricosa*); il est donc possible d'en trouver tandis que Küchler *et al.* (2001) y ont reculé et décrit des ammonites campaniennes.

D'après nos observations près d'Imiscoz (sur le territoire de la carte de Garralda), les ammonites sont peu communes. Les inocérames sont plus nombreux mais ces mollusques sont concentrés dans quelques niveaux riches séparés de larges portions sans témoignage et, donc, sans repérage temporel relatif. Il s'y ajoute la difficulté des déterminations même dans les affleurements favorables (comparer Odin, 2001c avec Walaszczyk *et al.*, 2002). Dans la macrofaune de Navarre, les échinides sont beaucoup plus fréquents et auraient pu assurer un repérage pratique sur le terrain. Pourtant, nous n'avons pas retrouvé la succession biostratigraphique remarquablement claire des couches de Tercis (Néraudeau & Odin, 2001). Il paraissait donc nécessaire de rechercher des éléments de microfaune utilisables.

Le présent travail expose essentiellement les résultats paléontologiques et donne les éléments permettant d'affirmer qu'avec une technique adaptée il est possible de dater précisément les couches campaniennes en Navarre par la microfaune. Ceci permettrait, entre autres applications, d'améliorer localement la carte géologique au moins pour le faciès de plate-forme car sur la carte de Gulina (Berrois Pi *et al.*, 1978), immédiatement à l'ouest de Garralda, le faciès flysch est présent au Crétacé supérieur et le Campanien (C25) est distingué du Maastrichtien (C26) par la microfaune (*G. elevata*, *G. ventricosa*, *Contusotruncana fornicata*), le Campanien supérieur étant identifié par la présence de *Radotruncana calcarata* (anciennement *Globotruncanita calcarata*) et le sommet de l'étage est accepté au niveau de sa disparition.

2. MATÉRIEL ET MÉTHODES

Les sections ayant fait l'objet d'une étude préliminaire pour repérer les niveaux à minéraux pyroclastiques se situent dans un cadre géographique compris entre Dax, Pau, Pampelune et Zumaya (Fig. 1). En France, divers affleurements ont été considérés dans les environs de Dax (faciès de plate-forme), près d'Orthez, au Sud de Pau et près de la frontière espagnole (faciès de bassin flysch). En Espagne, la coupe entre Zumaya et Deva (faciès flysch) et une coupe en Navarre (faciès de plate-forme) ont été examinées; cette dernière est l'objet principal de la présente étude. La stratigraphie des couches campano-maastrichtiennes de Navarre a été établie par Küchler *et al.* (2001) d'après la succession des ammonites.

La section la plus prometteuse décrite par ces auteurs (contrôle continu par les ammonites, longueur de la section, bon développement des couches du Campanien supérieur) se situe à environ 25 km au NE de Pampelune, localité du Mont Juandehaco, près du village d'Imiscoz en Navarre. Il s'agit d'un affleurement faisant face au Sud, légèrement couvert de buissons épineux (Fig. 2) qui permet, le long d'une pente peu escarpée, de gravir des couches au pendage très faiblement incliné (15°) vers le Nord Est. Un nouveau levé a été réalisé du fait de la grande homogénéité de la lithologie (calcaires peu argileux indurés, monotones tout le long de la section). Cette homogénéité ne permet pas de se repérer par rapport aux observations lithologiques telles qu'elles ont été publiées. Divers repères topographiques ont été fixés (Fig. 3): à la base, la limite avec le Santonien dolomitique rouge constitue un bon repère; le levé est aisé à partir d'un chemin bas situé vers notre cote Ju10; un poteau de ligne électrique à moyenne tension (P sur la photographie) se situe à notre cote Ju65; un arbre mort († sur la photographie) correspond à notre cote Ju100; un chemin dessinant une ligne blanche horizontale dans le paysage (LB sur la photographie) correspond à notre cote Ju126.

Une difficulté tectonique a été observée sur le terrain: la présence d'un panneau déplacé, épais de quelques mètres, intercalé localement vers la cote Ju50 et dont les couches recourent de part et d'autre la succession stratigraphique.

Des éléments de macrofaune ont été récoltés: 88 échinides, 2 bivalves; 8 inocérames; 2 *Baculites* et 18 autres ammonites spiralées ou hétéromorphes. Les inocérames sont généralement en mauvais état, groupés en peu de niveaux et difficiles à dégager de leur matrice. Une quinzaine de prélèvements ont été faits pour l'étude de la microfaune entre les cotes Ju70 et Ju124, là où le marqueur *Radotruncana calcarata* (foraminifères) qui accompagne, à Tercis, la présence des minéraux pyroclastiques, devait se trouver d'après les ammonites communes aux deux affleurements de Tercis et du Mont Juandechaco.

Quelques fossiles ou leur matrice ont aussi servi de matériel pour extraire des microfossiles. En tout 17 niveaux ont été traités de diverses manières pour être dissociés. La seule approche ayant permis une dissociation efficace à partir de laquelle des tris ont pu être réalisés est l'acétolyse.

La technique de dissociation par acétolyse consiste à plonger des morceaux de roche carbonatée dans un bain d'acide acétique concentré. Le sédiment est disposé dans un bocal en verre puis l'acide est ajouté et le récipient est fermé non hermétiquement. La concentration de l'acide et

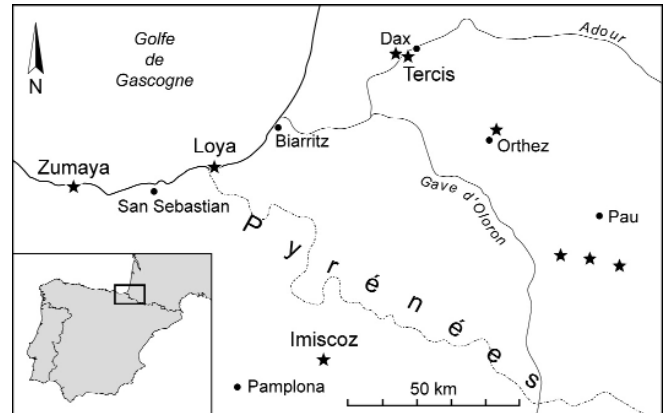


Figure 1. Localisation des affleurements étudiés dans le cadre de ce travail (étoilés).

Figure 1. Location of the outcrops studied for this work (stars).

la température favorables à la dissociation dépendent du sédiment; des essais doivent être faits pour chaque affleurement. Des concentrations de l'acide allant de 80 à 100 % peuvent être utilisées; la température peut aller de la température ambiante jusqu'à celle d'un bain de sable à 80 °C. On doit opérer soit à l'extérieur, par exemple sur le terrain pour repérer les niveaux favorables (si l'on dispose d'une source d'eau et de quelques jours), soit sous



Figure 2. Vue de l'affleurement du Mont Juandechaco (Navarre). Les trois repères topographiques sont P: poteau de ligne électrique à moyenne tension, t: arbre mort, LB: ligne blanche.

Figure 2. The outcrop at the Juandechaco Mount (Navarra). Topographic marks are P: post carrying electric cables, t: dead tree, LB: white line.

une sorbonne en dépression. Le lavage s'effectue à grande eau, sur tamis à mailles de nylon ou d'acier inoxydable. La durée de la réaction est d'autant plus longue que l'acide est plus pur et va de quelques heures à quelques semaines. Il est impératif de surveiller la réaction car, lorsqu'elle est avancée, la dissociation est immédiatement suivie d'une recristallisation rapide qui cimente le sédiment dans le récipient. Sur le terrain, la pollution est évitée en rejetant les solutions dans les déblais calcaires qui neutralisent aussitôt les restes d'acide et non dans la source d'eau. Jusqu'à 5 traitements différents ont été réalisés pour certains niveaux avant d'obtenir une dissociation satisfaisante. Pour les microfossiles de taille supérieure à 250 µm des quantités de 100 à 200 g ont été traitées; il a suffi de 50 g pour les microfossiles de taille inférieure à 250 µm.

3. MACROFOSSILES

3.1. Échinides

Dans la figure 3, les deux sections de Juandechaco (Navarre) et de Tercis ont été mises en parallèle d'après le repérage biostratigraphique obtenu à partir des ammonites, des foraminifères planctoniques et des microproblematica présents dans les deux sections. Pour la section type de Tercis, les unités lithologiques usuelles (Odin & Odin, 1994) sont localisées avec une unité sans silex (Unité d'Avezac subdivisée en 5 sous unités identifiées d'après leur teneur en glauconie: A1 jusqu'à A5) à la base et une unité à silex au sommet (Unité les Vignes avec sa première sous unité: V1, où les silex sont gris clair).

Dans cette section type de Tercis, le genre *Micraster* a donné un signal biostratigraphique aisé d'application dans le Campanien supérieur. Trois espèces se succèdent sans se recouvrir: *M. coranguinum simpsoni* entre les cotes Ts0 et Ts13,4 puis *M. corcolumbarium* entre les cotes Ts16,2 et Ts67, enfin *M. aturicus* entre les cotes Ts69 et Ts94,3 (Néraudeau & Odin, 2001). Ces trois espèces se distinguent immédiatement par leurs tailles moyennes respectivement proches de 50 mm, 30 mm et 65 mm successivement (Fig. 3); au-dessus, le genre n'a donné que peu de restes dont la détermination est délicate sauf pour 2 spécimens attribués à l'espèce *M. brongniarti*.

Le même exercice effectué en Navarre permet de séparer à la base, entre les cotes Ju10 et Ju20, un ensemble où le genre *Micraster* est de taille moyenne proche de 40 mm, puis un second ensemble entre les cotes Ju29 et Ju66 où la taille est plutôt grande autour de 60 mm, puis un troisième ensemble, entre les cotes Ju86 et Ju95 où le genre est représenté par une espèce de taille moyenne 46 mm, enfin un quatrième ensemble, au dessus de la cote Ju104, avec une espèce de taille plutôt grande de nouveau proche de 60 mm.

Il en résulte que, malgré leur proximité et un faciès de plate-forme commun, les successions de Tercis et de Navarre ne renferment pas une évolution commune pour le genre *Micraster*. La morphologie des taxons présents est elle-même distincte comme le montre le critère de taille. L'espèce *M. aturicus* a bien été citée en Navarre mais le spécimen figuré (Küchler, 2000, pl. 6 figs. 4-7) est plus petit que 60 mm, sa forme est bien plus globuleuse, bien moins dissymétrique antéro-postérieurement que l'espèce *M. aturicus* définie à Tercis. En outre, le taxon de Navarre figuré provient d'une partie basale du Campanien supérieur (sous la zone d'existence de l'ammonite *Bostrychoceras polyplacum*) alors que l'espèce de Tercis est localisée dans le Campanien plus élevé au dessus de la zone d'existence du foraminifère *Radotruncana calcarata*. (cf. Fig. 6). Par ailleurs, le même auteur (Küchler, 2000, Fig. 8) signale *M. aturicus* dans ce qu'il attribue à la base du Maastrichtien (avec les ammonites index *Pachydiscus neubergicus* et *Pachydiscus epiplectus*) d'une autre coupe navarroise tandis qu'à Tercis, *M. aturicus* a disparu bien avant que l'on rencontre ces mêmes ammonites et c'est *M. brongniarti* qui vient le relayer dans les couches du Campanien terminal et la base du Maastrichtien. Plus généralement, la présence de *M. aturicus* est citée comme continue en Navarre, dans la région d'Urdirroz-Imiscoz depuis la base des couches du Campanien supérieur jusqu'aux couches inférieures du Maastrichtien plus de 210 m au dessus (Küchler & Kutz, 1989); à Juandechaco même, le taxon est signalé entre les cotes 22 et 205 de ces auteurs. Il s'ensuit que les "*Micraster aturicus*" de Tercis et de Navarre n'appartiennent probablement pas au même taxon.

Il reste, de la présence commune du genre *Micraster*, que le site de Navarre étudié se situait sur une plate-forme de

faciès proche de celui de Tercis pour le Campanien supérieur non terminal avec une paléo-profondeur estimée à 50-100 m là où ce genre est dominant chez les échinides (Néraudeau & Odin, 2001, Fig. 1, p. 615) alors que le genre *Echinocorys* qui dénote une profondeur un peu supérieure (100-150 m) est présent mais jamais dominant dans notre section de Navarre.

3.2. Ammonites

Dans la succession de Tercis, les niveaux dans lesquels des indices de volcanisme ont été mis en évidence sont situés entre les cotes Ts52 et Ts60 avec des reprises jusqu'à la cote Ts70 (Odin, 2001b). Ce sont les ammonites hétéromorphes (plus ou moins déroulées) qui permettent de

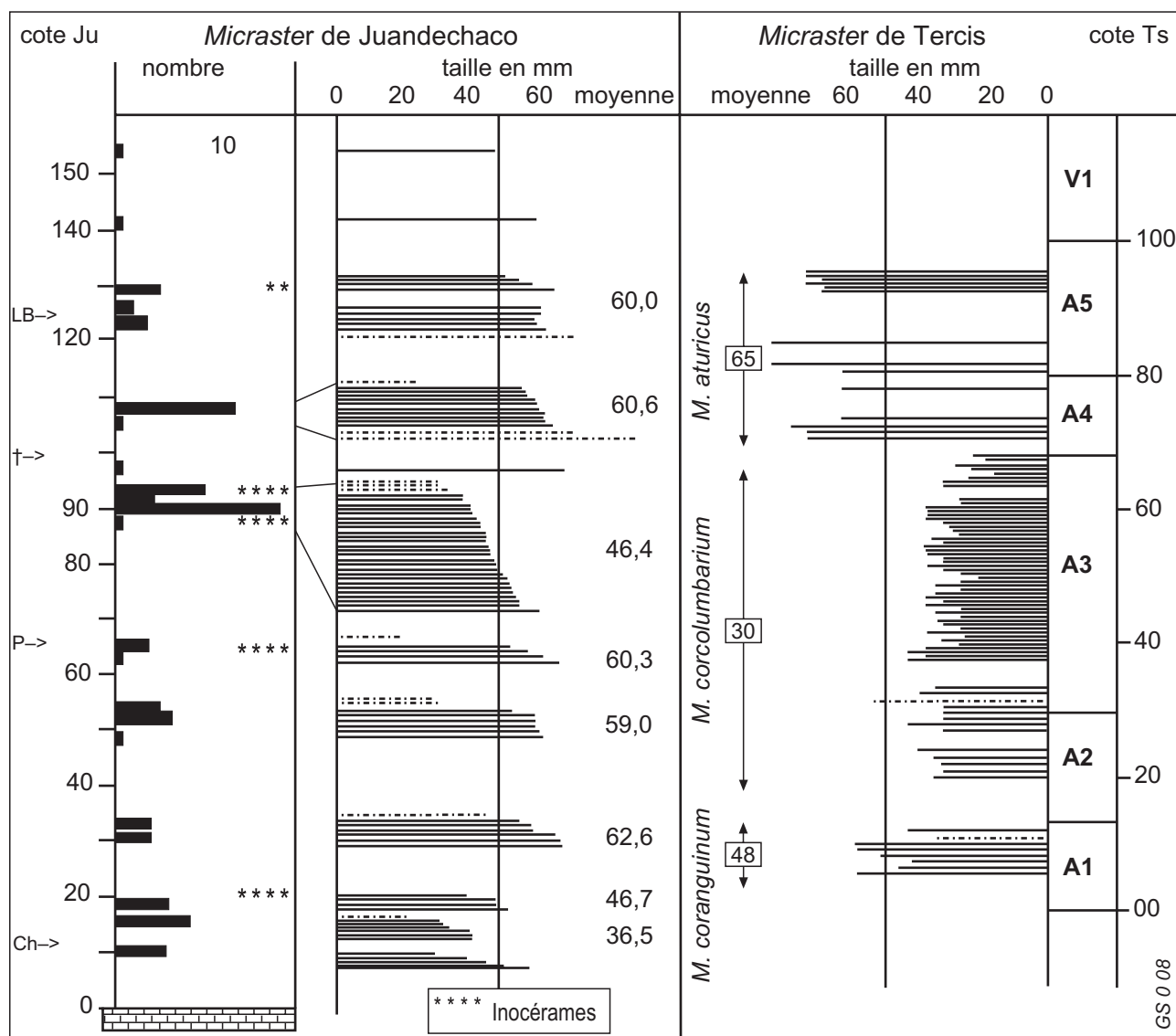


Figure 3. Distribution de la taille du genre *Micraster* dans les sections de Tercis et du Mont Juandechaco. Chaque trait horizontal représente 1 spécimen; les spécimens de taille exceptionnelle pour le niveau sont notés en tiretés; pour la section de Navarre, la présence de niveaux riches en inocérames à été notée (astérisques) ainsi que les repères Ch: chemin, P: poteau de ligne électrique à moyenne tension, t: arbre mort, LB: ligne blanche. Trois ensembles observés à Tercis correspondent à quatre ensembles en Navarre et les taxa sont de taille différente.

Figure 3. Size distribution of specimens of the genus *Micraster* collected from Tercis (right) and the Juandechaco Mount (left). Each line represents 1 specimen; broken lines show specimens of locally uncommon size; inoceramid-rich levels (stars) are shown in the Navarra section as well as field marks such as Ch: way, P: post carrying electric cables, t: dead tree, LB: white line. Three groups of size observed at Tercis correspond to four groups in Navarra and the taxa are different in size.

caractériser au mieux cet intervalle. *Bostrychoceras polyplacum* et diverses formes morphologiquement proches sont présentes entre les cotes Ts20 et Ts45 à Tercis (Küchler & Odin, 2001) et sont donc plus anciennes que les couches à minéraux pyroclastiques. *Nostoceras hyatti* et diverses formes proches (caractérisées par une loge d'habitation en U) et plus ou moins contemporaines en Europe (*N. helicinum*, *N. approximans*) sont présentes entre les cotes Ts66 et Ts105 essentiellement (Küchler & Odin, 2001); elles se situent au dessus de l'intervalle contenant des indices de volcanisme.

En Navarre, bien que les ammonites récoltées l'aient été en petit nombre au cours des prélèvements sur notre section, des éléments utiles ont été observés. Trois spécimens de *B. polyplacum* ont été récoltés en place aux cotes Ju63 (Fig. 4), Ju55 et Ju53,5. Il faut noter que Küchler *et al.* (2001) ont signalé la présence de *B. polyplacum* sur une épaisseur de 30 m (entre leurs cotes 70 et 100) trois fois supérieure à celle que nous avons caractérisée ce qui indique que nous n'avons observé qu'une partie de l'intervalle d'existence du taxon marqueur.

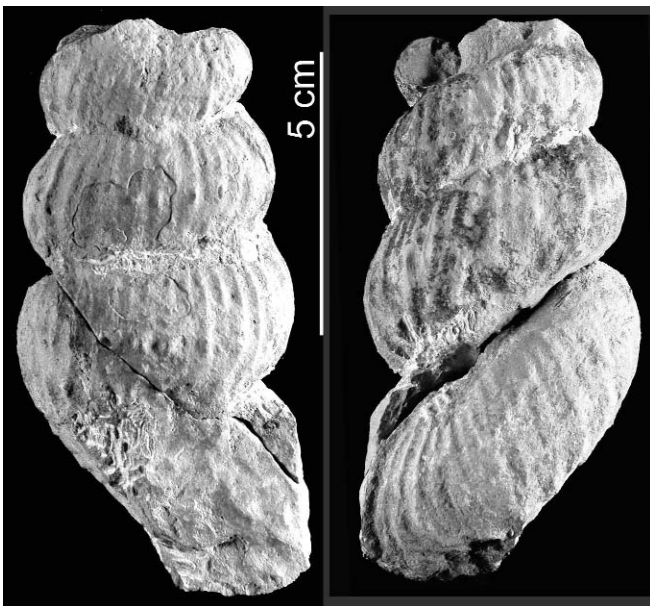


Figure 4. *Nostoceras (Bostrychoceras) polyplacum* (Römer, 1841) de la cote Ju63 caractérisé par des rides fines, nombreuses, jusqu'à 40 par tour; une alternance entre rides avec et rides sans tubercules; des rides continues entre les tubercules (Clichés C. Abrial).

Figure 4. *Nostoceras (Bostrychoceras) polyplacum* (Römer, 1841) from level Ju63 showing fine, dense ribbing, up to 40 per whorl; tubercles are present each 2 ribs; ridges are continuous between the tubercles (picture by C. Abrial).

Quant aux *Nostoceras* à loge d'habitation en U, aucun n'a été récolté en place mais des débris ont été observés à des cotes voisines de Ju108 et Ju122. Un spécimen de *Pachydiscus perfidus* a aussi été récolté à la cote Ju125. Ce spécimen possède 20 rides secondaires par demi tour ce qui conduit à un secteur moyen entre rides de 9° d'angle; avec cette caractéristique (Odin, 2001 d), ce taxon se distingue de *P. neubergicus* dont le secteur moyen ne dépasse pas 8° et pourrait être son ancêtre comme illustré dans la série de Tercis (Odin *et al.*, 2001). *P. perfidus* a vécu au Campanien supérieur, *P. neubergicus* au Maastrichtien. La répartition de ces quelques ammonites est logique et situe les niveaux à considérer pour l'étude micropaléontologique dans l'intervalle compris entre nos cotes Ju70 et Ju100 si l'on veut trouver le marqueur *Radotruncana calcarata* des foraminifères.

4. MICROFOSSILES

4.1. Présence de microfossiles

La dissociation des sédiments récoltés en Navarre a permis de récolter des microfossiles dans les 17 prélèvements soumis à l'acétolyse. Ces restes sont diversifiés; leur préservation est modérée (Fig. 5): la recristallisation a souvent lissé les formes et les tests sont usés. Ceci n'est pas principalement le résultat du mode de dissociation mais celui de l'histoire du sédiment qui a subi divers effets diagenétiques. Les identifications en sont rendues délicates. La liste des groupes représentés en Navarre est très proche de celle établie à Tercis (Odin, 2001e, pl. 1, p. 136).

Pour les éléments appartenant à des formes usuellement de grande taille, les prismes d'inocérames sont parfois communs, parfois rares (entre les cotes Ju83,6 et Ju74,5). Comme à Tercis, ce sont les micro-restes d'échinodermes qui caractérisent le mieux ces sédiments avec à la fois des éléments squelettiques d'échinides, de crinoïdes, d'astérides mais surtout des ossicules d'ophiures (Pl. 1, vues 2-3). Très variés, omniprésents, ces restes d'échinodermes se reconnaissent grâce à la structure en réseau visible sur certains spécimens en partie dissous (cf. Pl. 1, vues 4-5). La récolte ne dépasse pas quelques dizaines de spécimens pour 100 g traités chez les ophiures (à la fois dans la fraction supérieure et dans la fraction inférieure à 250 µm) et

quelques unités, dans la fraction supérieure à 250 µm, pour les ossicules d'astérides et de crinoïdes. Des microbrachiopodes sont aussi présents sous forme de coquilles entières (Pl. I, vue 7) ou de valves isolées dans la majorité des échantillons; leur abondance est restreinte: quelques unités seulement, au mieux 7 (avec 2 espèces) pour 100 g dissociés dans la fraction supérieure à 1 mm au niveau Ju89. Pour terminer cette liste non exhaustive, citons la présence d'un otolithe de poisson (Pl. 1, vue 6) de petite taille (pour un otolithe).

