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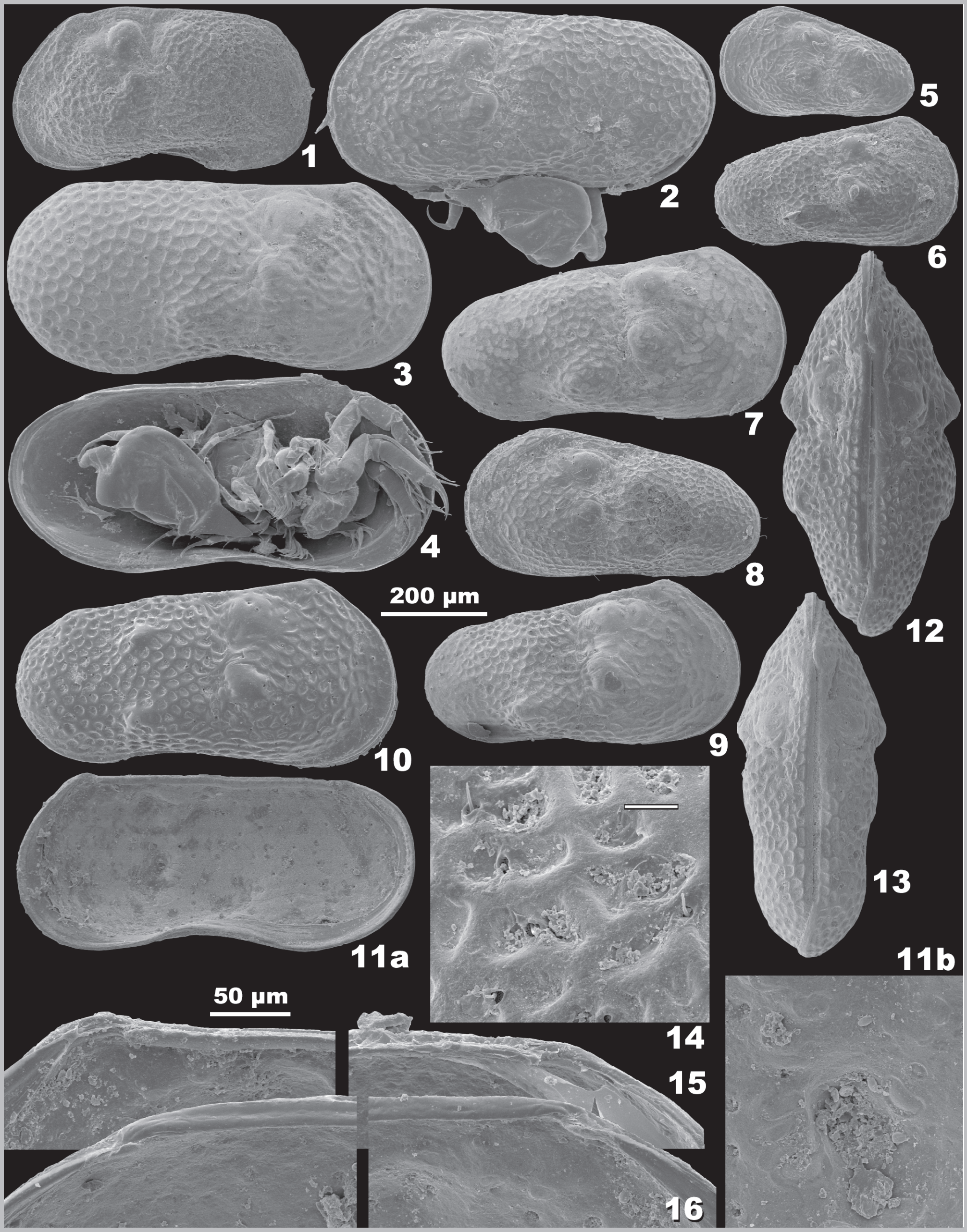

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Portada: Ostrácodos lacustres actuales de los géneros *Leucocytherella* y *Limnocythere* de Nam Co, Tibet. Microfotografías de Claudia Wrozyna, Peter Frenzel, Philip Steeb, Liping Zhu y Antje Schwalb.

Cover: Leucocytherella *and* Limnocythere*, Recent lacustrine ostracods from Nam Co, Tibet. Microphotograhies by Claudia Wrozyna, Peter Frenzel, Philip Steeb, Liping Zhu and Antje Schwalb.*

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Recent lacustrine Ostracoda and a first transfer function for palaeo-water depth estimation in Nam Co, southern Tibetan Plateau

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Resumen

Se analizan las asociaciones de ostrácodos de Nam Co con el objetivo de diseñar la toma de datos para reconstruir los cambios del nivel de agua que sufrió este lago salado durante el Holoceno. Con el fin de analizar las tafocenosis recientes de ostrácodos, se realizó un transecto en el que se recogieron noventa muestras tomadas entre 2 y 64 m de profundidad. Las muestras contenían abundantes ostrácodos, más de 1.000 valvas por gramo de sedimento, pero presentaron una baja diversidad de especies. Las seis especies documentadas son, en orden decreciente de dominancia, *Leucocytherella sinensis* Huang 1982, ?*Leucocythere dorsotuberosa* Huang 1982, *Fabaeformiscandona danielopoli* Yin & Martens 1997, *Ilyocypris* cf. *mongolica* Martens 1991, *Candona candida* (O.F. Müller 1776) and *Limnocythere inopinata* (Baird 1843). En conjunto, *L. sinensis* y ?*L. dorsotuberosa* integraron alrededor del 90% de las asociaciones. ?*L. dorsotuberosa* mostró una alta variabilidad morfológica. *Leucocythere postilirata* Pang 1985 se considera en este trabajo como un morfotipo de ?*L. dorsotuberosa* con carenas posteriores, medio-ventrales y anteriores semejantes a pliegues sobresalientes de la concha. Esta forma apareció por debajo de la termoclina (20-30 m de profundidad) y llegó a ser más abundante según aumentaba la profundidad. *I.* cf. *mongolica* y *L. inopinata* fueron especies típicas de aguas someras (<10 m). Por debajo de esta profundidad sólo se encuentran unas pocas valvas desarticuladas de ambas especies. El género *Candona* se halló en gran número, probablemente representado por dos especies diferentes en aguas someras (*C. candida)* y profundas (*C. xizangensis*). La especie *F. danielopoli* mostró una mayor abundancia alrededor del nivel de termoclina. Considerando los resultados obtenidos, ?*L. dorsotuberosa* f. *postilirata, I.* cf. *mongolica, F. danielopoli*, *Candona* spp. y *L. inopinata* pueden ser usadas como indicadores de la profundidad de las aguas en Nam Co. Si excluímos a *L. inopinata*, teniendo en cuenta los datos de dominancia del resto de las especies identificadas, se ha construido una función de transferencia para inferir la paleoprofundidad de las aguas en Nam Co, que cubre un intervalo de profundiades entre 3,7 y 64 m y presenta un error estándar de 7,6 m.

Palabras clave: *Crustacea, Ostracoda, paleolimnología, ecología acuática, aguas salobres athalásicas, nivel de aguas lacustres, Tibet.*

Abstract

Ostracod assemblages from Nam Co were analyzed to design a training set for reconstructing Holocene water level changes in this saline lake. A transect consisting of nineteen surface sediment samples taken from 2 m to 64 m water depth was used to analyze Recent ostracod taphocoenoses. The samples contained abundant ostracods of up to about 1000 valves per gram sediment but display low species diversity. The six documented species are, in descending order of dominance, *Leucocytherella sinensis* Huang, 1982, ?*Leucocythere dorsotuberosa* Huang, 1982, *Fabaeformiscandona danielopoli* Yin & Martens, 1997, *Ilyocypris* cf. *mongolica* Martens, 1991, *Candona candida* (O.F. Müller, 1776) and *Limnocythere inopinata* (Baird, 1843). *L. sinensis* and ?*L. dorsotuberosa* together composed about 90 % of the associations. ?*L. dorsotuberosa* showed high morphological variability. *Leucocythere postilirata* Pang, 1985 is regarded here as a morphotype of ?*L. dorsotuberosa* with pronounced posterior, medio-ventral and anterior carinae as protruding foldings of the shell. This form occurred below the thermocline (20 – 30 m water depth) and became more abundant with increasing depth. *I.* cf. *mongolica* and *L. inopinata* were typical of shallow water (<10 m). Below this depth only very few single valves of both species were found. The genus *Candona* occurred in larger numbers probably with two different species in shallow (*C. candida)* and deep (*C. xizangensis)* water. *F. danielopoli* showed highest abundance around the thermocline level. Regarding our results, ?*L. dorsotuberosa* f. *postilirata, I.* cf. *mongolica, F. danielopoli*, *Candona* and *L. inopinata* can be used as water depth indicators in Nam Co. Based on the dominance data of these taxa, except *L. inopinata*, we set up a transfer function for palaeo-water depth in Nam Co which covers a water depth interval of 3.7 to 64 m and displays a standard error of 7.6 m.

Keywords: *Crustacea, Ostracoda, palaeolimnology, aquatic ecology, athalassic brackish water, lake level, Tibet.*

1. INTRODUCTION

Nam Co (other names are Namu Cuo and Tengri Nor) and its catchment is the highest and largest lake system on the Tibetan Plateau. The lake is influenced by the intersection of the Southasian or Indian and Eastasian summer monsoon and the winter monsoon, which is composed of the Northeast monsoon and the Eastasian winter monsoon as well as the Westerlies. These all brings moisture in different amounts to the lake system and makes it a very sensitive and therefore well-suited area for studying monsoon dynamics. The lake level is an important indicator for modeling hydrological system changes within the Nam Co area. It can be reconstructed in time and space using different methods such as geomorphology, sedimentology and geochemistry. Here, we want to highlight the potential of micropalaeontological proxies from sediment cores for lake level reconstruction. Ostracods are, besides diatoms, the most abundant aquatic taxa with well preserved hard parts in Nam Co. In contrast to diatoms, they are preserved in both surface sediments and sediment cores. Thus, they are the biological proxies with the highest potential for palaeoenvironmental reconstructions in the lacustrine environment of Nam Co. The value of ostracods as proxies in palaeolimnological research has been shown for other areas before (e.g. Löffler, 1997; Griffiths & Holmes, 2000; Holmes, 2001; Boomer *et al.*, 2003; Curry, 2003; Schwalb, 2003). Transfer functions are still rare within the published ostracod literature (Mezquita *et al.*, 2005; Viehberg, 2006; Mischke *et al.*, 2007). A first and so far only transfer function for water depth was presented by Mourgiart & Roux (1990) and Mourgiart & Carbonel (1994) for the Bolivian Altiplano. They demonstrated a valuable application for this parameter because a transfer function allows the quantitative reconstruction of parameters and the estimation of an error of prediction. This is of course very promising for the reconstruction of palaeo-lake levels in the Nam Co area also. Because the knowledge of ostracod taxonomy, ecology and distribution is rather poor for the Tibetan Plateau and there are only few publications on Recent ostracods from this region and most of them are published in Chinese (Chen, 1982; Yang *et al.*, 1982; Huang *et al.*, 1985; Li *et al.*, 2001) and are thus not easily accessible for the international research community, we documented taxonomy and morphology of the present taxa a little more in detail. On this base, we analyzed Recent ostracod associations from a water depth transect in Nam Co and designed an ostracod-based water depth transfer function in order to reconstruct Holocene lake level variations from sediment cores.

2. STUDY AREA

Nam Co is situated in the southeastern part of the Tibetan Plateau (30°30′-35′ N, 90°16′-91°03′ E; Fig. 1). The lake is located in an altitude of 4718 m a.s.l. (T. Yao, pers. comm.) and covers an area of 1961 km^2 (Williams, 1991) with a maximum depth of 105 m (G. Daut, pers. comm.). A hydrological study in August and September 2005 found the lake water to be well mixed (Zhang *et al.*, 2006). The catchment area is at the earth's surface a hydrologically closed basin. Precipitation arrives mainly with the Southwest Asian Monsoon during the summer months with 300 to 400 mm per year. Annual evaporation exceeds 2400 mm (T. Yao, pers. comm.). The temperature varies strongly between -10 and 9 °C with an annual mean of 0 °C (Fig. 2). The dominating anions of Nam Co surface water are HCO_3^- and SO_4^{2-}, the main cations Na^+ and Mg^{2+} (Table 1). The Ca^{2+} concentration is very low (Zhang *et al.*, 2006).

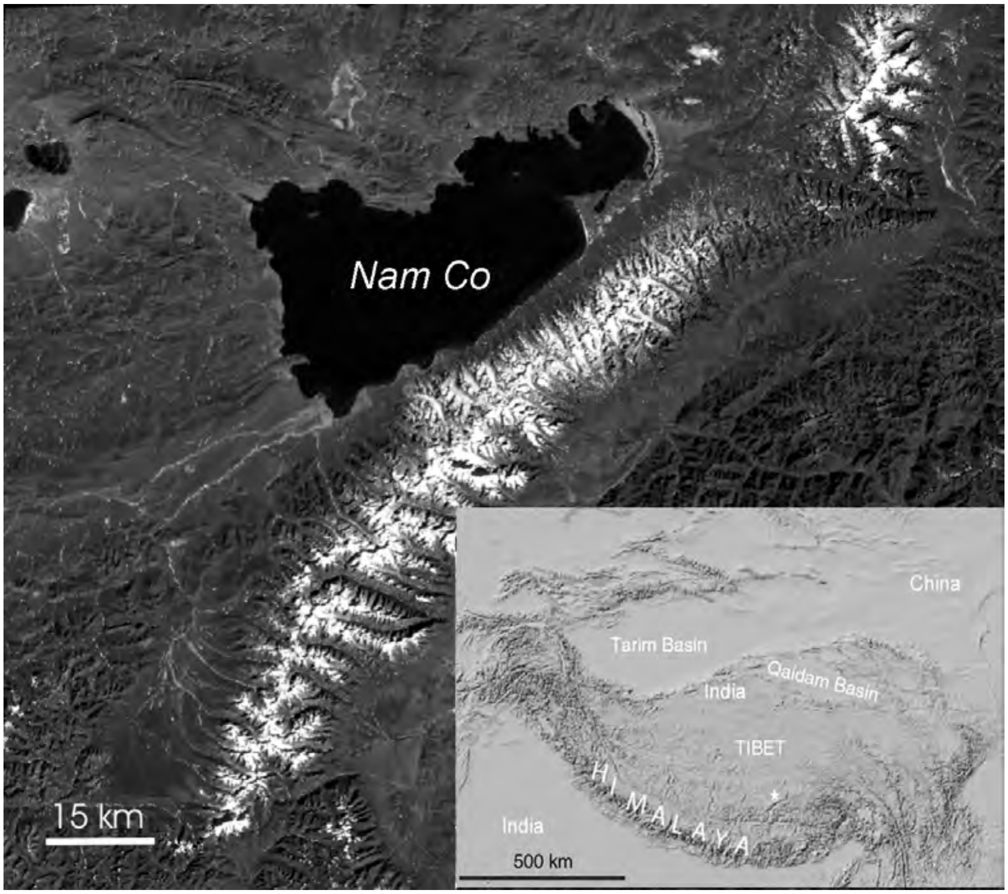

Figure 1. Position of Lake Nam Co within the Himalayan Region (inset) and topography of the Nam Co area (A Datasource Landsat ETM 2007, B modified after Owen *et al.*, 2006).

Ions	Concentration [mg l^{-1}]
Na^+	170.5
NH_4^+	0.34
K^+	19.90
Mg^{2+}	44.59
Ca^{2+}	5.92
Cl^-	44.76
NO_3^-	0.20
SO_4^{2-}	147.6
HCO_3^-	464.46
TDS	898.2

Table 1. Average concentration of main ions in surface water samples taken from Nam Co in August/September 2005 (compiled from Zhang *et al.*, 2006).

3. MATERIAL AND METHODS

Eighteen samples from Nam Co were collected with an Ekman grab (225 cm^2) in August 2005 from water depths ranging between 2 and 64 m in the eastern part of the lake (Table 2, Fig. 3). The uppermost 1 – 2 cm of oxidized sediment were isolated and used for ostracod analysis. One additional sediment sample, taken in August, 2004, was provided by Ines Mügler (MPI Jena). The geographical position was documented by GPS.

In September, 2005, physico-chemical water characteristics were measured in the water column down to a water depth of 53 m (Fig. 3) within the embayment where most of our stations are situated. These were then interpolated for the water depths of our sediment sampling stations within the lake. Water samples were collected in 1 l bottles and measured with a multi-probe (temperature, pH, conductivity, O_2 concentration) immediately after reaching the water surface. The water sample temperature differed less than 7 K between sampling and processing. The salinity was calculated from conductivity values following Fofonoff & Millard (1983).

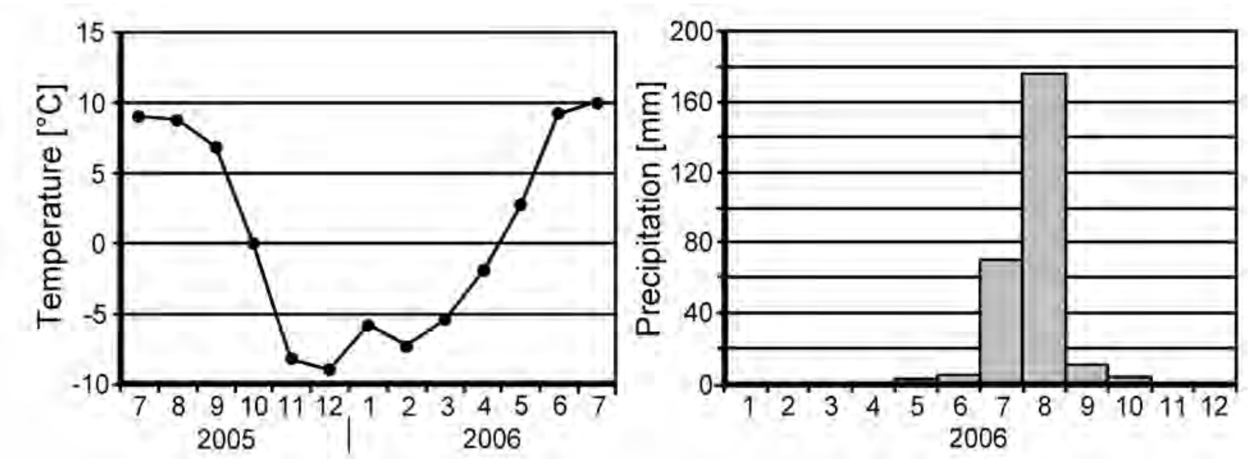

Figure 2. Monthly average temperature and monthly precipitation at Nam Co in 2005/2006 compiled from data of You *et al.* (2006).

Sample	Date	Water depth	Habitat
Nam300805-02	8/2005	2.0 m	dark-brown greyish silt
Nam300805-01	8/2005	3.7 m	grey beige sandy silt
Nam300805-03	8/2005	5.7 m	dark brown coarse sand
Nam300805-04	8/2005	7.2 m	dark grey coarse sand, detritus
Nam300805-05	8/2005	9.2 m	dark grey coarse sand
NamSC001-1.5	8/2004	10 m	grey beige silt, plants
Nam300805-06	8/2005	11 m	reddish brown coarse sand
Nam300805-07	8/2005	15 m	dark grey brown coarse sand
Nam300805-08	8/2005	20 m	grey beige silty fine sand
Nam300805-09	8/2005	25 m	grey beige sandy silt
Nam300805-10	8/2005	30 m	grey beige silty fine sand
Nam310805-03	8/2005	35 m	grey beige silt
Nam310805-01	8/2005	40 m	grey beige sandy silt
Nam310805-02	8/2005	45 m	grey beige fine sand
Nam290805-01	8/2005	47 m	grey brown silt
Nam Co 4-2-2	9/2005	49 m	grey beige silt
Nam290805-02	8/2005	53 m	grey beige sandy silt
Nam-SCII-2	8/2005	60 m	grey beige silt, detritus
Nam Co 6-1-2	9/2005	64 m	grey beige silt

Table 2. Sampling dates with water depths and sediment character.

For isolating the ostracods from the sediment, about 5 g of each sample were placed in a plastic bottle. A teaspoon of sodium bicarbonate and 250 ml hot deionized water were added. The sample was then placed in a freezer for 24 h and frozen solid. After thawing, the disintegrated sediment sample was washed through a 63 µm mesh sieve. The residue was rinsed with deionized water and air dried. Ostracods were picked from dry residues using a fine paint brush until a minimum of 300 valves, if present, was reached. Counting of splits served as a base for total ostracod number calculation.

We estimated proportions of hyaline, opaque and colored valves, articulated valves, abraded/corroded and encrusted specimens, and documented carapaces containing soft parts for distinguishing autochthonous and allochthonous/subfossil components of the ostracod associations. Hyaline valves were considered as autochthonous specimens in general. This is a simplification because short distance or floated transport without deterioration of the valve surface may have occurred. Analyzing the population age structure of ostracod associations is in general a powerful tool to distinguish between autochthonous and allochthonous components (see Boomer *et al.*, 2003). However, ratios of adults versus juveniles of the abundant species were not easily applicable for identifying allochthonous components in Nam Co because of very similar species compositions in space and time. First results from short cores of Nam Co showed the same dominant species in similar proportions as today. Hence, species represented by well preserved specimens and with a high number of juveniles and individuals with soft parts were regarded as collected from their natural habitat.

The ostracods were checked through stereo microscope in reflected light and in some cases at higher magnification in transmitted light for the identification of species. In addition, SEM photographs of selected specimens were used. The material is stored in the collection of the authors at the Institut für Umweltgeologie, Technische Universität Braunschweig.

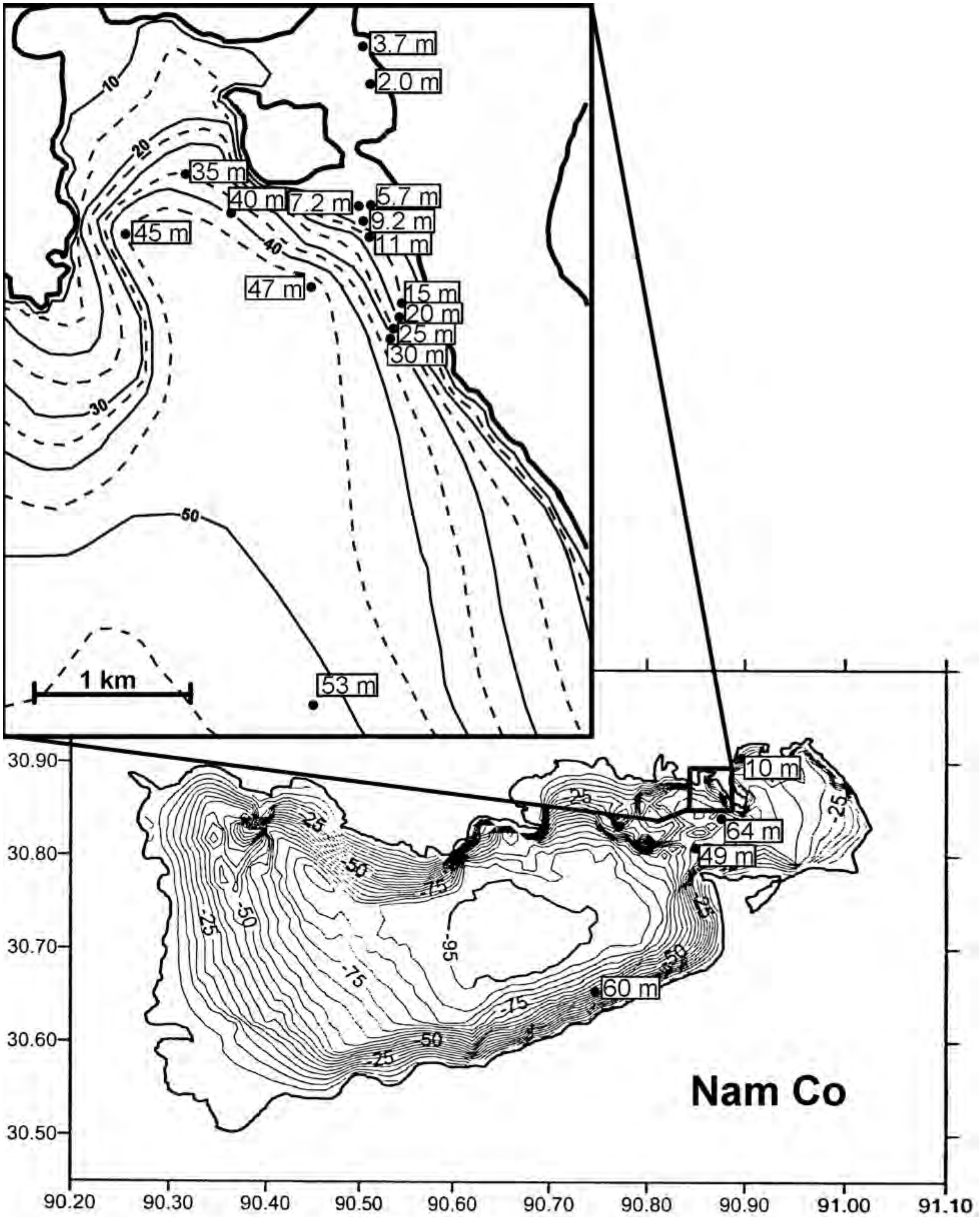

Figure 3. Locations of sampling stations in and around Lake Nam Co. Bathymetric map of entire lake from Wang & Zhu (2006). Isobaths in detail map approximative.

Diversity was measured using the Shannon-Wiener diversity index (compare Spellerberg & Fedor, 2003).

We carried out Spearman Rank correlation and Canonical Correspondence Analysis (CCA) using the program PAST version 1.80 (Hammer *et al.*, 2001). All samples with less than 100 counted specimens were excluded from multivariate statistical analysis. This limit excludes the samples from 2 and 5.7 to 11 m water depth from ostracod analysis. Also, *Limnocythere inopinata* was excluded because it occurs in one sample only. The Spearman Rank correlation (Table 3) was used in order to show relationships between ostracod species dominances on one hand as well as water and sediment parameters on the other hand. We replaced pairs of highly correlating (>0.9) faunistic and environmental parameters by one of these parameters each for excluding distorting impacts onto the data matrix before starting a CCA. Furthermore, conductivity was excluded because its low variability is regarded as ecologically insignificant for the ostracods here. The CCA should reveal factors that drive the distribution of ostracod species and forms.

As a tool for reconstructing palaeo-water depths in Nam Co from Holocene sediments, we created an ostracod based transfer function. The principle of a transfer function was formulated by Imbrie & Kipp (1971) and consists of two steps: first, the mathematical description of the quantitative distribution of modern taxa in dependence of a selected environmental parameter; second, the reconstruction of this environmental parameter for past environments using abundance or dominance data of taxa from sediments of cores and outcrops. Details for our transfer function are given within the Results section.

4. RESULTS

4.1. Water data and sediment characteristics

A thermocline was present in the water column of Nam Co in September, 2005. Water temperature reached a maximum of up to 13 °C above 20 m, and a minimum of about 5.5 °C below 30 m water depth (Fig. 4). The pH values were relatively constant within water column (9.3 to

	depth	temperature	conductivity	O_2	silt	sand	LOI	diversity	ostracod number	*dorsotuberosa*	*postilirata*	*sinensis*	*mongolica*	*danielopoli*	*Candona*
depth		<0.001	0.003	0.300	0.385	0.090	0.570	0.651	0.533	0.726	<0.001	0.627	0.399	0.347	0.530
temperature	**-0.95**		<0.001	0.166	0.556	0.074	0.493	0.803	0.260	0.446	<0.001	0.405	0.705	0.244	0.313
conductivity	**0.83**	**-0.90**		0.069	0.556	0.054	0.610	0.676	0.214	0.467	0.014	0.627	0.497	0.214	0.211
O_2	0.36	-0.47	**0.60**		0.725	0.042	0.978	0.713	0.544	0.688	0.260	0.725	0.723	0.947	0.061
silt	0.31	-0.21	0.21	0.13		0.022	0.120	0.244	0.934	0.803	0.270	0.580	0.744	0.855	0.393
sand	**-0.56**	**0.59**	**-0.62**	**-0.65**	**-0.71**		0.736	0.200	0.467	0.276	0.019	0.187	0.770	0.726	0.372
LOI	0.24	-0.29	0.21	0.01	**0.60**	-0.14		0.095	0.323	-0.100	0.287	-0.643	0.101	0.071	0.143
diversity	-0.16	0.09	-0.15	0.13	0.41	-0.44	**0.82**		0.176	0.758	0.141	-0.830	0.725	0.552	0.097
ostracod number	0.22	-0.39	0.43	0.22	-0.03	-0.26	0.44	**0.63**		0.394	0.350	-0.382	0.425	-0.100	-0.330
dorsotuberosa	0.13	-0.27	0.26	0.15	0.09	-0.38	**0.82**	0.01	0.26		0.270	<0.001	0.021	0.676	0.530
postilirata	**0.89**	**-0.91**	0.74	0.39	0.39	**-0.72**	0.49	**0.70**	0.32	0.39		0.144	0.876	0.461	0.270
sinensis	-0.18	0.30	-0.18	-0.13	-0.20	0.46	0.09	<0.01	0.28	**-0.95**	**-0.50**		0.018	0.533	0.579
mongolica	-0.30	0.14	-0.24	-0.13	-0.12	0.11	**0.81**	0.02	0.22	**0.71**	-0.06	**-0.72**		0.532	0.741
danielopoli	-0.33	0.41	-0.43	0.02	0.07	-0.13	**0.87**	0.10	**0.78**	0.15	-0.26	-0.22	0.22		0.554
Candona	-0.23	0.36	-0.43	**-0.61**	0.30	0.32	**0.74**	**0.79**	0.35	-0.23	-0.39	0.20	0.12	0.21	

Table 3. Spearman Rank correlation for water, sediment and ostracod data of fourteen stations from Nam Co. Correlations with absolute values ≥0.9 are shaded, printed bold and double framed, ≥0.75 bold and double framed and ≥0.50 bold. The upper right half of the matrix displays the probability *p*.