Quant aux groupes de microfossiles, la première caractéristique notable des sédiments de la section de Navarre est la présence de *pithonelles* (localement quelques centaines par gramme de sédiment) dans la fraction plus petite que 250 µm (Fig. 5, noté pit.); ce sont des calcaires à *pithonelles*. Comme à Tercis, ces multiples microsphères indiquent un faciès de plate-forme avec une profondeur comprise entre 80 et 200 m (Berthou *et al.*, 2001). Les ostracodes sont aussi présents dans tous les niveaux soumis à l'acétolyse; des formes lisses (Fig. 5) et des formes ornées (Pl. 1, vue 8) existent. On peut en récolter quelques dizaines par 100 g de sédiment dissocié là où 500-1000 foraminifères planctoniques (globotruncanides) sont disponibles. La préservation des carapaces est inégale.

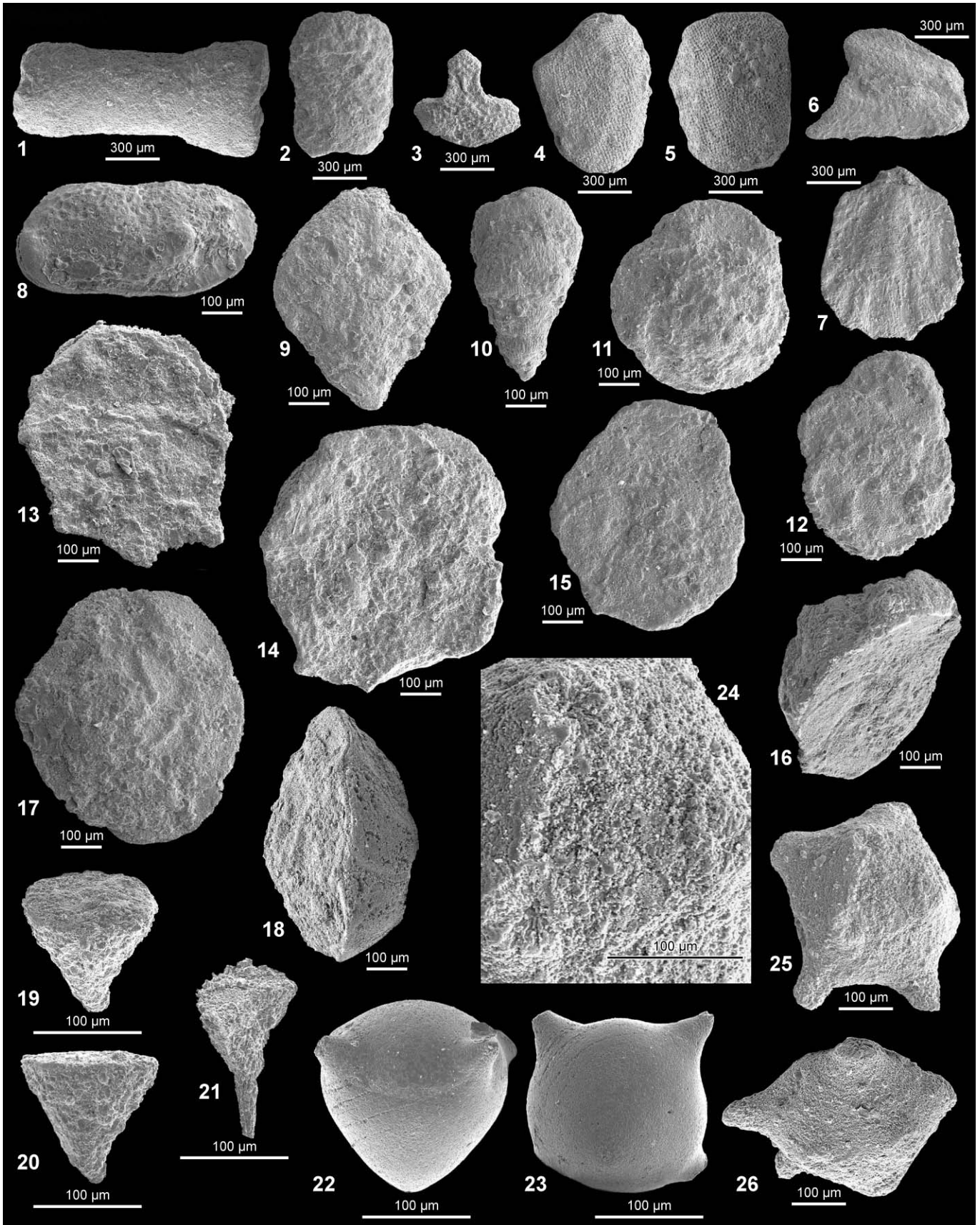
Les foraminifères constituent l'essentiel des microfossiles calcaires utilisables après dissociation. Dans la fraction la plus grossière (supérieure à 500 µm), les *Navarella* sont présentes. Ce grand foraminifère benthique arénacé peut être commun (niveau Ju100) dans la fraction supérieure à 1 mm et constitue un autre marqueur d'environnement de plate-forme (profondeur de 100-150 m). Dans la plupart des niveaux, le rapport foraminifères benthiques/foraminifères planctoniques est compris entre 0,6 et 1,5 ce qui dénote encore un environnement de plate-forme. Parmi les foraminifères benthiques utiles à la stratigraphie, le genre *Bolivinoïdes* est présent (Pl.1, vue 9). A Tercis, Tronchetti (2001), a mis en évidence une évolution continue des formes de ce genre au cours du Campanien supérieur et du Maastrichtien. Il en est de même dans d'autres portions de la Téthys comme en Égypte (El Nady, 2006). Les foraminifères planctoniques comprennent quelques hétérohélicides (Pl. 1, vue10) mais surtout des globotruncanides: 450 à 1100/100 g de sédiment dissocié et jusqu'à 2000/100g à la cote Ju83,6.

Pour terminer ce premier bilan d'ensemble, des attaques à l'acide fluorhydrique ont été réalisées pour tester la présence de restes organiques. Les Dinoflagellés ont été obtenus dans les 4 échantillons tests, en majorité des spécimens hirsutes de type hystrichosphère. Le marqueur *Corradinisphaeridium horridum* a été reconnu à la cote Ju74,5; à Tercis, il caractérise le Campanien supérieur, sous la limite avec le Maastrichtien (Antonescu *et al.*, 2001). Cette étude des restes organiques mériterait d'être approfondie en Navarre où l'on ne dispose pas d'études publiées à notre connaissance car ils ont montré un bon potentiel stratigraphique à Tercis.

Planche 1. Variété des microfossiles dans le faciès de plate-forme de Navarre. Vues au microscope électronique à balayage. Barre d'échelle = 300 µm (vues 1 à 7); ou 100 µm (vues 8 à 26).

1, ossicule colonnaire de crinoïde, vue latérale, niveau Ju111. 2, ossicule brachial latéral d'ophiure, niveau Ju111. 3, ossicule brachial ventral d'ophiure, niveau Ju91. 4-5, ossicule marginal d'astéride, 4: face articulaire, 5: face latérale, niveau Ju89. 6, otolithe de poisson, vue latérale, niveau Ju93, 7, microbrachiopode, vue dorsale, niveau Ju93. 8, carapace d'ostracode, *Bythoceratina* sp., vue latérale gauche. 9, foraminifère benthique, *Bolivinoïdes* sp., niveau Ju93. 10, foraminifère hétérohélicide, *Heterohelix* sp., vue latérale, niveau Ju93. 11-18, foraminifères planctoniques, 11: *Contusotruncana fornicata*, face spirale, niveau Ju93; 12: *Globotruncana linneiana*, face spirale, niveau Ju93; 13-16: *Radotruncana calcarata*, 13: vue spirale, niveau Ju83,6; 14: vue spirale, niveau Ju91; 15-16: vues spirale et cavalière du même spécimen, niveau Ju93; 17-18: *Globotruncanita stuartiformis*, vue spirale et latérale du même spécimen, niveau Ju91. 19-21, *Tubella hunzikeri*, microproblematica, 19-20: même spécimen, vue cavalière orale et profil, niveau 33; 21: vue cavalière orale d'un spécimen sectionné, niveau Ju74,5. 22-23, *Lucernellus aubouini*, même spécimen vu de profil et en vue cavalière aborale, niveau Ju63. 24-26, *Lucernellus* sp., microproblematica, même spécimen en vue aborale (vue 25) et cavalière aborale (vue 26) et détail de la vue 25 (24), niveau Ju91.

Plate 1. Diversity of microfossils in the platform facies of Navarre. Scanning electron microscopy. Scale bar = 300 µm (views 1 to 7); or 100 µm (views 8 to 26). 1, columnal ossicle of crinoid, lateral view, level Ju111. 2, lateral brachial ossicle of ophiuroid, level Ju111. 3, ventral brachial ossicle of ophiuroid, level Ju91. 4-5, marginal ossicle of asteroid, 4: articular side, 5: lateral side, level Ju89. 6, fish otolith, lateral view, level 93. 7, microbrachiopod, dorsal view, level Ju93. 8, ostracod carapace, *Bythoceratina* sp., left lateral view. 9, benthic foraminifer, *Bolivinoïdes* sp., level Ju93. 10, heterohelcid foraminifer, *Heterohelix* sp., lateral view, level Ju93. 11-18, planktonic foraminifers, 11: *Contusotruncana fornicata*, spiral face, level Ju93; 12: *Globotruncana linneiana*, spiral face, level Ju93; 13-16: *Radotruncana calcarata*, 13: spiral view, level 83,6; 14: spiral view, level Ju91; 15-16: spiral and sub-profile views of the same specimen, level Ju93; 17-18: *Globotruncanita stuartiformis*, spiral and lateral views of the same specimen, level Ju91. 19-21, *Tubella hunzikeri*, microproblematica, 19-20: same specimen, sub oral and profile views, level Ju33; 21: sub-oral view of a cut specimen, level Ju74.5. 22-23, *Lucernellus aubouini*, profile and sub-aboral views of the same specimen, level Ju63. 24-26, *Lucernellus* sp., microproblematica, aboral view (view 25) and sub-profile (view 26) and detail of view 25 (24), level Ju91.



4.2. Foraminifères planctoniques

Parmi les globotruncanides, un bon nombre de taxons ont été reconnus entre nos cotes Ju74,5 et Ju124: *Globotruncana linneiana*, *Globotruncana bulloides*, *Globotruncana arca*, *Globotruncana ventricosa*, *Globotruncanita stuartiformis*, *Globotruncanita subspinoso*, *Globotruncanita insignis*; *Globotruncanita elevata*, *Contusotruncana fornicata* et *Contusotruncana patelliformis*. La préservation est inégale, ici encore (Pl.1, Figs 11-18). Toutefois, notre objectif n'était pas d'établir une biostratigraphie détaillée pour les foraminifères mais seulement de reconnaître la distribution du marqueur clé *Radotruncana calcarata*.

Celui-ci a été reconnu pour la première fois dans ce faciès de plate-forme de Navarre grâce à ses épines périphériques et à son profil plano-convexe préservé même pour

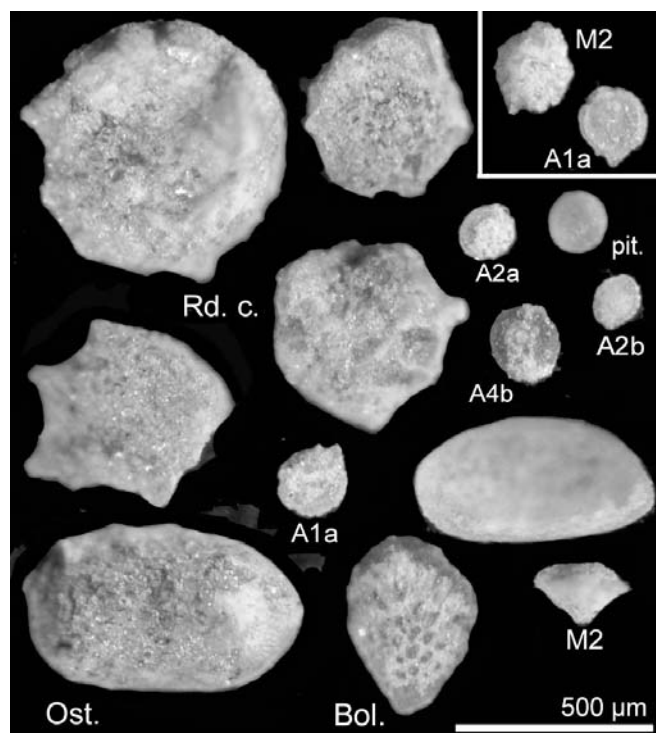


Figure 5. Vues au microscope optique de quelques spécimens de microfaune extraits du niveau Ju83,6 de la section du Mont Juandechaco. A1a, A2a, A2b, A4b, M2: diverses gilianelles (microproblematica); Ost.: ostracode; pit.: pithonelle (incertae sedis); Rd. c.: *Radotruncana calcarata* (foraminifère). Dans le cadre en haut à droite, autres vues des mêmes gilianelles A1a et M2 orientées différemment.

Figure 5. Optic microscopic views of the microfauna collected from level Ju83.6 (Juandechaco Mount section). A1a, A2a, A2b, A4b, M2: gilianellas (microproblematica); Ost.: ostracod; pit.: pithonellid (incertae sedis); Rd. c.: *Radotruncana calcarata* (foraminifer). Upper right corner: the same gilianellas A1a and M2 differently oriented.

certains tests très altérés (Pl. 1, vues 15-16). La présence est assurée dans les spécimens provenant des cotes Ju80, Ju83,6, Ju89, Ju91 et Ju93. Deux spécimens douteux ont été suspectés à la cote Ju79 et peut-être un à la cote Ju74,5. En tout, la zone d'existence de *R. calcarata* représente 13 à 18 m en Navarre ce qui est du même ordre d'épaisseur que pour le site de référence à Tercis. Pour chaque niveau, dont certains ont été dupliqués pour estimer la reproductibilité des trouvailles, les tris ont été arrêtés après l'observation d'un millier de globotruncanides et 2 à 4 spécimens du marqueur ont été récoltés chaque fois dans ces conditions. Le niveau le plus riche se situe à notre cote Ju83,6 où 12 spécimens ont été récoltés parmi 839 globotruncanides. Ainsi, ce niveau est en même temps le plus riche en microfaune planctonique comme noté plus haut; il a un rapport benthiques/planctoniques bas: 0,6; il est le plus riche en *R. calcarata*. Cette coïncidence suggère que le niveau où le marqueur abonde relativement est le plus "océanique".

4.3. Microproblematica

Lors de la découverte des microproblematica dans le site de référence à Tercis (Odin & Lethiers, 2006; Odin, 2007) un code alphanumérique simple leur a été attribué pour désigner temporairement les diverses formes. Ces codes ont été rappelés lors de leur récente détermination (Odin, 2008a) et permettent de les désigner brièvement. Les niveaux soumis à l'acétolyse en Navarre pour observer les foraminifères ont été testés ensuite pour rechercher la présence de ces formes énigmatiques. Rappelons que, si la plupart des foraminifères est présente dans la fraction supérieure à 250 µm, c'est dans la fraction inférieure à cette taille qu'il faut chercher les microproblematica. Un premier état des observations en Navarre a été soumis pour rendre compte de nos résultats et de leur intérêt pour la corrélation biostratigraphique inter-régionale (Odin, 2008b). L'information est complétée ici par l'illustration des formes observées et la présentation de quelques particularités de cette microfaune navarraise de petite taille.

Jusqu'ici, 17 taxons de microproblematica de Tercis (Landes) ont été dénombrés en Navarre dans les 13 niveaux examinés. Cinq niveaux sont très pauvres et l'information est concentrée à nos niveaux navarrais Ju33; Ju63; Ju74,5;

Ju83,6; Ju100; Ju111; Ju117 et Ju124. La préservation des restes est mauvaise à la fois par l'altération du test et par une déformation qui peut rendre impossible l'identification au delà du genre. La fréquence des microproblematica est maximale dans le niveau le plus ancien où ont été observés 50 spécimens par gramme de sédiment dissocié. Aux cotes Ju74,5 Ju117 et Ju124 une trentaine de spécimens ont été observés par gramme de sédiment dissocié. Les cinq niveaux très pauvres livrent moins d'un spécimen par gramme.

La planche 1 présente trois formes de microproblematica non rattachées aux gilianelles. *Tubella hunzikeri* (code L1; Pl. 1, vues 19-21) est une forme intéressante car, à Tercis, elle caractérise la base de la section et disparaît à la cote Ts50,2. La distribution relative du taxon est semblable en Navarre où elle comprend et entoure les niveaux renfermant l'ammonite *B. polyploum*.

Lucernellus aubouini (le lucernel d'Aubouin, code F1; Pl. 1, vues 22-23) est une forme potentiellement plus intéressante encore car, à Tercis, l'espèce n'existe qu'entre les cotes Ts47,2 et Ts57,9 c'est à dire au dessus de la zone d'existence de *B. polyploum* et en partie dans les niveaux à *R. calcarata* sus-jacents. Les deux spécimens récoltés en Navarre proviennent d'un niveau situé au dessus des spécimens de *B. polyploum* récoltés mais encore sous les niveaux à *R. calcarata*. Les spécimens de Navarre possèdent 4 bras régulièrement répartis autour de la face orale ce qui en fait peut-être une variété distincte de celle présente à Tercis où les spécimens comportent toujours 5 ou 6 bras. Cependant, la similitude des tests ne laisse pas de doute sur leur conspécificité. Une autre forme de microproblematica, que nous pensons apparentée à la précédente malgré sa dimension supérieure, a été récoltée en Navarre à notre cote Ju91. Elle est décrite plus loin et n'a pas été observée à Tercis.

Parmi les gilianelles, groupe de microproblematica défini récemment (Odin, 2007), le taxon le plus commun est la petite médaille tarbelle (*Numismella tarbellica*, code A1a; Pl.2, vues 1-2); elle est la forme dominante commune à la fois dans l'échantillon le plus ancien et dans les niveaux les plus récents examinés. À la cote Ju74,5 elle est localement remplacée par la scutellelle épaisse (*Scutellella crassa*, code A1b) comme forme dominante (Pl. 2, vues

6-7). La situation est la même à Tercis où ces deux formes dominant souvent l'association, tout au long de la série, la seconde prenant parfois la place dominante à la première. Observée dans cinq échantillons, la scutellelle à longue voile (*Scutellella longivelifera*, code A2b; Pl. 2, vues 3-5) n'est pas très commune en Navarre. Il en est de même de la scutellelle circulaire (*Scutellella circularis*, code A2a) souvent difficile à reconnaître en l'absence de sa collette équatoriale. Ces deux derniers taxons sont largement distribués dans tout le Campanien supérieur à Tercis comme en Navarre. Il n'en est pas de même de la scutellelle joliment voilée (*Scutellella pulchrevelifera*, code A3; Pl. 2, vues 8-9) qui est restreinte aux niveaux plus anciens et à la base des couches à *B. polyploum* à Tercis (cotes Ts5 à Ts25 de Tercis; Odin, 2008a) tandis qu'elle n'a été observée qu'à notre cote Ju33, sous ces mêmes couches à *B. polyploum* en Navarre. Cette scutellelle est un bon marqueur de temps et est contemporaine, à Tercis, de plusieurs espèces rapportées au genre *Pocillella* (code E3). En Navarre, un unique spécimen de *Pocillella* a été trouvé à la cote Ju33 confirmant ainsi une répartition relative semblable dans les deux successions.

Comme marqueur de niveaux plus récents, le petit corail chanterelle (*Coraliella cantharella*, code M2; Pl. 2, vues 16-17) est présent à Tercis depuis la base des niveaux à *R. calcarata* jusqu'au Maastrichtien inférieur compris (cotes Ts47,2 à Ts125,5 de Tercis; Odin, 2008a). En Navarre, quelques spécimens de cette gilianelle ont été rencontrés à nos cotes Ju74,5 et Ju83,6 c'est à dire dans l'équivalent de la partie basse de la distribution connue à Tercis. Plus haut, le petit corail simple (*Coraliella simplex*) n'est présent, à Tercis, que dans un intervalle de quelques mètres situé au dessus de la disparition de *R. calcarata*. En Navarre, un unique spécimen a été observé à la cote Ju100, quelques mètres au dessus de la disparition connue du même foraminifère dans cette série. Une autre gilianelle peut être considérée comme marqueur de temps; il s'agit de la terciennelle sphérique (*Tercensella globosa*, code N2b) une forme difficile à distinguer d'une pithonelle (Pl. 2, vue 15). Elle est pratiquement contemporaine du petit corail chanterelle à Tercis (couches situées au dessus de la cote Ts49 de Tercis; Odin, 2008a). En Navarre, elle a été reconnue dans des couches ayant le même âge qu'à Tercis, entre les cotes Ju83,6 et Ju124, c'est à dire dans et au dessus de l'intervalle d'existence de *R. calcarata*.

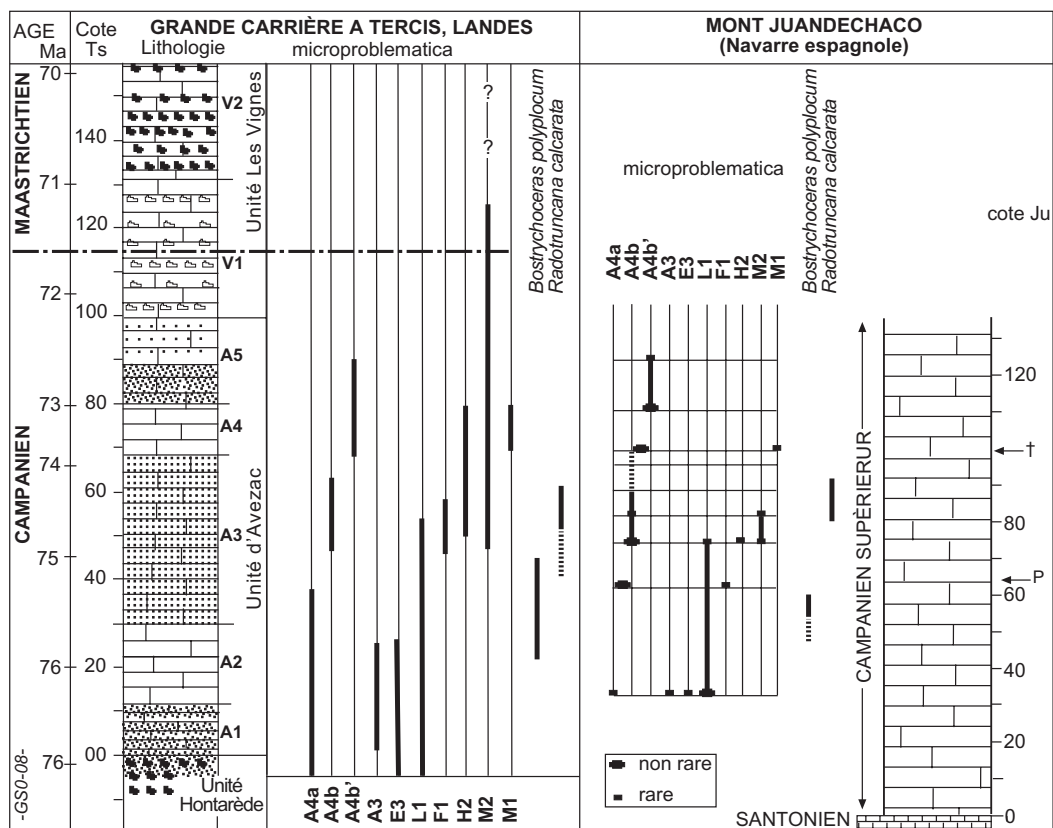


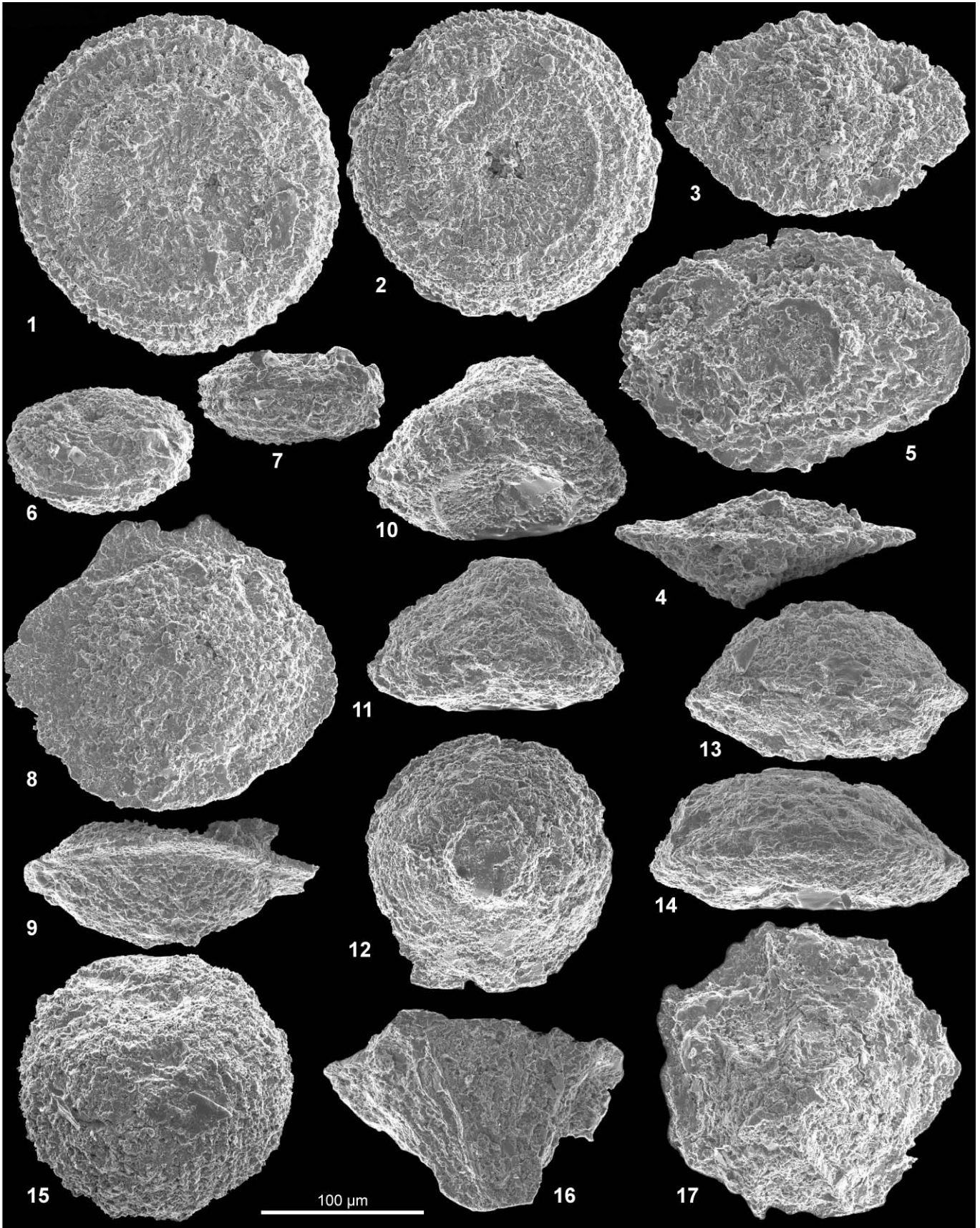
Figure 6. Corrélation entre le stratotype de Tercis et la coupe du Mont Juandechaco. À Tercis, les nodules de silex sont symbolisés dans les unités Hontarède, V1 (silex clair) et V2 (silex foncés); la présence de glauconie est notée en pointillés dans les unités A1 à A5.

Figure 6. Stratigraphical correlation between the stratotype at Tercis and the section of the Juandechaco Mount. At Tercis, flint nodules are shown in the Hontarède, V1 (light flint) and V2 (dark flint) units; dots indicate the presence of glaucony in units A1 to A5.

Un dernier marqueur chronologique très significatif est constitué par les diverses espèces d'aturelles, un genre qui évolue de façon continue à Tercis tout au long de la série campanienne et même au delà et pour lequel 4 espèces ont été formalisées (Odin, 2008a). En Navarre, le niveau Ju33 renferme une espèce dont le profil est nettement dissymétrique (*Aturella altodepressa*, code A4a; Pl. 2, vues 10-12). La face orale est bien plus développée que la face aborale et possède un col marqué entourant l'orifice situé au centre. Plus haut dans la série, le profil devient symétrique (*Aturella aequilatera*, code A4b; Pl. 2, vue 13) notamment dans les niveaux qui renferment *R. calcarata*. Au dessus encore, notamment à la cote Ju111, le profil de la face aborale est marqué par une sorte de couronne en relief qui caractérise l'espèce *Aturella angulata* (code A4b'). Plus haut encore, le profil se modifie encore mais l'on se trouve alors dans des couches dont l'équivalent n'a pas été examiné en Navarre. La succession des formes est la même dans les deux successions des Landes et de Navarre.

Planche 2. Gilianelles du faciès de plate-forme à pithonelles de Navarre. Vues au microscope électronique à balayage. Barre d'échelle commune: 100 µm. 1-2, *Numismella tarbellica*, vue 1: face aborale, niveau Ju83,6; vue 2: face orale, niveau 33. 3-5, *Scutellella longivelifera*, vue 3: face orale, niveau Ju74,5; vue 4: profil du même spécimen; vue 5: face aborale, niveau Ju83,6. 6-7, *Scutellella crassa*, vue 6: vue cavalière orale, niveau Ju74,5; vue 7: profil du même spécimen; 8-9, *Scutellella pulchrevelifera*, vue 8: vue orale, niveau Ju33; vue 9: profil cavalier aboral du même; 10-12, *Aturella altodepressa*, 10: vue cavalière aborale, niveau 33; vue 11: profil du même spécimen; 12, vue orale d'un autre spécimen, niveau Ju33. 13, *Aturella aequilatera*, profil, niveau Ju74,5. 14, *Aturella angulata*, 14: profil, niveau Ju100. 15, *Tercensella globosa*, vue cavalière orale, niveau Ju124. 16-17, *Coraliella cantharella*, 16: vue aborale, niveau Ju83,6; 17: profil du même spécimen.

Plate 2. Gilianelles from the platform pithonellid-rich facies of Navarra. Scanning electron microscopy. Common scale bar = 100 µm. 1-2, *Numismella tarbellica*, view 1: aboral side, level Ju83.6; view 2: oral side, level Ju33. 3-5, *Scutellella longivelifera*, view 3: oral side, level Ju74.5; view 4: profile of the same specimen; view 5: aboral side, level Ju83.6. 6-7, *Scutellella crassa*, view 6: sub oral side, level Ju74.5; view 7: profile of the same specimen; 8-9, *Scutellella pulchrevelifera*, view 8: oral side, level Ju33; view 9: sub-aboral profile of the same; 10-12, *Aturella altodepressa*, view 10: sub-aboral side, level Ju33; view 11: profile of the same specimen; 12, oral side of another specimen, level Ju33. 13, *Aturella aequilatera*, profile, level Ju74.5. 14, *Aturella angulata*, 14: profile, level Ju100. 15, *Tercensella globosa*, sub-oral view, level Ju124. 16-17, *Coraliella cantharella*, 16: aboral side, level Ju83.6; 17: profile of the same specimen.



4.4. Corrélation entre les coupes de plate-forme

Les fossiles marqueurs cités ci-dessus permettent de mettre en parallèle les deux successions où les microproblematica ont été observés. La figure 6 résume la situation en se limitant aux taxons communs significatifs.

Le niveau Ju33, avec A4a, A3, E3 et L1 est contemporain des niveaux Ts0-Ts20 de Tercis. Le niveau Ju63 contenant un intermédiaire A4a/A4b et F1, est contemporain des niveaux Ts39-Ts47 à Tercis. Le niveau Ju74 situé entre la disparition de *B. polyplacum* et l'apparition de *R. calcarata* et qui renferme A4b, L1, H2 et M2 est équivalent aux niveaux Ts47-Ts52 à Tercis. Pour le niveau Ju83 situé dans l'intervalle d'existence de *R. calcarata* contemporaine de A4b et M2, on se situe vers les niveaux Ts55-Ts60 à Tercis. Pour le niveau Ju100 postérieur à la disparition de *R. calcarata* et où l'on trouve un intermédiaire A4b/A4b' et M1, on a l'équivalent des cotes Ts64-Ts70 à Tercis. Au-dessus, pour les niveaux Ju111 et Ju124, on se trouve dans l'équivalent des niveaux Ts70 à Ts89 de Tercis.

Ainsi, les informations données par deux bons macrofossiles stratigraphiques: une ammonite et un foraminifère planctonique permettent de situer relativement les niveaux des deux successions de Tercis et du Mont Juandechaco. Ceci étant établi, l'examen de la succession relative des événements fournis par l'évolution des microproblematica conduit à observer une parfaite cohérence. Ces microproblematica permettent donc d'affiner les relations chronologiques entre les deux successions.

5. PALÉONTOLOGIE SYSTÉMATIQUE

Groupe MICROPROBLEMATICA

Genre *Lucernellus* Odin, 2008a

Espèce type: *Lucernellus aubouini* Odin, 2008a.

Description.- Corps cupulaire à symétrie axiale; expansions entourant la face orale constituées de diverticules de la loge; test formé de deux couches de cristallites; cou-

che interne, épaisse généralement bien préservée; couche externe, très fine, le plus souvent détruite dans l'espèce type; orifice discret, axial sur une face orale; présence de trace(s) d'expansion(s) brisée(s) sur la face aborale.

Espèces appartenant au genre:

L. aubouini, Odin (2008a, Pl. 15, vues 235 à 239)

L. sp. 1

Lucernellus sp. 1 nov. sp. (code H1, ce travail)
(Pl. 1, vues 25-26)

Description.- Corps en cupule de taille supérieure à celle des gilianelles (diamètre proche de 300 µm, hauteur 150 µm); face orale à peine convexe avec un orifice, simple trou dans la paroi du test; contour de la face orale sub-pentagonal (Pl. 1, vue 25) avec, à chaque angle, un bras épais, dirigé vers l'extérieur dans le plan équatorial, largement inséré sur le corps, de section elliptique aplatie; face aborale tronconique, de section sub-pentagonale en haut des flancs (test avec l'orifice vers le haut sur la vue 26) devenant grossièrement triangulaire et plane au niveau de la surface apicale (voir Fig. 7); structure se détachant en léger relief à chaque angle: cicatrice à lumière très réduite dont les parois révèlent une vague organisation radiale des cristallites qui composent la paroi; pas de nanostructure organisée à la surface de ce test.

Référence.- H1: Provenant du Mont Juandechaco, Navarre espagnole, niveau Ju91, le spécimen de référence de cette espèce laissée en nomenclature ouverte est illustré au microscope électronique à balayage (plot II, spécimen n° 20); il est préservé et inventorié au Musée du site de Tercis sous la référence ESP.X088.

Discussion.- Nous ne disposons pas d'une population pour illustrer d'éventuelles variations; son aspect général et divers détails de son organisation le classent très près de *Lucernellus aubouini* et il peut être attribué au même genre, il complète par là la connaissance de ce taxon marqueur de temps précis présent à Tercis et en Navarre.

Distribution.- Cote Ju91 au Mont Juandechaco où il est contemporain des dernières *R. calcarata*.

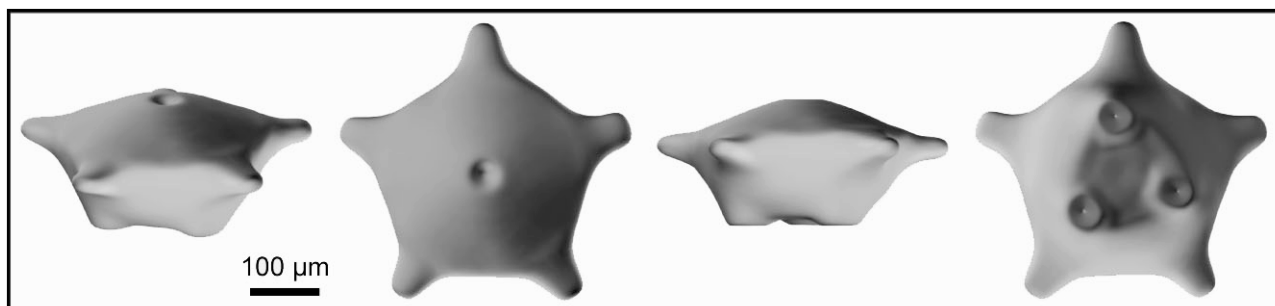


Figure 7. Modèle en 3 dimensions du microproblematica *Lucernellus* sp. 1 de Navarre (réalisation A. Lethiers).

Figure 7. Three dimensional model for the microproblematica *Lucernellus* sp. 1 from Navarre (drawing by A. Lethiers).

6. OBSERVATIONS SUR LES MINÉRAUX PYROCLASTIQUES DE NAVARRE

Connaissant la localisation stratigraphique de l'intervalle à minéraux pyroclastiques à Tercis, il était tentant de voir si des minéraux de même nature étaient présents aux mêmes niveaux sur la plate-forme navarraise espagnole. Rappelons que les événements pyroclastiques explosifs rejettent communément dans l'atmosphère, outre des débris de cendres qui ne se conservent pas souvent dans les sédiments, des cristaux automorphes de biotite (ou de hornblende), de feldspaths potassiques (ou de plagioclase), de zircon et d'apatite. A Tercis, des cristaux de biotite, sanidine, apatite et zircon volcaniques ont été identifiés formellement (Odin, 2001b). Jusqu'à cette première observation, on ne connaissait pas de traces d'événement éruptif dans la région pyrénéenne. Il en existe cependant, à la même époque, en Amérique du Nord. Il s'agit de bentonites interstratifiées dans les sédiments marins créacés du bassin du Western Interior (Obradovich & Cobban, 1976) résultant d'émissions explosives localisées dans l'ensemble des Montagnes Rocheuses durant l'intervalle de 76 à 70 Ma. Ces traces sont connues depuis le Saskatchewan au Nord (Baadsgaard *q.*, 1993) en passant par le Montana, le Wyoming (Hicks *et al.*, 1999), le Colorado, et jusqu'au Nouveau Mexique au Sud; d'autres traces sont connues 1200 km à l'Est du Nouveau Mexique, en Arkansas (Obradovich *et al.*, 1990) et c'est dans ce dernier état qu'elles sont associées à la présence de *Radotruncana calcarata* datée là à environ 75,2 Ma. On ne peut exclure que certains épisodes particulièrement imposants aient envoyé des débris jusqu'en Europe mais il semble peu probable que des apports continus aient pu traverser une partie des États-Unis et l'Atlantique pendant une durée de 1 Ma comme le montrent les sédiments de Tercis.

L'examen optique des échantillons navarraises soumis à l'acétolyse a permis d'observer des paillettes de biotite dans la fraction supérieure à 250 µm aux cotes Ju93 et Ju100. Quelques sédiments provenant des cotes Ju80 à Ju100 ont ensuite été dissous en milieu tamponné acétique afin de préserver les restes phosphatés dont les éventuels cristaux d'apatite. Décantation des résidus, séparation magnétique et séparation densitométrique au bromoforme ont été appliquées ensuite. La fraction fine (inférieure à 80 µm) dense a révélé, la présence d'apatite probable et de zircon dans les trois niveaux testés provenant des cotes Ju93, Ju83,6 et Ju80. Ils étaient accompagnés de baguettes vert bouteille. Quelques cristaux caractéristiques ont été soumis au microscope électronique équipé d'une sonde analytique. Les images obtenues (Fig. 8) indiquent que, parmi les cristaux de zircons (la sonde dénote la présence de 3 éléments: Si, Zr, O) certains sont parfaitement automorphes et sont sans trace de choc (Fig. 8, vues 1 et 3). D'autres portent des traces de choc et ne sont certainement pas parvenus dans le sédiment uniquement par la voie des airs, tandis que d'autres, très émoussés, ont subi une longue histoire détritique (Fig. 8, vue 4). Quant aux baguettes de couleur vert bouteille ou brunes, communes à très communes dans les échantillons Ju80, Ju83,6, Ju91, Ju93, Ju109, leur forme et leur composition: présence des éléments O, Al, Si, Mg, (Na, Fe, Ca) indique qu'il s'agit de cristaux de tourmaline dont la taille peut être supérieure à 250 µm; ce n'est pas un indice de volcanisme aérien mais de détritisme magmatique. Malgré cette provenance, leur préservation peut être bonne (Fig. 8, vue 2).

En résumé, l'étude minéralogique préliminaire des cristaux de haute température séparés des calcaires à pithonelles de Navarre espagnole laisse apparaître une

composate détritique mêlée à une probable contribution pyroclastique dans les niveaux qui renferment *R. calcarata* comme à Tercis. Dans les deux cas, il n'a pas été trouvé d'événement ponctuel considérable qui aurait marqué la série d'un niveau bentonitique. L'intérêt de cette observation est double et concerne la nature de l'événement et sa signification. Quant à sa nature, on n'a pas trouvé d'événement ponctuel considérable de type bentonite à Tercis ni en Navarre espagnole (non plus que dans le domaine du faciès flysch du Pays Basque); sans rejeter la possibilité d'en trouver un localement, on peut dire qu'il s'agit plutôt d'un épisode volcanique dont la durée (de l'ordre de 1 Ma d'après la chronologie illustrée à Tercis) n'est pas très longue mais dépasse le simple phénomène ponctuel.

Quant à son interprétation, cet intervalle volcanique éruptif acide paraît illustrer la première trace de collision entre la plaque ibéro-lusitanienne et la plaque Europe bien avant les phases usuellement admises pour ce phénomène supposé Paléocène-Éocène avant l'orogénèse pyrénéenne qui débute à l'Oligocène (Bilotte *et al.*, 2001, Fig. 2c).

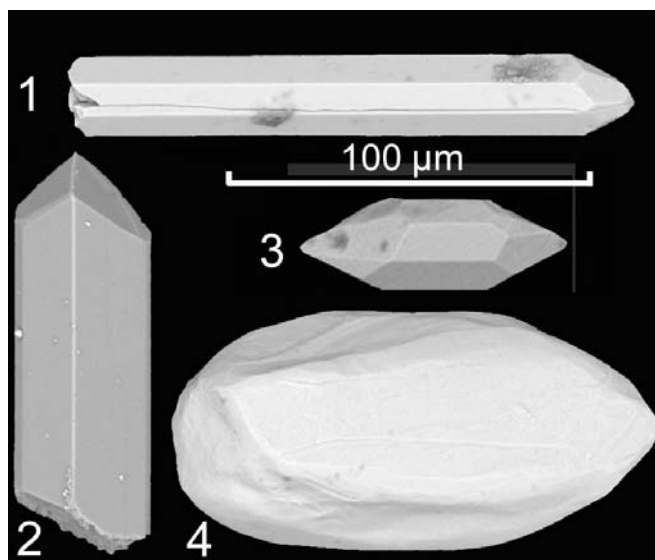


Figure 8. Cristaux séparés de la fraction fine, dense au bromoforme provenant du Mont Juandechaco, dans les niveaux contemporains de l'intervalle pyroclastique de Tercis. 1: zircon automorphe, Ju93; 2: tourmaline automorphe, Ju93; 3: zircon automorphe, Ju83; 4: zircon détritique, Ju93.

Figure 8. Crystals from the fine, dense fraction (density above 2.9) from the Juandechaco Mount in levels contemporaneous to those where pyroclastic minerals were observed at Tercis. 1: automorphic zircon, Ju93; 2: automorphic tourmaline, Ju93; 3: automorphic zircon, Ju83; 4: smoothed detrital zircon, Ju93.

7. CONCLUSION

L'application de la technique d'acétolyse sur les niveaux calcaires indurés du Campanien supérieur de Navarre a permis de dissocier des sédiments qui se sont révélés riches en microfossiles. Une parenté sédimentologique très proche peut être mise en évidence avec le faciès dit "Aturien" des dépôts du stratotype de Tercis où a été définie la limite Campanien-Maastrichtien. Dans les deux cas, il s'agit de calcaires à pithonelles riches en éléments d'échinodermes variés. Ceci caractérise un environnement de plate-forme favorable, notamment, au développement des échinides du genre *Micraster*. Cependant, la succession des espèces de ce genre, très bien caractérisée à Tercis pour le Campanien supérieur, n'est pas reproduite en Navarre, laissant entendre que ce taxon se développait et évoluait indépendamment dans les deux endroits pourtant séparés de moins d'une centaine de km de part et d'autre d'un même bassin.

L'examen des sédiments dissociés a aussi conduit à la découverte de foraminifères variés suffisamment abondants pour permettre une datation stratigraphique des niveaux et compléter ainsi l'approche chronologique de ces dépôts jusqu'ici stratigraphiquement localisés par leur macrofaune. Malgré une préservation pas toujours idéale, on est en droit d'espérer des foraminifères benthiques comme des foraminifères planctoniques une datation relative continue. L'attribution des couches à un âge plus précis que Campanien-Maastrichtien peut alors être obtenu après l'examen de petites quantités de sédiment ce qui devrait faciliter le repérage stratigraphique pour préciser la carte géologique. Rappelons à ce propos que la définition mondiale de la limite Campanien-Maastrichtien à Tercis (Odin & Lamaurelle, 2001) situe le sommet de la zone à *R. calcarata* (situation de la limite autrefois admise en Mésogée) près de 3 Ma au dessous de la limite d'étage définie à Tercis d'après notre plus récente estimation (Odin & Walaszczyk, 2003). Ce déplacement a été rendu nécessaire afin de normaliser la limite utilisée dans les bassins mésogéens avec celle des bassins nordiques où les bélemnites constituent l'outil pratique utilisé alors que ces mollusques sont absents en Mésogée.