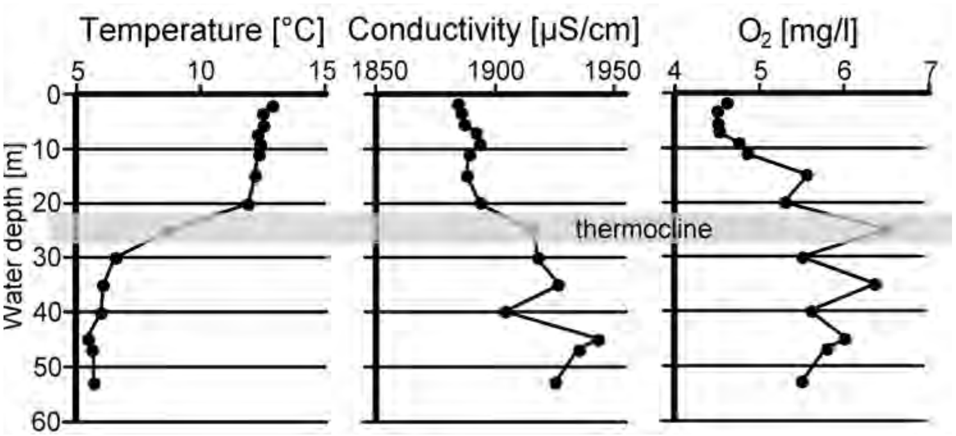

Figure 4. Depth related variation of selected physico-chemical parameters measured in the water column. The shaded box shows the position of the thermocline.

9.4). Conductivity values varied between 1885 and 1943 µS cm^{-1} within the lake. This corresponds roughly to a (calculated) salinity value of 1.3 ‰. A slight increase of conductivity from approximately 1890 to 1920 µS cm^{-1} with water depth and water temperature within the thermocline is documented between 20 and 30 m water depth. The oxygen concentration was 4.7 mg l^{-1} in 0 to 11 m water depth and reached concentrations of about 6 mg l^{-1} below 15 m.

Nam Co sediments consisted mostly of clayey silts with some fine and coarse sand. An additional sample taken in 10 m water depth from the 2004 sampling campaign yielded silts with abundant plant fragments.

4.2. Ostracod abundance

All sediment samples yielded ostracods. The maximum total abundance of all samples was 910 valves per gram sediment in sample NamSC001-1.5 (Table 1) collected from a water depth of 10 m in 2004. The minimum (2 valves per gram) was found in sample Nam300805-04 in 7.2 m water depth. Mean total abundance for Nam Co was 115 valves per gram sediment.

Five of the nineteen surface sediment samples from Nam Co showed a high proportion of opaque and coated valves. This was associated with a very high proportion of complete carapaces that were characterized by incrustations or distinct corrosion/abrasion marks (Fig. 5). These

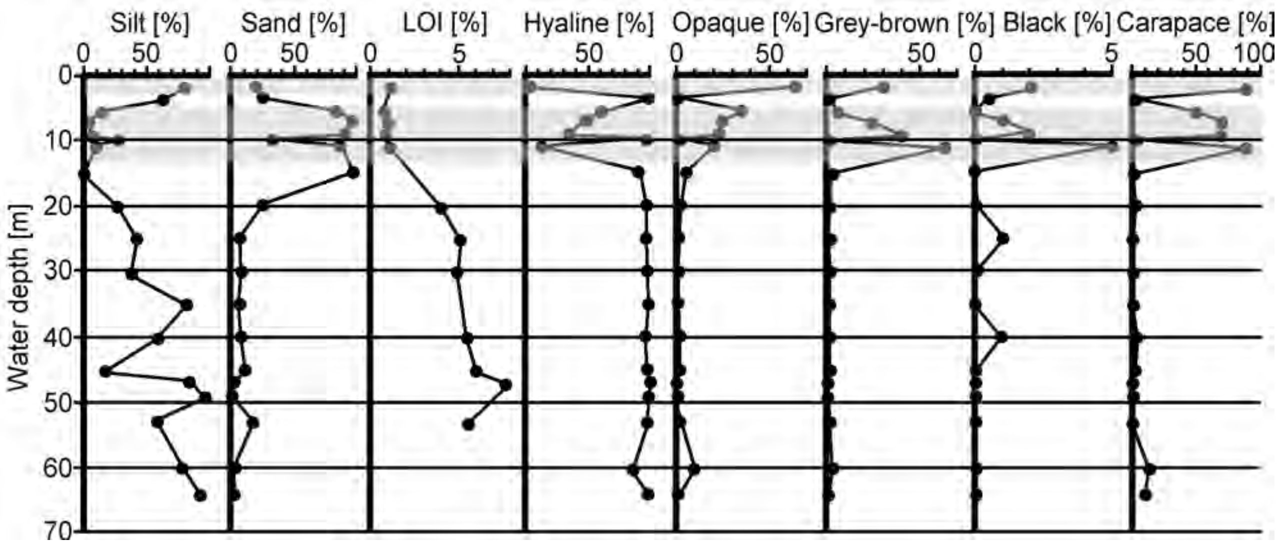

Figure 5. Sediment character and preservation status of ostracods in surface sediments. Samples that are dominated by allochthonous or subfossil valves are indicated by shaded boxes. 'Sand' comprises medium to coarse sand, 'LOI' shows loss on ignition and 'Carapace' the proportion of articulated valves.

associations in samples collected from 2 m to 11 m water depth are regarded as taphocoenoses, i.e. they do not represent Recent autochthonous communities by a thanatocoenosis. Therefore, the hyaline valves from these samples were counted separately as actual thanatocoenoses. In consequence, the total number of identified autochthonous ostracods within these samples was rather small with less than 100 valves per sample.

The autochthonous abundance of ostracods from Nam Co varied between 1 and 910 valves per gram sediment with a mean of 104 valves per gram sediment (Fig. 6). Looking into the abundance variance along the water depth profile, we found an increase of autochthonous ostracod abundance within the thermocline and a second peak at about 45 m water depth. The sampling of the only phytal habitat of our sample series (NamSC001-1.5) showed an extraordinary high abundance at 10 m water depth in contrast to the other sediment samples from macrophyte-barren shallow water.

4.3. Taxonomy

We found six ostracod species in our samples. Their valves are extensively documented on plates 1 – 3 and discussed in the following because of the still poor knowledge on most of these taxa.

1. *Candona candida* (O.F. Müller, 1776) = *Cypris candida* O.F. Müller – [plate 1, fig. 9]

Except one female valve all specimens recorded are juveniles, which can not be certainly ascribed to *C. candida*. We found subfossil valves of *Candona xizangensis* Huang, 1982 (in Huang *et al.*, 1982) in short core samples from Nam Co more frequently than *C. candida*. It is possible that many of the juvenile *Candona* valves of the superficial sediment samples belong to *C. xizangensis*.

2. *Fabaeformiscandona danielopoli* Yin & Martens, 1997 [plate 1, fig. 10-11]

Only juvenile specimens could be documented. Therefore, the identification remains uncertain. However, *F. danielopoli* is present in subfossil samples from Nam Co.

3. ?*Leucocythere dorsotuberosa* Huang, 1982 (in Huang *et al.*, 1982) – [plate 2]

Following Danielopol *et al.* (1989) and Martens (2000), the genus *Leucocythere* possesses a characteristic hinge with the anterior tooth on right valve considerably smaller than the posterior tooth and a crenulated intercardinal bar. In contrast, our specimens (plate 2, fig. 4) bear a lophodont hinge. The assignment of *Leucocythere dorsotuberosa* Huang, 1982 to the genus *Leucocythere* has been questioned by Danielopol *et al.* (1989: 78-80). *Leucocythere postilirata* Pang, 1985 (in Pang *et al.*, 1985) is regarded here as a morphotype of ?*L. dorsotuberosa* with pronounced medio-ventral and anterior and often posterior carinae as protruding foldings of the shell (plate 2, fig. 3, 6, 8-14). This morphological combination is more distinct in males than in females and goes hand in hand with a thinner shell with less pronounced reticulation in our material (e.g. plate 2, fig. 8). The form *postilirata* is connected to the typical *L. dorsotuberosa* by transient morphotypes. A few carapaces with well developed posterior, medio-ventral and anterior carinae on one valve and less pronounced anterior and lacking posterior carinae on the other valve were found within subfossil material from the Nam Co area indicating a varying morphology rather than a different species. Further investigations on soft parts is needed to be carried out in order to review the systematic position of ?*Leucocythere dorsotuberosa* and the *postilirata* form.

4. *Leucocytherella sinensis* Huang, 1982 (in Huang *et al.*, 1982) – [plate 3, fig. 2-16]

Valves lacking nodes and others with up to four lateral nodes occur within our material. *Limnocytherellina bispinosa, L. trispinosa* and *L. kunlunensis*, all described by Pang (1985) and characterised by a different number of lateral nodes, seem to be synonyms of *Leucocytherella sinensis.*

5. *Limnocythere inopinata* (Baird, 1843) = *Cythere inopinata* Baird – [plate 3, fig. 1]

6. *Ilyocypris* cf. *mongolica* Martens, 1991 – [plate 1, fig. 1-8]

Lateral shape, size and surface ornamentation of our specimens are very similar to those of *I. mongolica* described from eastern Mongolia. A mummified specimen from Nam Co (pl. 1, fig. 4) shows the long natatory setae given

Plate 1

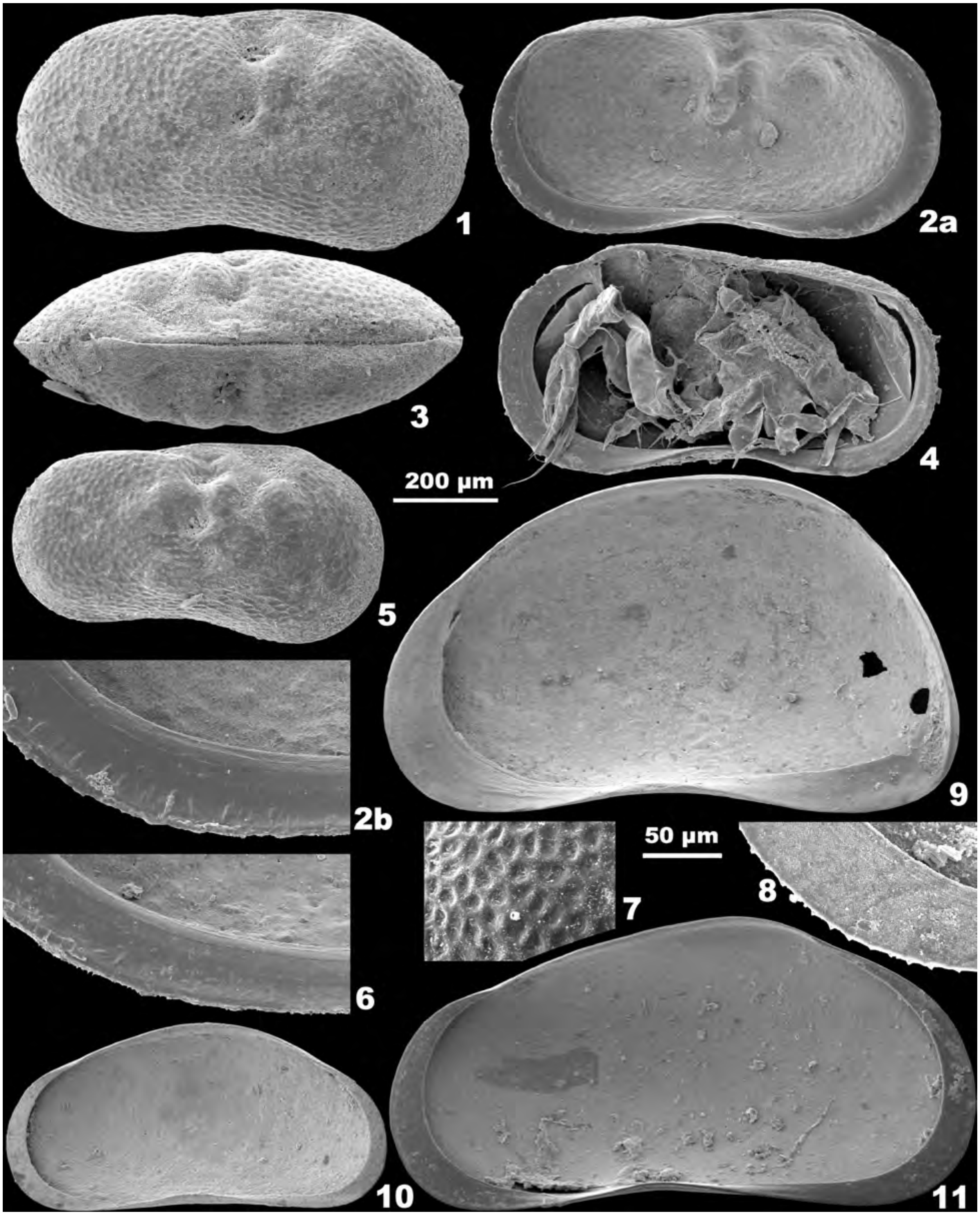

Plate 1. *Ilyocypris* and Candoninae from Nam Co. ***1-8***, *Ilyocypris* cf. *mongolica* Martens, 1991, sample Nam300805-01 if not otherwise stated: 1) RV in external view; 2) LV in internal view, with (b) conspicuous marginal ripplets on the posteroventral inner lamella; 3) carapace in dorsal view; 4) ♂ RV in internal view with preserved soft parts; 5) juvenile RV in external view, Nam300805-09; 6) inconspicuous marginal ripplets on the posteroventral inner lamella of a LV; 7) exterior ornamentation detail of a RV; 8) fine denticulation on the anteroventral margin of a RV in internal view. ***9***, *Candona candida* (O.F. Müller, 1776), internal view of a ♀ RV, sample NamSC001-1.5. ***10-11***, *Fabaeformiscandona danielopoli* Yin & Martens, 1997, internal views of juvenile RVs: 10) sample Nam310805-02; 11) Nam300805-08. 200 µm scale bar: fig. 1, 2a, 3-5, 9-11; 50 µm scale bar: fig. 2b, 6-8

Plate 2

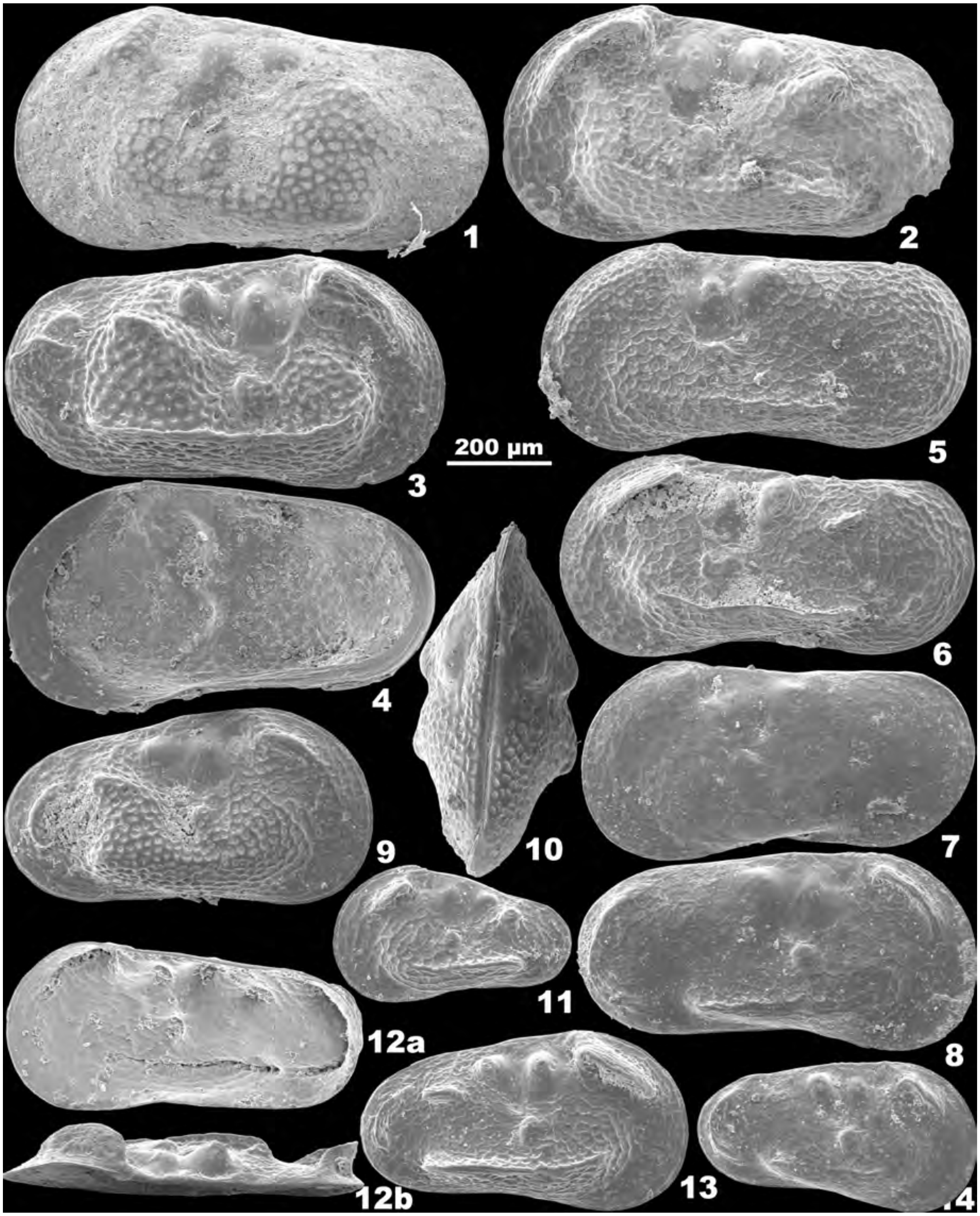

Plate 2. ?*Leucocythere dorsotuberosa* Huang, 1982 from Nam Co. ***1-2***, ♀ LVs: 1) without ribs or nodes, Nam290805-02; 2) antero-dorsal rib and two dorso-lateral nodes, Nam310805-02. ***3-4***, ♀ RVs: 3) f. *postilirata*, with antero-dorsal, ventro-lateral and short posterior-dorsal ribs and four lateral nodes, Nam310805-01; 4) without ribs, internal view, Nam300805-08. ***5-7***, ♂ LVs: 5) without ribs, but with two dorso-lateral nodes, Nam310805-01; 6) f. *postilirata*, with antero-dorsal and ventro-lateral rib and three dorso-lateral nodes, but atypical distinct reticulation, Nam310805-01; 7) smooth form, Nam310805-03. ***8***, ♂ RV, f. *postilirata,* with antero-dorsal, ventro-lateral and short posterior-dorsal ribs and two lateral nodes, Nam290805-01. ***9-10***, juvenile *dorsotuberosa* forms: 9) RV of a pre-adult ♀ with short antero-dorsal and postero-dorsal ribs and weak nodes, transient form to *postilirata*, Nam300805-10; 10) dorsal view of a carapace, Nam300805-01. ***11-14***, juvenile f. *postilirata*: 11) LV, Nam290805-01; 12) RV of a pre-adult ♂, Nam310805-02: a) internal view with well visible extrusions of the shell forming carinae and nodes, b) dorsal view; 13) RV, Nam310805-02; 14) RV, Nam290805-01.

Plate 3

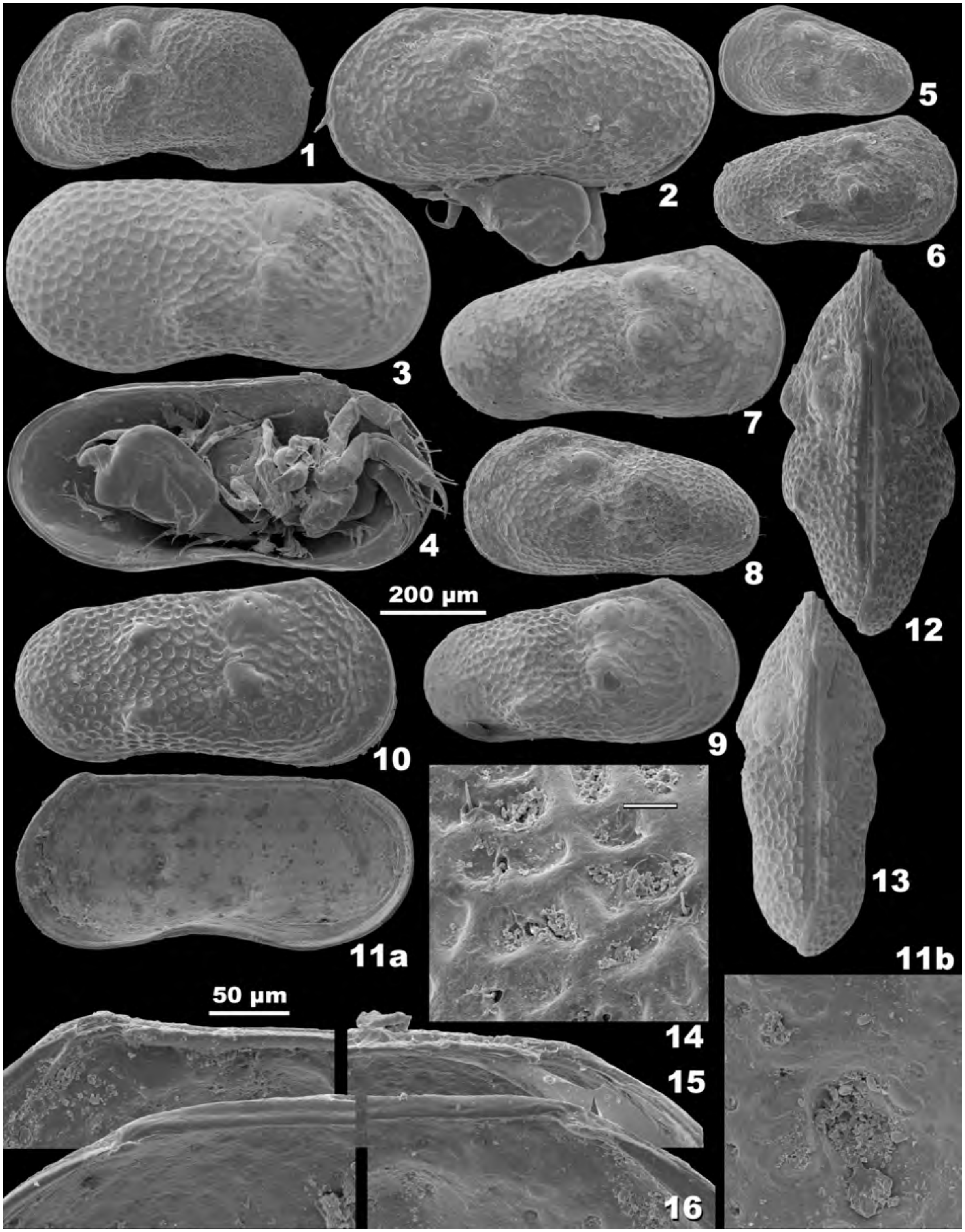

Plate 3. *Leucocytherella* and *Limnocythere* from Nam Co. ***1***, *Limnocythere inopinata* (Baird, 1843), ♀LV, Nam300805-01. ***2-16***, *Leucocytherella sinensis* Huang, 1982: 2) left side of a ♂ carapace with soft parts, Nam300805-01; 3) ♂ RV, Nam300805-09; 4) ♂ LV with soft parts, Nam300805-08; 5) juvenile LV, Nam300805-08; 6) juvenile RV, Nam300805-09; 7) juvenile RV, Nam310805-01; 8) juvenile LV, Nam310805-03; 9) juvenile RV, Nam310805-01; 10) ♀ RV, Nam300805-08; 11) ♂ RV, Nam310805-01: a) internal view, b) central muscle scar field; 12) ♀ carapace in dorsal view, Nam300805-08; 13) ♂ carapace in dorsal view, Nam310805-02; 14) low-lying sieve pores of a ♂ LV, Nam310805-01; 15) anterior and posterior lophodont hinge parts of a ♂ RV, Nam300805-01; 16) anterior and posterior lophodont hinge parts of a ♂ LV, Nam310805-01.

in Marten's diagnosis. However, the marginal denticulation is rather weak or even missing in our material in contrast to wart-like tubercles along the posterior margin of *I. mongolica*. Unfortunately, a description of the characteristic marginal ornamentation on the posteroventral inner lamella of the left valve is not given by Martens (1991) and cannot compared with our findings therefore. Additionally, our material matches the valves presented by Yang *et al.* (2004) and Mischke *et al.* (2006) as *I. sebeiensis*. However, the marginal ripplets on the posteroventral inner lamella of the left valve of specimens from Nam Co are faint and strongly vary in number in contrast to the very distinct ripplets of *I. sebeiensis* Yang & Sun, 2004 (in Yang *et al.*, 2004). They lay in a distal band on the posteroventral inner lamella in a similar position as the only four to five distinct ripplets of *Ilyocypris bradyi* Sars, 1890 and *I. lacustris* (compare Van Harten, 1979; Janz 1994). *I. getica* Masi, 1906 displays inconspicuous marginal ripplets like our specimens, but the carapace is larger (length 1.00 – 1.25 mm; Meisch, 2000) and possesses a dorsal expansion overlapping the valve margin. Another similar species is *Ilyocypris dentifera* Sars, 1903. Victor and Fernando (1981) redescribed *I. dentifera* and considered *I. angulata* Sars, 1903 as being a variant of *I. dentifera*. Their description matches our material well in size, shape, adductor muscle scar pattern and ornamentation, except the lateral nodes and marginal denticulation of the shell, which are lacking respectively indistinct in our form. Our specimens show some features typical of the genus *Qinghaicypris* Huang, 1979. Rodríguez-Lázaro and Martín-Rubio (2005) list a group of four anterior and two posterior adductor muscle scars and a large anterior hinge element (compare our plate 1, fig. 2a) as diagnostic features typical for *Qinghaicypris* in comparison with *Ilyocypris*. However, the medium grade of carapace calcification, the relatively small size (about 0.9 mm length), the more sub-rectangular than sub-cylindrical carapace shape and the relatively broad anterior marginal zone of our species are closer to *Ilyocypris* (compare Rodríguez-Lázaro & Martín-Rubio, 2005: table 2). Furthermore, *I. dentifera* (as figured by Victor and Fernando, 1981) and *I. decipiens* show the same 4 + 2 adductor muscle scar pattern. The extended diagnosis for *Qinghaicypris* given by Yang *et al.* (2004) supports the exclusion of our species from this genus.

4.4. Ostracod diversity and distribution

The relatively low species number corresponded with a low evenness and species diversity (average of Shannon-Wiener index 0.8). The clearly dominating species were *Leucocytherella sinensis* and ?*Leucocythere dorsotuberosa* that made up more than 90 % of specimens in almost all samples. All other species provided less than 10 % of the remaining valves – the most important forms of these rare species were juvenile candonids. The diversity trend showed decreasing values with increasing water depth in general. A broad diversity peak around and below the thermocline at 25 – 40 m water depth was also visible (Fig. 6).

Leucocytherella sinensis and ?*Leucocythere dorsotuberosa* occurred in all water depths in variable proportions without any clear trend. However, ?*L. dorsotuberosa* f. *postilirata* was practically restricted to water depths below the thermocline. In general, *Ilyocypris* cf. *mongolica* and *Limnocythere inopinata* were only present in shallower water of less than 10 m depth. Both species became more abundant in the shallowest autochthonous samples. Juvenile *Candona* valves were found both in very shallow and deep water whereas *Fabaeformiscandona danielopoli* showed highest dominances around the thermocline.

Results by a Canonical Correspondence Analysis (CCA; Fig. 7) indicate that the environmental parameter sand is bound to axis 1 and loss on ignition (LOI) to axis 2. Water depth (also representing temperature in our analysis) and oxygen concentration show the highest loadings on axis 3. The distribution pattern of *Ilyocypris* cf. *mongolica* and ?*Leucocythere dorsotuberosa* f. *postilirata* seems to be driven by water depth and oxygen concentration – ?*L. dorsotuberosa* f. *postilirata* occuring in deep water and *I.* cf. *mongolica* prefering shallow water. This fits well the depth distribution pattern of both taxa. The dominance of the genus *Candona* is positive correlated to sand proportion within the sediment. This is similar but less significant for *Leucocytherella sinensis* and *Fabaeformiscandona danielopoli*, whereas ostracod abundance is higher in samples with lower sand proportion. *Leucocythere dorsotuberosa* dominance (also representing general ostracod diversity in our analysis) is weakly bound to loss on ignition.

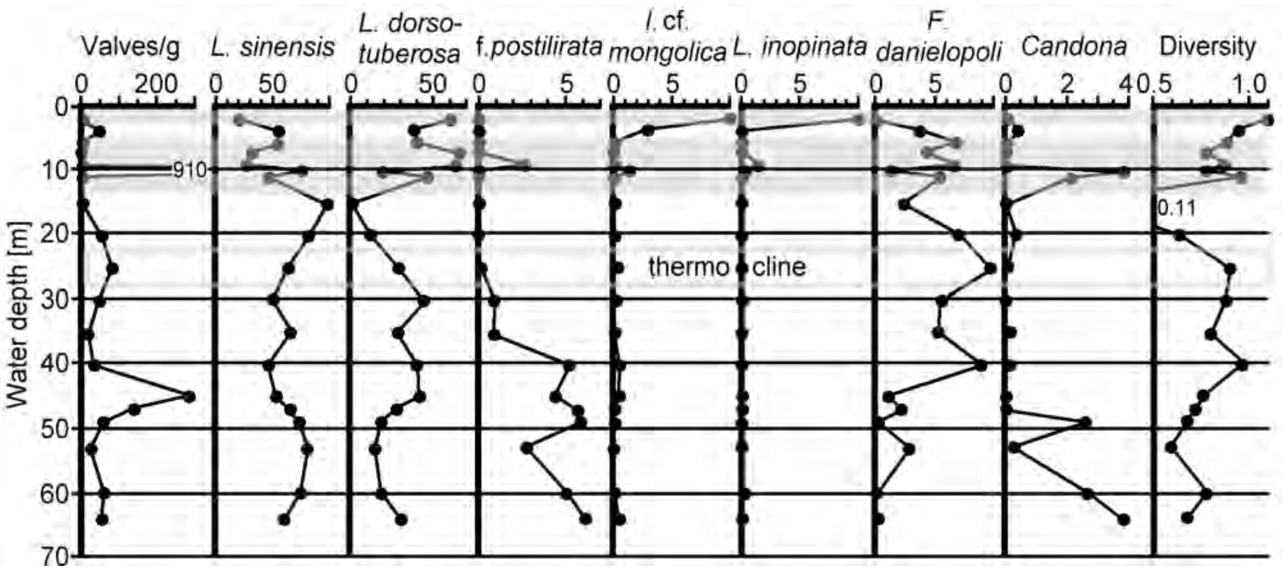

Figure 6. Abundance, vertical distribution of ostracod dominances [%] and diversity (Shannon Wiener index) with water depth. The shaded boxes indicate samples with dominating allochthonous/subfossil associations, however, the data represent autochthonous ostracods. The thermocline position is shown by a grey box in about 25 m water depth.