Outre la présence des foraminifères planctoniques, les couches de Navarre ont livré des microproblematica dont une grande variété avait été découverte dans les niveaux

du stratotype de limite où ils permettent un découpage stratigraphique plus précis que celui résultant de l'examen des nombreux autres groupes de restes organiques présents sur la plate-forme. L'étude entreprise en Navarre a montré que non seulement ces microproblematica étaient présents mais aussi 1- qu'ils comprenaient des restes similaires à ceux de Tercis, 2- qu'ils se succédaient dans le temps dans le même ordre et 3-qu'ils avaient la même position stratigraphique par rapport aux trouvailles de macrofaune ammonitique et de microfaune planctonique. Une bonne corrélation peut ainsi être proposée entre les Landes et la Navarre.

Enfin, les niveaux contemporains de ceux qui renferment des minéraux pyroclastiques dans la section stratotypique de Tercis repérés par rapport à la zone d'existence du foraminifère *Radotruncana calcarata* ont aussi livré des indices probablement volcaniques en Navarre; ils renferment aussi des minéraux manifestation d'origine magmatique qui ne portent pas toujours les traces de leur remaniement ce qui rend l'identification de l'origine indubitablement volcanique des cristaux de biotite ou de zircon délicate.

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ANNEXE

Note taxinomique sur les genres *Globotruncanita-Radotruncana*

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Loeblich & Tappan (1988, p. 469-470) reconnaissent le genre *Radotruncana* El Naggar, 1971 avec "*Globotruncana calcarata*" comme espèce-type, ce que suivent les auteurs qui se réfèrent usuellement à Loeblich & Tappan (par exemple: Ion & Odin, 2001). Officiellement, c'est donc le genre *Radotruncana* qui devrait être utilisé pour l'espèce *calcarata*; c'est ce qui est accepté, par exemple, par Premoli Silva & Verga (2004, p. 25 et Pl. 119-120).

Toutefois, *Radotruncana calcarata* appartient à une lignée comprenant les formes *Globotruncanita stuartiformis* > *G.(?)-R.(?) subspinosa* > *G.(?)- R.(?) calcarata* avec des formes de transition ce qui peut justifier le maintien du nom de genre *Globotruncanita* pour les 3 espèces comme cela est pratiqué par de nombreux auteurs à la suite de Robaszynski *et al.* (1984, p. 224).

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Análisis bioestratigráfico mediante nanofósiles calcáreos para el Oligoceno–Mioceno medio del norte de Colombia. Sección de superficie del Arroyo Alférez, Colombia

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Resumen

Se analizaron muestras provenientes del registro sedimentario de la Formación El Carmen cuya sección de superficie analizada fue tomada del Arroyo Alférez. Dicha sección de la Formación analizada consiste principalmente en sucesiones muy gruesas de arcillolitas limosas con ocasionales intercalaciones de arenitas glauconíticas. Pocos estudios estratigráficos y bioestratigráficos basados en fósiles marinos, han sido propuestos para el noroeste de Suramérica. Además, no existe ningún modelo bioestratigráfico y paleoceanográfico moderno basado en nanofósiles calcáreos. Diversos esquemas de biozonaciones con nanofósiles calcáreos han sido sugeridos para el Cenozoico. Para la biozonación clásica que se presenta en este estudio, se han escogido los esquemas de Martini (1971) y Bukry (1973, 1975) para subdividir el Oligoceno y Mioceno porque estas zonaciones se establecieron con base en secuencias muy detalladas del Caribe. Además, se tienen en cuenta eventos adicionales propuestos por varios autores. La base del intervalo estudiado comprende desde el Oligoceno inferior NP23 (CP18) hasta el Mioceno medio NN5 (CN4). El registro es continuo y la preservación de la asociación coccolitofores es excelente. El intervalo estudiado contiene en líneas generales, de abundante a común, especímenes de *Cyclicargolithus floridanus*, *Cyclicargolithus abisectus*, *Reticulofenestra minuta*, *Reticulofenestra minutula*, *Reticulofenestra media*, *Reticulofenestra pseudoumbilicus*. En abundancia común aparecen taxones del género *Helicosphaera*. En tanto que los *Asterolites* aparecen en poca abundancia, registrándose un considerable incremento hacia el final de la secuencia, lo que estaría en concordancia con la idea de que prefieren aguas más cálidas. La futura correlación con otras secciones ya propuestas para transeptos oceánicos continuos, permitirá plantear un modelo paleoceanográfico para el área de estudio.

Palabras clave: Nanofósiles calcáreos, Neógeno, Bioestratigrafía, Mar Caribe, Colombia

Abstract

[*Biostratigraphical analysis from calcareous nannofossils of the Oligocene–Middle Miocene of North Colombia. Outcrop of Arroyo Alférez, Colombia*] A calcareous nannofossil-based biostratigraphy is presented for northern Colombia. The samples were taken from the Arroyo Alférez on-shore section belonging to El Carmen Formation. Mostly it consists of a massive succession of dark gray silty mudstones with occasional glauconitic sandstone intercalations. Very few stratigraphic and biostratigraphic studies have been done in the land areas of NE South America based on marine fossil faunas and there are not any modern paleoceanographic and biostratigraphic calcareous nannofossil reconstruction. In this research, the classical biostratigraphic schemes proposed by Martini (1971) and Bukry (1973, 1975) for the subdivision of Oligocene and Miocene have been chosen, because those were established in detailed sequences of the Caribbean Sea. In addition, other events proposed by several authors have been considered. The base of the Arroyo Alférez sequence studied is localized in the lower Oligocene NP23 (CP18) to Middle Miocene NN5 (CN4), showing a continuous record and an excellent preservation of coccolithophore assemblages. The most representative taxa identified in the sequence are *Cyclicargolithus floridanus*, *Cyclicargolithus abisectus*, *Reticulofenestra minuta*, *Reticulofenestra minutula* and *Reticulofenestra pseudoumbilicus*. We also note that the *Helicosphaera* spp. was abundant in some intervals, while discoasterids increase toward the top of the section indicating more temperate superficial waters. It also shows a potential paleoceanographic key for the future correlation with the off-shore record.

Keywords: Calcareous nannofossils, Neogene, Biostratigraphy, Caribbean Sea, Colombia

1. Introducción

La sección de superficie de la Formación Carmen estudiada se encuentra ubicada en cercanías a los municipios de Carmen de Bolívar, San Jacinto y San Juan Nepomuceno, departamento de Bolívar (Colombia) (Fig. 1). En el Arroyo Alférez (Carmen de Bolívar), específicamente en el sector del flanco oriental del anticlinal de El Tigre se midieron 1885,5 m de la Formación Carmen. En esta sección se tomaron muestras de roca fresca para su posterior

análisis microscópico. La sección de superficie de la Formación Carmen consiste principalmente en sucesiones muy gruesas de arcillolitas limosas con ocasionales intercalaciones de arenitas glauconíticas. Suprayace la Formación San Jacinto e infrayace la Formación Rancho (Fig. 2).

A pesar de su alto valor biocronológico, los nanofósiles calcáreos aun no han sido utilizados en Colombia para generar una bioestratigrafía de alta resolución, aplicable a la correlación del registro geológico. El objetivo de este

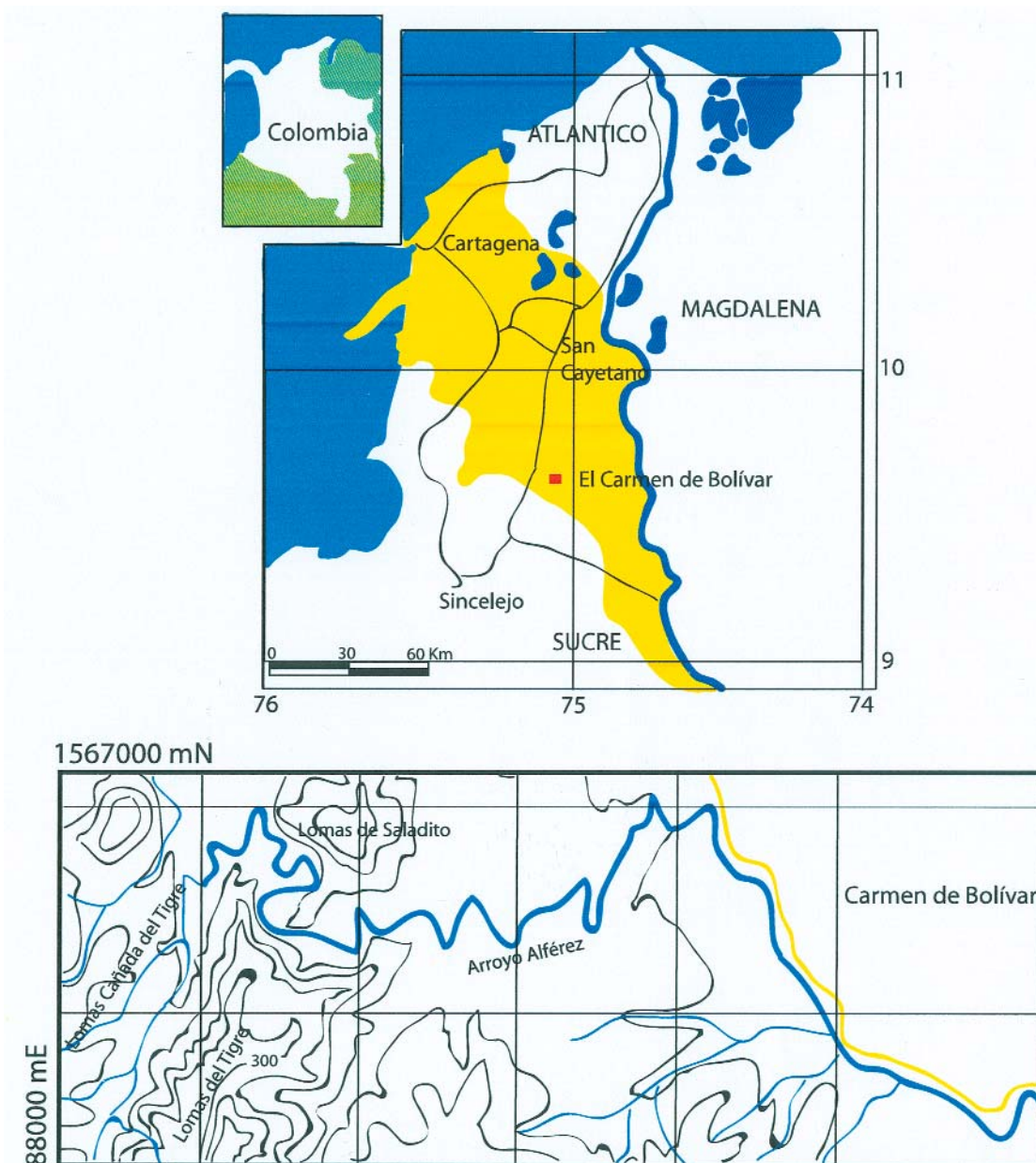


Figura 1. Localización geográfica de la sección del Arroyo Alférez, Colombia.
 Figure 1. Geographical setting of Arroyo Alférez section, Colombia.

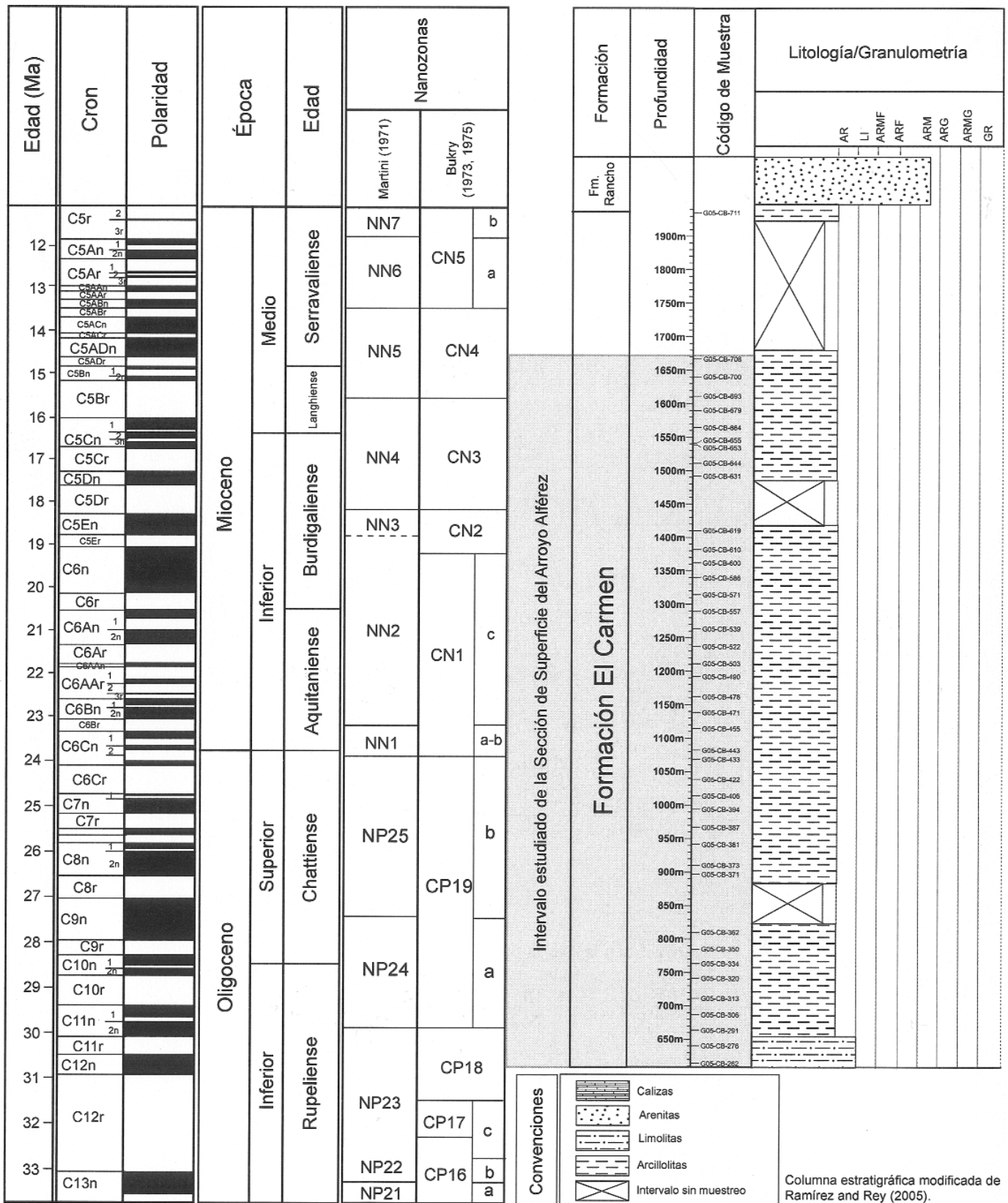


Figura 2. Escala y polaridad del tiempo geológico para el intervalo Oligoceno–Mioceno medio. Esquemas de zonación de nanofósiles calcáreos propuestos por Martini (1971) y Bukry (1973, 1975) considerados en este estudio. Columna litoestratigráfica para la sección estudiada.

Figure 2. Geological and polarity timescale of Oligocene-Middle Miocene Interval. Calcareous nannoplankton zonation schemes proposed by Martini (1971) and Bukry (1973, 1975) considered for the present review. Lithostratigraphic column for the studied section.

estudio es mostrar la distribución de eventos bioestratigráficos de nanofósiles calcáreos para el intervalo Oligoceno-Mioceno inferior de la Formación El Carmen en la sección de superficie del Arroyo Alférez. Esta sección ha sido utilizada como referencia para el norte de Colombia a partir del trabajo de Petters and Sarmiento (1956). Del análisis de su registro sedimentario, la presencia de sus diferentes taxones con sus respectivas características ecológicas, su evolución y momentos de aparición o extinción cronológicamente datados pueden reconstruirse las condiciones paleoceanográficas de las aguas superficiales y su relación con las variaciones paleoclimatológicas (McIntyre and Bé, 1967; Geitzenauer *et al.*, 1977; Kinkel *et al.*, 2000, entre otros). Además, de ser una excelente herramienta bioestratigráfica donde en el modelo bioestratigráfico aquí planteado, se registran los bioeventos clásicos y otros propios del complejo entorno paleoceanográfico de la región del caribe colombiano, además de constituirse en el primer estudio moderno que presenta las características de la asociación coccolitoforal identificada.

La futura correlación con otras secciones a estudiar permitirá plantear un modelo paleoceanográfico para el área de estudio, donde la calibración astronómica de los eventos identificados con la curva global de $\delta^{18}\text{O}$ genera gran expectativa.

2. TÉCNICAS DE PREPARACIÓN DE NANOFÓSILES CALCÁREOS PARA ESTUDIOS CON MICROSCOPIA ÓPTICA

Las muestras fueron tratadas en el Laboratorio de Micropaleontología de la Universidad de Salamanca. Inicialmente se prepararon 40 frotis (*smear slides*) de algunos intervalos seleccionados al azar de las muestras colectadas con el propósito de tener una idea general de la preservación y abundancia relativa de la nanoflora. Además, porque es una técnica sencilla y rápida, la cual ofrece la suficiente confiabilidad para estimaciones preliminares. La preparación definitiva de las muestras se realizó mediante la implementación de la técnica de decantación de Flores and Sierro (1997).

2.1 Análisis microscópico

El análisis microscópico para el reconocimiento e identificación taxonómica de cocolitos se hizo utilizando un microscopio petrográfico Leica DMRP de 1000, 1250 y 1500 aumentos. La taxonomía propuesta en este estudio es de acuerdo con Bolli *et al.* (1985) y Bown (1998). Apéndice A. Además de la planteada por otros autores en diversos artículos científicos y de la del software *Electronic Calcareous Nannofossils, 2002* de la INA (*The International Nannoplankton Association*). Se presentan imágenes de los taxones más representativos y su taxonomía correspondiente (Láms. 1 y 2).

En general la nanoflora es abundante y bien preservada, donde incluso en algunos niveles, se pueden observar estructuras muy delicadas de los escudos de algunos taxones, las cuales difícilmente se encuentran preservadas en secuencias tan antiguas. Sin embargo, otros niveles presentan un pobre contenido en nanofósiles donde es evidente la extrema disolución. En muestras aisladas no se registra nanoflora.

3. ZONACIÓN BIOESTRATIGRÁFICA

Diversos esquemas de biozonaciones con nanofósiles calcáreos han sido propuestos para el Cenozoico (Martini, 1971; Okada and Bukry, 1980). Para la biozonación clásica propuesta en este estudio, se han escogido los esquemas de Martini (1971) y Bukry (1973, 1975) para subdividir el Oligoceno y Mioceno porque estas zonaciones se establecieron con base en secuencias muy detalladas del Caribe. Además, se tienen en cuenta eventos adicionales propuestos por Gartner (1992), Okada and Bukry (1980), Raffi and Flores (1995), Theodoridis (1984), Varol (1989) y los registrados por Bown (1998) pertenecientes a varios autores. La edad de la mayoría de los datos de nanofósiles y de los bioeventos fueron tomados de Berggren *et al.* (1995) y Raffi and Flores (1995).

3.1 Biozonación

Las muestras de sedimento del intervalo estudiado del Arroyo Alférez contiene en líneas generales, de abundante a común, especímenes de *Cyclicargolithus floridanus*

(Lám. 1, Fig. 5), *Cyclicargolithus abisectus* (Lám. 1, Fig. 4), *Reticulofenestra minuta*, *Reticulofenestra minutula*, *Reticulofenestra media*, *Reticulofenestra pseudoumbilicus* (Lám. 1, Fig. 19). En abundancia común aparecen taxones del género *Sphenolithus* y en algunos niveles se registran frecuentes individuos de *Helicosphaera*. En tanto que los *Asterolitos* aparecen en poca abundancia, registrándose un considerable incremento hacia el final de la secuencia, lo que estaría en concordancia con la idea de que prefieren aguas más cálidas, condiciones que habrían prevalecido después del óptimo climático del Mioceno que finalizaría hacia ~15 Ma (Zachos et al., 2001).

A continuación se describen las biozonas definidas para la sección de superficie del Arroyo Alférez, las cuales abarcan un periodo comprendido entre el Oligoceno inferior (Rupeliense) hasta el Mioceno medio (Langhiense-Serravallense), correspondientes a las zonas NP23 (CP18) hasta la NN5 (CN4) de Martini (1971) y Okada and Bukry (1980) (Fig. 2). Las zonas se han organizado de acuerdo a Martini (1971) y entre paréntesis se relaciona la zona correspondiente de acuerdo a Bukry (1973, 1975). FO y LO, corresponden al primer registro y último registro, sucesivamente.

3.2 Oligoceno

El Oligoceno fue un periodo de tiempo relativamente corto, pero caracterizado por algunos de los mayores cambios geológicos. El enfriamiento que prevaleció a través del Oligoceno (Aubry, 1992) modificó la vida y el hábitat de muchos organismos, siendo los especímenes marinos unos de los más afectados.

3.2.1 Inferior (Rupeliense)

NP23 *Sphenolithus predistentus* Zone

(CP17) *Sphenolithus predistentus* Zone y (CP18) *Sphenolithus distentus* Zone

Intervalo.- De G05-CB-262 hasta G05-CB-394.

Profundidad: 614,625m a 994,625 m

Definición.- LO de *Reticulofenestra umbilicus* hasta FO de *Sphenolithus ciperoensis*

Investigaciones en secciones del Oligoceno del Norte de Europa (Müller, 1976; Benedek and Müller, 1974) han mostrado que *C. abisectus* y *Helicosphaera recta* (Lám. 1, Fig. 13) tienen sus primeras apariciones aproximadamente hacia el límite de las zonas de *Sphenolithus predistentus* (Lám. 2, Fig. 9) y *Sphenolithus distentus* (NP23/24) (Lám. 2, Fig. 6) de la zonación estándar (Martini, 1971; Martini and Müller, 1986). En: Garecka (2005). Lo anterior, sumado al resto de la asociación de nanoplacton identificada, permite situar la base de la secuencia en el final de NP23 (CP18), después del primer registro de *C. abisectus*, *Helicosphaera recta* y *Discoaster adamanteus* (Lám. 1, Fig. 6). *S. predistentus* está presente pero es escaso. *Helicosphaera compacta* (Lám. 1, Fig. 11) es frecuente.

El límite entre NP23/NP24 (CP18/CP19a) estaría marcado por la LO de *H. compacta* y FO de *Sphenolithus ciperoensis* (Lám. 2, Fig. 1), lo que estaría en concordancia por lo sugerido por Bolli et al. (1985).

3.2.2 Superior (Chattiense)

NP24 *Sphenolithus distentus* Zone

(CP19) *Sphenolithus ciperoensis* Zone (CP19a)

Cyclicargolithus floridanus Zone

Intervalo.- De G05-CB-406 hasta G05-CB-490. Profundidad: 1014,625 m a 1192,125 m

Definición.- FO de *Sphenolithus ciperoensis* hasta LO de *Sphenolithus distentus*

La asociación presenta un importante aumento de *Helicosphaera euphratis* (Lám. 1, Fig. 12) y *C. abisectus*. *S. predistentus* es frecuente y desaparece antes de *Sphenolithus distentus*, aunque la presencia de este último es escasa en todos los niveles. Escasos individuos de *Triquetrorhabdulus carinatus* (Lám. 2, Fig. 11), levemente disueltos, se registran en esta zona. Estas características estarían de acuerdo a lo descrito por Bolli et al. (1985) para NP24. *S. ciperoensis* aparece en poca abundancia, pero en general, bien preservados y fácilmente distinguibles de los otros *Sphenolithus*. Es común la presencia de Reticulofenestridos y se destaca la abundancia de *Reticulofenestra bisecta* (Lám. 1, Fig. 18).

El final de esta zona está caracterizado por la última ocu-

rrencia de *Pontosphaera (Discolithina) enormis* (Müller, 1976; Martini, 1981; Martini and Müller, 1986; Benedek and Müller, 1974, en: Garecka, 2005). Pero, aunque *Pontosphaera multipora* aparece en algunos niveles como frecuente, la presencia de *P. enormis* no se ha registrado en la sección o su identificación no ha sido posible dada las características de preservación de los especímenes. De acuerdo con varios autores (Báldi-Beke, 1981; Melinte, 1995; Bizon and Müller, 1979; Biolzi et al., 1981), la primera aparición de *Sphenolithus conicus* (Lám. 2, Fig. 3) podría ser usada como un marcador sustituto de LO *P. enormis*. Sin embargo, la LO de *S. conicus* se observa más arriba al final de NN1. Este evento podría estar presentando un carácter diacrónico. Además de lo anterior, el hecho de que la primera muestra considerada como de NN1 (G05-CB-586) presenta una pésima preservación y un avanzado estado de disolución, habría podido impedir la conservación de estos pequeños *Sphenolithus*.

NP25 *Sphenolithus ciperensis* Zone

(CP19) *Sphenolithus ciperensis* Zone (CP19b)

Dictyococcites bisectus Subzone

Intervalo.- De G05-CB-503 hasta G05-CB-571.

Profundidad: 1211,375 m a 1314,375 m

Definición.- LO de *Sphenolithus distentus* hasta LO de *Helicosphaera recta* y/o LO de *Sphenolithus ciperensis*

Está basada en la presencia continuada de *S. conicus*, *Sphenolithus dissimillis* (Lám. 2, Fig. 5) y *T. carinatus*, seguida por la desaparición de *R. bisecta*. Ha sido recomendado durante muchos años el uso del último registro de *S. ciperensis* para definir la base de NN1 (Okada and Bukry, 1980). Sin embargo, esta especie es común en latitudes bajas y está casi siempre ausente en latitudes altas. La secuencia del Arroyo Alférez muestra claramente el último registro de *S. ciperensis* y *R. bisecta*, siendo más difícil en el caso de *S. distentus* dado su escasa abundancia en la secuencia. En este nivel se registra también la LO de *Chiasmolithus altus* (Lám. 1, Fig. 1). Mientras *H. recta* y *S. ciperensis* han mostrado ser marcadores útiles en muchas secciones a latitudes bajas, los últimos registros de *R. bisecta* y *Zygrhablithus bijugatus* (Lám. 2, Fig. 14) establecerían el límite aproximado entre NP25-NN1 (Bolli et al., 1985). Sin embargo, el LO de *H. recta* se registra en NN1. Estos últimos registros serían eventos sincrónicos con la primera aparición de *T. carinatus* y correspondería a la

base de NN1 (Martini, 1971). No obstante, el mismo autor (Martini, 1971) registra la ocurrencia de *T. carinatus* también en la zona de NP25 y aún más abajo en la parte superior de NP24. Esto último ha sido registrado en la sección estudiada donde el material no está tan mal preservado como para no diferenciar este taxón de elementos alargados de calcita. Además de lo anterior, Perch-Nielsen (1985), Berggren et al. (1995), Fornaciari et al., (1990) y Young (en Bown, 1998) sugieren redefinir la base de NN1 (y por consiguiente el techo de NP25) como en el último registro de *R. bisecta*.

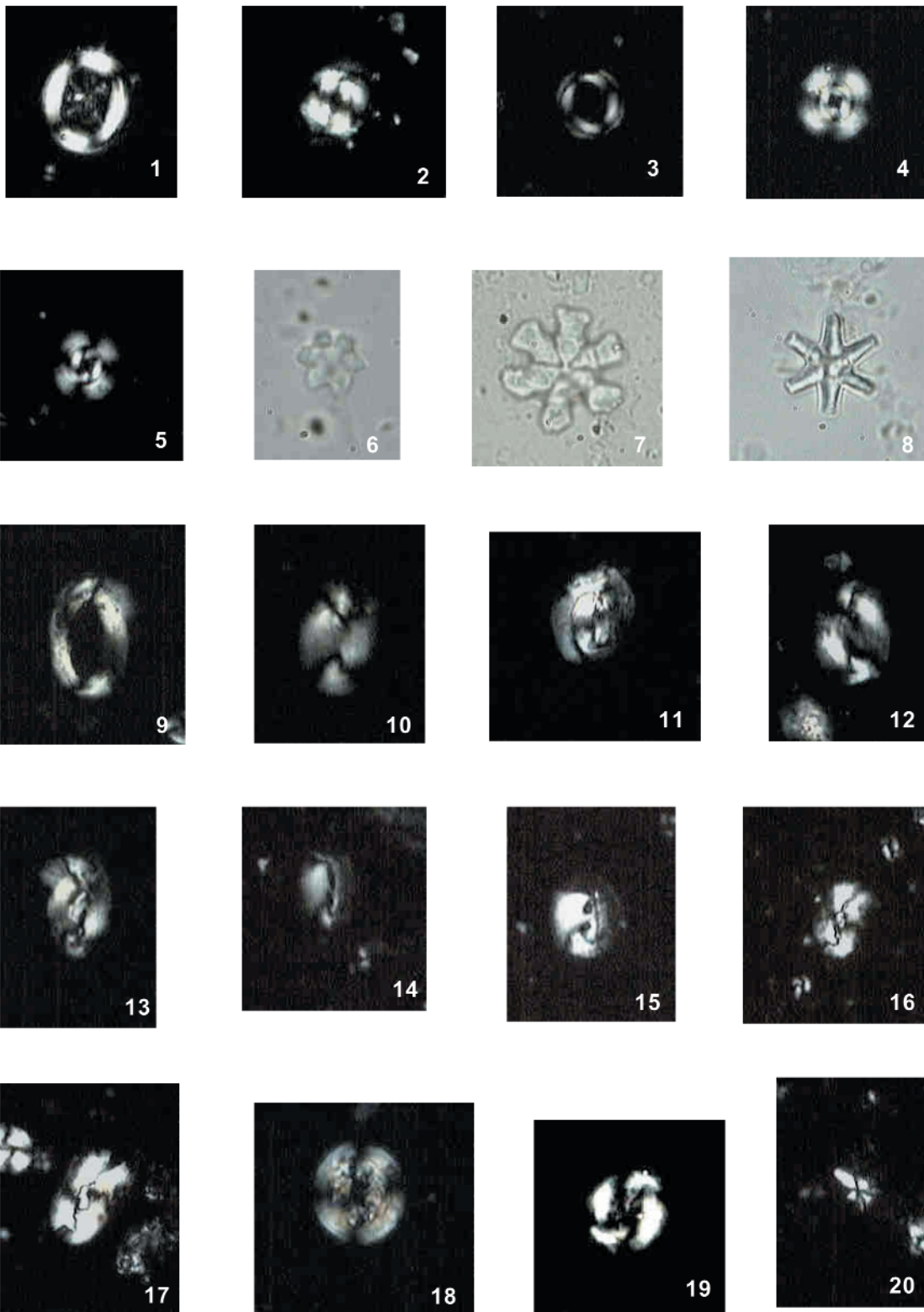
3.3 Eventos bioestratigráficos en el límite Oligoceno-Mioceno

El límite Oligoceno/Mioceno en términos de nanofósiles calcáreos es localizado en el techo de NP25 por algunos autores y en la base de NN1 por otros. La secuencia de desaparición de *H. recta*, *S. ciperensis*, *R. bisecta* y *Z. bijugatus* suelen ser usados como marcadores (Bolli et al., 1985), pero este conjunto de eventos pueden variar de acuerdo a los marcadores seleccionados por diferentes autores, además de que en algunos casos ciertos taxones están restringidos por la latitud. De acuerdo a lo expuesto por Aubry and Villa (1996) la primera aparición de *Sphenolithus delphix* es el único evento que marca el límite

Lámina 1. Nanofósiles calcáreos del Oligoceno-Mioceno Medio de Arroyo Alférez (Colombia). 1. *Chiasmolithus altus* Bukry and Percival, 1971; 2. *Coccolithus pelagicus* (Wallich, 1877) Schiller, 1930 (<13 µm); 3. *Coronocyclus nitescens* (Kamptner, 1963) Bramlette and Wilcoxon, 1967; 4. *Cyclicargolithus abisectus* (Müller, 1970) Wise, 1973 (>10 µm); 5. *Cyclicargolithus floridanus* (Roth and Hay in: Hay et al., 1967) Bukry, 1971 (<10 µm); 6. *Discoaster adamanteus* Bramlette and Wilcoxon, 1967; 7. *Discoaster deflandrei* Bramlette and Riedel, 1954; 8. *Discoaster druggii* Bramlette and Wilcoxon, 1967 (>15 µm); 9. *Helicosphaera ampliapertura* Bramlette and Wilcoxon, 1967; 10. *Helicosphaera carteri* (Wallich, 1877) Kamptner, 1954; 11. *Helicosphaera compacta* Bramlette and Wilcoxon, 1967; 12. *Helicosphaera euphratis* Haq, 1966; 13. *Helicosphaera intermedia* Martini, 1965; 14. *Helicosphaera obliqua* Bramlette and Wilcoxon; 15. *Helicosphaera recta* (Haq, 1966) Jafar and Martini, 1975; 16. *Helicosphaera walbersdorfensis* Mueller, 1974; 17. *Helicosphaera waltrans* Theodoridis, 1984; 18. *Reticulofenestra bisecta* (Hay, Mohler and Wade, 1967) Roth, 1970; 19. *Reticulofenestra pseudoubilicus* (Gartner, 1967) Gartner, 1969 (>7 µm); 20. *Sphenolithus belemnus* Bramlette and Wilcoxon, 1967. Todas las microfotografías se han realizado con nicoles cruzados, excepto 6, 7 y 8, y se encuentran ampliadas x 1000. Escala gráfica = 10µm.

Plate 1. Calcareous nanofossils from the Oligocene-Middle Miocene of Arroyo Alférez (Colombia). All specimens x 1000 and in crossed nicols, except 6, 7 and 8. Scale bar equals 10µm.

Lámina 1



10 μm

Oligoceno– Mioceno. Sin embargo, Fornaciari y otros (Fornaciari *et al.*, 1990) indica que esta especie está restringida a la parte superior del Mioceno inferior, Subzona CN1c (NN2), donde aparecería con frecuencia. En este estudio no se ha identificado *S. delphix*, lo cual es factible dado su pequeño tamaño, lo que lo hace muy difícil de identificar en análisis de microscopía óptica. Además el inicio del Mioceno está caracterizado por la ausencia de nanoflora en las muestras (G05-CB-610 y G05-CB-619).

El evento que quizá presenta más confiabilidad es el último registro de *R. bisecta*, el cual ha sido utilizado para fijar el límite NP25/NN1 (Rio *et al.*, 1990 para el Océano Índico y Berggren *et al.*, 1995 en 23.9 Ma). En el Mediterráneo este evento se habría registrado en la parte inferior de la zona de NN1 (Fornaciari and Rio, 1996) y se considera la mejor aproximación al límite Oligoceno/Mioceno. En este estudio se ha seleccionado el LO de *R. bisecta* para marcar el límite Oligoceno/Mioceno.

3.4 Mioceno

Durante el Mioceno inferior (~24 Ma hasta ~16 Ma), la circulación termohalina era muy diferente a la actual porque los pasajes oceánicos a bajas latitudes (por ejemplo, entre Istmo de Panamá y Tethys) permitían una circulación ecuatorial bien desarrollada. El Mioceno medio a superior es conocido como un intervalo de grandes cambios en el sistema climático terrestre, como lo fueron la expansión de los casquetes polares de la Antártida, el enfriamiento y hundimiento de las masas de agua superficial e inicio del levantamiento del Istmo de Panamá y del Himalaya (Zachos *et al.*, 2001). Estas condiciones tan cambiantes tuvieron un impacto significativo en la circulación oceánica, en el suministro de nutrientes y por ende, en la productividad de los océanos.

3.4.1 Inferior (Aquitaniense)

NN1 *Triquetrorhabdulus carinatus* Zone

(CN1) *Triquetrorhabdulus carinatus* Zone (CN1a)
Cyclicargolithus abisectus y (CN1b) *Discoaster deflandrei* Subzone

Intervalo.- G05-586. Profundidad: 1339,125 m

Definición.- LO de *Helicosphaera recta* y/o LO *Sphenolithus ciperoensis* hasta FO de *Discoaster druggii*

NN1 es usualmente reconocida como la zona base del Mioceno. Bukry (1973) resalta en la parte más baja de esta zona (CN1a) la presencia común de *C. abisectus* y en la siguiente (CN1b) caracterizada por poca diversidad, la presencia relativamente común de *Discoaster deflandrei* (Lám. 1, Fig. 7). Lo anterior es coherente con lo encontrado en la sección estudiada, aunque los Asterolitos aún no son muy frecuentes en la asociación. Aumenta la abundancia de *T. carinatus* y *C. floridanus*. *Discoaster druggii* (Lám. 1, Fig. 8) puede ser difícil de distinguir de otros Asterolitos cuando hay recrecimiento. Aunque la recristalización es evidente en varios individuos, se ha podido identificar bien su presencia en la base de esta zona, registrándose mayores abundancias hacia el límite con NN2. El rango bioestratigráfico de *S. delphix* es aún problemático. Este taxón fue registrado por Aubry (1985) desde NP25 y en NN1 por Young (Young, en: Bown, 1998), donde esta especie sería característica sólo en la parte superior de NN1, lo cual podría marcar el límite Oligoceno/Mioceno (Oszczypko *et al.*, 2005). La no presencia de *S. delphix* en el registro ya fue discutida en un apartado anterior.

El último registro de *H. recta* fue formalmente adoptado por Martini and Worsley (1979) como la base de NN1, pero hay indicios en otros estudios de la presencia de este taxón en secuencias más jóvenes (Rio *et al.*, 1990; en: Bown, 1998). *H. recta* se presenta como un taxón frecuente en la asociación donde su LO se ha identificado en la base de NN2 (CN1c), lo que está en concordancia con lo sugerido por Gartner (1992) y De Kaenel and Villa (1996). De acuerdo con Okada and Bukry (1980) la LO de *C. abisectus* estaría ubicada en la base de CN1b. En este estudio este evento está justo en la parte inferior-media de CN1c. Es importante resaltar que en esta zona y/o en la base de NN2 el Mioceno está caracterizado por la ausencia de nanoflora en las muestras (G05-CB-610 y G05-CB-619), lo que impide que algunos eventos se registren con una mayor precisión.

NN2 *Discoaster druggii* Zone

(CN1) *Triquetrorhabdulus carinatus* Zone (CN1c)

Discoaster druggii Subzone

Intervalo.- G05-CB-600 hasta G05-CB-679.

Profundidad: 1362,750 m a 1590,125 m

Definición.- FO de *Discoaster druggii* hasta LO de *Triquetrorhabdulus carinatus*

La base de esta zona estaría representada por la primera aparición de *Helicosphaera ampliaperta* (Lám. 1, Fig. 10) aunque en la asociación no llega a ser abundante en ningún intervalo y la presencia frecuente de *D. druggii*, eventos que ya han sido definidos (en Bolli *et al.*, 1985). Además de la LO de *Helicosphaera recta*, evento que se ha discutido en el apartado anterior. De acuerdo con (Oszczypko *et al.*, 2005) la presencia simultánea de *S. conicus*, *Sphenolithus disbelemnus* (Lám. 2, Fig. 4), *R. pseudoumbilicus* y *T. carinatus*, caracterizan esta zona. En la zonación estándar de Martini (1971) se propone el FO de *R. pseudoumbilicus* en NN5 con un reconocido valor estratigráfico. Sin embargo, en el intervalo analizado, ejemplares de más de siete micras de *Reticulofenestra* con las características propias de *R. pseudoumbilicus* se identifican claramente es este nivel de NN2. Esto ya ha sido registrado por Oszczypko *et al.* (2005). En la sección estudiada, la primera aparición de *S. disbelemnus* es identificada, lo que estaría de acuerdo con lo sugerido por Young (en: Bown, 1998), donde su FO y la de *Umbilicosphaera rotula* son eventos bioestratigráficos característicos de la parte inferior de NN2. En la asociación no se identificó *U. rotula*, aunque se registra la presencia de algunos individuos de *Umbilicosphaera* spp. *T. carinatus* en algunos niveles es muy abundante.

De Kaenel and Villa (1996) mencionan la LO de *Helicosphaera euphratis* (morfortipo grande) como un evento adicional útil para la parte superior de NN2. En la sección analizada, *H. euphratis* es muy frecuente en el Oligoceno, pero hacia NN2 se observa su disminución sin que se precise claramente si es en este nivel o más arriba su último registro. Lo que si es claro es que hacia este nivel su presencia es ya muy escasa. Estos autores también registran el LO de *S. conicus* en la parte superior de NN2. Esto estaría en concordancia con la posición de *S. conicus* documentada antes de la FO de *Sphenolithus belemnus* (Lám. 1, Fig. 20) por Gartner (1992). En este estudio se ha iden-

tificado la LO de *S. conicus* en la parte superior de NN2 antes de la FO de *S. belemnus*, lo que confirma lo anterior. Sin embargo, Fornaciari *et al.* (1990) registra la LO de *S. conicus* al mismo nivel con la presencia de *S. belemnus*.

La distribución no continuada de *Coronocyclus nitescens* (Lám. 1, Fig. 3) se ve reflejada en la secuencia del Arroyo Alférez, donde aparece frecuente en los sedimentos del Oligoceno inferior para desaparecer del registro hasta este nivel de NN2, a partir del cual permanece (en poca abundancia) hasta el final de la secuencia estudiada. Además la LO de *H. ampliaperta* en este intervalo supone una anomalía, la cual será detallada más adelante.

3.4.2 Inferior (Burdigaliense)

NN3 *Sphenolithus belemnus* Zone

(CN2) *Sphenolithus belemnus* Zone

Intervalo.- G05-CB-693. Profundidad: 1611,125 m

Definición.- LO de *Triquetrorhabdulus carinatus* hasta LO de *Sphenolithus belemnus*

Martini (1971) propone la LO de *T. carinatus* para distinguir la base de NN3, pero este marcador se considera, en general, no muy fiable (ver discusión en Maiorano and Monechi, 1998). Rio *et al.* (1990) y Fornaciari *et al.* (1990) consideran que la disminución en la abundancia de *T. carinatus* en la base de CN1c es un dato de mayor fiabilidad.

Bukry (1973) sugiere que primera aparición de *S. belemnus* para reconocer la base de CN2; en tanto que la LO de esta especie sería un marcador fiable para el límite NN3/NN4 y un evento secundario para definir el final de CN2. La LO de *T. carinatus* para la sección del Arroyo Alférez se habría presentado aquí, justo antes de la FO de *S. disbelemnus* reconocida en un nivel más joven, evento ya descrito en Bown (1998).

NN4 *Helicosphaera ampliaperta* Zone

(CN3) *Helicosphaera ampliaperta* Zone. Aproximadamente.

Intervalo.- G05-CB-700. Profundidad: 1640,625 m

Definición.- LO de *Sphenolithus belemnus* hasta LO de *Helicosphaera ampliaperta*

La presencia de *Sphenolithus heteromorphus* (Lám. 2, Fig. 7) caracteriza este intervalo, siendo en general abundante. Este es también un intervalo en el que se comienza a registrar una alta diversidad en las especies coccolitoforales: la mayoría de los taxones del Mioceno inferior, como *Helicosphaera obliqua* (Lám. 1, Fig. 14) y *C. nitescens* aún persisten y forman parte de la asociación junto con nuevas especies donde se destacan *Calcidiscus premacintyreii* y *Discoaster exilis*. (Bown, 1998). En un apartado anterior se destaca el carácter no continuo en el registro de *C. nitescens*. Se ha reconocido que taxones diferentes de *Asterolites* están presentes en este intervalo y hasta el final de la secuencia, pero la intensa recristalización que presentan ha impedido su identificación, siendo mencionados como *Discoaster* spp.

La primera aparición de *S. heteromorphus* define la zona de CN3 de la zonación propuesta por Bukry (1973). En la sección estudiada, especímenes de *S. belemnos* aparecen junto con la primera aparición de *S. heteromorphus*. Esta ocurrencia simultánea ya ha sido documentada por Bukry (1972) en el Site 140 en el Atlántico, Pujos (1985) en el Pacífico ecuatorial y Takayama and Sato (1987) en el Atlántico Norte. Contrario a lo antes mencionado, otros autores (Olafsson, 1989 en el Atlántico ecuatorial; Fornaciari *et al.*, 1990 en el océano Índico y Gartner, 1992 en el Atlántico Norte) no registran la simultaneidad entre estas dos especies.

3.4.3 Medio (Langhiense)

NN5 *Sphenolithus heteromorphus* Zone

(CN4) *Sphenolithus heteromorphus* Zone

Intervalo.- G05-CB-708. Profundidad: 1666,875 m

Definición.- LO de *Helicosphaera ampliaperta* hasta LO de *Sphenolithus heteromorphus*

Este nivel representa el techo de la secuencia estudiada, dado que la muestra más joven de la sección (G05-CB-711) no presenta nanoflora. Ambos, Martini (1971) y Okada and Bukry (1980) usan la LO de *H. ampliaperta* para subdividir el largo intervalo entre NN4 y NN5. Su ocurrencia, sin embargo, es frecuentemente esporádica (como se observa en los sedimentos estudiados), particularmente hacia su LO, lo que hace que no se presente como un marcador muy fiable (Bown, 1998). Aún más,

en la sección de superficie estudiada, la LO de *H. ampliaperta* se registra mucho antes, en NN2 (?); lo que confirma su esporádica continuidad en el registro. De acuerdo con Olafsson (1989) y Raffi *et al.* (1995) el repentino incremento en la abundancia de *Triquetrorhabdulus rugosus* y *Triquetrorhabdulus rioensis* (Lám. 2, Fig. 13) es un evento útil para correlacionar niveles antes de la LO de *S. heteromorphus*. En esta sección la FO de *T. rioensis* se presenta coincidente con pocos especímenes de *S. heteromorphus*, lo que podría indicar que el nivel corresponde justo antes de la LO de *S. heteromorphus*. Además la presencia de *Helicosphaera waltrans* (Lám. 1, Fig. 17) y de la pequeña *Helicosphaera walbersdorfensis* (Lám. 1, Fig. 16) confirma que corresponde a esta zona (Müller, 1981 y Fornaciari *et al.*, 1986; en: Bown, 1998).