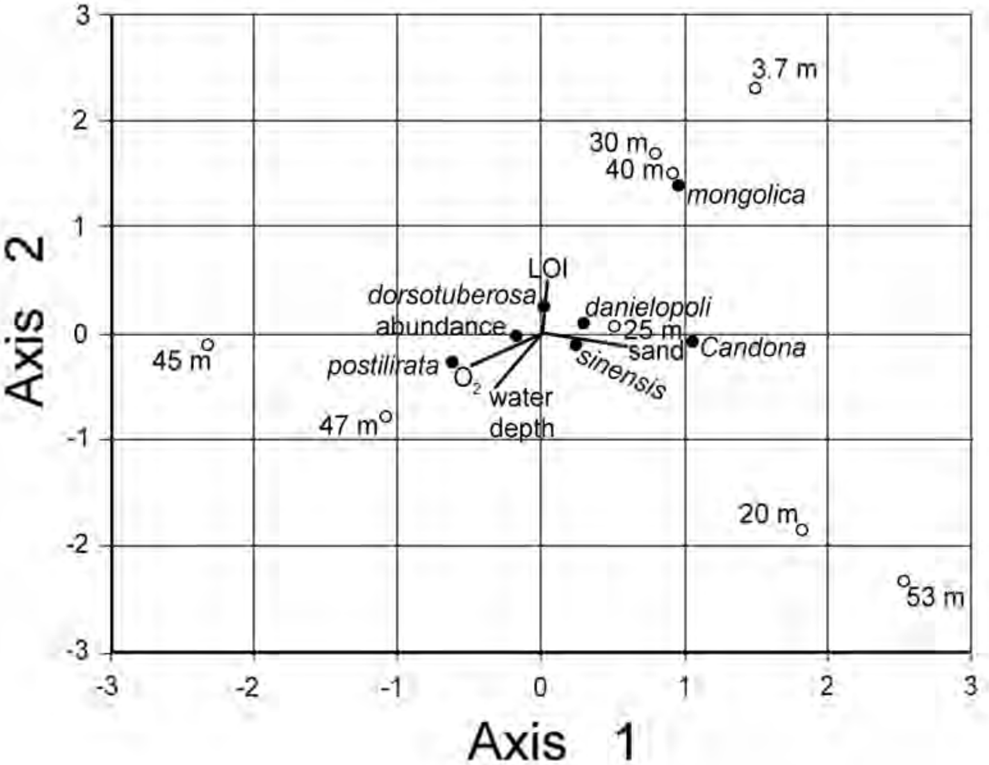

Figure 7. Canonical Correspondence Analysis for ostracod (6 taxa + abundance), water depth, oxygen concentration, sand proportion and loss on ignition of eight samples from Nam Co. Environmental parameters are indicated by lines, samples by open circles and ostracod data by solid circles. Temperature, silt proportion and diversity were excluded because of their high correlation with water depth, sand proportion and ?*Leucocythere dorsotuberosa* dominance respectively. The first two axes have eigenvalues of 0.04282 and 0.02093 respectively. Sand proportion is bound to axis 1 and loss on ignition to axis 2. Water depth is best reflected by dominances of ?*L. dorsotuberosa* f. *postilirata*, *Fabaeformiscandona danielopoli* and *Ilyocypris* cf. *mongolica*. Water depth shows to be mainly connected to oxygen concentration and is bound to axis 3 (eigenvalue 0.00944).

4.5. Transfer function

We selected ostracod taxa with significant water depth dependant distribution for creating a transfer function. *Limnocythere inopinata* was excluded because it was found in single specimens only. For the remaining taxa ?*Leucocythere dorsotuberosa* f. *postilirata, Ilyocypris* cf. *mongolica, Fabaeformiscandona danielopoli* and *Candona*, quadratic equations and a logarithmical equation were fitted to show a minimum variance of differences with empirical data (Fig. 8). The palaeo-water depth is estimated by using a weighted average between the water depth values deriving from each of these four taxa. Weighting is based on significance of depth-dominance correlation and actual dominance classes. That means that water depth estimations of these four taxa are weighted with two factors each; first the corresponding correlation coefficient (f. *postilirata*: 0.7502; *F. danielopoli*: 0.4418; *Candona*: 0.4633; *I. mongolica*: 0.6611) and second the corresponding dominance class (f. *postilirata* and *F. danielopoli*: 1; *Candona*: 0.5; *I. mongolica*: 0.25). Taxa with a higher mean dominance is given a greater weight because of their higher statistical significance within the random samples. The equations for candonids deliver two solutions normally for a given dominance value (Fig. 8). A minimized difference between these solutions and the estimations indicated by ?*L. dorsotuberosa* f. *postilirata* and *I.* cf. *mongolica* is the main criterion for choosing one of both values for the calculation of palaeo-water depth. The second rated criterion is the water depth calculated for the neighbouring samples within the transect – or, in palaeoenvironmental analysis, for the neighbouring samples in a sediment section. A correlation of estimated and measured values was done by bootstrapping (Fig. 9). The correlation coefficient is 0.86, the standard error ±7.58 m.

5. DISCUSSION

5.1. Hydrology

Our calculated salinity of 1.3 ‰ is slightly higher than the reported 0.9 ‰ by Zhang *et al.* (2006) measured in the same year. This difference may be attributed to the calculation of our value from conductivity data whereas Zhang *et al.* used concentrations. Such a calculation of salinity from conductivity is problematical because of the athalassic character of the lake. The pH measurements, how-

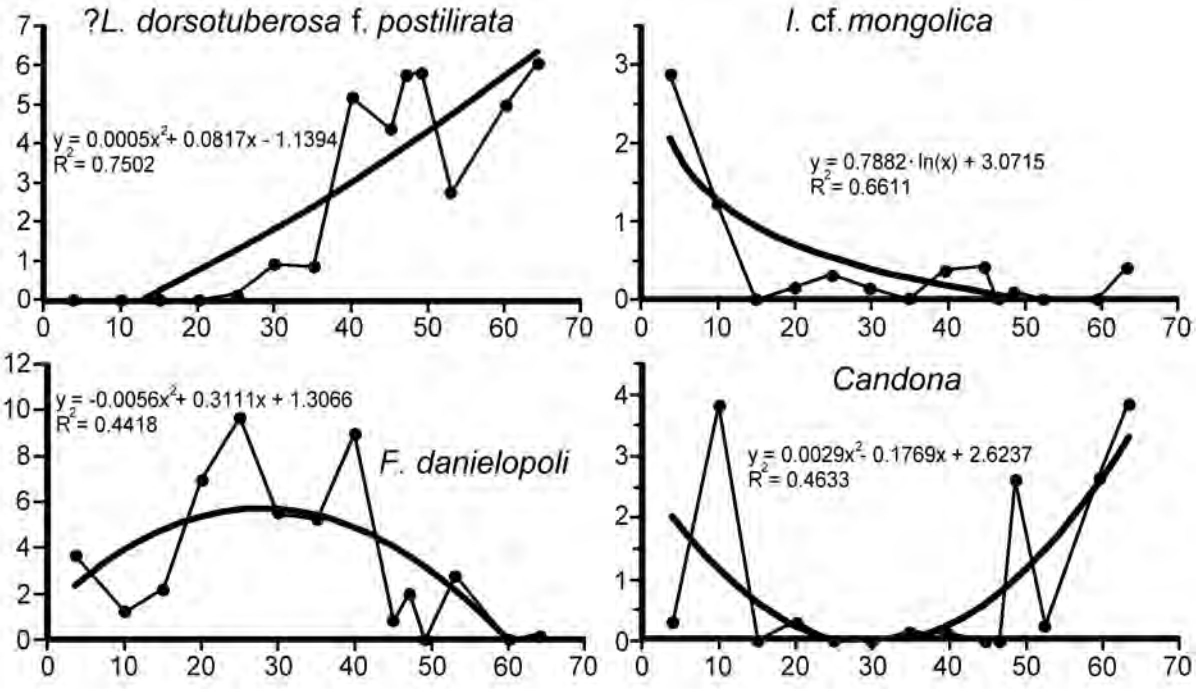

Figure 8. Water depth dependant distribution of the four most significant ostracod taxa of Nam Co and fitting of quadratical and logarithmical equations to distribution data. The equation and correlation coefficient are given in each diagram.

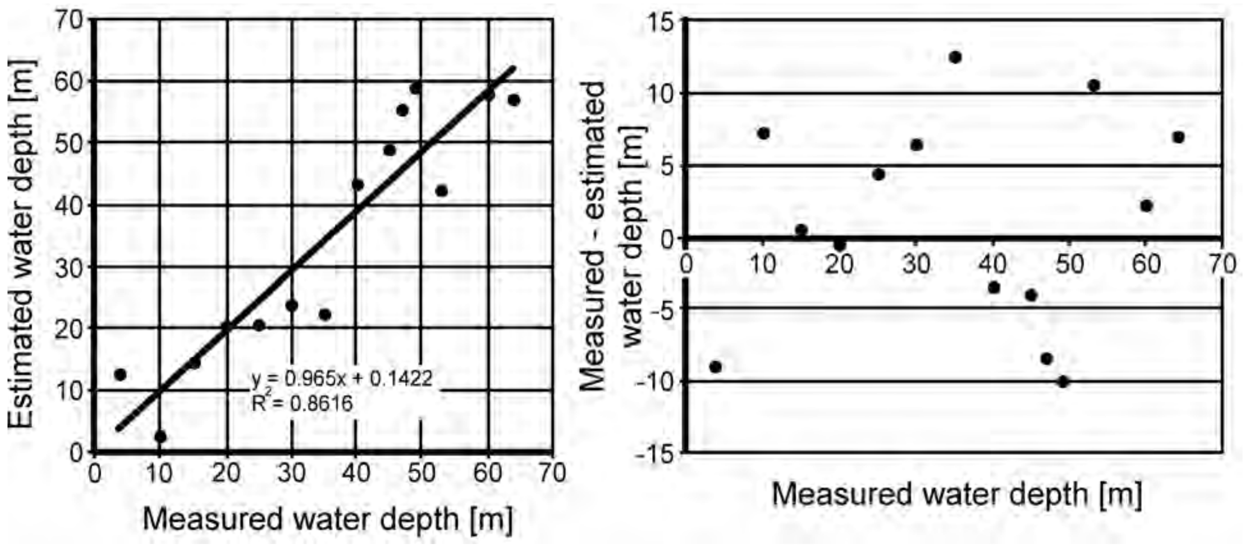

Figure 9. Correlation of measured versus estimated water depth and residuals of our ostracod based transfer function for water depth using bootstrapping.

ever, show the same values in our and Zhang *et al*. measurements (9.4). The low Ca^{2+} concentration in combination with Na^{+}- and SO$_4^{2-}$-rich water points to evapoconcentration and aquatic carbonate precipitation (Zhang *et al.*, 2006). The orthograde curve of oxygen is typical for the oligotrophic lake system, where oxygen concentration increases with depth because of the lower temperature in deeper water. The generally low oxygen concentration is caused by the high altitude with about 50 % oxygen concentration in the air compared to concentrations at sea level sites.

5.2. Faunistics

All species found in Nam Co are coldwater forms and tolerate saline water. *Candona candida* occurs in waters with salinities of up to about 1.5 ‰ in the Qaidam Basin (Sun *et al.*, 1995) and at <2 ‰ in other Tibetan lakes (Huang *et al.* 1985). This species is also known from the Baltic Sea area with salinities of up to 5.3 ‰ (Meisch, 2000). *Fabaeformiscandona danielopoli* was described from a lake in the Chinese Qinghai Basin with a salinity of about 1 ‰ (Yin & Martens, 1997). *Leucocythere dorsotuberosa* is a halophilic species (Sun *et al.*, 1995) and lives in waters with salinities from 0 – 1 ‰ on the NE Tibetan Plateau (Mischke *et al.*, 2007) and in other Chinese lakes with up to 2 ‰ (Wu quoted in Yu *et al.*, 2001). *Leucocytherella sinensis* is reported from lakes in Tibet in water with salinities of 0 – 13 ‰ (Huang *et al.*, 1985).

The two dominant species in Nam Co, ?*Leucocythere dorsotuberosa* and *Leucocytherella sinensis,* are today endemic to the Tibetan Plateau (e.g. Huang *et al.*, 1985; Zhang *et al.*, 2006).

?*L. dorsotuberosa* was also documented from Quaternary sediments of adjacent Sichuan Province (Wang & Zhu, 1991). *L. sinensis* is known from fossil associations from Tibet since the Early/Middle Pleistocene (Pang, 1985; Pang *et al.*, 1985). The special environmental conditions including high altitude, low temperature, dryness and the short vegetation period are limiting factors. They isolate associations on the Tibetan Plateau and cause a high proportion of endemic elements. Three of our six documented ostracod species are listed in a preliminary checklist of 47 Recent ostracod species from China (Yin & Martens, 1997). We add *Ilyocypris* cf. *mongolica* and ?*L. dorsotuberosa* to this list. *Ilyocypris* cf. *mongolica* is also new to the 22 species listed by Huang *et al.* (1985) for modern lakes in Tibet.

5.3. Ostracod diversity and distribution

A low diversity of the species assemblage is in general typical for stressed and unstable environments. Stress factors in Nam Co include the slightly brackish water chemistry of the lake that is problematic for most freshwater ostracod species occurring in continental athalassic waters, the low temperature of high altitude settings causing freezing of the lake for the larger part of the year, and a short vegetation period limiting the food resources and thus the time window for reproduction. Within the lake, diversity should decrease with increasing water depth because of diminishing habitat structure due to the lack of phytal microhabitats. The diversity trend shows this expected picture within the uppermost 15 m (Fig. 6). A second broad diversity maximum occurred between about 25 and 40 m water depth tracing approximately the thermocline level. The higher diversity index is caused by a more evenly distributed dominance of species rather than a higher species number characteristic for shallow water. This pattern is probably generated by regularly changing environmental parameters within the oscillating level of the thermocline and a resedimentation of allochthonous valves. Interestingly, loss on ignition values and diversity show a high correlation (Table 3) suggesting food availability as a crucial factor for ostracod assemblages.

Changes of salinity with water depth were neglectable in Nam Co and certainly did not affect the ostracod distribution. Williams (1991) cites values of around 3 ‰ from Chinese measurements of unknown date, whereas Zheng *et al.* (1989) give values of 1.3 ‰ for Nam Co. These data may point to a freshening in recent years as indicated by a rising lake level during the last years (Zhou *et al.*, 2006). From an evolutionary point of view, rapid and unpredictable environmental changes may be responsible for relatively low species diversity. This is what is theoretically expected in an unstable environment. Because of the high importance of salinity as a driving factor for ostracod communities in brackish water (Frenzel & Boomer, 2005), decadal or centennial changes in salinity have to be taken into account when interpreting subfossil and fossil associations, even in such a large and relatively stable lake. This partly limits the comparability of Recent depth distribution of ostracod species with distribution patterns in the past.

One of the main questions is: Which are the main factors influencing the vertical distribution of ostracods? Water depth itself does not act as a driving factor; rather some factors correlated with water depth are important. One of these factors is, for example, light penetration driving autotrophic production by aquatic plants providing food and shelter (e.g., Liebau, 1984; Griffiths & Holmes, 2000). Another important water depth-related factor is the position of the wave base controlling changes of water movement and sediment disturbance. The normal water depth position of the mean wave base ranges between 5 and 10 m (Liebau, 1984) and is indicated by distinct taphocoenoses in our samples. In marginal marine environments, the storm wave base is traced by the Pterygokline (the uppermost occurrence of the strongly ornamented ostracod genus *Pterygocythereis*) at 20 – 40 m water depth (Liebau, 1980). In Nam Co, we assume that the position of the storm wave base is located at the upper limit of this interval slightly above the thermocline as shown by the lowermost sample dominated by taphocoenoses. Other parameters, such as water temperature, salinity, oxygen concentration and stability of the environment, are changing with water depth as well. Temperature, conductivity and proportion of the sand fraction display a high correlation with water depth (Table 3). Temperature and grain size are important factors potentially influencing the distribution of ostracod assemblages in our example.

The Spearman Rank correlation analysis (Table 3) shows a high positive correlation of ?*Leucocythere dorsotuberosa* f. *postilirata* dominance with water depth and a high negative one with water temperature and coarsening of the sediment. The CCA supports these findings and reveals a connection between the dominance of this form and higher oxygen concentration (Fig. 7). We assume that f. *postilirata* avoids the turbulent water where coarser sediments are reworked and redeposited. The shells of f. *postilirata* are extremely thin and fragile and so they have to be stabilized by outfoldings that form the distinctive costae (plate 2, fig. 6, 8 11-14). Hence, a good preservation of these delicate valves indicates a sedimentation below the storm wave base similar to *Pterygocythereis* in the marine realm (cf. Liebau, 1980). The restriction of ?*L. dorsotuberosa* f. *postilirata* to deeper water below the thermocline (Fig. 6) makes this morphotype an index form for deep water environments. The small dominance peak at only 9.2 m water depth, as shown in Figure 6, is based on two single valves within an association dominated by allochthonous/subfossil specimens. This shallow occurrence is interpreted here as allochthonous. Species indicative of shallow water environments are, for example, *I.* cf. *mongolica* and *Limnocythere inopinata* (see Fig. 6, Table 3). A shallow water preference is stated from European populations of *L. inopinata* (Griffiths & Holmes, 2000; Meisch, 2000) and Donggi Cona, Northeast Tibetan Plateau

(Bookhagen, 2005). ?*L. dorsotuberosa* and *I.* cf. *mongolica* show a correlation to loss on ignition values (Table 3, Fig. 7) what may indicate food availability as limiting factor for these species. *F. danielopoli* and *Candona* prefer the higher sand proportion of samples from the thermocline level respectively shallow water. Yin & Martens (1997) assumed this species to be rheophilic what fits its distribution pattern in Nam Co. The distribution of the dominating ostracod species *L. sinensis* cannot be attributed clearly to any documented environmental parameter (Table 3). The investigation leads one to suppose that this species posses a wide ecological tolerance as previously assumed by Zhu *et al.* (2002).

Although we measured water column data only once in September 2005, and long-term monitoring is not yet existing, we sampled at time with well developed thermocline and within the ice-free vegetation period. We suspect ostracod reproduction takes place in this vegetation period when temperature is higher. Thus the timing of our sampling should well reflect the water depth dependant variance of parameters related to ostracod distribution.

Distinguishing autochthonous and allochthonous/subfossil ostracod associations by degree of valve preservation, carapace proportion, population age structure and the presence of soft parts provides us with a key to interpret long term distributions of species as species associations (see results) despite lacking discrimination of living and dead specimens in our samples.

5.4. Water depth transfer function

Ostracod based transfer functions for water depth were published by Mourgiart and coauthors for lakes of the Bolivian Altiplano (Mourgiart & Roux, 1990; Mourgiart & Carbonel, 1994). They used 115 modern samples collected between 0 and 14 m water depth for creating a transfer function with a correlation coefficient of 0.98 and a standard error of ±0.82 m. The better estimation and lower error of this function compared with ours can be explained by a much higher number of modern samples and included ostracod species as well as the shallower water depth studied that displays a narrower distribution pattern of assemblages. This transfer function was used by Mourgiart *et al.* (1992) and Argollo & Mourgiart (2000) for reconstructing lake levels during the Holocene.

Our transfer function allows a quantitative reconstruction of Holocene and late Quaternary lake levels for the Nam Co area. Caution is needed in interpretation of lake levels much higher and especially much lower than today because of probable different salinity conditions that may affect the ostracod assemblages.

6. CONCLUSIONS

The low diversity of Recent ostracod associations is typical of harsh aquatic environments such as the brackish water conditions, low temperatures and short vegetation period characteristic of Nam Co. Three of the six documented species are endemic on the Tibetan Plateau. These are *Ilyocypris* cf. *mongolica,* ?*Leucocythere dorsotuberosa* and *Leucocytherella sinensis,* for which we provide a SEM documentation of the shells because they are poorly known so far. The assignment of ?*Leucocythere dorsotuberosa* to the genus *Leucocythere* is questioned here, because of the lophodont hinge of this Tibetan species, whereas *Leucocythere* species bear a crenulated intercardinal bar. *Leucocytherella sinensis* can only be assigned to the given genus. These two endemic limnocytherid species clearly dominate the associations.

With increasing water depth the ostracod association changes. *Limnocythere inopinata* and *Ilyocypris* cf. *mongolica* are limited to the uppermost approximately 10 m water depth, where light penetration enables submergent macrophyte and benthic microalgae production. Below this level only single valves of both species were found. Higher proportions of *F. danielopoli* were found broadly scattered around the thermocline level. Below the thermocline level (at about 30 m water depth) a conspicuous morphological variant of ?*L. dorsotuberosa,* the forma *postilirata*, appears and becomes more frequent with increasing depth. Hence, *L. inopinata, I.* cf. *mongolica* and ?*L. dorsotuberosa* f. *postilirata* can be used as index forms for specific water depths in Lake Nam Co.

The high abundance of ostracod shells in surface and core sediments of Nam Co improves their potential as palaeoenvironmental proxies. Although our sample set is restricted to a rather low sample number, we propose that ostracods are well suited to reconstruct past lake levels of Nam Co indicating three depth levels: 1) shallow water (<10 m), 2) the thermocline level (20 – 30 m) and 3) water depths below the thermocline level. A first ostracod based transfer function for water depth for the Nam Co area estimates palaeo-water depths with a standard error of 7.6 m. Using this transfer function a quantitative reconstruction of past lake levels is possible for the Nam Co area.

7. ACKNOWLEDGEMENTS

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8. REFERENCES

Argollo, J. & Mourgiart, P. 2000. Late Quaternary climate history of the Bolivian Altiplano. *Quaternary International*, 72 (1), 37-51.

Baird, W. 1843. Notes on British Entomostraca. Zoologist 1, 193-197.

Bookhagen, B. 2005. *Subrezente Entwicklung des Sees Donggi Cona, NO-Tibet-Plateau, anhand von Ostrakoden-Vergesellschaftungen.* Diploma thesis, Free University of Berlin, 86 pp. [unpublished]

Boomer, I., Horne, D.J. & Slipper, I.J. 2003. The use of ostracods in palaeoenvironmental studies, or what can you do with an ostracod shell? *Paleontological Society Papers*, 9, 153-179.

Chen S. 1982. *Atlas of animals in China: Crustacea, subclass Ostra*coda. Science Press, Beijing, 48-63. [in Chinese]

Curry, B.B. 2003. Linking ostracods to climate and landscape. *Paleontological Society Papers*, 9, 223-240.

Danielopol, D.L., Martens, K. & Casale, L.M. 1989. Revision of the genus *Leucocythere* KAUFMANN, 1892 (Crustacea, Ostracoda, Limnocytheridae), with the description of a new species and two new tribes. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, Biologie 59, 63-94.

DIN 38409-7: 2004-03. German standard methods fort he examination of water. Waste water and sluge – General measures of effects and substances (group H) – Part7: Determination of acid and base capacity (H7).

Fofonoff, P. & Millard Jr., R. C. 1983. *Algorithms for computation of fundamental properties of seawater.* Unesco Technical Papers in Marine Science, 44, 53 pp.

Frenzel, P. & Boomer, I. 2005. The use of ostracods from marginal-marine, brackish waters as bioindicators of modern and Quaternary environmental change. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 225, 68-92.

Griffiths, H. & Holmes, J.A. 2000. *Non-marine ostracods & Quaternary palaeoenvironments.* Quaternary Research Association, Technical Guide no. 8, London, 179 pp.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. 2001. PAST: Palaeontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4 (1), 9 pp.

Holmes, J.A. 2001. Ostracoda. In: J.P. Smol, H.J.B. Birks & W.M. Last (Eds.), *Tracking Environmental Change Using Lake Sediments, Volume 4: Zoological Indicators*. Kluwer Academic, Dordrecht etc., 125-151.

Huang B. 1979. In: *Report of Combined Investigations into Chinghai Lake*. Beijing Science Press, Beijing, 270 pp. [in Chinese]

Huang B., Yang H. & You K. 1982. Pliocene and Quaternary Ostracoda from southern and southwestern Xizang. *Paleontology of Xizang*, 4, 326-348. [in Chinese with English abstract]

Huang B., Yang L. & Fan Y. 1985. Ostracodes from surface deposits of Recent lakes in Xizang. *Acta Micropalaeontologica Sinica*, 2, 369-376, 3 plates. [in Chinese with English abstract]

Imbrie, J. & Kipp, N.G. 1971. A new micropaleontological method for quantitative paleoclimatology: application to a late Pleistocene Carribean core. In: *Late Cenozoic Glacial Ages* (Ed. Turekian), Yale University Press, New Haven, Conn., 71-181.

Janz, H. 1994. Zur Bedeutung des Schalenmerkmals ‚Marginalrippen' der Gattung *Ilyocypris* (Ostracoda, Crustacea). *Stuttgarter Beiträge zur Naturkunde*, Serie B (Geologie und Paläontologie), 206, 1-19.

Liebau, A. 1980. Paläobathymetrie und Ökofaktoren: Flachmeerzonierungen. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 160, 173-216.

Liebau, A. 1984. Grundlagen der Ökobathymetrie. In: *Paläobathymetrie* (Ed. H.P. Luterbacher; Paläontologische Kursbücher, 2), Paläontologische Gesellschaft, München, 149-184.

Li Y., Zhu L. & Li B. 2001. Ostracoda and environmental changes of South Hongshan lake on Tibetan Plateau during the past 150 years. *Geographical Research*, 20, 199-205. [in Chinese with English abstract]

Löffler, H. 1997. The role of ostracods for reconstructing climate change in Holocene and Late Pleistocene lake systems in Central Europe. *Journal of Paleolimnology*, 18, 29-32.

Martens, K. 1991. On a small collection of non-marine ostracods from

Mongolia, with the description of a new species (Crustacea, Ostracoda). *Miscellanea Zoologica Hungarica*, 6, 53-60.

Martens, K. 2000. Factors affecting the divergence of mate recognition systems in the Limnocytherinae (Crustacea, Ostracoda). *Hydrobiologia*, 419, 83-101.

Masi, I. 1906. Contributo alla systematica delle Ilyocyprinae. *Bollettino della Società Zoologica Italiana*, seria 2, 7, 133-146.

Meisch, C. 2000. Crustacea: Ostracoda. In: *Süßwasserfauna von Mitteleuropa 8 (3)* (Eds. J. Schwoerbel & P. Zwick), Spektrum Akademischer Verlag, Heidelberg, Berlin, 522 pp.

Mezquita F., Roca, J.R., Reed, J.M., Wansard, G. 2005. Quantifying species–environment relationships in non-marine Ostracoda for ecological and palaeoecological studies: Examples using Iberian data. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 225, 93-117.

Mischke, S., Herzschuh, U., Massmann, G. & Zhang C. 2007. An ostracod-conductivity transfer-function for Tibetan lakes. *Journal of Paleolimnology*, 38, 509-524.

Mischke, S., Herzschuh, U., Sun Z., Qiao Z., Sun N. & Zander, A.M. 2006. Middle Pleistocene Ostracoda from a large freshwater lake in the presently dry Qaidam Basin (NW China). *Journal of Micropalaeontology*, 25, 1-8.

Mourgiart, P. & Carbonel, P. 1994. A quantitative method of palaeolake-level reconstruction using ostracod assemblages: an example from the Bolivian Altiplano. *Hydrobiologia*, 288, 183-193.

Mourgiart, P. & Roux, M. 1990. Une approche nouvelle du problème posé par les reconstructions des paléoniveaux lacustres: utilisation d'une fonction de transfert basée sur les faunes d'ostracodes. *Géodynamique*, 5 (2), 151-165.

Mourgiart, P., Wirrmann, D., Fournier, M. & Servant, M. 1992. Reconstruction quantitative des niveaux du petit lac Titicaca au cours de l'Holocene. *Comptes Rendus de l'Académie des Sciences*, 315, Série II, 875-880.

Müller, O.F. 1776. *Zoologiae danicae prodramus, seu animalium Daniae et Norvegiae indigenarum characters, nomina et synonyma imprimis popularium*. Leipzig & Copenhagen, 282 pp.

Owen, L.A., Finkel, R.C., Haizhou, M. & Barnard, P.L. 2006. Late Quaternary landscape evolution in the Kunlun Mountains and Qaidam Basin, Northern Tibet: A framework for examining the links between glaciation, lake level changes and alluvial fan formation. *Quaternary International*, 154-155, 73-86.

Pang Q. 1985. On a new Ostracoda genus from Pleistocene in the pass of Kunlun Mountain, Qinghai—Xizang (Tibet) Plateau. In: *Contribution to the geology of the Qinghai—Xizang (Tibet) Plateau*, 16, 269-279. [in Chinese with English abstract]

Pang Q., Zheng M. & Liu W. 1985. The Late Cenozoic Ostracoda of the Siling Lake and Bangkog Lake District in the Xizang (Tibet) and its stratigraphic significance. In: *Contribution to the geology of the Qinghai—Xizang (Tibet) Plateau*, 16, 243-268. [in Chinese with English abstract]

Rodríguez-Lázaro, J. & Martín-Rubio, M. 2005. Pliocene Ilyocyprididae (Ostracoda) from the Ebro Basin (N. Spain). *Revue de micropaleontology,* 48, 37-49.

Sars, G.O. 1890. Oversigt af Norges Crustaceer med foreløbige Bemaerkniger over de nye eller mindre bekjendte Arter. Forh. Selsk. Christiania, I commission hos J. Dybwad [1892] 1890 (1), 1-80. [in Norwegian]

Sars, G.O. 1903. Fresh-water entomostracan from China and Sumatra. *Archiv for Mathematik og Naturvidenskab,* 25 (8), 44 pp., 4 plates.

Schwalb, A. 2003. Lacustrine ostracods as stable isotope recorders of late-glacial and Holocene environmental dynamics and climate. *Journal of Paleolimnology*, 29, 265-351.

Spellerberg, I.F. & Fedor, P.J. 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. *Global Ecology & Biogeography*, 12, 177-179.

Sun Z., Li J., Zhan S., Wang P., Wang T. & Li Y. 1995. Areal distribution of Quaternary ostracod assemblages and its main controlling factor in Chaidamu Basin, NW China. In: *Ostracoda and Biostratigraphy* (Ed. J. Ríha), Balkema, Rotterdam, 277-281.

Van Harten, D. 1979. Some new shell characters to diagnose the species of the *Ilyocypris gibba-biplicata-bradyi* group and their ecological significance. In: *The Taxonomy, Biostratigraphy and Distribution of Ostracodes* (Ed. N. Krstic), Serbian Geological Society, Belgrade, 71-78.

Victor, R. & Fernando, C.H. 1981. *Ilyocypris dentifera* Sars, 1903 versus *Ilyocypris angulata* Sars, 1903. A taxonomic study of two species of *Ilyocypris* Brady and Norman, 1889 (Crustacea, Ostracoda) described from China. *Canadian Journal of Zoology*, 59, 1103-1110.

Viehberg, F.A. 2006. Freshwater ostracod assemblages and their relationship to environmental variables in waters from northeast Germany. *Hydrobiologia*, 571 (1), 213-224.

Wang J. & Zhu D. 1991. Quaternary Ostracoda from Hongyuan and Zoige regions, Sichuan. *Acta Micropalaeontologica Sinica*, 8, 111-120. [in Chinese with English abstract]

Wang, J. & Zhou L. 2006. Preliminary study on the field investigations of Nam Co. Annual Report of Nam Co Monitoring and Research Station for Multisphere interactions, CAS 1, 42-46. [in Chinese with English abstract]

Williams, W.D. 1991. Chinese and Tibetan saline lakes: a limnological overview. *Hydrobiologia*, 210, 39-66.

Yang F., Sun Z., Qiao Z. & Zhang Y. 2004. Revision of the diagnosis of the genus *Qinghaicypris* Huang, 1979 (Ostracoda) and the environmental significance of its type species. *Acta Micropalaeontologica Sinica*, 21, 367-381.

Yang L., Fan Y. & Huang W. 1982. Relation between ostracode distribution in surface deposits and water salt of Recent lakes in Xizang Plateau. *Transactions of Oceanology and Limnology*, 1, 19-28. [in Chinese with English abstract]

Yin Y. & Martens, K. 1997. On a new species of *Fabaeformiscandona* KRSTIC, 1972 (Crustacea, Ostracoda) from China, with a preliminary checklist of Recent Chinese non-marine ostracods. *Hydrobiologia*, 357, 117-128.

You Q., Kang S., Li C., Li M. & Liu J. 2006. Features of Meteorological Parameters at Nam Co station, Tibetan Plateau. Annual Report of Nam Co Monitoring and Research Station for Multisphere Interactions 1, 1-8. [in Chinese with English abstract]

Yu G., Harrison, S.P. & Xue B. 2001. *Lake status report from China: Data Base Documentation*. MPI-BGC Technical Report 4, 247 pp.

Zhang L., Sun Z., An Z., Liu W. & Li X. 2006. A preliminary analysis on Ostracoda of different water bodies from Qinghai Lake area, NW China. *Acta Micropalaeontologica Sinica*, 23 (4), 425-436. [in Chinese with English abstract]

Zhang Q., Kang S., Wang F., Li C. & Xu Y. 2006. *Major ion chemistry in the Nam Co Basin, Tibetan Plateau*. Annual Report of Nam Co Monitoring and Research Station for Multisphere Interactions 1, 86-96.

Zheng M., Xiang J., Wei X. & Zheng Y. 1989. *Saline lakes on the Qinghai – Xizang (Tibet) Plateau*. Beijing Scientific and Technical Publishing House, Beijing, 431 pp. [in Chinese and English]

Zhou S., Kang S., Liu J. & Wang S. 2006. *Preliminary results for hydrological observations in the Nam Co drainage area*. Annual Report of Nam Co Monitoring and Research Station for Multisphere Interactions 1, 54-57. [in Chinese with English abstract]

Zhu L., Li Y. & Li B. 2002. The ostracoda assemblages and their environmental significance in the Chen Co area, southern Tibet in recent 1400 years. *Journal of Geographical Sciences*, 12 (4), 451-459. [in Chinese with English abstract]

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Foraminíferos bentónicos del Holoceno del Golfo Nuevo, Argentina: inferencias paleoclimáticas

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Resumen

Se analizaron los foraminíferos bentónicos de un testigo correspondiente al Holoceno reciente del Golfo Nuevo. La fauna recuperada fue bentónica y las especies predominantes fueron *Buccella peruviana* f. *campsi* (Boltovskoy), *Buliminella elegantissima* (d'Orbigny) y *Bulimina patagonica* d'Orbigny. Los análisis cualitativos y cuantitativos confirman condiciones marinas marginales con menor oxigenación que las actuales. Ello sería la consecuencia de un desmejoramiento climático que por su magnitud y persistencia habría llegado a invertir el sentido de la actual circulación termohalina del golfo, representando entonces una probable consecuencia de la denominada Pequeña Edad de Hielo.

Palabras clave: Foraminíferos bentónicos, Pequeña Edad de Hielo, Golfo Nuevo, paleoecología, plataforma continental argentina.

Abstract

[*Benthic Foraminifera of the Holocene from Golfo Nuevo, Argentine: paleoclimatical inferences*]. Benthic Foraminifera from a recent Holocene core from Golfo Nuevo were analyzed. The fauna recovered was benthonic, and the predominant species were *Buccella peruviana* f. *campsi* (Boltovskoy), *Buliminella elegantissima* (d'Orbigny) and *Bulimina patagonica* d'Orbigny. Qualitative and quantitative analyses confirmed marginal marine conditions with lower oxygenation levels than under present-day conditions. This may have been a consequence of deterioration in climate which, due to its magnitude and persistence could have inverted the direction of the gulf's current thermohaline circulation, in which case it would represent a probable consequence of the so-called Little Ice Age.

Keywords: Benthic Foraminifera, Golfo Nuevo, Little Ice Age, paleoecology, Argentinean continental shelf.

1. INTRODUCCIÓN

Los foraminíferos bentónicos del Océano Atlántico Sudoccidental se hallan ampliamente estudiados, sin embargo en áreas engolfadas se puede mencionar sólo el trabajo de Boltovskoy (1954) quien analizó los foraminíferos del golfo San Jorge y más recientemente los trabajos de Bernasconi y Cusminsky (2005) y Bernasconi (2006) quienes estudiaron los foraminíferos provenientes de los golfos San Matías y Nuevo, tanto de sedimentos superficiales como de sedimentos correspondientes a testigos de fondo.

Los golfos San Matías, Nuevo y San José forman parte de la región de los Golfos Nordpatagónicos y constituyen una de las regiones oceanográficas más importantes de la plataforma continental Argentina, siendo cuencas con similares características morfológicas (Parker *et al*., 1996; Tonini *et al*., 2007).

Oceanográficamente, una cuenca es una depresión que es llenada con aguas del mar y que está parcialmente separada por barreras submarinas del océano abierto, con el cual posee una comunicación horizontal restringida a profundidades menores que la mayor profundidad en la cuenca. La entrada de agua desde el océano abierto a la cuenca se realiza por encima del umbral que se halla en su boca (Panzarini, 1984).

La circulación en la región de los golfos Norpatagónicos está forzada por mareas excepcionales, vientos y un importante intercambio de calor y humedad con la atmósfera (Tonini *et al.*, 2007). Desde el punto de vista hidrológico, estas cuencas se clasifican según la forma en que se produce la entrada de agua desde el mar abierto hacia el interior de la cuenca o bien por la manera en que se produce la salida del agua. Es así que la entrada de agua puede darse por la superficie (cuenca con carga a nivel de la superficie) o a nivel del umbral y la salida a nivel del umbral o bien a nivel de la superficie (Sverdrup *et al.*, 1942).

La dinámica del flujo del agua de cada cuenca se ve reflejada en su biología y en su geología (Mouzo, 1996). Las cuencas con carga al nivel de la superficie muestran mayor salinidad, mayor evaporación y consecuentemente una mayor densidad del agua en la cuenca que en el exterior. Hay un intercambio de agua muy importante, produciéndose corrientes convectivas que llegan a las aguas profundas, las que contienen oxígeno y no sulfuro de hidrógeno en los sedimentos, sugiriendo que hay vida bentónica profunda (Mouzo, *op. cit.*) (Fig. 1.1). En cambio, en las cuencas con carga a nivel del umbral la renovación del agua se hace lentamente, su salinidad es baja en superficie y regular en la profundidad y su contenido de oxígeno es alto en la superficie y pobre en la profundidad, y consecuentemente el contenido de sulfuro de hidrógeno en el fondo es alto (Panzarini, 1984; Mouzo, 1996) (Fig. 1.2).

En la actualidad, el golfo Nuevo se comporta como una cuenca con carga a nivel de la superficie, es decir que posee altas concentraciones de oxígeno en el fondo dadas por una buena ventilación o renovación del agua profunda y por lo tanto se caracteriza por poseer una abundante vida bentónica (Mouzo, op. cit.).

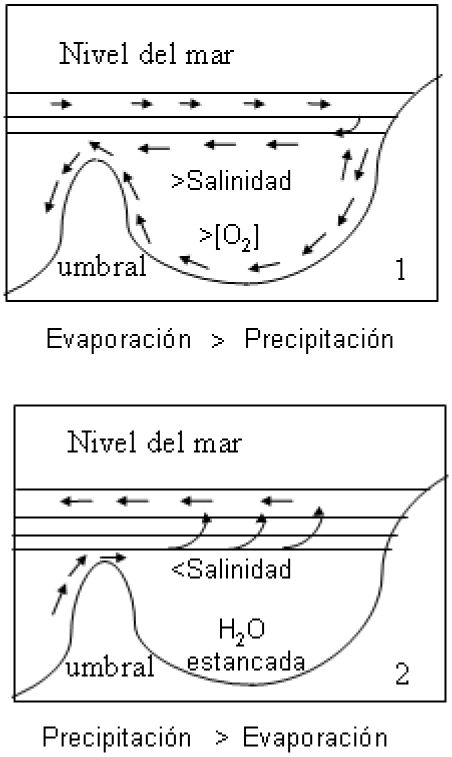

Figura 1. 1, Modelo de cuenca con carga a nivel de la superficie. 2, Modelo de cuenca con carga a nivel del umbral.

Figure 1. 1, Model of basin with inflow of water across the surface. 2, Model of basin with inflow of water across the sill.

Como consecuencia de sus características fisiográficas, los ambientes engolfados podrían ser sensibles a los cambios de las condiciones ambientales, haciendo posible realizar inferencias palaeocológicas. Es por ello, que el estudio de ambientes semicerrados, sobre la base de su contenido foraminiferológico, podría brindar mucha información en el área bajo análisis.

2. ÁREA DE ESTUDIO

El golfo Nuevo se encuentra entre los 42° y 43° de latitud Sur y los 64 y 65° 10′ de longitud Oeste, plataforma continental Argentina (Fig. 2.1). Su forma es elíptica con el eje mayor de 67 km en dirección OSO-ENE y su eje menor de 48 km orientado al NNO-SSE. La superficie del golfo es de 2.500 km^2 y su profundidad máxima de 184 m superando a la profundidad de la plataforma continental adyacente (Mouzo *et al.*, 1978; Mouzo, 1996).

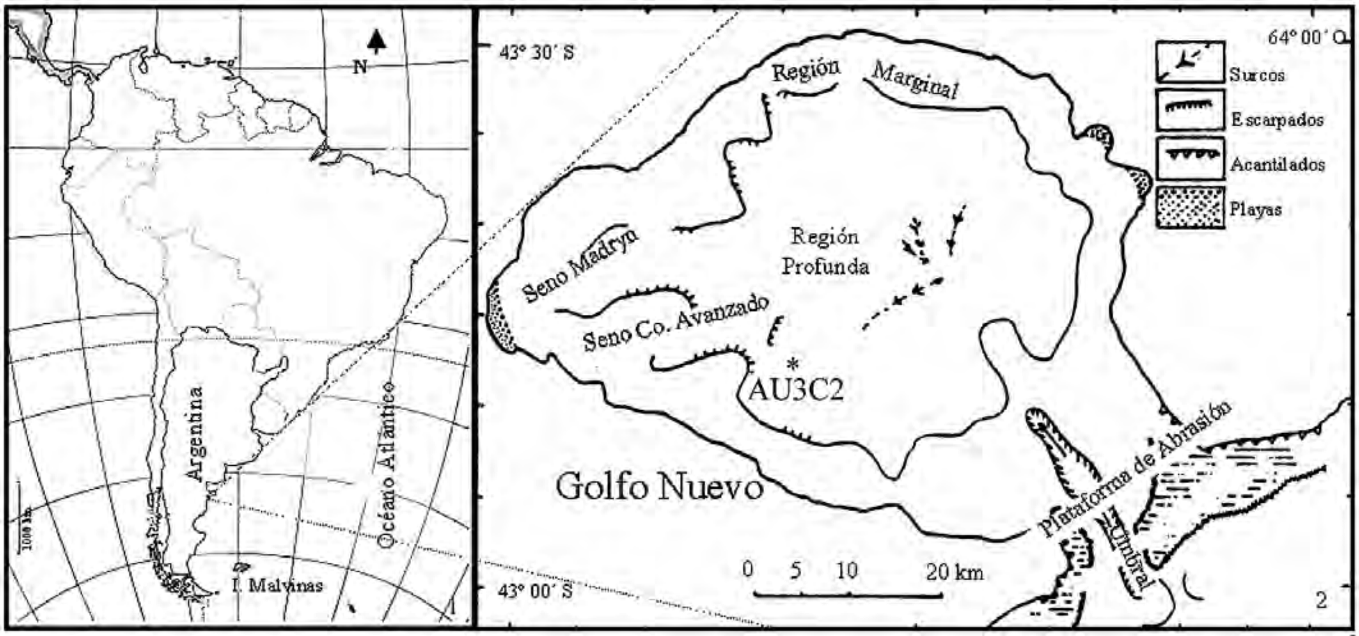

Figura 2. 1, Localización del golfo Nuevo. 2, Morfología del golfo (modificado de Mouzo *et al*., 1978) y ubicación geográfica del testigo.

Figure 2. 1, Location of Nuevo Gulf. 2, Morphology of Nuevo Gulf (modified from Mouzo et al.*, 1978) and location map showing the position of the core.*

Desde el punto de vista geomorfológico, el golfo Nuevo es una depresión semicerrada por barreras submarinas. El agua interior sólo puede comunicarse libremente con el mar a través de un angosto estrecho, el cual posee una profundidad de 75 m, muy inferior a las mayores profundidades alcanzadas dentro del golfo (Mouzo *et al*., 1978; Mouzo, 1996; Parker *et al*., 1996). En función de la batimetría, en el golfo se diferencian dos regiones: una periférica llamada Marginal que se extiende desde la costa hasta aproximadamente los 100 m de profundidad y otra central denominada Profunda de profundidades mayores. La región Marginal es de relieve rugoso y está cubierta por sedimentos gruesos, arenas, rodados, fragmentos de conchillas y afloramientos de la roca de base, correspondiente a sedimentos marinos y continentales del Terciario. La región Profunda posee un relieve suave y está constituida por sedimentos arcillosos entre los que se encuentran capas de arena estratificada y bancos de rodados de matriz arenosa (Mouzo *et al*., 1978) (Fig. 2.2).

La distribución de los sedimentos se encuentra en relación con la batimetría, pudiéndose diferenciar tres zonas. La primera zona está constituida casi totalmente por arena con gravas y conchillas, abarca desde la costa hasta profundidades de 50-70 m e incluye a la región del estrecho, donde hay profundidades algo mayores. La otra zona es paralela a la anterior y posee arenas limosas y limos arenosos, extendiéndose hasta profundidades de 100-120 m. Por último y con profundidades mayores a los 120 m, se encuentra la zona central que está cubierta por arcillas limosas o limos arcillosos (Mouzo *et al*., 1978).

El golfo se halla bajo la influencia de las aguas costeras argentinas que se desplazan desde el Sur hacia el Norte y se ubican entre la región costera occidental y la corriente Patagónica que tiene su origen en aguas subantárticas (Boltovskoy *et al*., 1980). La cuenca evoluciona desde un estado de mezcla casi completa, en otoño e invierno, hasta uno estratificado que alcanza sus máximos valores de estabilidad hacia fines del verano (Rivas y Ripa, 1989). Estos autores mencionan que el golfo está fuertemente estratificado en verano alcanzando los 18ºC en la superficie y 11ºC en el fondo, en enero y bien mezclado en invierno con temperaturas que llegan a los 12ºC tanto en la superficie como en el fondo, en julio y a los 10ºC en septiembre.

Actualmente, el golfo Nuevo muestra las características de una cuenca con carga a nivel de la superficie (Sverdrup *et al*., 1942; Mouzo, 1996). En esta cuenca se produce un aumento de la densidad superficial que se origina en invierno por enfriamiento y por el aumento de la salinidad causado por la evaporación. La salinidad es siempre superior dentro del golfo aumentando desde abril a septiembre provocando corrientes convectivas que alcanzan el fondo de la cuenca (Rivas y Ripa, 1989; Rivas y Beier, 1990). El efecto de los procesos convectivos que remueven las aguas, aportando un alto contenido de oxígeno al fondo y elevando las aguas más frías y ricas en nutrientes hacia la superficie, ha sido observado reiteradamente (Esteves *et al.*, 1992 y Esteves y De Vido, 1980 en Mouzo, 1996).

De los datos disponibles para el golfo Nuevo surge que los tenores de oxígeno determinados en las aguas profundas son altos, cercanos a los valores de saturación (Piola, comunicación personal).

3. MATERIALES Y MÉTODOS

Se estudió el testigo AU3C2 de 428 cm de largo, ubicado a los 42° 48′ 5″ LS y a los 64° 37′ 6″ LO, extraído a 143 m de profundidad (Fig. 2.2). Se obtuvo con un extractor tipo Ewing a pistón de media tonelada con el buque oceanográfico ARA El Austral, durante la campaña realizada por el Instituto Argentino de Oceanografía (IADO) entre 1970 y 1973.

El testigo AU3C2 está constituido por arcillas limosas gris oliva, con una reducida cantidad de arena fina y restos de organismos marinos, representando depósitos marinos relativamente modernos (Mouzo *et al.*, 1978). Para este trabajo se utilizó el tramo 10-230 cm, no disponiéndose de material entre los niveles 50-80 cm y 110-150 cm.

El testigo fue muestreado a intervalos de 15 cm, aproximadamente. Se procesaron 40 gramos de sedimento mediante los métodos convencionales ponderándose la cantidad de individuos presentes en 1 gramo de sedimento. La clasificación sistemática a nivel genérico se basó en Loeblich y Tappan (1988). Para la identificación de las especies se siguió a Boltovskoy (1954), Boltovskoy *et al.* (1980), Bertels *et al.* (1982), Cusminsky (1992), Laprida (1998), Laprida y Bertels-Psotka (2003) y Malumián (1972), entre otros.

Se determinó la abundancia total (A total) y la riqueza específica (S). Se fotografiaron los ejemplares más representativos mediante el microscopio electrónico de barrido (Philips, Modelo SEM 515). Estos ejemplares se encuentran depositados en el laboratorio de Micropaleontología del Museo de La Plata bajo el número MLP-Mi 1699 al 1710.

Se calcularon los índices de diversidad de Shannon-Wiener (H′) (Buzas y Gibson 1969) y ∝ de Fisher (Fisher *et al.*, 1943; Murray 1991), que tienen gran utilidad en la determinación de paleoambientes.

Para ello se usó el paquete estadístico TILIA Versión 2.1 (Grimm, 1991). Este análisis se basó en las especies que alcanzaron el 2 % o más de abundancia relativa en al menos 2 niveles del testigo. Se empleó la transformación de datos por estandarización a media 0 y desviación típica 1.

Se efectuaron dos análisis con el fin de inferir las condiciones de paleooxigenación del Golfo Nuevo. Se calculó el índice de Kaiho o BFOI (Índice de oxigenación basado en foraminíferos bentónicos) para todas las muestras. Para ello, se dividieron los foraminíferos bentónicos calcáreos recuperados en tres grupos de indicadores: disóxicos, subóxicos y óxicos, tomando como base la relación entre sus características morfológicas específicas, los niveles de oxígeno y sus microhábitats (Kaiho, 1994, 1999). Complementariamente, se obtuvo el índice mediante la siguiente ecuación matemática: $BFOI = \{[O /(O + D)] \times 100\}$, donde O y D número de especímenes óxicos y disóxicos respectivamente. En las muestras donde el número de especímenes óxicos fue nulo, $O = 0$ y $D + S > 0$, donde S es la suma de número de individuos subóxicos; se aplicó la expresión $BFOI =\{[S / (S + D)] - 1\} \times 50$. Los valores del BFOI permitieron determinar las condiciones de paleoxigenación; cuando el índice del Kaiho es –55 (0-0,1 ml/l) la condición es anóxica; entre –50 y –40 (0,1-0,3 ml/l) la condición es disóxica; entre –40 y 0 (0,3-1,5 ml/l) la condición es subóxica; entre 0 y 50 (1,5 – 3,0 ml/l) la condición es óxica baja y entre 50 y 100 (3,0 - +6,0 ml/l) la condición es óxica alta (Kaiho, 1994, 1999).

Por otro lado, se determinó la relación de individuos infaunales-epifaunales calculándose el porcentaje de especies infaunales (Corliss, 1985; Corliss y Chen, 1988), para cada muestra de los testigos de Golfo Nuevo.

A fin de poder ubicar cronológicamente el testigo se efectuó una datación radimétrica de C^{14} AMS (Acceleration Mass Spectrometry) en la Australian Nuclear Science y Technology Organization (Ansto). Para ello se separaron caparazones de foraminíferos bentónicos sin retrabajo.

4. RESULTADOS

Se recuperaron individuos representantes de los Subórdenes Rotaliina (98 %), Lagenina (2 %) y Miliolina (0,01 %).

En general, la abundancia total fue mayor en los niveles inferiores del testigo decreciendo un poco en los niveles medios, aunque se registró un pico máximo de abundancia en el nivel 80 cm. La abundancia de los niveles superiores fue mucho menor. Las curvas de la riqueza específica S y del índice de diversidad de Shannon-Wiener (H´) tuvieron un comportamiento general coincidente a excepción de los niveles 160 cm y 80 cm que se comportaron en forma opuesta. La riqueza específica fue muy variable a lo largo de todo el testigo. En la curva de diversidad H' se determinaron valores relativamente homogéneos hasta el nivel 180 cm, a partir de allí hasta el nivel 150 cm los valores decrecen, siendo más altos hacia el tope del testigo (Fig. 3). Los valores del índice α de Fisher varió entre 1,5 y 5 en los niveles 100 cm y 30 cm, respectivamente (Fig. 4).

A lo largo del testigo analizado se reconoció un predominio de la especie *Buccella peruviana* f. *campsi* (Boltovskoy) (12-79 %). Además se encontraron bien representadas *Buliminella elegantissima* (d´Orbigny) (2-71 %), *Bulimina patagonica* d´Orbigny (7-30 %), *Bolivina pseudoplicata* Heron-Allen y Earland (2-17 %), *Bolivina ordinaria* Phleger y Parker (2-16 %), *Bulimina marginata* d´Orbigny (1-11 %) y *Cibicides dispars* (d´Orbigny) (1-9 %). En los niveles superiores se destacaron pequeños máximos de abundancia de *Nonionella auris* (d´Orbigny) (1-23 %), *Nonion depressulus* (Walker y Jacob) (2-9%) y *Bulimina gibba* Fornasini (1-9 %). El resto de las especies registraron proporciones menores al 5 % (Fig. 5).

Los valores del índice de Kaiho variaron entre -7 y 36 y el contenido de oxígeno disuelto estimado varió entre 1,3 y 2,5 ml/l en los niveles 50 cm y 220 cm, respectivamente.

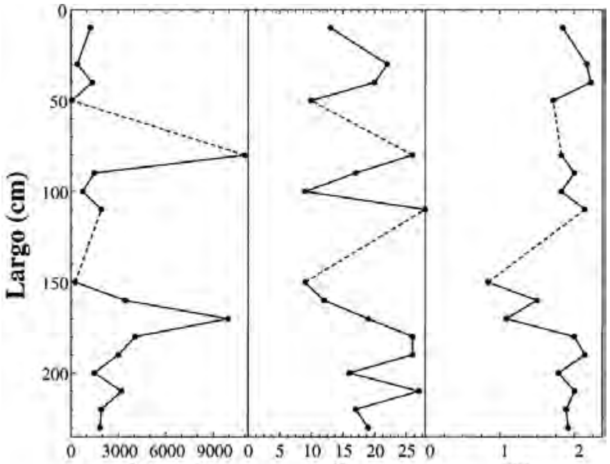

Figura 3. Abundancia total (A total), riqueza específica (S) e índice de diversidad de Shannon-Wiener (H') para el testigo AU3C2.

Figure 3. Total abundance (Total A), Specific richness (S) and Shannon-Wiener diversity (H´) for core AU3C2.

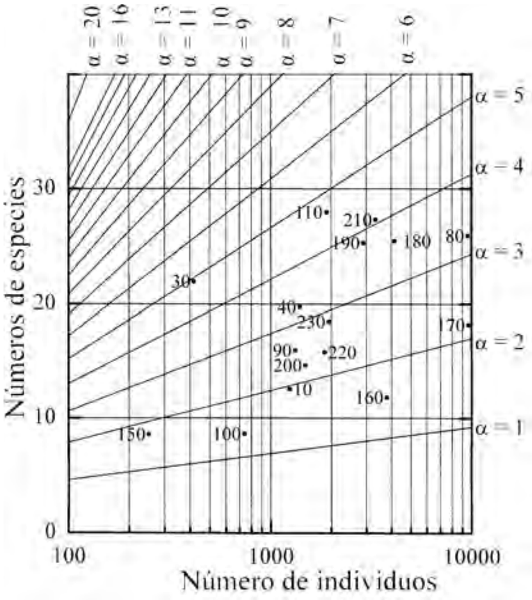

Figura 4. Valores del índice α de Fisher.

Figure 4. Values of Fisher's index (α).

Esto estaría describiendo una fauna de foraminíferos calcáreos constituida fundamentalmente por indicadores disóxicos, subóxicos y pocos indicadores óxicos sugiriendo una condición de oxígeno óxica baja (1,5-3,0 ml/l); los niveles 150 cm y 50 cm estarían compuestos de indicadores disóxicos y altos valores de indicadores subóxicos sugiriendo una condición de oxígeno subóxica (0,3-1,5 ml/l), (Fig. 6.1).

Los porcentajes de los ejemplares infaunales variaron entre 21 % en el nivel 150 cm y 87 % en el nivel 170 cm (Fig. 6.2).

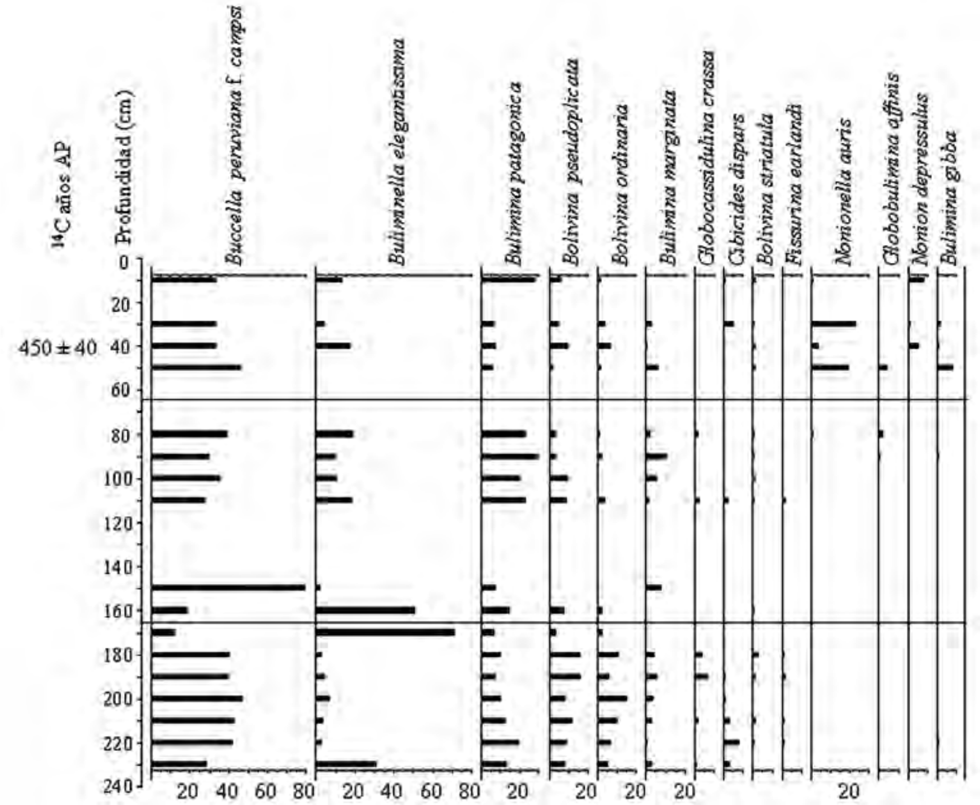

Figura 5. Distribución específica de los foraminíferos en el testigo AU3C2.

Figure 5. Foraminiferal distribution in core AU3C2.

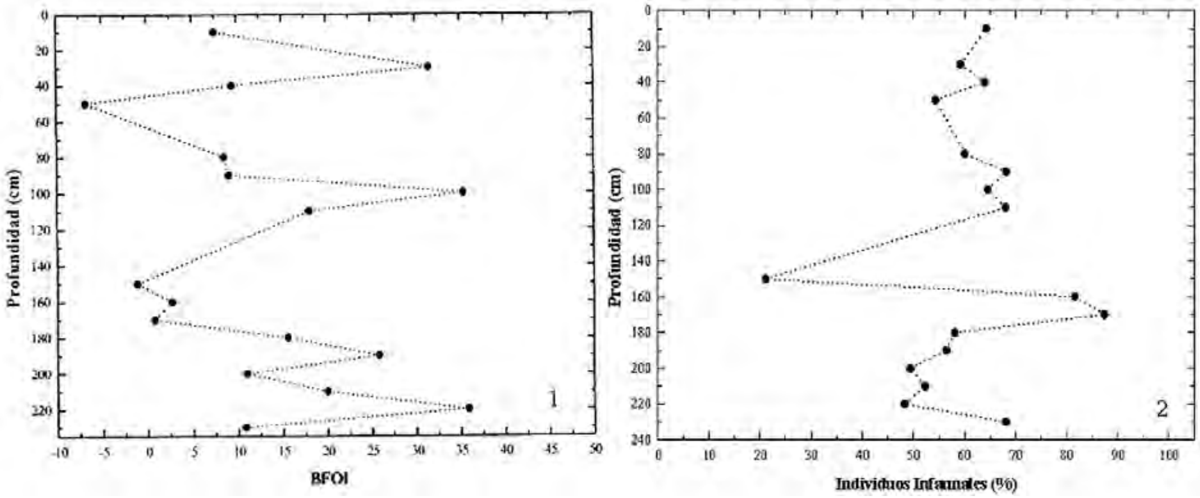

Figura 6. 1, Valores del índice de Kaiho (BFOI). 2, Porcentajes de individuos infaunales.

Figure 6. 1, Values of Kaiho's index (BFOI). 2, Percent of infaunal individuals.