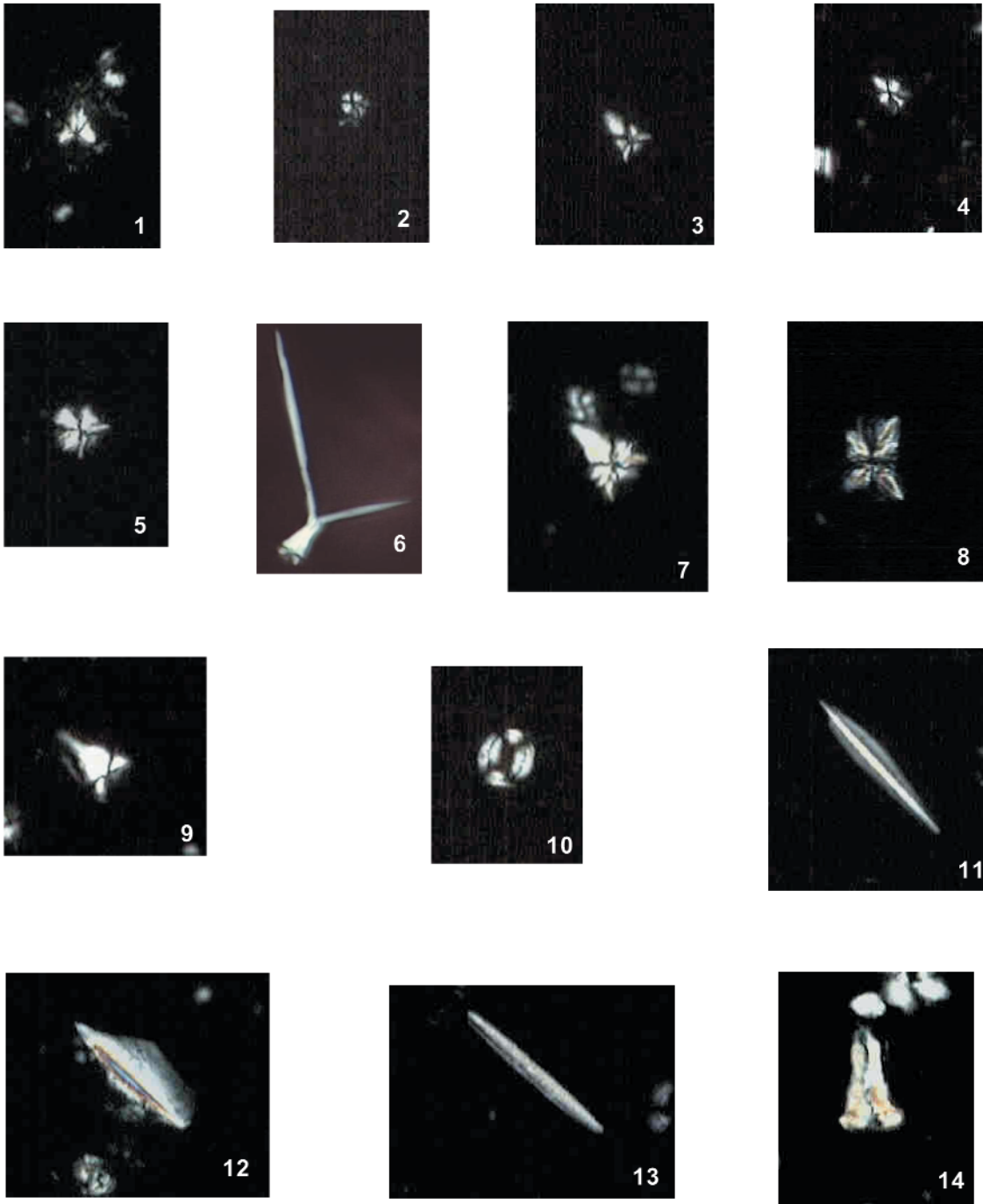
4. CONCLUSIONES

Se identificaron 50 especies pertenecientes a 17 géneros diferentes de algas coccolitoforales y nanofósiles calcáreos. Algunas de ellas son reconocidas como indicadores paleotérmicos y paleoceanográficos. Su distribución geográfica y en la columna de agua, está controlada por eventos climáticos globales de orden orbital y suborbital, que le confieren características específicas a las masas de agua donde se establecen.

Lámina 2. Nanofósiles calcáreos del Oligoceno-Mioceno Medio de Arroyo Alférez (Colombia). 1. *Sphenolithus ciperensis* Bramlette and Wilcoxon, 1967; 2. *Sphenolithus compactus* Backman, 1980; 3. *Sphenolithus conicus* Bukry, 1971; 4. *Sphenolithus disbelemnos* Fornaciari and Rio, 1996; 5. *Sphenolithus dissimilis* Bukry and Percival, 1971; 6. *Sphenolithus distentus* (Martini, 1965) Bramlette and Wilcoxon, 1967; 7. *Sphenolithus heteromorphus* Deflandre, 1953; 8. *Sphenolithus moriformis* (Bronnimann and Stradner, 1960) Bramlette and Wilcoxon, 1967; 9. *Sphenolithus predistentus* Bramlette and Wilcoxon, 1967; 10. *Transversopontis* spp. Mohler and Wade, 1966; 11. *Triquetrorhabdulus carinatus* Martini, 1965; 12. *Triquetrorhabdulus milowii* Bukry, 1971; 13. *Triquetrorhabdulus rioensis* Olafsson, 1989; 14. *Zygrhablithus bijugatus* (Deflandre, En: Deflandre and Fert, 1954) Deflandre, 1959. Todas las microfotografías se han realizado con nicols cruzados y se encuentran ampliadas x 1000. Escala gráfica = 10µm.

Plate 2. Calcareous nannofossils from the Oligocene-Middle Miocene of Arroyo Alférez (Colombia). All specimens x 1000 and in crossed nicols. Scale bar equals 10µm.

Lámina 2



10 μm

Las muestras contienen en líneas generales, de abundante a común, especímenes de *C. floridanus*, *C. abisectus*, *R. minuta*, *R. minutula*, *R. media*, *R. pseudoumbilicus*. Común aparecen taxones del género *Sphenolithus* y en algunos niveles de *Helicosphaera*. En tanto que, los *Asterolitos* aparecen en poca abundancia, registrándose un considerable incremento hacia el final de la secuencia, lo que estaría en concordancia con la idea de que prefieren aguas más cálidas, condiciones que habrían prevalecido después del Óptimo Climático del Mioceno que finalizaría hacia ~15 Ma (Zachos et al., 2001).

Las biozonas identificadas abarcan un periodo comprendido entre el Oligoceno inferior (Rupeliense) hasta el Mioceno medio (Langhiense-Serravallense), correspondientes a las zonas NP23 (CP18) hasta la NN5 (CN4) de Martini (1971) y Okada and Bukry (1980). La mayoría de los eventos bioestratigráficos clásicos han sido identificados en el intervalo de la Formación Carmen estudiada. Se destacan principalmente los referidos al género *Helicosphaera*, cuya presencia es abundante en la asociación y cuyos ejemplares presentan un grado de preservación excelente.

La abundante presencia de múltiples taxones de algas colitoforales y nanofósiles calcáreos razonablemente bien preservados, caracterizan la secuencia del Arroyo Alférez, lo que la hace óptima para potenciales estudios paleoceanográficos de mayor resolución y profundización. Tales estudios requieren un muestreo sistemático más resolutivo, la comparación con otras secciones de continente y de sedimentos de mar abierto; donde la posibilidad de obtener otros indicadores importantes, como los estudios isotópicos, permitirían una datación de la secuencia más fiable.

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APÉNDICE 1: LISTA DE ESPECIES IDENTIFICADAS

Reino PROTISTA Haeckel, 1866
Phylum PRYMNESIOPHYTA Hibberd, 1976
Clase PRYMNESIOPHYCEAE Hibberd, 1976
Orden COCCOLITHOPHORALES Schiller, 1926

- Chiasmolithus altus* Bukry and Percival, 1971
Chiasmolithus spp. Hay, Mohler and Wade, 1966
Coccolithus pelagicus (Wallich, 1877) Schiller, 1930 (<13 µm) (Lám. 1, Fig. 2)
Coccolithus spp. Schwarz, 1894
Coronocyclus nitescens (Kamptner, 1963) Bramlette and Wilcoxon, 1967
Cyclicargolithus abisectus (Müller, 1970) Wise, 1973 (>10 µm)
Cyclicargolithus floridanus (Roth and Hay en Hay et al., 1967) Bukry, 1971 (<10 µm)
Discoaster adamanteus Bramlette and Wilcoxon, 1967
Discoaster deflandrei Bramlette and Riedel, 1954
Discoaster druggii Bramlette and Wilcoxon, 1967 (>15 µm)
Discoaster spp. Tan Sin Hok, 1927 (ex *Eu-discoaster*, corregido por Tan Sin Hok, 1931)
Helicosphaera ampliaperta Bramlette and Wilcoxon, 1967
Helicosphaera carteri (Wallich, 1877) Kamptner, 1954 (Lám. 1, Fig. 10)
Helicosphaera compacta Bramlette and Wilcoxon, 1967
Helicosphaera euphratis Haq, 1966
Helicosphaera intermedia Martini, 1965 (Lám. 1, Fig. 13)
Helicosphaera obliqua Bramlette and Wilcoxon, 1967
Helicosphaera recta Haq, 1966) Jafar and Martini, 1975
Helicosphaera walbersdorfensis Mueller, 1974
Helicosphaera waltrans Theodoridis, 1984
Holodiscolithus spp. Roth, 1970
Pedinocyclus larvalis (Bukry and Bramlette, 1969) Loeblich and Tappan, 1973
Pontosphaera multipora (Kamptner, 1948) Roth, 1970 emend. Burns, 1973
Pontosphaera spp. Lohmann, 1902
Rhabdosphaera spp. Haeckel, 1894
Reticulofenestra bisecta (Hay, Mohler and Wade, 1967) Roth, 1970
Reticulofenestra minuta Roth, 1970 (<3 µm)
Reticulofenestra minutula (Gartner, 1967) Haq and Berggren, 1978 (3–5 µm)
Reticulofenestra pseudoumbilicus (Gartner, 1967) Gartner, 1969 (>7 µm)
Sphenolithus belemnos Bramlette and Wilcoxon, 1967
Sphenolithus ciperoensis Bramlette and Wilcoxon, 1967
Sphenolithus compactus Backman, 1980
Sphenolithus conicus Bukry, 1971
Sphenolithus disbelemnos Fornaciari and Rio, 1996
Sphenolithus dissimilis Bukry and Percival, 1971
Sphenolithus distentus (Martini, 1965) Bramlette and Wilcoxon, 1967
Sphenolithus heteromorphus Deflandre, 1953
Sphenolithus moriformis (Bronnimann and Stradner, 1960) Bramlette and Wilcoxon, 1967 (Lám. 2, Fig. 8)

Sphenolithus predistentus Bramlette and Wilcoxon, 1967

Transversopontis spp. Mohler and Wade, 1966

Triquetrorhabdulus carinatus Martini, 1965

Triquetrorhabdulus milowii Bukry, 1971 (Lám. 2, Fig. 12)

Triquetrorhabdulus rioensis Olafsson, 1989

Umbilicosphaera rotula (Kamptner, 1956) Varol, 1982

Zygrhablithus bijugatus (Deflandre, En: Deflandre and Fert, 1954) Deflandre, 1959

Ostracodes from the Nagrota Formation, Upper Siwalik Subgroup, Jammu, India

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Resumen

Se han identificado dieciséis especies de ostrácodos, entre ellas dos nuevas especies, en los horizontes lutíticos que se encuentran por encima y por debajo de la banda de bentonita del Miembro Nagrota B de la Formación Nagrota (Subgrupo Siwalik Superior, Jammu, Norte de la India). Los ostrácodos registrados fueron *Cypris subglobosa*, *Cypris* cf. *C. decaryi*, *Cypridopsis* sp. A, ?*Cypridopsis* sp., *Candona* sp. A, *Candona* sp. B, *Eucypris* sp. A, *Eucypris* sp. B, *Hemicypris pyxidata*, *Stenocypris major*, *Stenocypris* sp., *Zonocypris barakhetarensis* sp. nov., *Ilyocypris bradyi*, *Ilyocypris* sp., *Vestalenula jammuensis* sp. nov. y ?*Sclerocypris* sp. indet. Una probable edad pliocena tardía se ha inferido a partir del estudio de los ostrácodos así como por datos proporcionados por micromamíferos y huellas de fisión. Los sedimentos en donde se encontraron los ostrácodos fueron depositados en un medio alcalino lacustre somero de 2-6 m de profundidad.

Palabras clave: Ostrácodos, Siwalik superior, Formación Nagrota, Plioceno tardío, Medio ambiente lacustre

Abstract

Sixteen species including two new species of ostracodes are recorded from the mudstone bearing horizons immediately overlying and underlying the bentonite band, of the Nagrota Member B, Nagrota Formation, Upper Siwalik Subgroup, north India Jammu. The ostracodes recorded are: *Cypris subglobosa*, *Cypris* cf. *C. decaryi*, *Cypridopsis* sp. A, ?*Cypridopsis* sp., *Candona* sp. A, *Candona* sp. B, *Eucypris* sp. A, *Eucypris* sp. B, *Hemicypris pyxidata*, *Stenocypris major*, *Stenocypris* sp., *Zonocypris barakhetarensis* sp. nov., *Ilyocypris bradyi*, *Ilyocypris* sp., *Vestalenula jammuensis* sp. nov., and ?*Sclerocypris* sp. indet. The above ostracodes and recovered micro mammals and fission track dating suggest a probable Late Pliocene age and sediments were deposited in shallow alkaline lacustrine environment with water depth 2-6 m.

Keywords: Ostracodes, Upper Siwalik, Nagrota Formation, Late Pliocene, lacustrine environment

1. INTRODUCTION

The name Siwalik, originally applied to a range of the hills exposed as an arcuate belt, stretching from the Ganges to Jammu and separating the Dehradun from the plains, has been extended by geographers, northwestwards as far as

the Beas river and south-eastwards in Nepal. The Siwalik Group is known for its treasure of mega fossils. The Jammu region exhibit excellent exposures of Siwaliks which stretches for tens of kilometers along the strike. The Siwaliks have traditionally been divided into Lower, Middle and Upper subgroups. The Upper Siwalik Subgroup in the Jammu region is best exposed in the southwestern limb of Suruin-Mastgarh anticline. Ranga Rao *et al.* (1988) subdi-

vided Upper Siwalik strata into Purmandal Sandstone (=Purmandal Formation), Nagrota Formation and Boulder Conglomerate Formation in ascending order (Fig. 1).

The ostracode fauna of the Upper Siwalik has received little attention from micropaleontologists. Recently, Bhatia *et al.* (2001) reported five taxa of Ostracoda from the Upper Siwaliks. With the intention of working in detail on ostracode fauna from the Upper Siwalik of Jammu, one of us (SNK) systematically collected samples from four sections of the Nagrota Formation at Barakhetar, Utterbehani, Khanpur and Anandpur (Fig. 2). An interesting ostracode assemblage has been recorded from the mudstone bearing horizons immediately below and above the bentonite band in the Nagrota Member B (NB) in the Na-

grota Formation (see Table 1). These ostracodes are systematically described, and illustrated in plates 1-2.

2. PREVIOUS WORK

Studies on the megafossils of the Upper Siwalik subgroups of Jammu region were carried out by number of Indian Paleontologists from time to time such as Sahni and Mathur (1964), Sahni and Khan (1964), Nanda (1981), Tripathi (1986), Nanda and Seghal (1993), but the microfossils such as ostracodes, charophytes, gastropods and microvertebrates of Jammu region are less studied in this region in comparison to the other sections, both in India and Pakistan. Bhatia and Khosla (1967) recovered for the

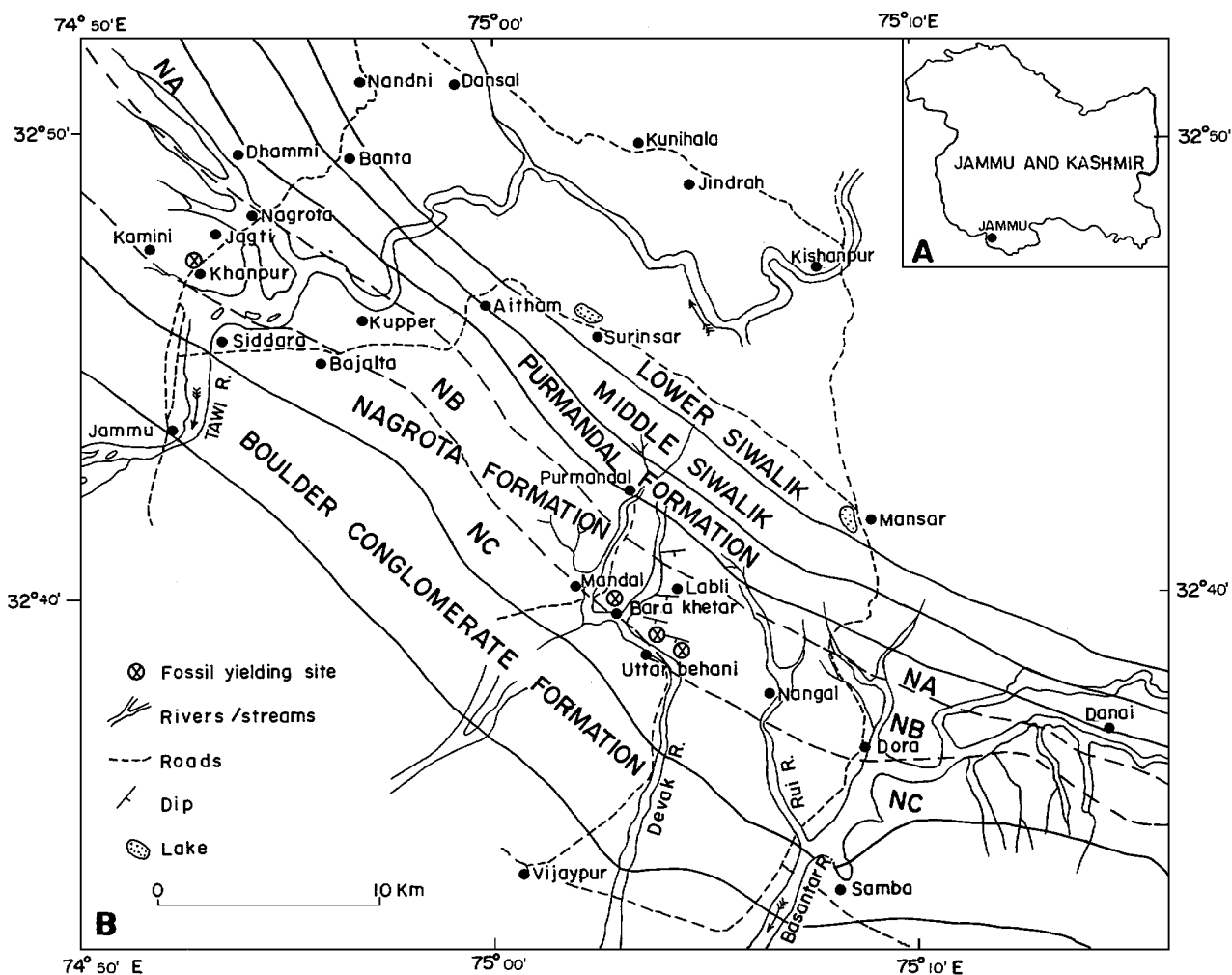


Figure 1. Geological map of southeastern limb of the Suruin-Mastgarh anticline showing fossil yielding of sample localities of Upper Siwalik strata. NA, NB, and NC are members of Nagrota Formation (modified after Bhatia *et al.* 2001).

first time ostracodes from the Tatrot beds of the Upper Siwalik subgroup near Chandigarh in India. Subsequently, studies on ostracodes of Siwaliks are carried by Mathur (1972, 1976, 1977), Khosla *et al.* (1993), Raghavan (1990), Bhatia (1995, 1996) and Bhandari and Tewari, and (2003). The microfossils from the mudstone bearing horizons of Jammu region are not much known to micropaleontologists of India. Few studies have been carried out on some of the sections. Suneja *et al.* (1980) reported the presence of ostracode taxa such as *Hemicypris* sp., gastropods *Planorbis* and an identifiable fish remains from a locality near Khanpur village near Nagrota, District Jammu, but they have neither been described nor figured them. Recently, Bhatia *et al.* (2001) described microfossils both ostracodes and charophytes from Barakhetar and Utterbehani sections from the Upper Siwalik subgroup of Jammu region. The ostracodes recovered from above sections are *Hemicypris megalops* Sars, *H. pyxidata* Moneiz, *Candona lacta* Baird, *Cypridopsis* sp. indet. and *Sclerocypris* ? sp. indet.

3. MATERIALS AND METHODS

Three tonnes of mudstone samples from Nagrota Formation were collected from four sections of Barakhetar, Anandpur, Utterbehani and Khanpur (Fig. 2) immediately above and below the bentonite band of the Upper Siwalik subgroup of Jammu region. These mudstone samples were treated with the kerosene method. In this method, the mudstone samples are broken to the size of a few centimeters and dried in the sunlight so that the moisture evaporates from the samples. After drying in sunlight or in oven, the samples are put in a plastic tubs and are immersed in kerosene for 2 hours, then the kerosene was decanted from the tubs and the samples are kept immersed in water for two hours. Because of the difference in the specific gravity of the water and oil, water pushes/forces its way into the samples and expels the kerosene out. This results in the breakdown of samples into slurry, which is then washed in running water using 40, 60, and 100, mesh sets of sieves. The volume of samples was reduced to

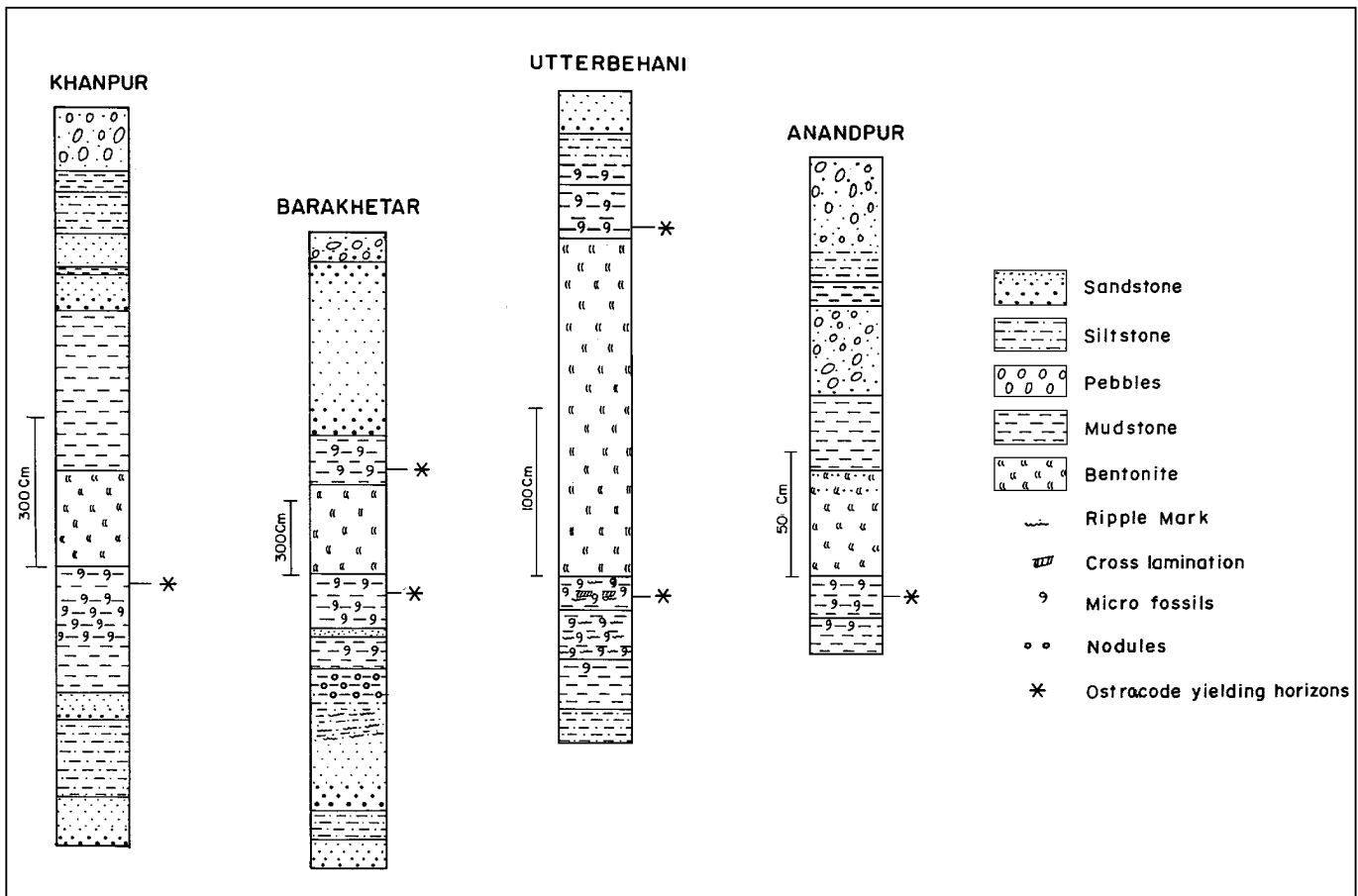


Figure 2. Lithological columns of the studied localities of Nagrota Formation.