5. EDAD DE LOS SEDIMENTOS

La edad del nivel 40 cm fue de 450±40 años AP (Edad convencional radiocarbónica). Sin embargo, los organismos que obtienen su C del mar presentan generalmente un envejecimiento aparente variable que se denomina Efecto de Reservorio (ER), por el que es necesario efectuar una corrección previa a fin de poder obtener finalmente la edad sideral o calendario de la muestra en cuestión, ya que la producción de 14C en la atmósfera no se ha mantenido constante a lo largo del tiempo. Si bien para la costa atlántica de la Patagonia el valor de ER previo a las pruebas nucleares en la atmósfera es desconocido, se cuenta con las estimaciones posnucleares obtenidas por Cordero *et al*. (2003). Estos autores presentan dos mediciones del ER posnuclear para el golfo Nuevo, por lo que se empleó su valor promedio (230 años) como corrección por ER. Una vez efectuada esta corrección, mediante el programa CALIB 5. 0.2 (http://calib.qub.ac.uk/calib/) y considerando la base de datos para Sudamérica (SHCal04, McCormac *et al*., 2004), se obtiene un rango de edad calendario de 311-142 AP a 1 σ.

6. CONSIDERACIONES PALEOECOLÓGICAS Y DISCUSIÓN

La asociación de especies estuvo caracterizada fundamentalmente por *Buccella peruviana* f. *campsi, Buliminella elegantissima* y *Bulimina patagonica*. *Buccella peruviana* f. *campsi* está ampliamente distribuida a lo largo de la plataforma continental argentina (Boltovskoy, 1976, 1979), mientras que el género *Buliminella* es reconocido como un género infaunal (Murray, 1991; Corliss y Chen, 1985; Kaiho, 1994). *Buliminella elegantissima* fue mencionada como una especie predominante en áreas confinadas bajo condiciones de stress (Páez y Zúñiga, 2001). Esta especie estaría adaptada a ambientes o subambientes en condiciones disóxicos o anóxicos (Vilela, 2003; Vilela *et al*., 2002). Su ocurrencia y abundancia confirmarían su utilidad como una especie bioindicadora (Vilela *et al*., 2003, 2004). Además, se registró la asociación de especies del género *Bulimina* tales como *B. gibba, B. marginata* y *Globobulimina affinis*, como así también una asociación de especies del género *Bolivina* como ser *B. pseudoplicata, B. ordinaria* y *B. striatula* (Fig. 7).

Bulimina es descripta como infaunal con dudas y *Bolivina* como infaunal-epifaunal por Murray (1991), sin embargo otros autores citan a estos dos últimos géneros como infaunales (Severin, 1983; Corliss, 1985; Corliss y Chen, 1988; Kaiho, 1994).

Siguiendo los criterios de Corliss y Chen (1988) y otros investigadores, se reconoce en los sedimentos analizados, un predominio de las formas infaunales. Según Sen Gupta y Machain-Castillo (1993), la distribución de estas especies estaría reflejando un ambiente con bajo contenido de oxígeno. Dado que cuando los niveles de oxígeno comienzan a volverse un factor limitante las primeras especies afectadas en abundancia son las especies epifaunales mientras que las especies infaunales son más tolerantes a prevalecer por largos períodos (Smart, 2002). Por ejemplo *Buliminella elegantissima* y *Bulimina marginata* han sido consideradas como oportunistas, o sea capaces de habitar zonas con bajo contenido en oxígeno Alve (1995), Silva *et al*. (1996), Bernhard (1996), Sen Gupta *et al*. (1997) y Malumián y Caramés (2002).

Se observó pirita sustituyendo la materia orgánica de los caparazones, otorgándoles un aspecto metálico, indicando propiedades hidrodinámicas distintas siendo menos susceptibles a una redistribución postmorten cobrando importancia en estudios paleoecológicos (Murray, 1968). La piritización en los caparazones de foraminíferos no es un indicador directo de aguas anóxicas sino más bien de microambientes con bajas concentraciones de oxígeno (Ferrero, 2006), razón por la que se procedió a calcular el índice de Kaiho. Este índice, denotó poca variabilidad en el testigo, determinando una condición de oxígeno baja bastante homogénea, entre 1,3 y 2,5 ml/l. Los niveles con menor contenido de oxígeno fueron los 170 cm, 160 cm y 80 cm, donde predominaron los morfotipos disóxicos y subóxicos, reconociéndose en particular en los niveles 170 cm y 160 cm un predominio de *Buliminella elegantissima*.

Desde el punto de vista de los análisis cuantitativos, los bajos valores del ∝ de Fisher, menores a 5, indicarían un ambiente marino marginal (Murray, 1991); mientras que los valores de H´, menores a 2,5, reflejarían además condiciones de alta inestabilidad (Buzas y Gibson, 1969; Bertels, 1994) (Fig. 8).

Teniendo en cuenta las características de las asociaciones registradas, se infiere que uno de los factores que determinaron dicha composición faunística habría sido el oxígeno como se señala en trabajos precedentes (Bernhard, 1986; Vilela, 1995; Smart, 2002; Sagasti y Ballent, 2002). Ello indica que durante la depositación de estos sedimentos habrían prevalecido condiciones de menor oxigenación que las actuales. Es así que la presencia de ambientes o microambientes con bajos contenidos de oxigenación puede inferirse no sólo a partir de la presencia de pirita en parte del material sino también del hecho de que proporciones importantes de las asociaciones presentaron afinidad con ambientes pobres en oxígeno, como lo hallado por Ferrero (2006) para el Sudeste de la provincia de Buenos Aires.

Las asociaciones faunísticas y los resultados de los análisis cuantitativos indican, que en el pasado, en el golfo Nuevo habrían prevalecido condiciones de poca oxigenación, comportándose éste como una cuenca con carga a nivel del umbral. Ello estaría entonces evidenciando un cambio en la dinámica circulatoria de este golfo, el cual probablemente se haya debido a la ocurrencia de un desmejoramiento climático persistente que condujo una disminución en la evaporación, un aumento en las precipitaciones y probablemente al incremento en la descarga fluvial adentro del golfo Nuevo.

Desde el punto de vista climático originalmente se pensó que el Holoceno era estable pero existen registros paleoclimáticos bien datados que muestran que el clima holoceno estuvo caracterizado por muchos eventos fríos (de Menocal, 2001). Estudios paleoustáticos y paleoambientales del Holoceno sugieren fuertemente la ocurrencia de desmejoramientos climáticos de escala global causados por oscilaciones en la radiación del sol que se agrupan siguiendo un período del orden de los 2300 años (Gómez, 2004; Gómez *et al.,* 2005a y b, 2006). Dentro de este ciclo, el último máximo frío se correspondería con la denominada Pequeña Edad de Hielo (PEH), evento que esta muy bien documentado principalmente en el hemisferio Norte y que aconteció entre los 1300 y 1870 años DC (650 y 80 años AP), aproximadamente.

En Argentina, se han desarrollado varias investigaciones que muestran desmejoramientos climáticos coincidentes con la PEH. Estudios dendrocronológicos en los bosques Fueguinos permitieron reconocer períodos fríos alrededor de los 1750-1780, 1820, 1875-1880, 1900-1945 y 1950 años A.D, representando las primeras aproximaciones ambientales al desarrollo de la PEH en el extremo sur de Sudamérica (Rabassa *et al.*, 1986, 1992; Planas *et al.*, 2002).

Para la provincia de Buenos Aires Rabassa *et al.* (1985), en base a evidencias geológicas, históricas y arqueológicas, mencionan la ocurrencia de un evento árido durante los siglos 17 a 19 que se correlaciona con la PEH definida para el hemisferio Norte. Martínez *et al.* (2000) hallaron evidencias sedimentológicas, geomorfológicas y edáficas de la PEH en ambientes sedimentarios del Sudeste Bonaerense comprendidos entre Santa Clara y Mar Chiquita.

El rango de edad calendario obtenido para la parte superior del testigo AU3C2 (311-142 años AP) corresponde a la finalización de la Pequeña Edad de Hielo (PEH). Es por ello que aunque aun no se cuente con otras mediciones radiocarbónicas del testigo, sería posible suponer que los sedimentos ubicados por debajo del nivel de 40 cm se depositaron mayoritariamente durante el transcurso de tal desmejoramiento climático global. Es así que la inversión circulatoria del golfo Nuevo, evidenciada por una menor oxigenación que la que ocurre en la actualidad, habría sido consecuencia de la PEH, siendo estos por lo tanto los

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Figura 7. ***1***, *Bolivina ordinaria* Phleger y Parker, MLP-Mi. 1699. ***2***, *Bolivina striatula* Cushman, MLP-Mi.1700; 3, *Buccella peruviana* f. *campsi* (Boltovskoy), vista umbilical, MLP-Mi. 1701. ***4***, *Bulimina marginata* d'Orbigny, MLP-Mi. 1702. ***5***, *B. marginata*, MLP-Mi. 1703. ***6***, *B. marginata*, MLP-Mi. 1704. ***7***, *Bulimina patagonica* d'Orbigny, MLP-Mi. 1705. ***8***, *B. patagonica*, MLP-Mi. 1706. ***9***, *Buliminella elegantissima* (d´Orbigny), MLP-Mi. 1707. ***10***, *B. elegantissima*, MLP-Mi. 1708. ***11***, *Globobulimina affinis* (d´Orbigny), MLP-Mi. 1709. ***12***, *Uvigerina peregrina* Cushman, MLP-Mi. 1710. Escala = 50 µm (figuras 1, 6, 8, 10, 11, 12); 100 µm (figuras 2, 3, 4, 5, 7, 9).

Figure 7. **1**, Bolivina ordinaria *Phleger y Parker, MLP-Mi. 1699.* **2**, Bolivina striatula *Cushman, MLP-Mi.1700.* **3**, Buccella peruviana *f.* campsi *(Boltovskoy), umbilical view, MLP-Mi. 1701.* **4**, Bulimina marginata *d'Orbigny, MLP-Mi. 1702.* **5**, B. marginata*, MLP-Mi. 1703.* **6**, B. marginata*, MLP-Mi. 1704.* **7**, Bulimina patagonica *d'Orbigny, MLP-Mi. 1705.* **8**, B. patagonica*, MLP-Mi. 1706.* **9**, Buliminella elegantissima *(d´Orbigny), MLP-Mi. 1707.* **10**, B. elegantissima*, MLP-Mi. 1708.* **11**, Globobulimina affinis *(d´Orbigny), MLP-Mi. 1709.* **12**, Uvigerina peregrina *Cushman, MLP-Mi. 1710. Scale = 50 µm (figures 1, 6, 8, 10, 11, 12); 100 µm (figures 2, 3, 4, 5, 7, 9).*


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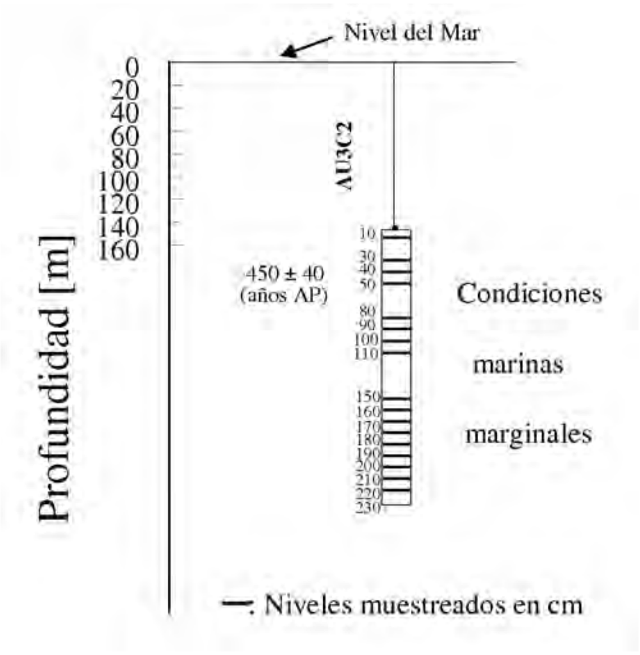

Figura 8. Posición relativa del testigo respecto del nivel del mar con los niveles en cm, edad de los sedimentos en años AP y la interpretación paleoambiental.

Figure 8. Relative position with regard to the sea level (levels in cm, ages in yrs. B.P. and paleoambiental interpretation).

primeros indicios de la influencia de este desmejoramiento climático global en el ambiente marino en Sudamérica.

7. CONCLUSIONES

Los análisis cualitativos y cuantitativos de los foraminíferos bentónicos provenientes del golfo Nuevo confirman condiciones de ambientes marinos marginales como así también una circulación inversa a la actual que habría dado condiciones de menor oxigenación que en el presente. Ello obedecería a la ocurrencia de un desmejoramiento climático persistente que habría conducido a una disminución en la evaporación, a un aumento en las precipitaciones y a un posible incremento en la descarga fluvial en el golfo Nuevo. La edad radiocarbónica obtenida en el testigo AU3C2 indica que tal desmejoramiento climático se correspondería con la denominada Pequeña Edad de Hielo, por lo que estos resultados serían entonces los primeros indicios de su influencia en el ambiente marino de Sudamérica.

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8. BIBLIOGRAFÍA

Alve, E.1995. Benthic foraminiferal responses to estuarine pollution: a review. *Journal of Foraminiferal Research*, 25, 190-203.

Bernasconi, E. 2006. *Los foraminíferos del Holoceno de testigos de la plataforma continental argentina (40º 30´-42º 48´LS y 59º 25´-64º 40´LO)*. Tesis Doctoral, Universidad Nacional del Comahue, Argentina, 210 pp.

Bernasconi, E. y Cusminsky, G. 2005. Distribución de *Nonionella auris* (d'Orbigny) Orden Foraminiferida en el golfo San Matías, Provincia de Río Negro, Argentina. *Ameghiniana*, 42, 167-174.

Bernhard, J. 1986. Characteristic assemblages y morphologies of benthic foraminifera from anoxic, organic-rich deposits: Jurassic through Holocene. *Journal of Foraminiferal Research*, 16, 207-215.

Bernhard, J. 1996. Microaerophilic and facultative anaerobic benthic foraminifera: a review of experimental and ultrastructural evidence. *Revue de Paleobiologie*, 15 (1), 261-275.

Bertels, A. 1994. Foraminíferos (Protozoa) y paleoambientes de las Lutitas de Río Foyel (Oligoceno medio bajo), Cuenca de Ñirihuau-Ñorquinco-Cushamen, Provincia de Río Negro, República Argentina. *Revista Española de Micropaleontología*, 26, 99-123.

Bertels, A., Kotzian, S., Madeira-Falcetta, M. 1982. Micropaleontología (Foraminíferos y Ostrácodos) del Cuaternario de Palmares Do Sul (Formacióin Chui) Brasil. *Ameghiniana*, 19, 125-156.

Boltovskoy, E. 1954. Foraminíferos del Golfo San Jorge. *Revista Instituto Nacional Investigaciones Naturales y Museo Argentino Bernardino Rivadavia Ciencias Geológicas*, 3, 85-246.

Boltovskoy, E. 1966. *Los Foraminíferos recientes*. Ed. Universitaria de Buenos Aires, 510 pp.

Boltovskoy, E. 1976. Distribution of Recent Foraminifera of the South American Region. *Foraminifera*, 2, 171-236.

Boltovskoy, E. 1979. Palaeoceanografia del Atlántico Sudoccidental desde el Mioceno, según estudios foraminiferológicos. *Ameghiniana*, 16, 357-389.

Boltovskoy, E., Giussani, G., Watanabe, S., Wright, R. 1980. *Atlas of benthic shelf foraminifera of the southwest Atlantic*. W. Junk. Publishers, The Hague, 147 pp.

Buzas, M.A. y Gibson, T.G. 1969. Species diversity: Benthonic foraminifera in the Western North Atlantic. *Science*, 163, 72-75.

Cordero, R.R., Panarello, H., Lanzelotti, S. y Favier Dubois, C. 2003. Radiocarbon age offsets between living organisms from the marine and continental reservoir in coastal localities of Patagonia (Argentina). *Radiocarbon*, 45 (1), 9-15.

Corliss B.H. 1985. Microhabitats of benthic foraminifera within deep-sea sediments. *Nature*, 314, 435-438.

Corliss, B.H. y Chen, C. 1988. Morphotype patterns of Norwegian Sea deep-sea benthic foraminifera and ecological implications. *Geology*, 16, 716-719.

Cusminsky, G. 1992. Foraminifers bentónicos provenientes de testigos del océano Atlántico Sudoccidental austral. *Revista Española de Micropaleontología*, 24, 5-32.

De Menocal, P. Ortiz, J., Guilderson, T. y Sarnthein, M. 2001. Coherent High-and Low-Latitude Climate Variability During the Holocene Warm Period. *Science*, 288, 2198-2202.

Ferrero, L. 2006. *Micropaleontología y Paleoecología del Cuaternario del sudeste de la provincia de Buenos Aires*. Tesis Doctoral, 371 pp. (Inédito).

Fisher, R.A., Corbet, A., S. y William, C.B. 1943. The relation between the number of species y the number of individuals in a random sample of an animal population. *Journal Animal Ecology*, 12, 42-58.

Gómez, E.A., 2004. Sea Level Oscillations Related to Past Global Climatic Changes. *Inter-American Institute for Global Change Research, IAI News Letter*, 36, 11-13.

Gómez, E.A., Martínez, D.E., Borel, C.M., Guerstein, G.R. y Cusminsky, G.C. 2005a. Submarine evidence of Holocene sea-level fluctuations in the Bahía Blanca Estuary, Argentina. *Journal of South American Earth Sciences*, 20 (1-2), 135-155.

Gómez, E.A., Martínez, D.E. y Cusminsky, G.C. 2005b. A cycle in solar irradiance as trigger of abrupt Holocene global climatic changes and negative sea level oscillations. Proceedings of *Holocene environmental catastrophes in South America: From the lowlands to the Andes, ICSU Dark Nature – IGCP 490, third Joint Meeting*. Laguna Mar Chiquita, Córdoba, 25-26.

Gómez, E.A., Martínez, D., Borel, C.M., Guerstein, G.R. y Cusminsky, G.C. 2006. Negative sea-level oscillation at the Bahía Blanca Estuary related to a ca. 2650 yr BP global climatic change. *Journal of Coastal Research*, Special Issue 39, 181-185.

Grimm, E. 1991. Tilia State Museum. *Research Collection Center*, Springfield.

Kaiho, K. 1994. Benthic foraminiferal dissolved-oxygen index and dissolved-oxygen levels in the modern ocean. *Geology*, 22, 719-722.

Kaiho, K. 1999. Effect of organic carbon flux and dissolvedoxygen on the benthic foraminiferal oxygen index (BFOI). *Marine Micropaleontology*, 37, 67-76.

Laprida, C. 1998. Micropaleontological assemblages (Foraminiferida and Ostracoda) from Late Quaternary marginal marine environments (Destacamento Río Salado Formation), Salado Basin, Argentina. *Revue Paleobiologie*, 17, 461-478.

Laprida, C. y Bertels-Psotka, A. 2003. Benthic foraminifers and paleoecology of a Holocene shelly concentration, Salado Basin, Argentina. *Geobios*, 36, 559-572.

Loeblich A. y Tappan, H. 1988. *Foraminiferal Genera and their Classification*. Van Nostrand Reinhold, (New York), 2 vol., 969 pp. y 847 láms.

Malumián, N. 1972. Foraminíferos del Oligoceno y Mioceno del subsuelo de la provincia de Buenos Aires. *Ameghiniana*, 9, 97-137.

Malumián, N. y Caramés, A. 2002. Foraminiferos de sedimentitas ricas en carbono orgánico Formación La Barca, Paleoceno Superior, Tierra del Fuego, República Argentina. *Revista de la Asociación Geológica Argentina*, 57, 219-231.

McCormac, F.G., Hogg, A.G., Blackwell, P.G., Buck, C.E., Higham, T.F.G. y Reimer, P.J. 2004. SHCal04 Southern Hemisphere Calibration 0-11.0 cal kyr BP. *Radiocarbon*, 46, 1087-1092.

Martínez, G., Osterrieth, M.L. y Borrelli, N. 2000. Registro de la Pequeña Edad de Hielo en ambientes sedimentarios del Sudeste bonaerense, Argentina. *2º Congreso Latinoamericano de Sedimentología-8ª Reunión Argentina de Sedimentología*, (Mar del Plata), Resúmenes, 113.

Mouzo, F.H. 1996. Los golfos patagónicos renuevan sus aguas. *Petrotecnia,* 72-84.

Mouzo, F.H. Garza, M.L., Izquierdo, J.F. y Zibecchi, R.O. 1978. Rasgos de la geología submarina del golfo Nuevo (Chubut). *Acta Oceanográfica Argentina*, 2, 69-91.

Murray, W. 1968. *The living Foraminiferida of Christchurch Harbour, England*. Heinemann Educational Books, London, 271 pp.

Murray, W. 1991. *Ecology and Paleoecology of Benthic Foraminifera*. Longman, London, 397 pp.

Páez, M. y Zúñiga, O. 2001. Foraminifers recientes en el área del Río Loa (21° 25'S; 70° 04'W). Chile. *Estudio Oceanológico*, 20, 3 -12.

Panzarini, R. 1984. Introducción a la Oceanografía general. Ed. Universitaria de Buenos Aires, 199 pp.

Parker, G., Violante, R. y Paterlini, M. 1996. Fisiografía de la Plataforma Continental. In: Ramos, V., Turic, A. (Eds.), Geología y Recursos Naturales de la Plataforma Continental Argentina. *Relatorio del XIII Congreso Geológico Argentino y 3er Congreso de Exploración de Hidrocarburos*, Buenos Aires, 1, 1-16.

Planas, X., Ponsa, A., Coronato, A. y Rabassa, J. 2002. Geomorphological evidence of diffent glacial stages in the Martial cirque, Fuegian Andes, southernmost South America. *Quaternary International*, 87, 19-27.

Rabassa, J., Heusser, C. y Stuckenrath, R. 1986. New Data on Holocene Sea Transgresion in the Beagle Channel: Tierra del Fuego, Argentina. *Quaternary of South America and Antarctic Peninsula*, 4, 291-309.

Rabassa, J., Brandani, A., Politis, G. y Salemnme, M. 1985. La pequeña edad del Hielo (siglos 16 a 19) y su posible influencia en la aridización de áreas marginales de la pampa húmeda (provincia de Buenos

Aires). *1ras Jornadas Geológicas Bonaerenses*, Tandil, Resúmenes, 559-577.

Rabassa, J., Bujalesky, G.G., Meglioli, A., Coronato, A., Gordillo, S., Roig, C. y Salemme, M. 1992. The Quaternary of Tierra del Fuego, Argentina: the status of our knowledge. *Sveriges Geologiska Undersökning,* 81, 249-256.

Rivas, A. y Beier, E. 1990. Temperature and salinity fields in the Northpatagonic Gulfs. *Oceanológica acta*, 13, 15-20.

Rivas, A. y Ripa, P. 1989. Variación estacional de la estructura termohalina del Golfo Nuevo, Argentina. *Geofísica Internacional*, 28, 3-24.

Sagasti, G. y Ballent, S. 2002. Caracterización microfaunística de una trangresión marina: Formación Agrio (Cretácico Inferior), Cuenca Neuquina, Argentina). *Geobios*, 35 (6), 721-734.

Sen Gupta, B. y Machain-Castillo, M.L. 1993. Benthic foraminifera in oxygen-poor habitats. *Marine Micropaleontology*, 20, 183-201.

Sen Gupta, B., Platon, E., Bernhard, M.J. y Aharon, P. 1997. Foraminiferal colonization of hydrocarbon-seep bacterial mats and underlying sediment, gulf o Mexico slope. *Journal of Foraminiferal Research*, 27, 299-300.

Severin, K. 1983. Test morphology of benthic Foraminifera as a discriminator of biofacies. *Marine Micropaleontology*, 8, 65-76.

Silva, K., Corliss, B., Rathburn, A. y Thunell, R. 1996. Seasonality of living benthic foraminifera from the San Pedro basin, California Borderland. *Journal of Foraminiferal Research*, 26, 71-93.

Smart, C. 2002. Environmental Applications of Deep-Sea Benthic Foraminifera. In: Haslett (Ed.), *Quaternary Environmental Micropaleontology*, 3, 14-58.

Sverdrup, H., U., Johnson, M., W. y Fleming, R. 1942. *The Oceans, their Physics, Chemistry, General Biology*. Prentice Hall, Inc., (New York), 2º Printing, 1946, 1087 pp.

Tonini, M., Palma, E. y Rivas, A. 2007. Simulación numérica de la circulación y frentes térmicos en los golfos Norpatagónicos. *Mecánica Computacional,* 26, 3757-3768.

Vilela, C. 1995. Ecology of Quaternary benthic foraminiferal assemblages on the Amazon shelf, northern Brazil. *Geo-Marine Letters*, 15, 199-203.

Vilela, C. 2003. Diagnóstico ambiental da Baia Da Guanabara e Regioes adjacentes. *9 Congresso da Associacao Brasileira de estudos do Quaternario-II congreso do Quaternário de países de línguas ibéricas-II congreso sobre plaejamento e gestáo da zona costeira dos países de expressao portuguesa*, (Brasil) 3 pp.

Vilela, C., Batista, D., Baptista-Neto, A., Crapez, M. y Mcallister, J. 2004. Benthic foraminifera distribution in high polluted sediments from Niterói Harbor (Guanabara Bay), Rio de Janeiro, Brazil. *Anais da Academia Brasileira de Ciências*, 76 (1), 161-171

Vilela, C., Baptista-Neto, A., Mendonca-Filho, J., Sanjinés, A., Batista, D. y Barbosa, C. 2002. Benthic foraminifer's occurrence in subenvironments on Guanabara Bay, Río de Janeiro, southeast Brasil. *Forams: International Symposium Perth on Foraminifera western Australia, Volume of Abstracts*, 7.

Vilela, C., Sanjinés, E., Ghiselli, R., Mendonca-Filho, J., Baptista-Neto, A., Barbosa, C. 2003. Search for Bioindicators of Pollution in the Guanabara Bay: Integrations of Ecologic Patterns. *Anuário do Instituto de Geociéncias- UFRJ*, 26, 26-35.

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APÉNDICE: LISTA DE ESPECIES

Orden FORAMINIFERIDA Eichwald, 1830

Quinqueloculina seminulum (Linné) = *Serpula seminulum* Linné, 1758.

Amphicoryna scalaris (Batsch) = *Nautilus* (Orthoceras) *scalaris* Batsch, 1791.

Lenticulina limbosa (Boltovskoy) = *Robulina limbosa* Reuss, 1863.

Lenticulina reniformis (d' Orbigny) = *Cristellaria reniformis* d' Orbigny, 1846.

Neolenticulina peregrina (Schwage) = *Cristellaria peregrina* Schwager, 1866.

Lagena aspera Reuss = *Lagena aspera* Reuss, 1861.

Lagena caudata (d' Orbigny) = *Oolina caudata* d' Orbigny, 1839.

Lagena clavata (d' Orbigny) = *Oolina clavata* d' Orbigny, 1846.

Lagena laevis (Montagu), f. *tenuis* = *Ovulina tenuis* Bornemann, 1855.

Lagena laevis (Montagu), f. *typica* = *Vermiculum laeve* Montagu, 1803.

Lagena substriata Williamson = *Lagena substriata* Williamson, 1848.

Lagena sulcata (Walker y Jacob) f. *lyellii* = *Serpula sulcata* Walker y Jacob, 1798.

Fissurina earlandi Parr = *Fissurina earlandi* Parr, 1950.

Fissurina laevigata Reuss = *Fissurina laevigata* Reuss, 1850.

Fissurina quadricostulata (Reuss) = *Lagena quadricostulata* Reuss, 1870.

Bolivina compacta Sidebottom = *Bolivina robusta* Brady var. *compacta* Sidebottom, 1905.

Bolivina ordinaria Phleger y Parker = *Bolivina simplex* Phleger y Parker, 1950.

Bolivina pseudoplicata Heron-Allen y Earland = *Bolivina pseudoplicata* Heron-Allen y Earland, 1930.

Bolivina striatula Cushman = *Bolivina striatula* Cushman, 1922.

Bolivina variabilis (Williamson) = *Textularia variabilis* Williamson, 1858.

Brizalina difformis (Williamson) = *Textularia variabilis* var. *difformis* Williamson, 1858.

Cassidulina carinata Silvestri = *Cassidulina laevigata* d´ Orbigny var. *carinata* Silvestri, 1896.

Globocassidulina crassa (d' Orbigny) = *Cassidulina crassa* d' Orbigny, 1839.

Globocassidulina subglobosa (Brady) = *Cassidulina subglobosa* Brady, 1881.

Bulimina elongata d´ Orbigny = *Bulimina elongata* d' Orbigny, 1826.

Bulimina gibba Fornasini = *Bulimina gibba* Fornasini, 1902.

Bulimina marginata d' Orbigny = *Bulimina marginata* d' Orbigny, 1826.

Bulimina patagonica d' Orbigny = *Bulimina patagonica* d' Orbigny, 1839.

Globobulimina affinis (d´ Orbigny) = *Bulimina affinis* d' Orbigny, 1839.

Buliminella elegantissima (d´Orbigny) = *Bulimina elegantissima* d´ Orbigny, 1839.

Uvigerina peregrina Cushman = *Uvigerina peregrina* Cushman var. *parvula* Cushman, 1923.

Angulogerina angulosa f. *occidentalis* (Cushman) = *Uvigerina occidentalis* Cushman, 1923.

Furksenkoina schreibersiana (Czjzek) = *Virgulina schreibersiana* Czjzek, 1848.

Discorbis peruvianus (d'Orbigny) *Rosalina peruviana* d' Orbigny, 1839.

Discorbis williamsoni (Chapman y Parr) = *Rotalina nitida* Williamson, 1858.

Discorbis malovensis Heron-Allen y Earland = *Discorbis malovensis* Heron-Allen y Earland, 1932.

Discorbinella bertheloti (d' Orbigny) = *Rosalina bertheloti* d' Orbigny, 1839.

Cibicides dispars (d' Orbigny) = *Truncatulina dispars* d' Orbigny, 1839.

Cibicides fletcheri Galloway y Wissler = *Cibicides fletcheri* Galloway y Wissler, 1927.

Nonion depressulus (Walker y Jacob) = *Nautilus depressulus* Walker y Jacob, 1798.

Nonionella auris (d' Orbigny) = *Valvulina auris* d' Orbigny, 1839.

Astrononion pussilum Hornibrook = *Astrononion pussilum* Hornibrook, 1961.

Melonis affine (Reuss) = *Nonionina affinis* Reuss, 1851.

Buccella peruviana f. *campsi* (Boltovskoy) = *Eponides peruvianus* f. *campsi* Boltovskoy, 1954.

Elphidium articulatum (d' Orbigny) = *Polystomella auriculata* d' Orbigny, 1839.