Sl. No.	Ostracode Taxa	Khanpur		Barakhetar		Uttarbehani		Anandpur	
		From Mudstone underlying bentonite band	From Mudstone overlying bentonite band	From Mudstone overlying bentonite band	From Mudstone underlying bentonite band	From Mudstone underlying bentonite band	From Mudstone overlying bentonite band	From Mudstone underlying bentonite band	From Mudstone overlying bentonite band
1	<i>Cypris subglobosa</i> Sowerby	-	-	-	-	+	-	+	-
2	<i>Cypris</i> cf. <i>C. decaryi</i> Gauthier	-	-	-	+	-	-	-	-
3	<i>Cypridopsis</i> sp. A	-	-	+	-	-	-	-	-
4	? <i>Cypridopsis</i> sp.	-	-	+	-	-	-	-	-
5	<i>Candona</i> sp. A	-	-	-	+	-	-	-	-
6	<i>Candona</i> sp. B	-	-	+	-	-	-	-	-
7	<i>Eucypris</i> sp. A	-	-	-	+	-	-	-	-
8	<i>Eucypris</i> sp. B	-	-	-	-	-	+	-	-
9	<i>Hemicypris pyxidata</i> (Moniez)	-	+	+	+	+	+	+	-
10	<i>Stenocypris major</i> (Baird)	-	-	+	+	-	+	-	-
11	<i>Stenocypris</i> sp.	-	-	+	-	-	+	-	-
12	<i>Zonocypris barakhetarensis</i> sp. nov.	-	-	-	+	-	-	-	-
13	<i>Ilyocypris bradyi</i> Sars	-	-	-	+	-	-	-	-
14	<i>Ilyocypris</i> sp.	-	-	-	+	-	-	-	-
15	<i>Vestalenula jammuensis</i> sp. nov.	-	-	-	+	+	-	+	-
16	<i>Sclerocypris</i> ? sp.	-	-	-	+	-	-	-	-

Table 1. Ostracode fauna from Nagrota Formation of the Upper Siwalik subgroup, Jammu.

about 10% of the original volume. The screened- washed residue so obtained by this method was dried in the sunlight and sorted under the binocular microscope for ostracodes. The photomicrographs of ostracodes were taken by using Scanning Electron Microscope (SEM). The ostracodes are deposited in the collection of the Department of Geology, Jammu University, Jammu, India with catalogue no. JU/VPL/SF/316-344.

4. STRATIGRAPHY

The Upper Siwalik subgroups in the Jammu region are best exposed in the southwestern limb of the Surui-Mastgarh anticline. Ranga Rao *et al.* (1988) classified the Upper Siwalik subgroup of Jammu area into three formations. These formations are Purmandal Sandstone, Nagrota Formation and Boulder Conglomerate. The base of the Purmandal Sandstone dates from 4.92 Ma; Nagrota Formation from 3.90 Ma and the Boulder Conglomerate from 0.60 Ma. Ranga Rao *et al.* (1988) gave this classification on the basis of vertebrate fauna recovered from the area, lithology and paleomagnetic polarity stratigraphy.

The fission track dating of the zircons extracted from the bentonite band of the Nagrota Formation by Ranga Rao *et al.* (1988) gave an age of 2.48 Ma which is equivalent to the Gauss-Matuyama boundary. The Nagrota Formation is rich in well preserved fossils (mega and microfossils) as compared to the Purmandal Sandstone and Boulder Conglomerate, which has fragmentary preserved bones.

Gupta & Verma (1988) classified the Siwalik area of Jammu into four formations. These formations are Dewal Formation, Mohargarh Formation, Utterbehani Formation and Dughor Formation. All these formations classified by above authors were based on structure and lithological characters. They kept the Dewal Formation and Mohargarh formations in the Middle Siwalik and the Utterbehani and Dughor formations in the Upper Siwalik of Jammu region. According to them the Upper Siwalik Subgroup of Jammu area starts at the base of the Utterbehani Formation, which is about 3.15 Ma and further divided the Utterbehani Formation into Labli Member and Marikhui Member and traced the bentonite band in the Labli Member of the Utterbehani Formation.

Agarwal *et al.* (1993) adopted the classification proposed by Ranga Rao *et al.* (1988) of the Upper Siwalik Subgroup of Jammu area and subdivided the Nagrota Formation into three members. These members are Nagrota A (NA), Nagrota B (NB), Nagrota C (NC). They studied the Upper Siwalik Subgroup of Jammu region and concluded that the bentonite band is occurred in the Nagrota Member B (NB) of the Nagrota Formation noting that there was a little change in the fauna about 75m below the Gauss-Matuyama boundary.

5. AGE CONSTRAINTS

Age determination of the bentonite band, immediately above and below of the Upper Siwalik subgroup of Jammu region has been attempted by number of Indian and British Paleontologists from time to time. Yokoyama *et al.* (1987) assigned an age of 1.6 ± 0.2 Ma for zircons extracted from the bentonite band of the Nagrota Formation exposed near Barakhetar village of the Upper Siwalik subgroup of Jammu. They also concluded that the Nagrota Formation consists of two faunal zones, one below the bentonite band and there is a little change in the faunal assemblage between lower faunal and upper faunal zone.

Ranga Rao *et al.* (1988) gave an age of 2.8 ± 0.56 Ma of zircon phenocryst extracted from the same Barakhetar bentonite band of the Nagrota Formation of the Upper Siwalik subgroup of Jammu. In conjunction with the magnetostratigraphy, they arrived at the conclusion that these bentonite bands straddle across Gauss-Matuyama boundary dated as 2.48 Ma. Furthermore, a major faunal change was shown to occur 60m below the Gauss-Matuyama magnetic polarity scale boundary.

A major faunal change about 75m below the Gauss-Matuyama boundary is given by Agarwal *et al.* (1993). Mehta *et al.* (1993) gave an age of 1.59 ± 0.32 Ma of zircon phenocryst extracted from the Utterbehani bentonite band of the Nagrota Formation and correlate age with the Barakhetar bentonite band given by Ranga Rao. *et al.* (1988).

Gupta & Prasad (2001) suggested an age of 2.5 Ma of the Marikhui Member (700m below the bentonite band) of the Nagrota Formation on the basis of micro mammals re-

covered from the Dhammi and Balli localities. These micro mammals are *Mus flynni*, *Golunda kellari*, *Abudhabia* cf. *A. kabulense* and *Rhizomyides sivalensis*.

As far as the microfossils are concerned, they are very useful for the age determination and paleoenvironmental analysis. Bhatia *et al.* (2001) suggested an age of Late Pliocene to the mudstone bearing horizons immediately below the bentonite band of the Barakhetar and Utterbehani sections on the basis of microfossils (ostracodes and Charophytes) recovered from above two sections.

The present ostracodes and micro mammals recovered from the same mudstones bearing horizons immediately below and above the bentonite band suggest Late Pliocene age which corroborates with Bhatia *et al.* (2001).

6. PALEOENVIRONMENT

Ostracodes inhabit every aquatic environment, which includes fresh, brackish and marine waters. They are very sensitive to change in the environment. In the present study ostracode taxa recovered from four sections of the Nagrota Formation, Jammu is used for paleoenvironmental reconstruction. They are dominated by *Hemicypris pyxidata* which represents about 90% of total population. *Hemicypris* prefers fresh water environment (Morkhoven, 1962). Recent specimens of *H. pyxidata* have been recorded in India by various workers. Jain (1977, 1979) recorded this species from dried mud of Chilka Lake and fresh water ponds of Kutch, respectively. Battish (1981) recorded it from an alkaline pond in Punjab, and Neale (1977) recorded it from rice fields, Sri Lanka and rock pools Madurai (Victor & Fernando, 1979). *H. pyxidata* in general tolerates fresh to brackish water is permanent to semi permanent water- bodies (Bhatia *et al.*, 2001). The next dominant ostracode in the assemblage is *Vestalenula* which represents about 4% of population. It inhabits fresh water springs, (Smith *et al.* 2006, semiterrestrial habitats (Pinto *et al.* 2003). The next important ostracod is *Stenocypris* which contributes about 2% of the total assemblage, it is commonly found in warm shallow – water ponds and lakes (Singh, 1977). In Kashmir Valley the species found to occur infrequently in the rice fields in association with *Ilyocypris bradyi* Sars (Singh, 1973). Rest of the ostracode assemblage is represented by *Zonocypris*,

Ilyocypris, *Cypris*, *Eucypris*, *Cypridopsis* and *Candona* etc. They indicate fresh-brackish water conditions. The study further indicates that the Barakheta section was deposited in the centre of lake with 2-6m water depth while the other three sections such as Utterbehani (2m), Khanpur (1.5m) and Anandpur (<1m) were deposited towards marginal side of the lake in relatively shallow water depth. The above depth conditions of standing water body are also given by Bhatia *et al.* (2001) on the basis of ostracodes recovered from this area. The other microfossils groups such as gastropods, charophytes and fishes recovered with ostracodes are also indicating the aquatic or lake conditions.

The fossil of micro mammals such as rodents suggests terrestrial conditions or terrestrial environment but these micro mammals are recovered with the aquatic fossils. This is due to the fact that these micro mammals were living on the edge of the lake, when they died; their body transported towards lake and was deposited in the lake. The cusps of molars of these micro mammals are sharp in nature it means that these micro mammals fossil are not much or little transported. If these micro mammal fossils are transported from a great distance, their cusps should be rounded nature.

7. SYSTEMATIC DESCRIPTION

Subclass OSTRACODA Latreille, 1806
 Order PODOCOPIDA Müller, 1894
 Suborder PODOCOPINA Sars, 1866
 Superfamily CYPRIDOIDEA Baird, 1845
 Family CYPRIDIDAE Baird, 1845
 Subfamily CYPRIDINAE Baird, 1845
 Tribe CYPRIDINI Baird, 1845

Genus *Cypris* O.F. Müller, 1776

Cypris subglobosa Sowerby, 1840
 (Pl. 1, Figs. 1-2)

1840 *Cypris subglobosa* Sowerby, pl.47, Fig.3

1859 *Cypris subglobosa* Sowerby. Baird, p. 232, Pl. 63,
 Fig. 2

Material.- Two carapaces, one open valve.

Diagnostic characters.- Carapace subglobular in lateral view; right valve larger than left valve; dorsal margin convex; ventral margin straight; anterior margin rounded; in dorsal view ends compressed, valve inflated with maximum width posterior to middle. Valve surface with minute pits all along surface.

Dimensions (mm).- Carapace (JU/VPL/SF/316): *Length*: 1.50, *Height*: 0.92, *Width*: 1.20

Remarks. - Specimens recorded from Jammu are comparable with *Cypris subglobosa* Sowerby, 1840 (locality not designated) but first found in situ near Munoor, in the Basaltic table-land north of the Koorn River, India.

Cypris cf. *C. decaryi* Gauthier, 1933
 (Pl. 1, Fig. 3)

1933 cf. *Cypris decaryi* Gauthier, p. 209, Figs. 1-4.

Material. - One carapace.

Diagnostic characters.- Carapace tumid; left valve slightly larger than right valve; dorsal margin smoothly arched; ventral margin concave near middle; anterior margin with distinct flange; posterior margin rounded. Valve surface finely pitted.

Dimensions (mm).- Carapace (JU/VPL/SF/317): *Length*: 2.20, *Height*: 1.18, *Width*: -

Remarks. - The present species closely resembles *Cypris decaryi* Gauthier, 1933 in overall lateral outline but differs in details. Unlike the present species, *Cypris decaryi* is smaller in size, anterior and posterior margin finely denticulate.

Subfamily CYPRIDOPSINAE Kaufmann, 1900
 Genus *Cypridopsis* Brady, 1867

Cypridopsis sp. A
 (Pl. 1, Fig. 4)

Material. - One carapace.

Diagnostic characters. - Carapace subtriangular in lateral view with greatest height anterior to middle; right valve slightly larger than left valve; dorsal margin strongly arched, angulated medially, truncated on either side from

greatest height; ventral margin straight; anterior margin obliquely rounded; posterior margin narrowly subrounded; in dorsal view carapace lanceolate, with maximum width near middle; anterior end narrowly compressed; posterior end subrounded. Valve surface smooth.

Dimensions (mm).- Carapace (JU/VPL/SF/318): *Length*: 0.55, *Height*: 0.32, *Width*: 0.25.

Remarks. - The present species resembles in overall lateral outline with *Cypridopsis vidua* Muller, 1776, but the latter has concave ventral margin.

?*Cypridopsis* sp.
(Pl. 1, Fig. 5)

Material. - One carapace.

Diagnostic characters. - Carapace subtriangular in lateral view, with greatest height near middle; left valve larger than right valve: overlapping distinctly along dorsal margin; dorsal margin convex; ventral margin straight; anterior margin obliquely rounded; posterior end narrowly rounded. Valve surface smooth; in dorsal view carapace with maximum width posterior to middle.

Dimensions (mm).- Carapace (JU/VPL/SF/319): *Length*: 0.82, *Height*: 0.50, *Width*: 0.51.

Remarks. - This species is questionably assigned to genus *Cypridopsis* in want more specimens.

Family CANDONIDAE Kaufmann, 1900
Subfamily CANDONINAE Kaufmann, 1900

Genus *Candona* Baird, 1845

Candona sp. A
(Pl. 1, Fig. 6)

Material. - One carapace.

Diagnostic characters. - Carapace elongate subreniform, compressed in lateral view, with greatest height posterior to middle; left valve slightly larger than right valve; dorsal margin gently convex, sloping anteriorly and posteriorly from greatest height; ventral margin curved anteromedially; anterior margin narrow, obliquely rounded; posterior

margin broad and obliquely rounded; posterodorsal straight, posteroventral rounded; anterior and posterior ends nearly at same height; in dorsal view carapace lanceolate; ends compressed, maximum width near posterior to middle.

Dimensions (mm).- Carapace (JU/VPL/SF/320): *Length*: 1.43, *Height*: 0.78, *Width*: 0.55

Remarks. - The present species resembles in overall lateral outline with *Candona cachensis* Swain, 1947 described from Plio-Pleistocene, Salt Lake Formation, Utah. Unlike the present species *C. cachensis* has maximum height posteriorly, is more rounded posterodorsally, and posteroventral and in dorsal view ends rounded.

Candona? sp. B
(Pl. 1, Fig. 7)

Material. - One carapace.

Diagnostic characters. - Carapace small subtriangular elongate in lateral view with greatest height near posterior to middle; left valve larger than right, overlapping all along margins; dorsal margin convex sloping from greatest height; ventral margin slightly curved in the middle; anterior margin narrowly rounded; posterior margin truncated forms rounded angle with posterior margin. Valve surface pitted.

Dimensions (mm).- Carapace (JU/VPL/SF/321): *Length*: 0.55, *Height*: 0.35, *Width*: 0.25

Remarks. - The present species has questionably kept in *Candona*. It resembles *Candona fabaeformis* (Fischer) in lateral outline but differs in details. Unlike present species *C. fabaeformis* is larger in size, maximum width posteriorly and valve surface smooth.

Subfamily EUCYPRIDINAE Bronstein, 1947
Tribe EUCYPRIDINI Bronstein, 1947

Genus *Eucypris* Varva, 1891

Eucypris sp. A
(Pl. 1, Fig. 8)

Material. - One carapace.

Diagnostic characters.- Carapace elongate-subovate moderately convex; left valve larger than right valve; overlapping all along margins, more pronounced along anterior and ventral; dorsal margin convex truncated behind and in front from the greatest height; ventral margin slightly concave or nearly straight; anterior margin obliquely rounded in the right valve; posterior margin evenly rounded; valve surface smooth. In dorsal view, carapace oval with maximum width in the middle.

Dimensions (mm).- Carapace (JU/VPL/SF/322): *Length:* 1.02, *Height:* 0.55, *Width:* 0.42

Remarks. - The present species resembles in lateral view with *Eucypris pigra* (Ficher). Unlike present species *E. pigra* has narrowly rounded and more truncated posterodorsally.

?*Eucypris* sp. B
(Pl. 1, Fig. 9)

Material. - One carapace.

Diagnostic characters. - Carapace small, subovate in lateral view and biconvex in dorsal view; greatest height near middle; left valve larger than right valve, overlapping distinctly all along margins; dorsal margin arched; ventral margin curved; anterior end lower than posterior; narrowly rounded; posterior margin broad, rounded; valve surface smooth.

Dimensions (mm).-Carapace (JU/VPL/SF/323): *Length:* 0.60, *Height:* 0.35, *Width:* 0.27

Remarks. - This species is questionably assigned to genus *Eucypris* on the basis of its shape.

Subfamily CYPRINOTINAE Bronstein, 1947

Genus *Hemicypris* Sars, 1903

Hemicypris pyxidata (Moniez)
(Pl. 1, Figs. 10-15)

1892 *Cyprinotus pyxidata* Moniez, p.134, Pl. 10, Figs. 23-27.

1903 *Hemicypris pyxidata* (Moniez). Sars, p. 25-26, Pl. 3, Fig. 1, 1a-t.

Material.- 123 carapaces from mudstone underlying bentonite at Barakhetar and 15 carapaces from mudstone overlying bentonite at Barakhetar; 159 carapaces from mudstone underlying bentonite at Uttarbehani and 24 deformed carapaces from mudstone overlying at Uttarbehani; 10 carapaces and two open valves from mudstone underlying at Khanpur and 26 carapaces from Anandpur.

Diagnostic characters. - Sexual dimorphism distinct males being more elongate, less high and wider than females. Carapace subovate; right valve overlap left valve all along margins; dorsal margin convex, arched with greatest height near middle in the males and posterior to middle in females; anterior and posterior margins rounded. Valve surface punctuate.

Dimensions (mm).-

Male Carapace (JU/VPL/SF/324): *Length:* 1.32, *Height:* 0.78, *Width:* 0.60

Female carapace (JU/VPL/SF/325): *Length:* 1.33, *Height:* 0.85, *Width:* 0.66

Open valve (JU/VPL/SF/326), Internal: *Length:*1.30, *Height:*0.85, *Width:* 0.65

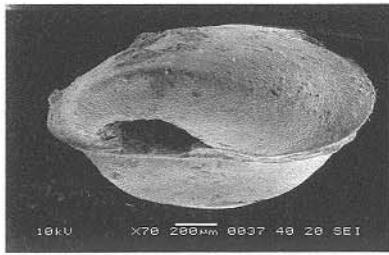
Open valve (JU/VPL/SF/327), internal: *Length:*1.30, *Height:* 0.80,*Width:* -

Carapace (JU/VPL/SF/328): *Length:*1.25, *Height:* 0.78, *Width:* 0.50

Carapace (JU/VPL/SF/329): *Length:* 1.20, *Height:*0.65, *Width:* 0.52

Plate 1. 1-2. *Cypris subglobosa* Sowerby: 1. Carapace, (JU/VPL/SF/316), right lateral view, x 29, 2. Dorsal view, x 24; 3. *Cypris* cf. *decaryi* Gauthier, broken carapace (JU/VPL/SF/317), right lateral view, x 19; 4. *Cypridopsis* sp. A, carapace (JU/VPL/SF/318), right lateral view, x 73; 5. *Cypridopsis* sp., carapace (JU/VPL/SF/319), right lateral view, x 55; 6. *Candona* sp. A, carapace (JU/VPL/SF/320), left lateral view, x 32; 7. *Candona* sp. B, carapace (JU/VPL/SF/321), right lateral view, x 80; 8. *Eucypris* sp. A, carapace (JU/VPL/SF/322), right lateral view, x 45; 9. *Eucypris* sp. B, carapace (JU/VPL/SF/323), right lateral view, x 72; 10-15. *Hemicypris pyxidata* (Moniez): 10. Male carapace, (JU/VPL/SF/324), left lateral view, x 34, 11. Female carapace (JU/VPL/SF/325) left lateral view, x 30, 12. Female right valve (JU/VPL/SF/326), internal view, x 35, 13. Male valve (JU/VPL/SF/327), internal view of left valve, x 30, 14. Deformed carapace, (JU/VPL/SF/328), left lateral view, x 35, 15. Deformed carapace, dorsal view, (JU/VPL/SF/329), x 25.