Elphidium discoidale (d' Orbigny) = *Polystomella discoidalis* d' Orbigny, 1839.

Elphidium excavatum (Terquem) = *Polystomella excavata* Terquem, 1876.

Elphidium incertum (Williamson) = *Polystomella umbilicatula*, var. *incerta* Williamson, 1858.

Elphidium magellanicum Heron-Allen y Earland = *Elphidium* (Polystomella) *magellanicum* Heron-Allen y Earland, 1932

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Recent marine Ostracoda from the Solomon Islands. Part 6: Cytheroidea; Paradoxostomatidae, Pectocytheridae, Trachyleberididae

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Resumen

Catorce especies pertenecientes a la familia Paradoxostomatidae, 6 especies de la familia Pectocytheridae y 15 especies y subespecies de Trachyleberididae, pertenecientes a 5 de sus subfamilias (Trachyleberidinae, Arculacythereinae, Cytherettinae, Ruggieriainae y Schizocytherinae) fueron registradas en las Islas Salomón. Todas ellas son discutidas o descritas e ilustradas en el presente trabajo. Se describen un nuevo género, *Hypocritecythere* y 15 nuevas especies y subespecies: *Paradoxostoma bilocus*, *P. dorsostriata*, *P. sophicos*, *Javanella dolichostracon*, *Keijia radiata*, *K. brachychthonus*, *Kotoracythere doratus*, *Hypocritecythere polymorphica*, *Neocaudites pacifica listrotus*, *Ponticocythereis pollostus*, *Arculacythereis polytrematus*, *Alocopocythere reticulata fultura*, *A. reticulata perfecta*, *Australimoosella polypleuron* y *Ruggeria caryonautes* ssp. nov. Once especies y subespecies han sido descritas previamente en las regiones Indo-Pacifica y Australásica, siete especies quedan en *nomina aperta* y dos paradoxostomátidos son referidos a, o comparados con otras especies de la familia. En conjunto, estas tres familias constituyen un componente importante de la fauna de ostrácodos marinos de las Islas Salomón, especialmente al presentar muchos taxones nuevos.

Palabras clave: Ostrácodos marinos, Reciente, Islas Salomón, Paradoxostomatidae, Pectocythereidae, Trachyleberididae, nuevos taxones.

Abstract

Fourteen species of the family Paradoxostomatidae, 6 species of the Pectocytheridae and 15 species and subspecies of the family Trachyleberididae, belonging to 5 of its subfamilies (Trachyleberidinae, Arculacythereinae, Cytherettinae, Ruggieriainae and Schizocytherinae) have been encountered in the Solomon Islands. All are discussed or described and illustrated. One new genus, *Hypocritecythere* and 15 new species and subspecies are described: *Paradoxostoma bilocus*, *P. dorsostriata*, *P. sophicos*, *Javanella dolichostracon, Keijia radiata*, *K. brachychthonus, Kotoracythere doratus*, *Hypocritecythere polymorphica*, *Neocaudites pacifica listrotus*, *Ponticocythereis pollostus*, *Arculacythereis polytrematus*, *Alocopocythere reticulata fultura*, *A. reticulata perfecta*, *Australimoosella polypleuron and Ruggeria caryonautes* ssp. nov. Eleven species and subspecies have been previously described from the Indo-Pacific and Australasian regions and seven species are left in open nomenclature and 2 paradoxostomatids are referred to or compared with other species. These three families make up an important component of the total Solomon Island fauna, especially since many of them are new.

Keywords: Marine Ostracoda, Recent, Solomon Islands, Paradoxostomatidae, Pectocythereidae, Trachyleberididae new taxa.

1. INTRODUCTION

Since the late 1980's there has been a resurgence of studies of Ostracoda in the Indo-Pacific area. A listing of the most important publications is given in the introduction of recent papers by the present authors (Titterton & Whatley, 2005, 2006a&b and Warne *et al.,* 2006). This contribution is the 6th paper in the current series on the Recent marine Ostracoda of the Solomon Islands. Quaternary marine and brackish Ostracoda from the islands are the subject of an additional study (Whatley *et al*., in press). Prior to this, apart from Harding's (1962) study of species recovered from the gut of freshwater fishes, and two papers by the present authors on marine taxa (Whatley & Titterton, 1981; Titterton & Whatley, 1988), which dealt with two trachyleberidid genera and the large fauna (21 species) of Bairdiinae respectively, the Ostracoda of the Solomon Islands had been sadly neglected.

The Solomon Islands are situated to the NE of Australia and to the SE of New Guinea between Lat. 5º-12ºS and Long. 155º-162ºE and enjoy an oceanic tropical climate. The samples on which this study is based were collected off the islands of Guadalcanal and Shortland (Fig. 1). The location of the samples is given in Figs 2 and 3. All of the samples are of largely biodetrital sand, ranging from very fine to medium in grain size. Much of the medium sand originated from coral and the samples were collected with a simple pipe dredge or by diving. Details of the individual samples can be found in Titterton (1984 MS) and Titterton & Whatley (1988).

The total ostracod fauna comprises some 160 species belonging to 56 genera. The overwhelmingly dominant group are the Cytheroidea (63%) the remainder are cyprids (15%), bairdiids (8%) and platycopids/cladocopids (13%).

It appears that species of *Paradoxostoma* are geographically restricted but this may in part be because in the Recent the genus is very diverse but with few individuals and because of the difficulties in identification of species and comparison with those already described. Over one hundred and twenty species have been described from the Southern Oceans and of these, only about 25 have been found by subsequent authors. For example Kajiyama (1913) described 7 new species from Japan; Schornikov (1974) 10 new species from the Kurile Islands and (1975) 8 new species from Japan; Hartmann (1964) described 4 new species from the Red Sea; (1974) 6 new species from South Africa; (1978) 17 new species from western Australia; (1979) 10 new species and 2 new subspecies from Southern Australia and (1980) 7 new species from south-

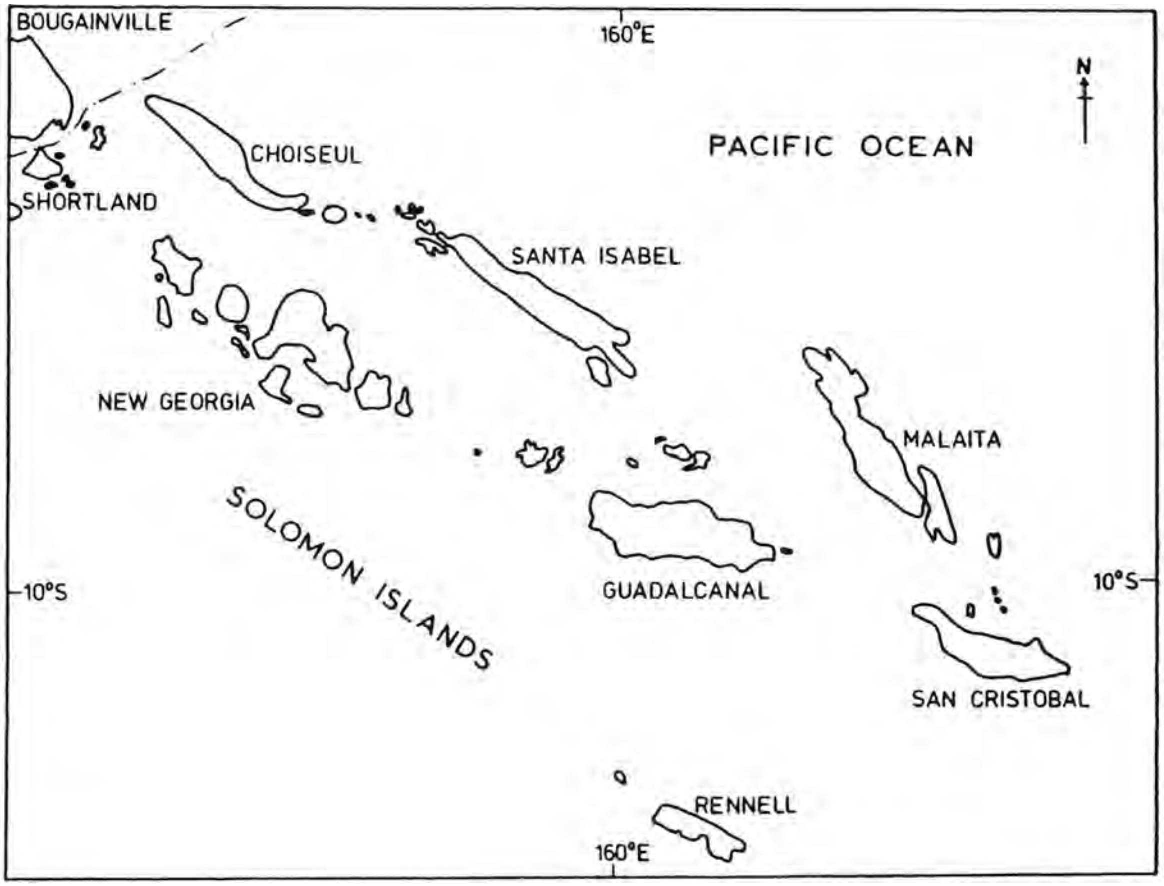


Figure 1. The Solomon Islands.

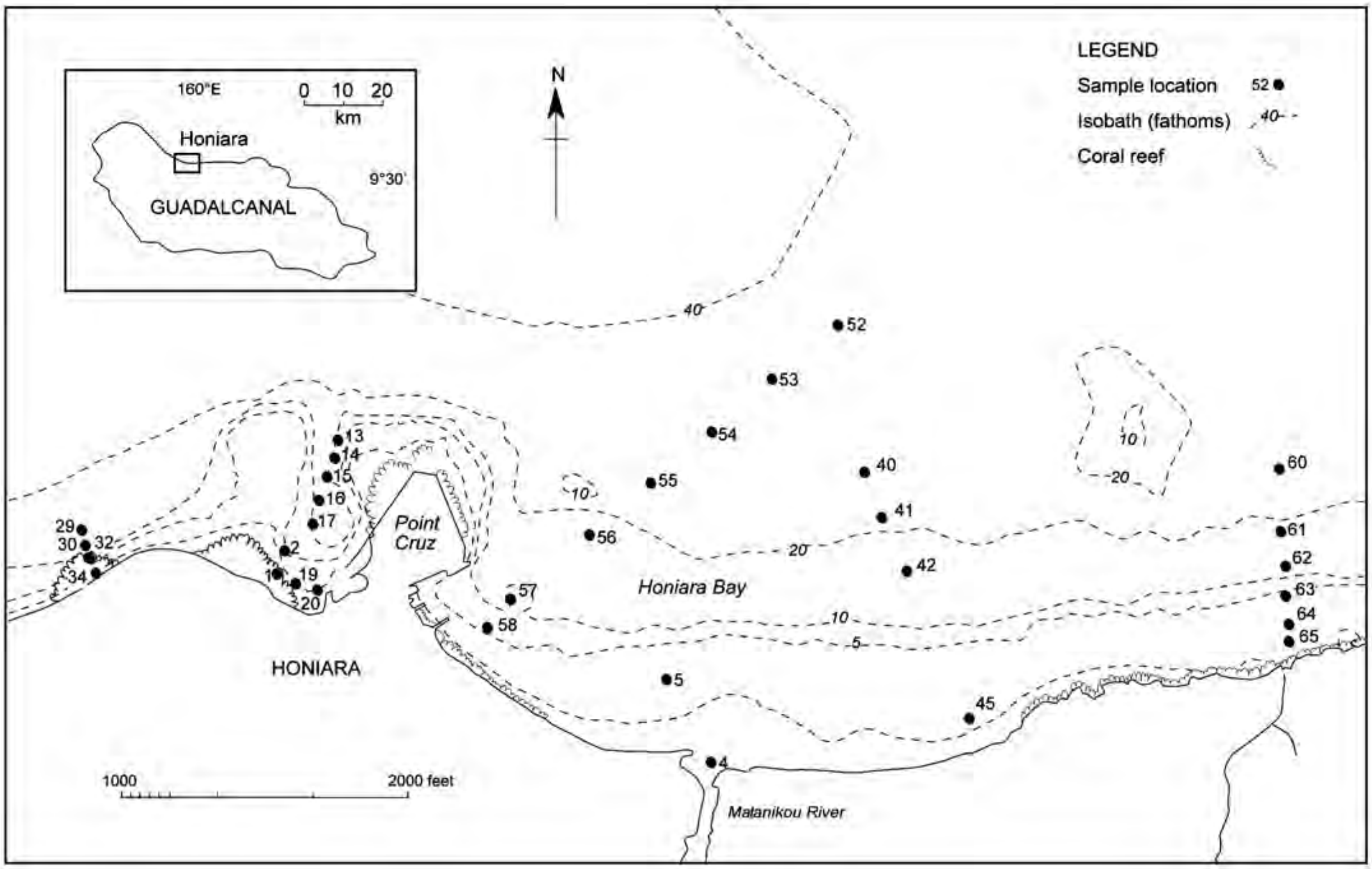


Figure 2. Location of sample stations, Honiara Bay, N. Guadalcanal, Solomon Islands.

eastern Australia; Whatley *et al.* (2000) described 5 new species of from Easter Island, one of which occurs in the Pitcairn group where Whatley *et al.* (2004) encountered no new species. Thirteen species of the genus were encountered in the present material, 6 appear to be new but there is insufficient material to substantiate them as new taxa. However, 2 species also occur in northeastern Australia (Hartmann, 1981) and 3 other species have been recorded as far away as the Java Sea (Watson, 1988 MS). Other authors have described 3 or less new species.

The Pectocytherids are represented by 6 species including the widely distributed species *K. demissa* and *K. inconspicua* but also by 1 new genus and 4 new species. The Trachyleberididae are represented by 15 species and make up some 8% of the total ostracod fauna. Notwithstanding this relatively small percentage, this family is important with such very conspicuous species as the 'armoured' *Ponticocythereis manis* one of the most spectacularly ornamented ostracods of all time. The character of the trachyleberids is very much SW Pacific/Australasian, although one species ranges as far afield as Kenya. However, within the regional aspect of the fauna there is a distinct component apparently endemic to the Solomon Islands with more than half the fauna being new.

2. SYSTEMATIC DESCRIPTIONS

The type specimens of all new taxa are housed in the collections of the Natural History Museum, London to which the catalogue numbers prefixed RT/SIR refer. Catalogue numbers prefixed OS refer to specimens deposited in the collections of the Department of Palaeontology, Natural History Museum, London. Specimens are of adults unless otherwise stated. All dimensions are given in millimetres and the size convention for adults is as follows: <0.40 very small, 0.40-0.50 small, 0.50-0.70 medium, 0.70-1.00 large, > 1.0 very large. Other conventions used throughout are: LV=left valve, RV=right valve, C=carapace, A=adult, juv.=juvenile, rpc=radial pore canal, npc=normal pore canal, LOC= line of concrescence, IM=inner margin, OM=outer margin. All new taxa are fully described.

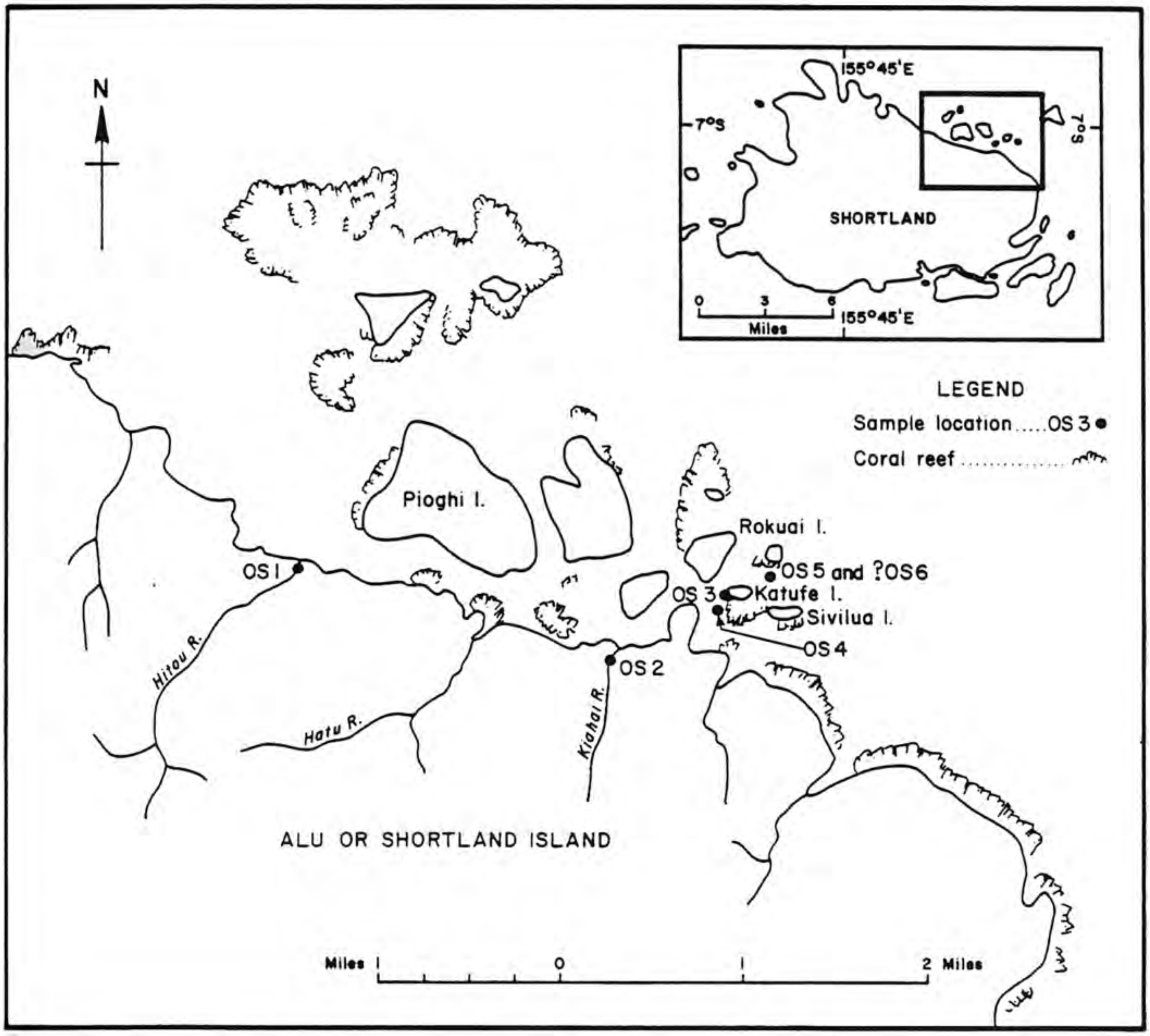


Figure 3. Location of sample stations, Shortland Island, Solomon Islands.

Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily CYTHEROIDEA Baird, 1850
Family PARADOXOSTOMATIDAE Brady & Norman, 1889
Subfamily PARADOXOSTOMATINAE Brady & Norman, 1889

Genus *Paradoxostoma* Fischer, 1855

Type species.- *Paradoxostoma dispar* Fischer, 1855.

Remarks.- Müller (1894) believed shape to be the most important character in distinguishing species of *Paradoxostoma* without soft-parts. He considered marginal pore canals less reliable as they may vary in distribution within a species. This may be because all the marginal pore canals are false, their length depending on their position relative to the line of concrescence. Normal pore canals which occur under the free part of the inner lamella in some specimens may appear in others as false marginal pore canals if the fused zone of the inner lamella is wider. It is, therefore, important to map the position of both marginal and normal pore canals. Only two species, *P. dorsostriata* and *P. sophicos* spp. nov. occurred in the present material in sufficient numbers to compare the distribution of pore canals between individuals and in both species it was found that the number and position of canals was constant.

Paradoxostoma fuscumaculosus Hartmann, 1981
(Fig. 4, Nos 20, 21; Pl. 1, Figs 12, 16, 17)

1981 *Paradoxostoma fuscumaculosum* Hartmann, p. 12, Text–Figs 72-75.

Material.-14 valves, A-2 to adult.

Dimensions.-

	Length	Height
RV, RT/SIR/504	0.54	0.32
LV, RT/SIR/505	0.60	0.34
RV, RT/SIR/506	0.59	0.33
RV, RT/SIR/507	0.59	0.33
A-1 RV	0.50	0.27
A-2 RV	0.39	0.21

Distribution.- Living on algae, Heron Island off the north-eastern coast of Australia (Hartmann, 1981). Present study samples: 1, 13, 14, 17, 20, 50, 55, OS6, Guadalcanal and Shortland islands.

Remarks.- This species is translucent with large, variable opaque patches, it is subtrapezoidal in lateral view and subelliptical in dorsal view. It is most similar in size and shape to *P. hoppei* Hartmann, 1978 (eulittoral, W Australia) but there are differences in the number and position of the marginal pore canals. *Paradoxostoma* sp. A of the present study, also belongs to the same species group but is less strongly caudate posteriorly.

Paradoxostoma heronislandensis Hartmann, 1981
(Fig. 4, No. 5; Pl. 1, Fig. 34)

1981 *Paradoxostoma heronislandensis* Hartmann, p. 127, Text-Figs 76-79.

Material.- 1 adult valve.

Dimensions.-

	Length	Height
RV, RT/SIR/538	0.60	0.25

Distribution.- Living on algae, Heron Island off the north-eastern coast of Australia (Hartmannn, 1981). Present study sample: 54, Guadalcanal.

Remarks.- The present species differs from *P. dorsostriata* sp. nov. in being slightly larger, the fused zone of the inner lamella is wider, the line of concrescence is gently sinuous, particularly anteroventrally, and it lacks the anterodorsal striations. It is also similar in shape to *Paradoxostoma* sp. 2 Whatley *et al.,* 2004 (Henderson Island, Pitcairn Group) although this species is much smaller (L = 0.34).

Paradoxostoma sp. cf. *P. mimicus* Whatley *et al*., 2000
(Fig. 4, Nos. 18, 19; Pl. 1, Figs 4, 5)

2000 *Paradoxostoma mimicus* Whatley *et al*., p. 156.

Material.- 3 adult valves.

Diagnosis.- A large, very thin-shelled, translucent species of *Paradoxostoma*, elongate subelliptical in lateral view and laterally compressed. Anterior margin sharply rounded subdorsally, straight and sloping obliquely anteroventrally. Posterior margin very strongly caudate with subdorsal extremity. Dorsal margin almost straight. Ventral margin gently convex. Greatest length subdorsal; greatest height at anterior quarter. Surface of valves smooth.

Dimensions.-

	Length	Height
RV, RT/SIR/541	0.93	0.26
RV, RT/SIR/543	broken	

Distribution.- Samples: 15, 14, Guadalcanal.

Remarks.- Although this species resembles certain bythocytherids, it is unquestionably a paradoxostomatid in that it possesses 4 rather than 5 adductor scars. There are a number of similar species in the Australia/Indo-Pacific region which perhaps warrant a new genus to embrace them, all of which differ in important details of size, shape and internal morphology from the present taxon. Among the species referred to are: *Paradoxostoma* sp. 2 Warne *et al.*, 2006. (Port Darwin, N Australia); *Xiphichilus lanceaformis* Mostafawi, 1992 (N Indonesia); *Paracytherois* sp. A Labutis 1977 MS (Great Barrier Reef); *Paradoxostoma* aff. *subtile* Bonaduce *et al.,* of Cabioch *et al.,* 1986 (New Caledonia); *Paradoxostoma lizardensis* Behrens, 1991 (Great Barrier Reef). However, it seems closest to *P. mimicus* Whatley *et al.,* 2000 (Easter Island), although it was absent from the Pitcairn Group fauna (Whatley *et al.*, 2004), from which it differs in details of shape, mainly in being somewhat less rounded anteriorly.

Paradoxostoma sp. aff. *P. angolensis* Hartmann, 1974
(Fig. 4, No. 28; Pl. 1, Figs 9-11)

1974 *Paradoxostoma angolensis* Hartmann, p. 333, Text-Figs 775-785, Pls 108, 109.

Material.- 1 adult carapace and 1 adult valve.

Description.- Medium. Thin-shelled. Translucent with opaque patches anteriorly and posteriorly. Subovate in lateral view; laterally compressed. Anterior margin narrow, well rounded; extremity just below mid-height. Posterior margin slightly caudate; extremity well rounded, above mid-height. Dorsal margin strongly arched towards posterior: cardinal angles rounded. Ventral margin almost straight. Greatest length at mid-height; greatest height at posterior third; greatest width median. Surface of valves smooth. Npcs few, small, regularly distributed. Inner lamella wide, LOC and IM widely divergent, forming a single large vestibulum. Approximately 11 anterior and 10 posterior rpc's canals, all false, some short, simple straight. Hinge lophodont. Four elongate adductor muscle scars; frontal scar not observed.

Dimensions.-

	Length	Height	Width
C, RT/SIR/512, 513	0.59	0.31	0.18
LV, RT/SIR/514	0.60	0.30	

Distribution.- Sample: OS6, Shortland Island.

Remarks.- The present species although very similar to *P. angolensis* Hartmann, 1964 (Recent, Angola), differs in the number and position of the marginal pore canals. It differs from *P. fuscumaculosum* Hartmann, 1981 in being more compressed laterally and less well calcified. *Paradoxostoma* sp. 1 Whatley *et al.*, 2004 (Henderson Island, Pitcairn Group) differs in its less regular inner margin and larger size (L = 0.64-0.65).

Paradoxostoma bilocus sp. nov.
(Fig. 4, Nos 23, 24; Pl. 1, Figs 18, 19)

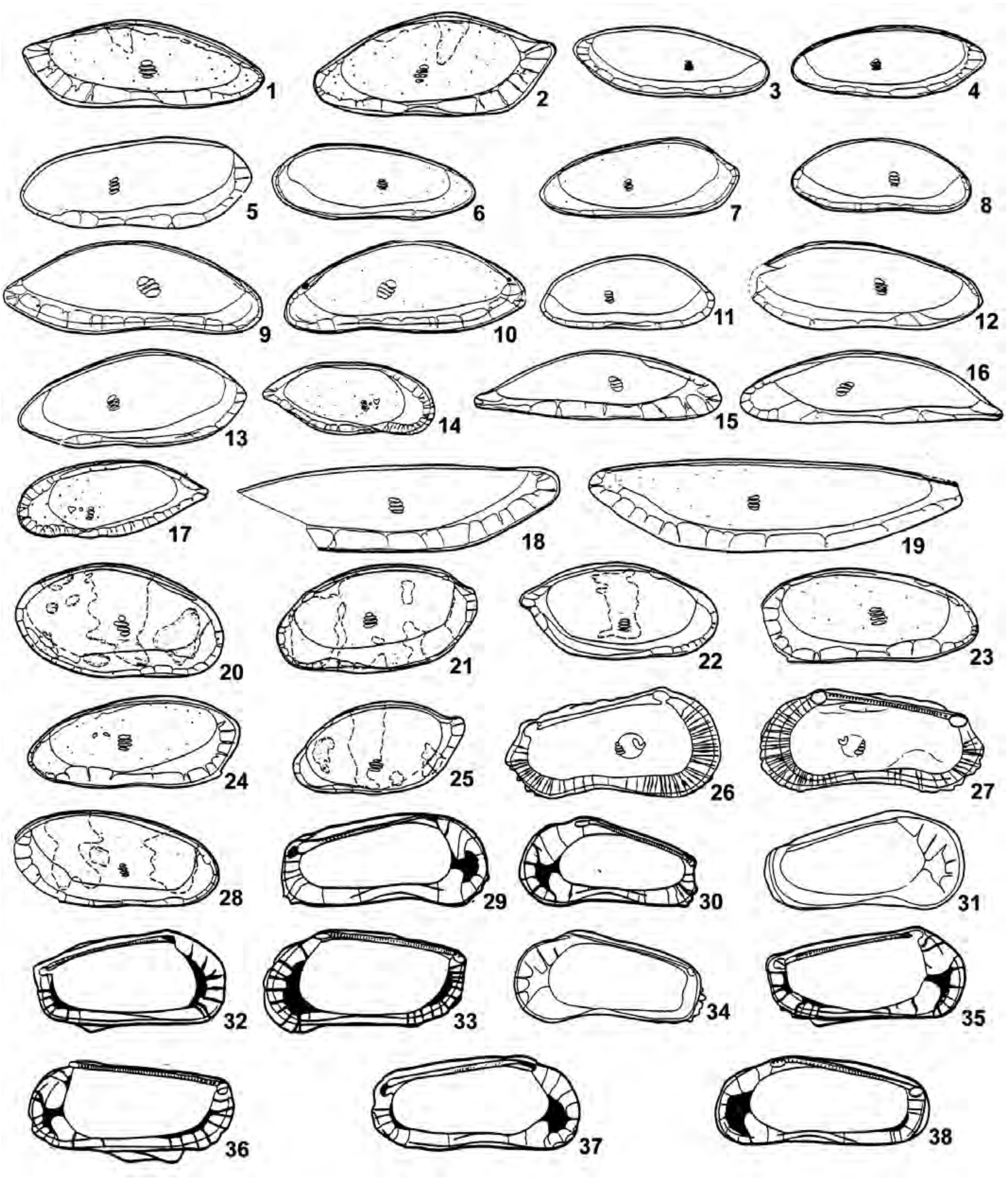
Derivatio nominis.- L. *bi* - two, plus *locus* - place. With reference to the two geographically separated localities where this species is found.

Holotype.- Female LV, RT/SIR/524. Plate 1, Fig. 18.

Type locality and horizon.- Shortland Island, sample OS6. Exact locality unknown but thought to be from the intertidal zone near a coral reef, on the NE coast of the island,

Figure 4. Internal lateral views. ***1-2***, *Paradoxostoma sophicos* sp. nov.*1,* Left valve RT/SIR/521 x 61.3. *2,* Right valve RT/SIR/520 x 61.3. ***3-4***, *Paradoxostoma* sp. B *3,* Left valve RT/SIR/515 x 57.7. *4,* Right valve RT/SIR/516 x 57.7. ***5***, *Paradoxostonma heronislandensis* Hartmann, 1981 right valve RT/SIR/538 x 60.8. ***6-7***, *Paradoxostoma dorsostriata* sp. nov. *6,* Left valve RT/SIR/537 x 66.0. *7,* Right valve RT/SIR/536 x 65.3. ***8, 11***, *Paradoxostoma* sp. E *8,* Left valve RT/SIR/539 x 61.7. *11,* Right valve RT/SIR/540 x 59.6. ***9-10***, *Paradoxostoma* sp. C *9,* Left valve RT/SIR/522 x 60.3. *10,* Right valve RT/SIR/523 x 58.2. ***12-13***, *Paradoxostoma*. sp. D *12,* Left valve RT/SIR/532 x 66.7. *13,* Right valve RT/SIR/530 x 62.1. ***14-17***, *Javanella dolichostracon* sp. nov. *14,* Right valve RT/SIR/552 x 59.6. *17,* Left valve RT/SIR/551 x 63.8. *15-16, Paradoxostoma* sp. F *15,* Left valve RT/SIR/546 x 57.4. *16,* Right valve RT/SIR/544 x 60.0. ***18-19***, *Paradoxostoma* sp. cf. *Paradoxostoma mimicus* Whatley *et al.*, 2000 *18,* Left valve RT/SIR/542 x 64.5. *19,* Right valve RT/SIR/541 x 64.5. ***20-21***, *Javanella dolichostracon* sp. nov. *20,* Left valve RT/SIR/505 x 55.0. *21,* Right valve RT/SIR/507 x 54.2. ***22-25***, *Paradoxostoma* sp. A *22,* Left valve RT/SIR/510 x 59.3. *25,* Right valve RT/SIR/511 x 51.9. *23-24, Paradoxostoma bilocus* sp. nov. *23,* Holotype female left valve RT/SIR/524 x 53.8. *24,* Paratype female right valve RT/SIR/526 x 50.8. ***26-27***, *Hypocritecythere polymorphica* gen. et sp. nov. *26,* Left valve RT/SIR/686 x 48.6. *27,* Right valve RT/SIR/687 x 51.5. ***28***, *Paradoxostoma* sp. aff. *P. angolensis* Hartmann, 1974 left valve RT/SIR/514 x 56.7. ***29-30***, *Keijia demissa* (Brady, 1868) *29,* Male left valve RT/SIR/564 x 67.3. *30,* Female right valve RT/SIR/563 x 80.6. ***31, 34***, *Keijia brachychthonus* sp. nov. *31,* Left valve RT/SIR/571 x 66.7. *34,* Right valve RT/SIR/572 x 61.2. ***32-33,*** *Kotoracythere inconspicua* (Brady, 1880) *32,* Female left valve RT/SIR/591 x 79.5. *33,* Male right valve RT/SIR/593 x 80.0. ***35-36***, *Kotoracythere doratus* sp. nov. *35,* Paratype left valve RT/SIR/596 x 78.0. *36,* Paratype right valve RT/SIR/597 x 73.3. *37-38, Keijia radiata* sp. nov. *37,* Male left valve RT/SIR/583 x 70.2. *38,* Male right valve RT/SIR/584 x 75.6.

Figure 4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in the vicinity of Rokuai Island. Coarse-grained coral sand. Recent.

Material.- 8 adult valves from the Solomon Islands and 15 adult valves from the Pulau Seribu in the Java Sea.

Diagnosis.- A medium, sexually dimorphic trapezoidal species of *Paradoxostoma* with males proportionally more elongate and less high than females. Most specimens with elongate excavation medianly in posterior third.

Description.-Medium. Subtrapezoidal. Males proportionally more elongate than females. Anterior margin narrowly rounded with extremity well below mid-height. Posterior margin wider and produced into a narrowly rounded caudal process with apex narrowly rounded and above mid-height; posteroventral slope straight, oblique and at an obtuse angle to ventral margin. Dorsal margin a gently convex arc. Ventral margin almost straight and shallow oral incurvature just anterior of mid-length. Lateral surface smooth but most specimens with elongate excavation medianly in posterior third. Inner lamella broad with large vestibulum around entire free margin. Seven short npc's anteriorly, 5 ventrally and 8-9 posteriorly. Hinge lophodont. Four large adductor muscle scars and 2 small, subovate frontal scars.

Dimensions.-

	Length	Height
Holotype female LV, RT/SIR/524	0.65	0.29
Paratype male RV, RT/SIR/525	0.62	0.27
Paratype female RV, RT/SIR/526	0.65	0.30
Paratype male RV, RT/SIR/527	0.63	0.29
Paratype female LV, RT/SIR/528	0.65	0.28

Distribution.- Samples: K40, K48, Pulau Kotok Kecil; PT2, PT3, PT9, PT10, PTN20, PSM47, Pulau Petundang Kecil, Pulau Seribu, Java Sea (Watson, 1988 MS). Present study samples: 1, 14, 17, 20, 58, OS6, Guadalcanal and Shortland islands.

Remarks.- The material described from the Java Sea is somewhat smaller but clearly of the same species. The present species belongs to the same Recent species group as *P. aculeoliferum* and *P. japonicum* Schornikov, 1975, (SE coast of Honshu, Japan) and *P. brunneum* Schornikov, 1974 (Kurile Islands), *P. romei* McKenzie, 1967 (S Australia), *P. albaniensis* Hartmann, 1979 (WSW Australia) and *P. heronsislandensis* Hartmann, 1981 (E Australia), *P. phaeophycicola* Hartmann, 1974 (South Africa), *P. attenuatum* Scott, 1905 (Ceylon), *P. subtile* Bonaduce *et al*., 1980 (Red Sea) and *P. angustum* Müller, 1894 (Bay of Naples). All these species differ in size, subtle details of shape and outline and in their internal characters. *Paradoxostoma novaecaledoniae* Brady, 1880 is very similar in shape but is much longer (L=0.87).

Paradoxostoma dorsostriata sp. nov.

(Fig. 4, Nos 6, 7; Pl. 1, Figs 31-33)

Derivatio nominis.- L. With reference to the longitudinal striations parallel to the dorsal margin.

Holotype.- LV, RT/SIR/534. Plate 1, Fig. 33.

Type locality and horizon.- Shortland Island, sample OS6. Exact location unknown but thought to be from the intertidal zone near a coral reef, off the NE coast of the island, in the vicinity of Rokuai Island. Coarse-grained, coral sand. Recent.

Material.- 12 valves and carapaces A-2 to adult and 10 specimens from the Pulau Seribu, Java Sea described by Watson (1988 MS).

Diagnosis.- A species of *Paradoxostoma*, subelliptical in shape in lateral view: strongly compressed in dorsal view. Anterior margin very narrow. Posterior cardinal angle obtusely rounded, below which 4 or 5 very fine striations extend longitudinally parallel to dorsal margin. Fused area of inner lamella narrow; inner margin gently sinuous anteriorly.

Description.- Small to medium. Very thin-shelled. Translucent. Sexual dimorphism not observed. Subelliptical in lateral view; compressed and elliptical in dorsal view. Anterior margin very narrow, sharply rounded; extremity below mid-height. Posterior margin broader; anterodorsal and posterodorsal slopes meeting with a rounded right angle; extremity at mid-height. Dorsal margin almost straight, sloping towards anterior; anterior angle rounded, posterior cardinal angle obtusely rounded. Ventral margin almost straight with very slight oral concavity. Greatest length just below mid-height; greatest height at posterior quarter; greatest width median. Valves subequal, RV overlaps LV posteriorly. Surface of valves smooth except for 4 or 5 very fine striations immediately below posterior cardinal angle, extending longitudinally parallel to dorsal margin. Npc's few, small, regularly distributed. Inner lamella moderately wide. A broad vestibulum around anterior, ventral and posterior margins; narrowest ventrally. Fused area very narrow; inner margin gently sinuous anteriorly. Rpc's few, widely spaced, short, simple canals; approximately 10 anterior and ventral canals observed. Hinge lophodont. Central muscle scar pattern comprises 4 elongate adductor scars, closely spaced; frontal scar not observed.

Dimensions.-

	Length	Height	Width
Holotype LV, RT/SIR/534	0.53	0.21	
Paratype C, RT/SIR/533	0.54	0.23	0.14
Paratype RV, RT/SIR/535	0.53	0.21	
RV, RT/SIR/536	0.49	0.20	
Paratype LV, RT/SIR/537	0.50	0.20	
A-1 RV	0.43	0.17	
A-2	0.32	0.13	

Distribution.- Samples: 24, 94, L5, Pulau Pari; K16, K29, Pulau Kotok Kecil; PT1, Pulau Petundang Kecil, Pulau Seribu, Java Sea (Watson, 1988 MS). Present study sample: OS6, Shortland Island.

Remarks.- The present species is somewhat similar in shape to *P. heronislandensis* Hartmann, 1981 and *Paradoxostoma* sp. B of the present study but may be distinguished by the very fine striations parallel on the dorsal margin. The fused zone of the inner lamella is narrower and the inner margin gently sinuous anteriorly.

Paradoxostoma sophicos sp. nov.

(Fig. 4, Nos 1, 2; Pl. 1, Figs 26, 27, 30)

Derivatio nominis.- Gr. *σοθικος* - sophikos, of wisdom. With reference to the wisdom of Solomon and an allusion to the type locality.

Holotype. - LV, RT/SIR/517. Plate 1, Fig. 26.

Type locality and horizon.- Shortland Island, sample OS6. Exact locality unknown but thought to be from the intertidal zone near a coral reef, on the NE coast of the island, in the vicinity of Rokuai Island. Coarse-grained coral sand. Recent.

Material.- 12 adult valves.

Diagnosis.- A species of *Paradoxostoma*, subtrapezoidal in shape in lateral view. Anterior margin narrowly rounded; posterior margin caudate; extremity subdorsal. Smooth but with short, poorly defined longitudinal ribs at end margins. Inner lamella wide; LOC and inner margin almost coincident posteriorly and ventrally with 2 small pocket-like vestibula; semicircular anterior vestibulum.

Description.- Medium. Thin-shelled. Translucent. Subtrapezoidal in lateral view; elliptical in dorsal view. Anterior margin very narrow, sharply rounded; extremity below mid-height. Posterior margin caudate; extremity subdorsal; posteroventral slope long, obliquely sloping, almost straight. Dorsal margin strongly arched; cardinal angles rounded. Ventral margin almost straight. Greatest length below mid-height; greatest height median; greatest width median. Valves laterally compressed, smooth except short, poorly defined longitudinal ribs at end margins. Npcs moderately numerous, small, evenly scattered. Inner lamella wide, LOC and inner margin almost coincident posteriorly and ventrally, with 2 small, pocket-like vestibula; divergent anteriorly with semicircular vestibulum. Mpcs few; approximately 9 anterior and 8 posterior canals, simple, straight; all false, some short, others almost to OM. Hinge lophodont. Four elongate adductor scars; frontal scar not observed.

Dimensions.-

	Length	Height
Holotype LV, RT/SIR/517	0.64	0.23
Paratype RV, RT/SIR/518	0.63	0.28
Paratype LV, RT/SIR/519	0.60	0.24
Paratype RV, RT/SIR/520	0.62	0.25
Paratype LV, RT/SIR/521	0.62	0.25

Distribution.- Sample: OS6, Shortland Island.

Remarks.- The present species is distinctive in that the fused area of the inner lamella is broad posteriorly with 2 small, pocket-like vestibula. *Paradoxostoma trapezoideum* Mckenzie, 1967 (Recent, S Australia) is similar in shape but is shorter (by almost 0.2 mm) than the present species and possesses a single large posterior vestibule. *Paradoxostoma* sp. C of the present study differs in that the posteroventral margin slopes more obliquely and merges with the ventral margin.

Paradoxostoma sp. A
(Fig. 4, Nos 22, 25; Pl. 1, Figs 13-15)

Material.- 7 adult valves.

Diagnosis.- A medium, moderately thin-shelled species of *Paradoxostoma*, translucent with variable opaque patches; 1 large, median patch extending from dorsal almost to ventral margin; smaller patches anteriorly and posteriorly. Subovate in lateral view: elliptical in dorsal view. Anterior margin narrow, well rounded, extremity at mid-height. Posterior margin caudate, extremity subdorsal, posterodorsal slope very short, posteroventral slope long and convex. Dorsal margin strongly arched: cardinal angles rounded. Ventral margin almost straight; very slight oral concavity.

Dimensions.-

	Length	Height
LV, RT/SIR/508	0.55	0.30
RV, RT/SIR/509	0.57	0.33
LV, RT/SIR/510	0.54	0.29
RV, RT/SIR/511	0.52	0.30

Distribution.- Samples: 2, 17, OS5, OS6, Guadalcanal and Shortland islands.

Remarks.- The present species belongs to the same species group as *P. bradyi* Sars, 1928 and *P. abbreviatum* Sars, 1866 (both from Europe) but is distinguished in its more dorsal caudal process. *Paradoxostoma hoppei* Hartmann, 1979, (eulittoral, S Australia), is also similar but the caudal process is less well developed. *Paradoxostoma* aff. *caudatum* Hartmann of Cabioch *et al.*, 1986 (New Caledonia) has a similar posterior margin but is more elongate and longer (L=0.68). Although the present species is probably new there was insufficient, well preserved material on which to erect a new species.

Paradoxostoma sp. B
(Fig. 4, Nos 3, 4; Pl. 1, Figs 28, 29)

Material.- 2 adult and 1 juv. valves.

Diagnosis.- A medium, very thin-shelled and translucent species of *Paradoxostoma*. Subelliptical in lateral view, laterally compressed. Anterior margin narrow, sharply rounded; extremity at mid-height. Posterior margin slightly caudate; extremity well above mid-height. Dorsal margin arched, cardinal angles rounded. Ventral margin almost straight. Surface of valves smooth.

Dimensions.-

	Length	Height
LV, RT/SIR/515	0.52	0.19
RV, RV/SIR/516	0.52	0.20

Distribution.- Sample: 17, Guadalcanal.

Remarks.- The present species is similar in shape to *P. albaniensis* Hartmann, 1978 (eulittoral, SW Australia), however, it is smaller and the number and position of the marginal pore canals differs between the two. The present species also resembles *P.* sp. aff. *P. angolensis* of the present study, but is smaller, the posterior extremity more rounded and the fused area of the inner lamella narrower.

Paradoxostoma sp. C
(Fig. 4, Nos 9, 10; Pl. 1, Figs 24, 25)

Material.- 2 adult and 1 juv. valve.

Diagnosis.- A medium, very thin-shelled, translucent species of *Paradoxostoma*. Subelliptical in lateral view, laterally compressed. Anterior margin narrow, sharply rounded; extremity sub-ventral. Posterior margin strongly caudate; extremity sharply rounded just below mid-height. Dorsal margin strongly arched, cardinal angles rounded. Ventral margin gently biconvex with broad oral concavity. Greatest length just below mid-height; greatest height just posterior to mid-length; greatest width median. Surface of valves smooth.

Dimensions.-

	Length	Height
LV, RT/SIR/522	0.68	0.26
RV, RT/SIR/523	0.67	0.26

Distribution.-Sample: OS6, Shortland Island.

Remarks.- Paradoxostoma promunturiumphsicicolum Hartmann, 1979 (Recent, S Australia) resembles the present species. The latter, however, is more strongly arched dorsally, the fused area of the inner lamella is broader and the marginal pore canals more numerous. *Paradoxostoma angustum* Müller, 1894 (Recent, Europe) is also very similar, but the posterior extremity is more dorsal.

Paradoxostoma sp. D
(Fig. 4, Nos 12, 13; Pl. 1, Figs 20, 21)

Material.- 4 adult valves and 1 adult carapace.

Diagnosis.- A medium sized, translucent, thin-shelled and trapezoidal species of *Paradoxostoma* which is very laterally compressed and narrowly rounded and sharply rounded at each end with apices just below mid-height. Dorsal margin arched towards posterior: cardinal angles rounded. Ventral margin with gentle oral concavity. Surface of valves smooth.

Dimensions.-

	Length	Height	Width
C, RT/SIR/529	0.58	0.25	0.16
RV, RT/SIR/ 530	0.58	0.24	
RV, RT/SIR/531	0.57	0.23	
LV, RT, SIR/532	0.57	0.25	

Distribution.- Samples: OS3, OS5, Shortland Island.

Remarks.- Similar to *P. sophicos* sp. nov. of the present study but is less caudate posteriorly and the fused area of the inner lamella is narrower anteriorly.

Paradoxostoma sp. E
(Fig. 4, Nos 8, 11; Pl. 1, Figs 22, 23)

Material.- 1 adult carapace (opened).

Diagnosis.- A medium sized species of *Paradoxostoma*, subelliptical in lateral view; laterally compressed. End margins narrow, well rounded. Dorsal margin strongly arched; cardinal angles rounded. Ventral margin almost straight; very gentle oral concavity. Greatest length well below mid-height; greatest height and width median. Surface of valves smooth.

Dimensions.-

	Length	Height
LV, RT/SIR/539	0.47	0.20
RV, RT/SIR/540	0.47	0.20

Distribution.- Sample: OS6, Shortland Island.

Remarks.- Similar in shape to *P. commune* McKenzie, 1967 (Recent, S Australia) but differs in the structure of the inner margin and radial pore canals. *Paradoxostoma propearcuatum* Hartmann, 1978 (Recent, W Australia) differs in being more strongly arched dorsally.

Paradoxostoma sp. F
(Fig. 4, Nos 15, 16; Pl. 1, Figs 1-3)

Material.- 3 adult valves.

Diagnosis.- A large, elongate, subelliptical species of *Paradoxostoma*. Anterior narrowly but well rounded. Posterior margin strongly caudate; extremity subventral. Dorsal margin strongly arched. Ventral margin almost straight. Greatest length subventral; greatest height median. Surface of valves smooth.

Dimensions.-

	Length	Height
RV, RT/SIR/544	0.70	0.19
LV, RT/SIR/545	0.68	0.19
LV, RT/SIR/546	0.68	0.19

Distribution.- Sample: R3, Palau Ringit Island, Pulau Seribu, Java Sea (Watson, 1988 MS). Present study samples: 13, 60, OS6, Guadalcanal and Shortland islands.

Remarks.- The subventral position of the caudal process distinguishes this species. The present authors consider it to be a new species but it must remain with open nomenclature because of the paucity of material.

Genus *Javanella* Kingma, 1948

Type species.- *Javanella kendengensis* Kingma, 1948.

Remarks.- We follow Keij (1957) and Warne *et al.,* 2006 in separating this genus from the closely related *Pellucistoma* Coryell & Fields, 1937. Species of *Javanella* are more angular than the more rounded species of *Pellucistoma*. While the former genus is probably most common in the Indo-Pacific, some clearly ovate species of *Pellucistoma* also occur in the Pacific, such as *Pellucistoma* sp. Whatley *et al.* (2004) from the Pitcairn Group (Pl. 4, Figs 18-20).

Javanella dolichostracon sp. nov.

(Fig. 4, Nos 14, 17; Pl. 1, Figs 6-8)

Derivatio nominis.- Gr. *δολιχος* - dolichos, long; plus *οστρακον* - ostrakon, a shell, meaning long shell. With reference to the elongate shape of this species.

Holotype.- LV, RT/SIR/548. Plate 1, Fig. 6.

Type locality and horizon.- Honiara Bay, Guadalcanal, sample 40, 3,100 feet offshore, east of the Matanikau River, 20 fathoms. Unconsolidated, medium-grained sand. Recent.

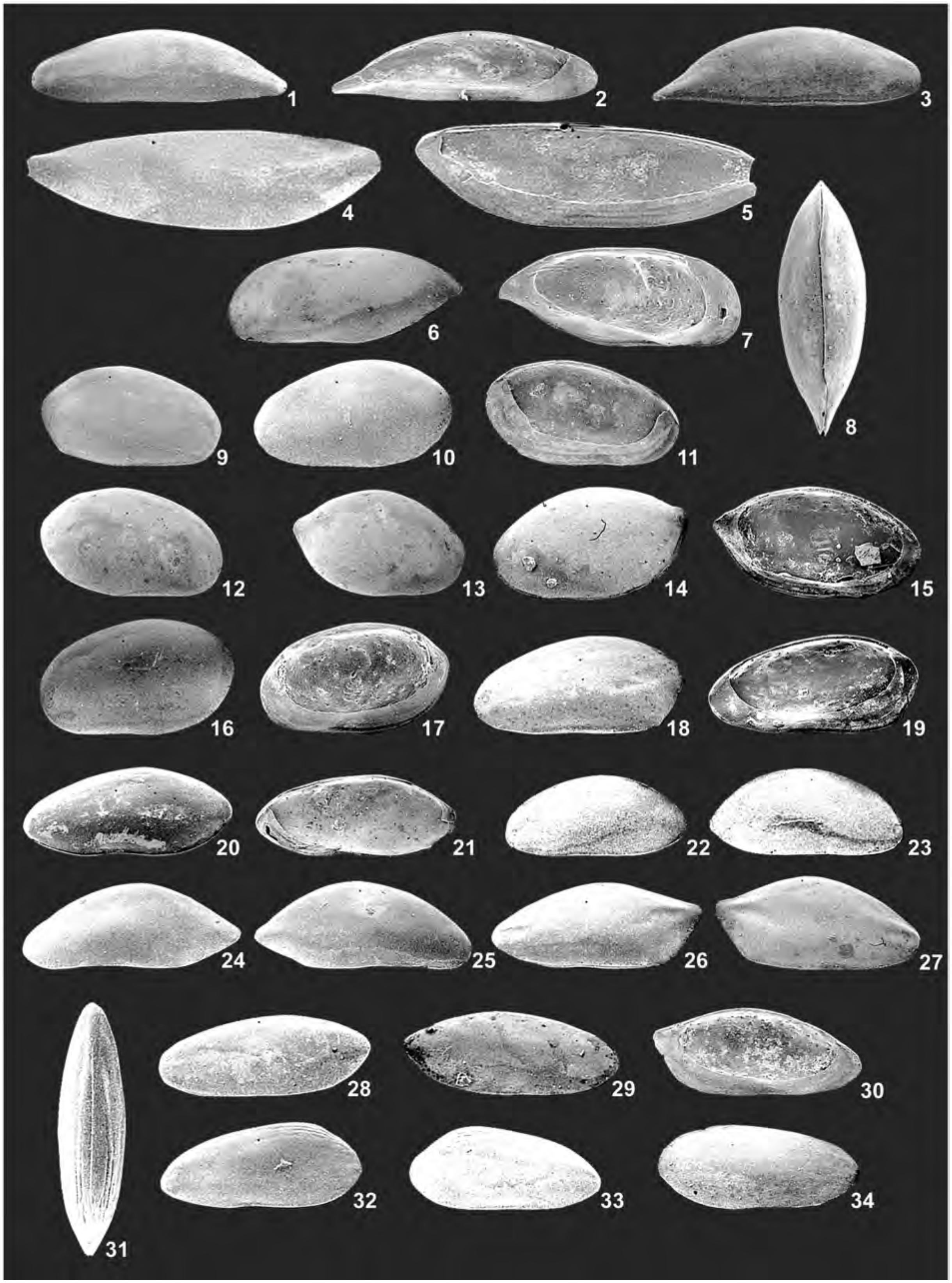
Material.- 37 valves and carapaces, all adults.

Diagnosis.- A small to medium, notably elongate species of *Javanella*, subelliptical in shape in dorsal and lateral views. Dorsal margin almost straight; posterior caudal process slightly downturned. Inner lamella broad with large, semicircular anterior vestibulum.

Description.- Small to medium. Thin-shelled. Translucent. Notably elongate subelliptical in lateral and dorsal views. Anterior margin rounded extremity just below mid-height. Posterior margin strongly and sharply caudate, extremity just above mid-height. Dorsal margin very gently arched: cardinal angles rounded. Ventral margin almost straight, obliquely sloping to caudal process. Greatest length just above mid-height; greatest height and width medianly. Valves subequal in size, evenly inflated medianly, narrow anteriorly and posteriorly. Surface smooth. Npc's numerous, large, evenly distributed. Inner lamella moderately wide with large semicircular anterior vestibulum and narrower, crescentic posteroventral vestibulum. Inner margin subparallel to outer margin. Approximately 19 anterior and 18 posterior true mpc's straight, slightly inflated medianly; approximately 15 false canals, evenly spaced about inner lamella. Selvage weak, peripheral anteriorly; subperipheral posteroventrally. Hinge weakly merodont. Central muscle scars towards anterior, 4 adductors, median 2 scars more elongate; heart-shaped frontal scar.

Plate 1. ***1-3**, Paradoxostoma* sp. F *1,* Left valve RT/SIR/546 external lateral view x 67.6, *2,* Left valve RT/SIR/545 internal view x 70.6, *3,* Right valve RT/SIR/544 external lateral view x 68.6. ***4-5**, Paradoxostoma* sp. cf. *Paradoxostoma mimicus* Whatley *et al*., 2000. *4,* Right valve RT/SIR/541 external lateral view x 74.2. *5,* Right valve RT/SIR/543 internal view x 76.3. ***6-8,** Javanella dolichostracon* sp. nov. *6*, Holotype left valve RT/SIR/548 external lateral view x 89.6. *7,* Paratype left valve RT/SIR/549 internal view x 93.6. *8,* Paratype carapace RT/SIR/547 dorsal view x 95.8. ***9-11**, Paradoxostoma* sp. aff. *P. angolensis* Hartmann, 1974 *9, 10,* Carapace RT/SIR/512/513 *9,* external lateral view of RV x 55.9, *10,* external lateral view of LV x 61.0, *11,* Left valve RT/SIR/514 internal view x 58.3. ***12, 16, 17**, Paradoxostoma fuscumaculosus* Hartmann, 1981. *12,* Right valve RT/SIR/504 external lateral view x 61.1, *16,* Left valve RT/SIR/505 external lateral view x 58.3, *17,* Right valve RT/SIR/506 internal view x 57.6. ***13-15**, Paradoxostoma sp. A. 13,* Right valve RT/SIR/509 external lateral view x 54.4, *14,* Left valve RT/SIR/508 external lateral view x 61.8, *15,* Left valve RT/SIR/510 internal view x 68.5. ***18-19**, Paradoxostoma bilocus sp. nov. 18,* Holotype female left valve RT/SIR/524 external lateral view x 56.9, *19,* Paratype male right valve RT/SIR/525 internal view x 59.7. ***20-21**, Paradoxostoma*. sp. D. *20,* Carapace RT/SIR/529, external lateral view of LV x 63.8. *21,* Right valve, RT/SIR/531, internal view x 63.2. ***22-23**, Paradoxostoma* sp. E. *22*, Left valve RT/SIR/539 external lateral view x 70.2, *23,* Right valve RT/SIR/540 external lateral view x 72.3. ***24-25**, Paradoxostoma* sp. C. *24,* Left valve RT/SIR/522 external lateral view x 57.4, *25,* Right valve RT/SIR/523 external lateral view x 58.2. ***26, 27, 30,** Paradoxostoma sophicos* sp. nov. *26,* Holotype left valve RT/SIR/517 external lateral view x 59.4, *27,* Paratype right valve RT/SIR/518 external lateral view x 60.3, *30,* Paratype left valve RT/SIR/519 internal view x 61.7. ***28-29,** Paradoxostoma* sp. B. *28,* Left valve RT/SIR/515 external lateral view x 73.1, *29,* Right valve RT/SIR/516 external lateral view x 73.1. ***31-33,** Paradoxostoma dorsostriata* sp. nov. *31,* Paratype carapace RT/SIR/533 dorsal view x 64.8, *32,* Holotype left valve RT/SIR/534 external lateral view x 66.0, *33,* Paratype right valve RT/SIR/535 external lateral view x 64.2. ***34,** Paradoxostoma heronislandensis* Hartmann, 1981, right valve RT/SIR/538 external lateral view x 60.0.

Plate 1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Dimensions.-

	Length	Height	Width
Holotype LV, RT/SIR/548	0.48	0.19	
Paratype C, RT/SIR/547	0.48	0.19	0.17
Paratype LV, RT/SIR/549	0.47	0.19	
Paratype LV, RT/SIR/550	0.46	0.18	
LV, RT/SIR/551	0.47	0.19	
RV, RT/SIR/552	0.47	0.19	

Distribution.- Samples: 14, 29, 30, 40, 41, 53-58, 60, 61, Guadalcanal.

Remarks.- The present species differs from other species of the genus in being more elongate with an almost straight dorsal margin, slightly down-turned caudal process and a large anterior vestibulum. It is probably closest to *Javanella kendegensis* Kingma, 1948 but differs in its greater length and its more pointed posterior. It resembles *Paradoxostoma rubrum* Müller, 1894 (Recent, Gulf of Naples) but differs from the latter in that the caudal process is shorter, the dorsal margin straighter, the marginal pore canals are more numerous and the central muscle scars are undivided.

Family PECTOCYTHERIDAE Hanai, 1957

Genus *Keijia* Teeter, 1975

Type species.- *Cythere demissa* Brady, 1868.

Keijia demissa (Brady, 1868)

(Fig. 4, Nos 29, 30; Pl. 2, Figs 1-8)

1868 *Cythere demissa* sp. nov. Brady, p. 180, Pl. 12, Figs 1, 2.
1990 *Keijia demissa* (Brady). Gou, p. 26, Pl. 3, Fig. 38a, b.
2001 *Keijia demissa* (Brady). Titterton, Whatley & Whittaker, p. 38, Pl. 2, Figs 13-19 (*q.v.* for synonymy).
2001 *Keijia demissa* (Brady). Mohan, Ravi, Hussain & Rao, p. 2, Pl. 1, Figs 14, 15.
2006 *Keijia demissa* (Brady). Warne, Whatley & Blagden, Pl. 6, Figs 7-9.

Material.- 80 valves and carapaces, A-1 to adult.

Dimensions.-

	Length	Height	Width
Female C, RT/SIR/553	0.39	0.18	0.15
Male C, RT/SIR/554	0.41	0.19	0.14
Male RV, RT/SIR/557	0.42	0.19	
Female LV, RT/SIR/558	0.39	0.19	
Female RV, RT/SIR 559	0.38	0.19	
Male RV, RT/SIR/560	0.42	0.19	
Female LV, RT/SIR 561	0.39	0.20	
Female RV, RT/SIR 563	0.36	0.18	
Male LV, RT/SIR 564	0.42	0.19	

Distribution.- The species is widely distributed in the Indo-Pacific, Australasia and also occurs in the Atlantic and Caribbean. It does not, however, occur at Easter Island or in the Pitcairn Group (Whatley *et al.* 2000 & 2004 respectively). See Witte (1993) and Titterton *et al.* (2001) for additional details of distribution. Present study samples: 1, 29, 30, 40-42, 53-58, 60, 61, Guadalcanal.

Remarks.- See Titterton *et al.* (2001).

Keijia radiata sp. nov.

(Fig. 4, Nos 37, 38; Pl. 2, Figs 9-15)

Derivatio nominis.- L. from the ribs of the surface ornament which seem to radiate from a mid-dorsal position.

Holotype.- Female LV, RT/SIR/577. Plate 2, Fig. 9.

Type locality and horizon.- Honiara Bay, Guadalcanal, sample 5, 800 feet offshore from the mouth of the River Matanikau. 3 fathoms. Medium-grained sand. Recent

Material.- 337 valves and carapaces, A-2 to adults.

Diagnosis.- A small species of *Keijia* possessing a strong reticulate ornament of which the muri parallel to the anterior, dorsal and posterior margins, are strengthened to form ribs which arch over the subcentral area. A characteristic, lipped, oval depression occurs just behind the main antero-marginal rib.