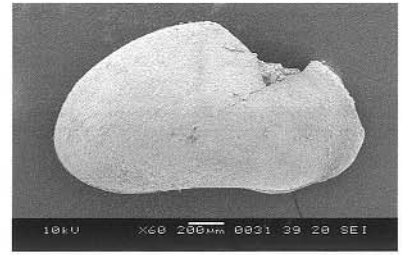
Plate 1



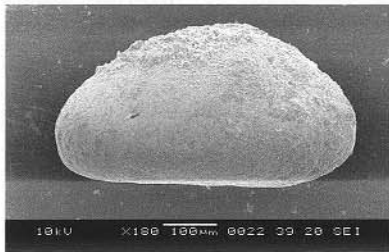
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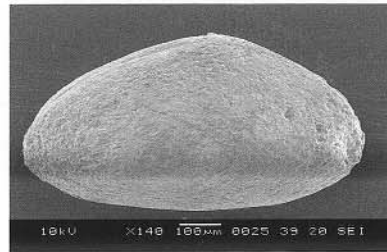
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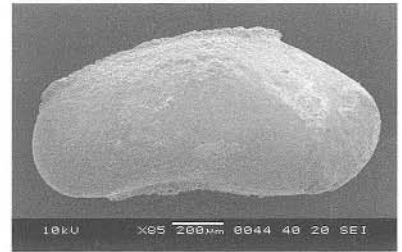
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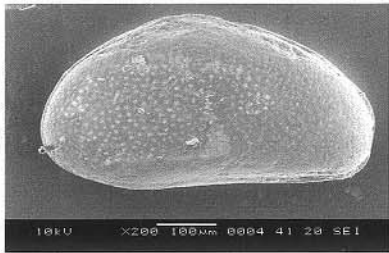
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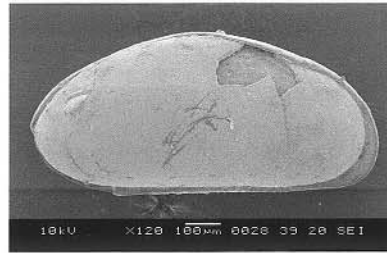
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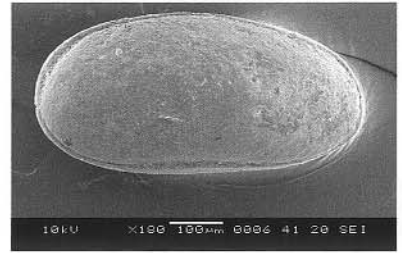
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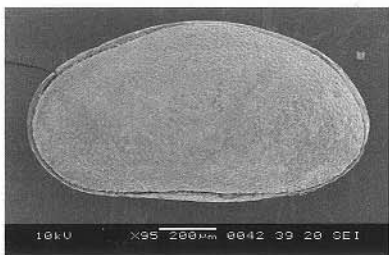
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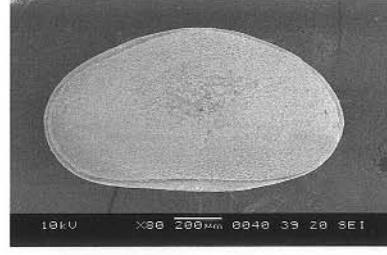
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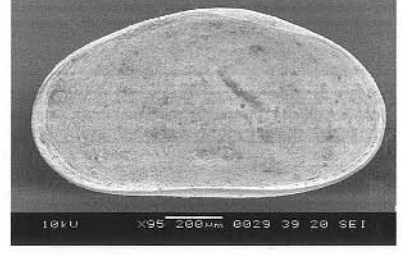
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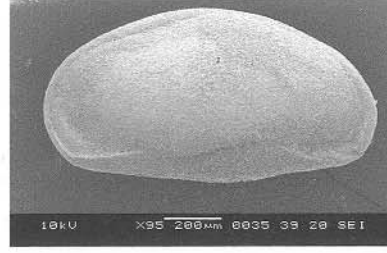
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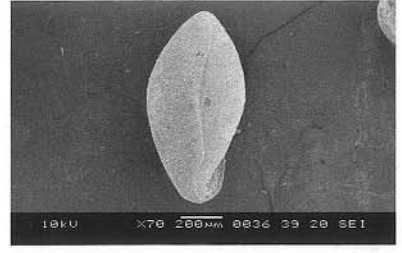
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Remarks. - The fossil form of this species was first recorded in India from Pinjor Formation of Siwalik Group near Chandigarh by Bhatia and Khosla (1967); Tatrot Formation, Pinjor by Mathur (1972), Bhatia (1995) recorded it from the Tatrot Formation at Kanthra (Locality VII) and recently, Bhatia *et al.* (2001) recorded from Badakheta and Uttarbehani, Jammu. Besides these fossil occurrences, recent specimens of this species have been reported from Chilka lake (Jain, 1977), fresh water ponds of Kutch (Jain, 1979), Punjab (Battish, 1981), rice fields of Srilanka (Neale, 1977), rock pools of Madurai (Victor and Fernando, 1979). Deformed specimens are recorded in the studied samples which suggest effect of tectonism on ostracodes (see Pl. 1, Figs. 14-15).

Subfamily HETEROCYPRIDINAE Kaufmann, 1900

Genus *Stenocypris* Sars, 1889

Stenocypris major Baird, 1859
(Pl. 2, Fig. 1)

1859 *Cypris cylindrica major* Baird, p. 233, Figs. 1, 4a-b.

1859 *Stenocypris major* (Baird). Victor and Fernando, p. 193-194, Figs. 126-204.

1886 *Cypris malcolmsonii* Brady, p. 297, Pl. 38, Figs. 5-7.

1889 *Stenocypris malcolmsonii* (Brady). Sars, p. 23-34, Pl.1, Figs.1-4.

1892 *Stenocypris malcolmsonii* (Brady). Moniez, p. 33.

1898 *Stenocypris major* (Baird). Daday, p. 69, Fig. v3-4a-d;

1906 *Stenocypris malcolmsonii* (Brady). Vavra, p. 426.

1907 *Stenocypris major* (Baird). Apstein, p. 226, Fig. 5.

1916 *Stenocypris malcolmsonii* (Brady). Gurney, p. 339.

1930 *Stenocypris malcolmsonii* (Brady). Lowndes, p. 975, Pl.1, Figs. 1-6, Pl. 2, Figs. 1-6.

1947 *Stenocypris malcolmsonii* (Brady). Bronstein, p. 148, Pl. 9, Fig. 2.

1964 *Stenocypris major* (Baird). Hartmann, p.121, Fig. 52.

1969 *Stenocypris cylindrica major* (Baird). Ferguson, p. 67, Fig. 3, 1-3.

Material.- Two carapaces.

Diagnostic characters. - Carapace elongate, elliptical with greatest height posterior to middle; valves more or less equal; dorsal margin straight and ventral margin weakly concave otherwise nearly straight; anterior and posterior margins rounded; valve surface smooth.

Dimensions (mm).- Carapace (JU/VPL/SF/330): *Length*: 2.20, *Height*: 0.90, *Width*: 0.62

Remarks. - Present specimens recorded from Barakheta and Uttarbehani are closely resembles *Stenocypris major*.

Stenocypris sp.
(Pl. 2, Figs. 2-3)

Material.- Two carapaces.

Diagnostic characters.- Carapace elongate in lateral view, with greatest height anteriorly; left valve larger than right valve, overlap all along margins; dorsal margin straight, truncate posteriorly; ventral margin curved in the middle; anterior end higher and rounded; posterior end lower, narrowly rounded; valve surface smooth.

Dimensions (mm).-

Carapace (JU/VPL/SF/331): *Length*: 2.03, *Height*: 0.85, *Width*: 0.40

Carapace (JU/VPL/SF/332): *Length*: 2.02, *Height*: 0.83, *Width*: 0.50

Remarks.- This species resembles *Stenocypris distincta* Victor and Fernando, 1979 in overall shape, but differs in length/height ratio. Unlike present species *S. distincta* which is larger in size.

Family ZONOCYPRIDIDAE Hou, 2002

Genus *Zonocypris* Müller, 1898

Zonocypris barakhetaensis sp. nov.
(Pl. 2, Figs. 4-6)

Name.- This species is named after locality Barakhetar, Jammu.

Material.- Six carapaces and three open valves.

Type locality and horizon.- About 0.40 km northwest of Barakhetar village, mudstone horizon immediately overlying Upper Siwalik bentonite band Nagrota Formation, Jammu.

Diagnosis.- The species of genus *Zonocypris* characterized by sub triangular carapace in lateral view: anterior margin obliquely rounded; posterior margin sub rounded. Valve surface ornamented by 13-14 very fine, concentrically arranged spiral ridges

Description.- Carapace subtriangular in lateral view, with greatest height anterior to middle; left valve larger than right valve; overlapping all along margins; overlap more pronounced along dorsal margin: dorsal margin arched in left valve and straight in right valve; anterodorsal margin steeply sloping, while posterodorsal margin gently sloping; ventral margin straight in left valve and inflated in right valve; anterior margin obliquely rounded; posterior margin narrowly rounded; in dorsal view anterior end compressed, maximum width posterior to middle. Valve surface ornamented by 13-14 very fine concentrically arranged spiral ridges.

Dimensions (mm).-

Holotype (JU/VPL/SF/333): *Length:* 0.75, *Height:* 0.43, *Width:* 0.45

Paratype I (JU/VPL/SF/334): *Length:* 0.75, *Height:* 0.45, *Width:* -

Paratype II (JU/VPL/SF/335): *Length:* 0.70, *Height:* 0.40, *Width:* -

Remarks.- The present species resembles *Zonocypris dadyai* Lowndes, 1932 in overall shape and ornamentation. However, differs in details. Unlike present species, *Z. dadyai* has concave ventral margin, anterior and posterior ends rounded and in dorsal view posterior end more rounded. It also resembles in overall shape with *Zonocypris gujaratensis* Bhandari and Colin 1999 described from the inter trapean of Anjar, in Kachchh District. But

differs in details of shape and ornamentation. Unlike present species *Z. gujaratensis* is inflated, biconvex in dorsal view and ornamented by 9-10 thick concentrically arranged spiral ribs.

Family ILYOCYPRIDIDAE Kaufman, 1900
Subfamily ILYOCYPRIDINAE Kaufman, 1900

Genus *Ilyocypris* Brady and Norman, 1889

Ilyocypris bradyi Sars, 1890
(Pl. 2, Fig. 7)

1890 *Ilyocypris bradyi* Sars, Fig. 30, 1-3, Pl. 3, 3-4.

Material.- One carapace.

Diagnostic characters.- Carapace elongate in lateral view; left valve larger than right valve, overlapping all along margins; dorsal and ventral margins weakly curved; anterior margin broadly rounded; posterior margin obtusely rounded. Valve surface pitted with two sulci; anterior sulcus starts near eye tubercle and reaches near middle; posterior sulcus does not reach up to middle, it ends half of the length of anterior sulcus.

Dimensions (mm).- Carapace (JU/VPL/SF/336): *Length:* 1.10, *Height:* 0.55, *Width:* 0.45

Remarks.- The present specimens recorded from Jammu resembles *Ilyocypris bradyi* (Sars) in overall shape and surface ornamentation.

Ilyocypris sp.
(Pl. 2, Figs. 8-9)

Material.- Two carapaces.

Diagnostic characters.- Carapace elongate; left valve slightly larger than right valve, overlapping all along margins, more distinct along anterior, ventral end posterior margins; dorsal margin weakly curved; ventral margin curved near middle; anterior margin broadly rounded; posterior narrowly rounded. Valve surface with rounded pits, looks like reticles; behind eye tubercle there are two sulci, anterior one starts from dorsal margin and reaching near middle; second sulci reaching half of the length of anterior sulci; rest of valve surface with scattered tubercles.

Dimensions (mm).-

Carapace (JU/VPL/SF/337): *Length:* 0.90, *Height:* 0.50, *Width:* 0.35

Carapace (JU/VPL/SF/338): *Length:* 0.90, *Height:* 0.52, *Width:* 0.37

Remarks.- The present species resembles *Ilyocypris gibba* (Ramdhor, 1808) in the lateral outline, but differs in the absence of lateral protuberans. Unlike present species, in *I. gibba* the anterior sulci do not reach near middle and ventral margin is straight.

Subfamily MEGALOCYPRIDINAE Rome, 1965

Genus *Sclerocypris* Sars, 1924

Sclerocypris ? sp.
(Pl. 2, Figs. 14-15)

Material.- Two broken valves.

Diagnostic character.- Carapace very large, subrectangular in lateral view; dorsal margin and ventral margins nearly straight; anterior margin rounded and compressed; posterior margin broadly rounded; valve surface finely pitted.

Dimensions (mm).-

Open valve (JU/VPL/SF/343): *Length:* 3.90, *Height:* 2.47, *Width:* -

Open valve (JU/VPL/SF/344): *Length:* 4.42, *Height:* 2.03 (Broken), *Width:* -

Remarks.- Bhatia *et al.* 2001 recorded similar type of ostracode from Barakhetar, Jammu and questionably assigned to genus *Sclerocypris*.

Superfamily DARWINULOIDEA Brady & Norman, 1889
Family DARWINULIDAE Brady and Norman, 1889

Genus *Vestalenula* Rossetti and Martens, 1998

Vestalenula jammuensis sp. nov.
(Pl. 2, Figs. 10-13)

Name.- This species is named after state Jammu, India.

Material.- Seven carapaces and one open valve (Barakhetar), six carapaces (Uttarbehani) and four carapaces (Anandpur).

Type locality and horizon.- About 0.40 km northwest of Barakhetar village, mudstone horizon immediately overlying and underlying Upper Siwalik bentonite band, Nagrota Formation, Jammu.

Diagnosis.- Carapace elongate oblong in lateral view; left valve larger than right valve; overlap distinct all along margins: anterior end narrowly rounded; posterior margin broadly rounded: dorsal margin straight: ventral margin slightly concave. Valve surface smooth

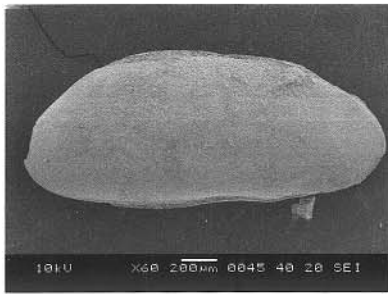
Description.- Carapace elongate, oblong in lateral view with greatest height posteriorly; sexual dimorphism observed, male carapace more elongate and less wider than female carapace: left valve larger than right valve, distinctly overlapping right valve all along margins; dorsal margins nearly straight; anterior end lower than posterior; anterior margin narrow, rounded; ventral margin straight in right valve and weakly curved in left valve; posterior margin broadly rounded; in dorsal view carapace cylindrical; anterior end narrow, posterior rounded with maximum width posteriorly.

Dimensions (mm).-

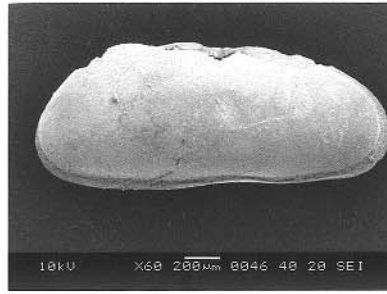
Holotype, a male carapace (JU/VPL/SF/339): *Length:* 0.94, *Height:* 0.42, *Width:* 0.30

Paratype I, a male carapace (JU/VPL/SF/340): *Length:* 0.95, *Height:* 0.45, *Width:* 0.30

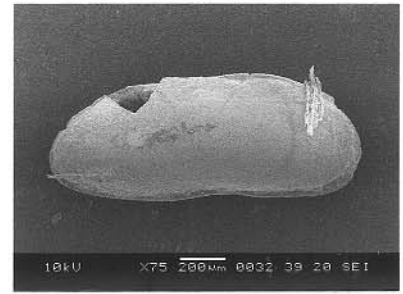
Plate 2. 1, *Stenocypris major* (Baird), carapace (JU/VPL/SF/330), right lateral view, x 22; 2-3. *Stenocypris* sp.: 2. Carapace I (JU/VPL/SF/331), right lateral view, x 23, 3. Carapace II, right view, x 20; 4-6. *Zonocypris barakhetarensis* sp. nov.: 4. Holotype (JU/VPL/SF/333), carapace, right lateral view, x 59, 5. Paratype I (JU/VPL/SF/334), left lateral view (JU/VPL/SF/335), x 57, 6. Hypotype II (JU/VPL/SF/336), right lateral view, x 64; 7. *Ilyocypris bradyi* Sars, carapace, (JU/VPL/SF/336), right lateral view, x 32; 8-9. *Ilyocypris* sp.: 8. Carapace (JU/VPL/SF/337), right view, x 49, 9. Carapace (JU/VPL/SF/338), right lateral view, x 50; 10-13. *Vestalenula jammuensis* sp. nov.: 10. Holotype (JU/VPL/SF/339), male carapace, right lateral view, x 44, 11. Paratype I (JU/VPL/SF/340), male carapace, left lateral view, x 45, 12. Paratype II (JU/VPL/SF/341), dorsal view, x 24, 13. Paratype III (JU/VPL/SF/342), carapace, right lateral view, x 48; 14-15. *Sclerocypris*? sp.: 14. Broken left lateral valve (JU/VPL/SF/343), x 12, 15. Broken left lateral valve (JU/VPL/SF/344), x 10.



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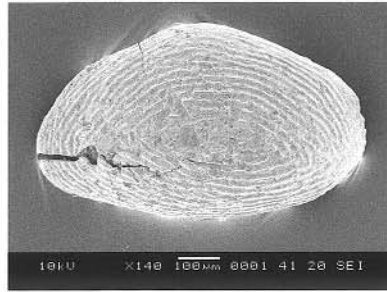
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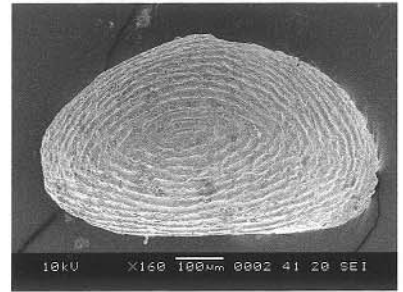
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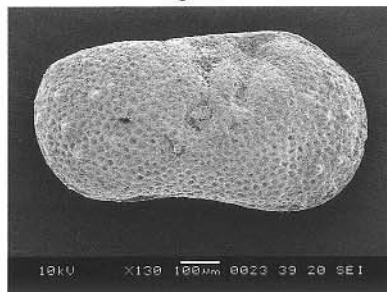
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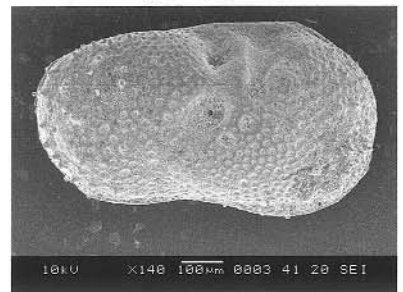
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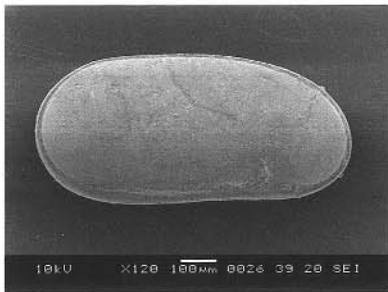
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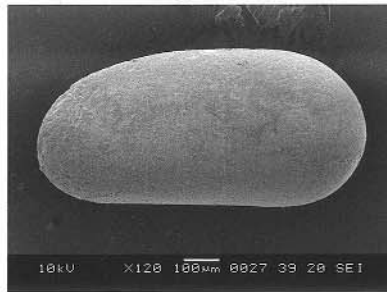
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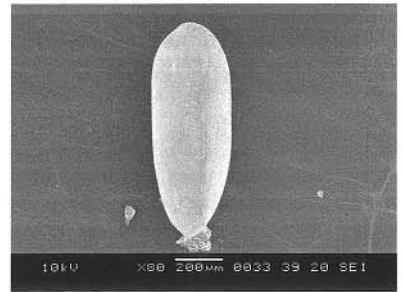
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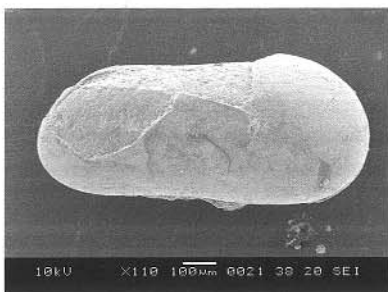
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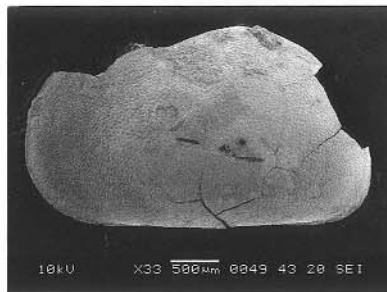
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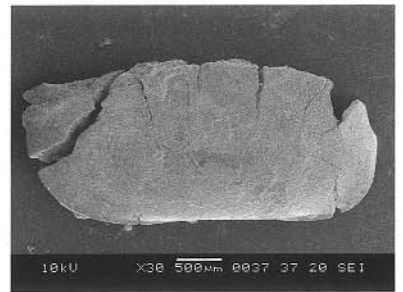
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Paratype II, a female carapace (JU/VPL/SF/341): *Length*: 0.90, *Height*:0.45, *Width*:0.35

Remarks.- This species resembles *Vestalenula corneliain* described by Smith, Kanya and Horne, 2006 from the gently flowing spring, Yakushima island, Japan in overall shape, overlap and length/ height ratios. Unlike present species *Vestalenula corneliain* has straight dorsal margin and overlap along dorsal margin is not distinct, anterodorsal margin steeply sloping, anterior end below mid height and carapace about more than four and half times larger than the present species.

8. CONCLUSIONS

The rich and diversified ostracod assemblage recorded from the Nagrota Formation, Upper Siwalik Subgroup of Jammu is indicative of fresh standing water body or lacustrine condition during deposition of mudstone. The recovered micromammals and fission track dating indicate a probable Late Pliocene age to the mudstone bearing stratigraphic horizon.

9. ACKNOWLEDGEMENTS

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In memoriam Yvette Tambareau (January 28, 1938 - February 26, 2008)

Jean-Paul Colin

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Yvette Tambareau was born in Toulouse on January 28th 1938 to parents who were both school teachers. Between 1954 and 1957 she followed the course of the Ecole Normale and then for one year taught in a primary school in the small village of Montesquieu Lauragais. In 1958 she registered at the Faculty of Sciences of the University of Toulouse and after successful graduation in 1964 she joined the Centre National de la Recherche Scientifique (CNRS), and in 1970 she presented her PhD Thesis "Thanétien supérieur et Ilerdien des Petites Pyrénées".

In 1981 she spent one year in Pau at ELF-Aquitaine research centre in which she worked under the supervision of H. J. Oertli on the inventory and palaeobiogeography of Cretaceous ostracodes of the Atlantic margins.

She retired in 1998, but during these last 10 years she never lost contact with her colleagues and friends. She used to come often to the University to help PhD students and she never missed any meeting of the ostracodologists' community. Despite her weak health, she was always ready to follow her colleagues and friends all over the world to attend symposiums or geological field trips: Japan, China, Australia, Mexico, Oman, ...

Her contribution to science is important (more than 60 publications), essentially concerning ostracodes from the Palaeogene and at the Cretaceous-Tertiary boundary in the continental realm, and to a lesser degree larger foraminifera. Her culture was not only scientific. She was very much interested in the arts, mostly theatre and opera, and by family tradition, rugby.

Yvette had many friends all over the world among scientist colleagues and any of them knew that they could rely on her on any occasion. Yvette was straight, courageous and devoted, faithful to her land and friends. We miss her.

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Portada: Hipotipos del foraminífero planctónico *Hendersonia carinata* (Cushman, 1938; Globigerinina, Heterohelicidae), del Santoniense Superior-Campaniense. Microfotografías de Marius Dan Georgescu y Sigal Abramovich.

Cover: Hypotypes of the planktonic foraminifer *Hendersonia carinata* (Cushman, 1938; Globigerinina, Heterohelicidae), from the Upper Santonian-Campanian. Microphotographies by Marius Dan Georgescu and Sigal Abramovich

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