Description.- Small. Thick-shelled. Opaque. Female notably shorter than male. Elongate, subrectangular in lateral view; subelliptical in dorsal view. Anterior margin obliquely rounded; in RV becoming gently concave anterodorsally, extremity mid-height. Posterior margin narrower, truncated; extremity mid-height. Dorsal margin straight, anterior cardinal angles rounded, posterior angle almost a right angle. Ventral margin very gently biconvex; oral concavity more pronounced in RV. Greatest length at mid-height; greatest height at anterior cardinal angle; greatest width at posterior third. Slight overlap of LV at anterior cardinal angle. Surface strongly reticulocostate with peripheral preferred alignment parallel to margins. Overall laterally, the ribs present the form of a reclined sigma and appear to radiate from about mid-dorsal, by virtue of ribs that are parallel to the anterior, dorsal and posterior margins then arch over the central area. A prominent anterior marginal rib extends subparallel to and at some distance from that margin and then extends along the ventral margin. Immediately behind the antero-marginal rib, at about mid-height, there is a small characteristic oval, ribbed depression. Single width reticulae occupy the intercostal areas. Mpc's few, small, evenly spaced on muri. Inner lamella moderately wide, broadest anteriorly. Inner margin subparallel to outer margin with a large, irregular anterior and a narrow, crescentic posterior vestibulum. Approximately 10 anterior and 7 posterior mpc's, simple, slightly sinuous. Hinge pentadont. RV anterior terminal element an irregular elongate tooth; median element long locellate groove widening distally; posterior terminal element a small, strong ovate tooth. Four closely spaced adductor muscle scars in a vertical row, median 2 more elongate; v-shaped frontal scar, open dorsally.

Dimensions.-

	Length	Height	Width
Holotype female LV, RT/SIR/577	0.39	0.19	
Paratype female C, RT/SIR/575	0.41	0.19	0.16
Paratype male C, RT/SIR/576	0.48	0.21	0.19
Paratype male RV, RT/SIR/578	0.45	0.20	
Female RV, RT/SIR/580	0.41	0.20	
Male LV, RT/SIR/581	0.45	0.20	
Male LV, RT/SIR/583	0.47	0.21	
Male RV, RT/SIR/584	0.45	0.20	

Distribution.- Samples: 1, 2, 5, 13, 14, 16, 17, 19, 40-42, 53-56, 58, 60-64, OS6, Guadalcanal and Shortland islands.

Remarks.- The present species is somewhat similar to *Pectocythere? broomensis* Hartmann, 1978 (Recent eulittoral, W Australia) but they differ in the detail of the ornament. In the former the dominant muri are concentric to the anterior, dorsal and posterior margins whereas in *P? broomensis* they are more concentric to the ventral margin. *Keijia parademissa* Warne *et al.,* 2006 (Port Darwin, Australia) is very similar but differs in the details of the ornament and in particular it lacks the ribbed depression anteriorly, so characteristic of the present species. Three specimens collected from Honiara Bay are presumed to be females as they are smaller than all the other specimens. The specimens from Shortland Island are conspicuously larger than those from Honiara Bay.

Keijia brachychthonus sp. nov.

(Fig. 4, Nos 31, 34; Pl. 2, Figs 16-22)

Derivatio nominis.- Gr. *βραχυς* - brachys, short, plus *χφονος* - cththonos, land, ground = shortland. With reference to the type locality of this species, Shortland Island.

Holotype.- LV, RT/SIR/566. Plate 2, Fig. 16.

Type locality and horizon.- Shortland Island, sample OS6. Exact locality unknown but thought to be from the intertidal zone near a coral reef, on the NE coast of the island, in the vicinity of Rokuai Island. Coarse-grained coral sand. Recent.

Material.- 23 valves and carapaces, all adults.

Diagnosis.- A small reticulo-costate species of *Keijia* in which the peripheral muri concentric to the margins are strengthened forming ribs, dominated by a strong, anterior submarginal rib. Two large fossae developed behind anterior rib, dorsal one extending to just below anterior cardinal angle. Marginal rib extending across ventrolateral surface and also parallels dorsal margin. Fourth rib from posterior margin extends ventrally to ventro-lateral rib.

Description.- Small. Thick-shelled. Opaque. Sexual dimorphism not observed. Elongate, subrectangular in lateral and dorsal views. Anterior margin broadly rounded, extremity well below mid-height. Posterior margin narrower, bluntly rounded, bearing 5 strong, spinose marginal denticles on ventral half, extremity mid-height. Dorsal margin straight. Ventral margin biconvex with broad, oral concavity. LV overlaps RV at anterior cardinal angle and anterior margin. Greatest length well below mid-height; greatest height through anterior cardinal angle; greatest width at posterior third. Surface strongly reticulo-costate with peripheral muri concentric to margins, strengthened to form ribs, dominated by a strong anterior submarginal rib that extends across the ventrolateral surface and then parallels posterior margin. Two large fossae, separated by a short horizontal rib, developed behind anterior rib; dorsal one extending to below anterior cardinal angle. The fourth rib from the posterior margin extends ventrally to the ventrolateral rib. The central area is largely covered with rather chaotic reticulae. Npcs small, simple, moderately numerous, regularly distributed. Inner lamella broad anteriorly, narrower posteriorly. Inner margin subparallel to outer margin with a mushroom-shaped anterior vestibulum. Mpc's few; 6-8 anterior and 5-6 posterior canals. Selvage sub-peripheral with narrow flange around entire margin. Hinge pentadont; RV anterior terminal element a short ridge, dentate on dorsal edge; median element a long, thin, finely crenulate groove; posterior terminal element a subquadrate tooth comprising 3 denticles; LV complementary. Four closely adjacent, subovate adductor muscle scars with a large, almost v-shaped frontal scar.

Dimensions.-

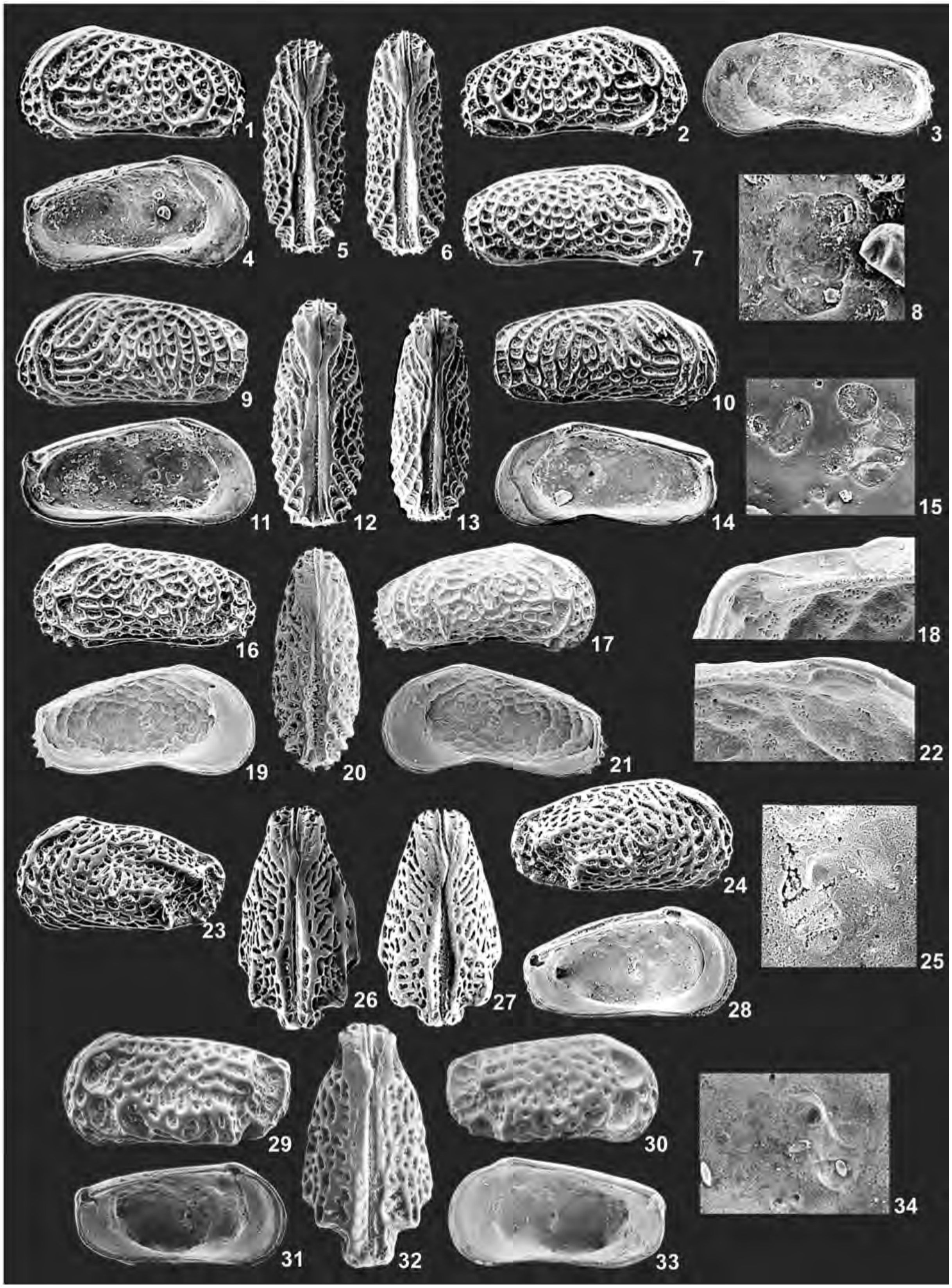
	Length	Height	Width
Holotype LV, RT/SIR/566	0.48	0.24	
Paratype C, RT/SIR/565	0.49	0.24	0.19
Paratype RV, RT/SIR/568	0.48	0.24	
Paratype LV, RT/SIR/570	0.48	0.24	
RV, RT/SIR/569	0.47	0.25	
LV, RT/SIR/571	0.48	0.23	
RV, RT/SIR/572	0.49	0.25	

Distribution.- Samples: 13, 17, 40, 54-56, 60, OS6, Guadalcanal and Shortland islands.

Remarks.- The present species is similar to some of the variants of *Keijia demissa* but none of these have the characteristic vertically orientated apophysis of the 4th rib from the posterior that extends to the ventrolateral rib, although two of the specimens figured by Teeter, 1973, from the Hawaiian Islands of that species Figs 2e, f (non Figs 2a-d) are most similar. However, the most similar species is *K. parademissa* Warne *et al*,. 2006 (N Australia). This species is a little smaller than the present one (L=0.40-0.46) and has a much less chaotic central reticular field. It also has the two large anterior fossae almost subdivided by small horizontal riblets that are entirely absent in the present species and the ventrally directed extension of the 4th from posterior rib is sometimes formed from the 3rd such rib and is never of the same configuration of the present species. There is no doubt, however, that the two species are closely related. Another similar species is *K. australis* Yassini *et al*., 1993, but the latter species bears large marginal spines posteriorly and lacks the ribs that parallel the dorsal margin. *K. tjokrosapoetroi* Dewi, 1997 is smaller (L = 0.40-0.42) and has ornament that differs significantly in detail.

Plate 2**. *1-8,*** *Keijia demissa* (Brady, 1868) *1,* Female left valve RT/SIR/558 external lateral view x 102.6, *2,* Female right valve RT/SIR/559 external lateral view x 105.3, *3,* Male right valve RT/SIR/560 internal view x 97.6. *4, 8,* Female left valve RT/SIR/561 *4,* internal view x 105.1, *8,* detail of central muscle scar x 449.7. *5,* Female carapace RT/SIR/553 dorsal view x 97.4. *6,* Male carapace RT/SIR/554 dorsal view x 97.6. *7,* Male right valve RT/SIR/557 external lateral view x 102.5. ***9-15,*** *Keijia radiata* sp. nov. *9,* Holotype female left valve RT/SIR/577 external lateral view x107.7. *10,* Paratype male right valve RT/SIR/578 external lateral view x 91.1. *11,* Male left valve RT/SIR/581 internal view x 93.3. *12,* Paratype female carapace RT/SIR/575, dorsal view x 100.0. *13,* Paratype male carapace RT/SIR/576, dorsal view x 79.2. *14, 15,* Female right valve RT/SIR/580 *14,* internal view x 97.6, *15,* detail of central muscle scar x 329.7. ***16-22,*** *Keijia brachychthonus* sp. nov. *16,* Holotype left valve RT/SIR/566 external lateral view x 83.3. *17,* Paratype right valve RT/SIR/568 external lateral view x 95.8. *18, 19, 22,* Paratype left valve RT/SIR/570 *18,* detail of posterior part of hinge x 359.7, *19,* internal view x 83.3, *22,* detail of anterior part of hinge x 359.7. *20,* Paratype carapace RT/SIR/565, dorsal view x 81.6. *21,* Right valve RT/SIR/569, internal view x 85.1. ***23-28,*** *Kotoracythere inconspicua* (Brady, 1880) *23*, Female left valve RT/SIR/587 external lateral view x 102.7. *24,* Male right valve RT/SIR/586 external view x 105.3. *25, 28,* Male left valve RT/SIR/590, *25,* detail of central muscle scars x 329.8, *28,* internal view x 95.0. *26,* Male carapace RT/SIR/585, dorsal view x 105.3. *27,* Female carapace RT/SIR/592, dorsal view x 90.7. ***29-34,*** *Kotoracythere doratus* sp. nov. *29,* Paratype left valve RT/SIR/596 external view x 100.0. *30-34,* Holotype carapace RT/SIR/594/595 *30,* external lateral view of RV x 95.0, *31,* internal view of LV x 95.0, *32,* dorsal view x 110.0, *33,* internal view of RV x 97.5, *34,* detail of central muscle scars of LV x 411.4.

Plate 2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Genus *Kotoracythere* Ishizaki, 1966

Type species.- *Cythere inconspicua* Brady, 1880.

Kotoracythere inconspicua (Brady, 1880)
(Fig. 4, Nos 32, 33; Pl. 2, Figs 23-28)

1880 *Cythere inconspicua* sp. nov. Brady, p. 70, Pl. 13, Fig. 1a-d.
1990 *Kotoracythere inconspicua* (Brady). Gou, p. 26, Pl. 3, Fig. 37a, b.
1993 *Kotoracythere inconspicua* (Brady). Jellinek, p. 121, Pl. 7, figs 157-165; Pl. 8, Figs 166-170.
1995 *Morkhovenia inconspicua* (Brady). Zhao, p. 71, Pl. 3, Figs 2a, b.
1995 *Morkhovenia inconspicua* (Brady). Tabuki & Nohara, p. 343, Pl. 4, Fig. 6.
1996 *Kotoracythere inconspicua* (Brady). Babinot & Degaugue-Michalski, p. 361.
2001 *Kotoracythere inconspicua* (Brady). Titterton, Whatley & Whittaker, p. 38, Pl 2, Figs 13-19 (q.v. for synonymy).
2006 *Kotoracythere inconspicua* (Brady). Warne, Whatley & Blagden, Pl. 6, Fig. 6.

Material.- 122 valves and carapaces, A-2 to adult.

Dimensions.-

	Length	Height	Width
Male C, RT/SIR/585	0.38	0.20	0.19
Male RV, RT/SIR/586	0.37	0.19	
Female LV, RT/SIR/587	0.37	0.19	
Male LV, RT/SIR/ 590	0.40	0.20	
Female LV, RT/SIR/591	0.39	0.20	
Female C, RT/SIR/592	0.43	0.22	0.24
Male RV, RT/SIR/593	0.40	0.22	

Distribution.- Widely distributed in tropical sublittoral environments across the Indo-Pacific (except eastern Pacific) and Australia. Believed by Witte & van Harten (1991) and Witte (1993) to have been transported by passive dispersal by ships (like *K. demissa*, into the Caribbean and Atlantic). Fossil records Miocene-Pleistocene of Midway Island; Neogene of the Andaman Islands and Quaternary of the Solomon Islands. Present study samples: 1, 2, 13-17, 32, 40, 57, 58, OS6, Guadalcanal and Shortland islands.

Remarks.- This species is readily distinguished from *Kotoracthere doratus* sp. nov. of the present study by its less cribrose reticulation.

Kotoracythere doratus sp. nov.
(Fig. 4, Nos 35, 36; Pl. 2, Figs 29-34)

Derivatio nominis.- *δορατος* doratos, a spear. With reference to the shape of this species in dorsal view.

Holotype.- RV, RT/SIR/594. Plate 2, Fig. 30.

Type locality and horizon.- Honiara Bay, Guadalcanal, sample 2, 500 feet offshore, west of Point Cruz, 1.5 fathoms. Medium-grained, coral sand. Recent.

Material.- 4 adult valves and one A-1 juvenile from the Solomon Islands plus 48 valves and carapaces from the Pulau Seribu, Java Sea in the Watson Collection housed in the NHM of which the type material bears the catalogue numbers KW/PS/717-722.

Diagnosis.- A very small to small, subrectangular species of *Kotoracythere* with maximum height at the anterior cardinal angle and a gradual convergence to the posterior. Hastate in dorsal view. Ornament robustly reticulo-costate. Fossae non cribrose.

Description.- Very small to small. Thick-shelled. Opaque. Sexual dimorphism not observed. Subrectangular in lateral view; hastate in dorsal view. Anterior margin broadly rounded; extremity at mid-height. Posterior margin narrower, bluntly rounded to straight posterodorsally, better rounded posteroventrally extremity at mid-height in RV, subdorsal in LV. Dorsal margin almost straight, slightly sloping posteriorly. Anterior cardinal angle obtusely rounded, posterior cardinal angle almost a right angle. Ventral margin almost straight, very gentle oral concavity. Greatest length at mid-height; greatest height through anterior cardinal angle; greatest width through postero-ventral inflation. LV slightly larger than RV with small overlap at dorsal cardinal angle. Valves inflated posterodorsally and posteroventrally. Eye tubercle inconspicuous. Surface of valves strongly reticulate; fossae irregular in size and shape, many coalesce. A coarse complex of fossae occurs ventro-laterally, mostly posterior of mid-length. A strong, anterior submarginal rib extends from the ocular region subparallel to the anterior margin and then extends around the ventral, posterior and dorsal margins back to the eye tubercle. Behind this rib anteriorly there are two scalloped areas bisected by a short horizontal rib at mid-height. A similar scalloped area, crossed by a number of thin horizontal ribs occurs dorsally. Posterolaterally, three short ribs are developed by the strengthening of the horizontal component of the muri. Npcs few, small, evenly distributed. Inner lamella broad, particularly anteriorly; LOC and inner margin coincident except for very small mid-anterior vestibulum; MPC's few, complex, branching; anteriorly a broad canal branches into 7-8 canals distally; 4 long, sinuous anterior canals and 7-8 long, sinuous posterior canals which may merge proximally to form the narrow vestibulum. Hinge pentadont, RV anterior terminal element a subovate tooth, median element a long locellate groove, posterior terminal element a strong ovate tooth; LV complementary but with a small ovate tooth below posterior distal end of median element accommodated by a shallow socket in RV. A vertical row of 4 closely spaced, subovate adductor scars; v-shaped frontal scar with anterior arm reduced.

Dimensions.-

	Length	Height
Holotype C, RT/SIR/594/595	0.40	0.20
Paratype LV, RT/SIR/596	0.41	0.20
Paratype RV, RT/SIR/597	0.40	0.19
Paratype A-1 LV, RT/SIR/598	0.35	0.19

Distribution.- Samples: 5, Pulau Pari; K9, K29, K39, K43, K47, K58, K62; Pulau Kotok Kecil; PT2, PT5, PT12, PT15, PT27, PSM47, Pulau Petundang Kecil; R2, R16, R17, Pulau Ringit, Java Sea (Watson, 1988 MS). Present study samples: 2, 17, 57, Guadalcanal.

Remarks.- The material from the Java Sea is rather smaller than the type material, being always no longer than 0.40 mm. It is also somewhat less strongly ornate and the scalloped anterior depressions are less strongly developed. This species differs from *K. inconspicua* in shape and ornament, especially in its lack of cribrose fossae. *Kotoracythere cuneola* (Brady, 1890) differs in shape and in its cribrose fossae.

Genus *Hypocritecythere* gen. nov.

Type species.- *Hypocritecythere polymorphica* gen. et sp. nov.

Derivatio nominis.- Gr. *υποκριτης* - hypocrites, an actor, dissembler plus *κυθερε* - *kythere* = *Hypocritecythere*. With reference to the fact that this species, although a member of the Pectocythereidae, externally mimics a number of genera of the Trachyleberididae.

Diagnosis.- A subrectangular genus, of the Pectocytheridae, heavily calcified with a robust reticulo-costate ornament with various nodes and tubercles. Distinct subcentral tubercle and anterior ocular rib; eye tubercle small, glassy. Sieve-type normal pore canals. Inner lamella well developed, avestibulate. Marginal pore canals closely spaced, particularly anteriorly, moderately numerous, slightly inflated medianly. Hinge pentadont. RV with anterior terminal boss; median locellate groove which expands distally and posterior terminal boss. Four adductor scars with a large v-shaped frontal scar.

Distribution.- Miocene? to Recent, Caribbean? and Solomon Islands.

Remarks.- Externally this genus superficially resembles a number of trachyleberid genera such as *Puriana* Coryell and Fields, 1953 and hemicytherid genera such as *Urocythereis* Ruggieri, 1950. *Puriana? congesticostata* Bold, 1963 (Upper Miocene, Trinidad) possibly belongs in this genus. The present genus differs from *Munseyella* Bold, 1957 in being much less acuminate posteriorly and less expansively rounded anteriorly, while being less flared anteriorly.

Hypocritecythere polymorphica gen. et sp. nov.
(Fig. 4, Nos 26, 27; Pl. 5, Figs 1-9)

Derivatio nominis.- Gr. πολυς *polys*, many plus μορφε morphe, form, many forms. With reference to the variable morphology demonstrated by individual members of this species.

Holotype.- LV, RT/SIR/679. Plate 5, Fig. 1.

Type locality and horizon.- Honiara Bay, Guadalcanal, sample 2, 500 feet offshore, west of Point Cruz, 1.5 fathoms. Medium-grained, coral sand. Recent.

Material.- 53 valves and carapaces, adult to A-3 juv.

Diagnosis.- A medium to large species of *Hypocritecythere*, elongate subrectangular in lateral and dorsal views. Characterised by a reticulate ornament of irregular reticulation and secondary riblets on crests of primary muri; subcentral tubercle and posteriorly 3 tubercles in an oblique row from posterior cardinal angle to ventral margin which vary in their development. Deep sulcus immediately behind and parallel to broad anterior, submarginal ocular ridge.

Description.- Medium to large. Very thick-shelled. Elongate subrectangular in lateral and dorsal views. Anterior margin broadly rounded with strong marginal frill anteroventrally: extremity below mid-height. Posterior margin narrower strongly caudate posterodorsal slope slightly concave; posteroventral slope straight, oblique, bearing 5 short, strong marginal denticles: extremity at mid-height in male, just above mid-height in female. Dorsal margin straight: anterior cardinal angle obtuse, posterior angle a prominent, rounded right angle. Ventral margin broadly through anterior cardinal angle; greatest width median, LV > RV with overlap at cardinal angles and along posterodorsal margin. Valves with subcentral tubercle and inflated posteriorly into 3 tubercles in an oblique row from posterior cardinal angle to ventral margin. Tubercles less well developed in ?male LV; in ?male RV joined by a ridge. ?Male RV with a deep concavity posteroventrally. Deep sulcus immediately behind and concentric to strong, broad anterior submarginal ocular ridge. Eye-tubercle conspicuous, small glassy. Surface of valves strongly reticulate, muri broad, fossae irregular, restricted but deep. Fine secondary reticulation on muri with secondary ribs on crests of primary muri. Npcs large, sieve-type moderately numerous, evenly distributed. Inner lamella well developed LOC and inner margin coincident and subparallel to OM. MPCs moderately numerous; approximately 30 anterior and 25 posterior canals, straight, slightly inflated medianly, closely spaced, particularly anteriorly. Selvage very strongly developed except at posterior extremity, subperipheral and subparallel to OM, well developed flange. Hinge pentadont: RV anterior terminal element a strong boss; median element a long locellate groove which expands distally; posterior terminal element a strong boss, LV complementary. Both valves with a strong ridge below anterior half of hinge reflected externally by a deep reticulum. Central muscle scars sited in subcentral depression, comprises 4 adductors, dorsal scar ovate, ventral scars more elongate, large v-shaped frontal scar open dorsally.

Dimensions.-

	Length	Height	Width
Holotype LV, RT/SIR/679	0.76	0.39	
Paratype C, RT/SIR/678	0.77	0.36	0.35
Paratype LV, RT/SIR/680	0.68	0.34	0.34
Paratype RV, RT/SIR/681	0.74	0.38	
Paratype RV, RT/SIR/682	0.76	0.37	
Paratype RV, RT/SIR/688	0.65	0.34	
RV, RT/SIR/683	0.72	0.38	
LV, RT/SIR/685	0.70	0.37	
LV, RT/SIR/686	0.70	0.35	
RV, RT/SIR/687	0.68	0.33	

Distribution.- Offshore Quaternary marine deposits from Guadalcanal (Williams, 1980 MS). Miocene, Nendø, Guadalcanal (Hughes, 1977 MS). Present study samples 1, 2, 5, 13-17, 19, 29, 30, 40-42, 53, 55, 58, 61, 62, OS5, Guadalcanal and Shortland islands.

Remarks.- The present species is more strongly tuberculate externally than *Puriana congestocostata* Bold, 1965 (Miocene, Trinidad). The reticulate ornament and three posterior tubercles distinguish the present species from *Puriana pacifica* Benson, 1959 (Recent, NW America).

Although two distinct size groups can be distinguished which may reflect sexual dimorphism, morphology varies within these groups. These variants are outlined below.

1. Large RV distinguishable by a conspicuous posterior rib extending almost vertically from just behind the posterior cardinal angle to the ventral margin. From this rib, a second rib branches obliquely at mid-height to the posteroventral margin. There is a marked concavity of the valve ventrally, just posterior to mid-length. Similar LV are also present, but this ventral concavity is less strongly developed.

2. Large RV and RV with ventral concavity absent but, al-

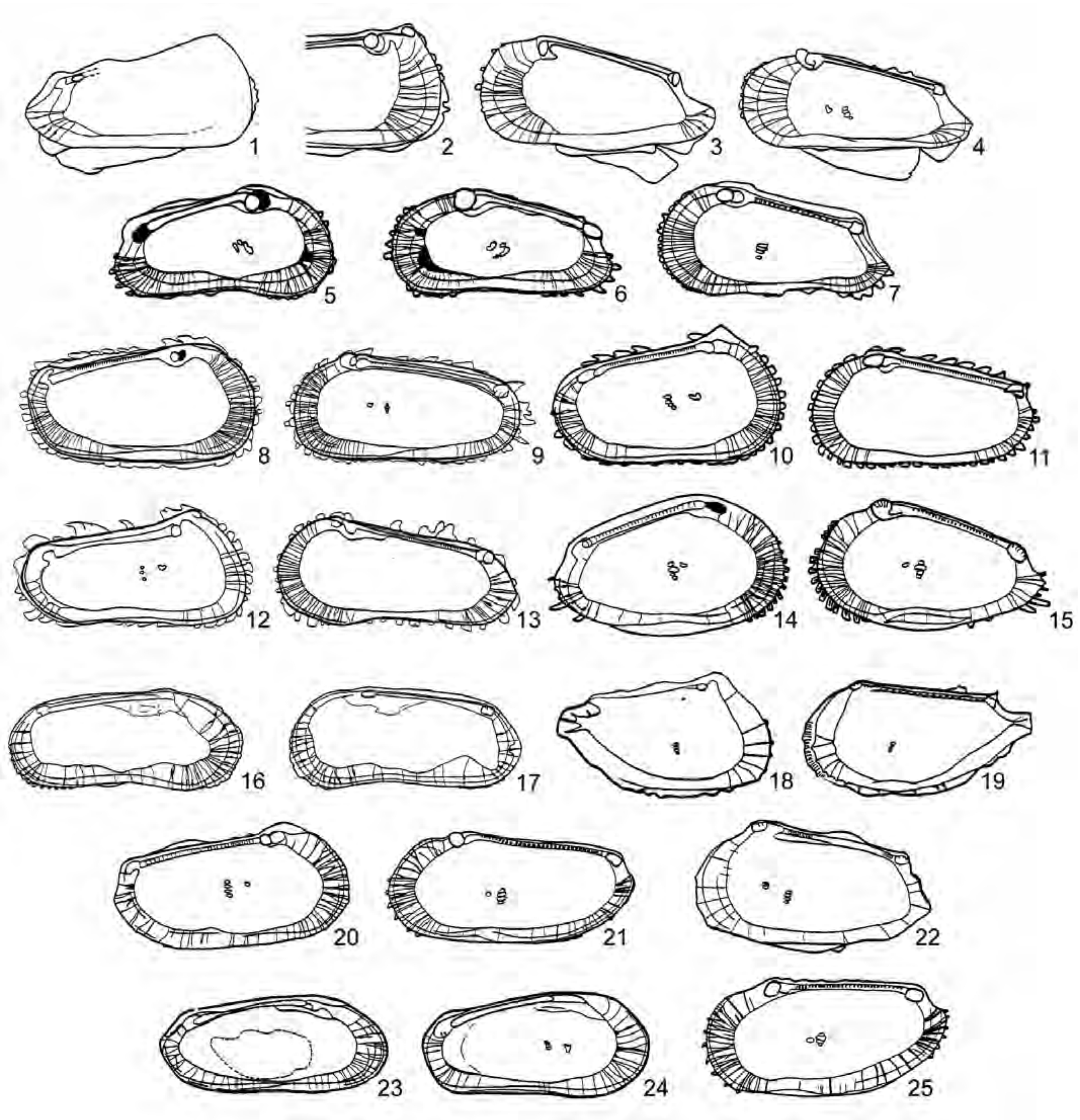


Figure 5. Internal lateral views. ***1-3**, Alatahermanites hastatus* Whatley and Titterton, 1981 *1,* Left valve RT/SIR/870 x 52.9. *2,* Left valve RT/SIR/871 x 53.0. *3,* Right valve RT/SIR/872 x 53.7. ***4**, Alatahermanites infundibulata* (Brady, 1890) right valve OS 11765 x 54.7. ***5-6**, Neocaudites pacifica* Allison and Holden, 1971 *listrotus* sub sp. nov. *5,* Paratype left valve RT/SIR/332 x 70.8. *6,* Paratype right valve RT/SIR/331 x 68.0. ***7**, Cletocythereis rastromarginata* (Brady, 1880) female right valve RT/SIR/626 x 58.3. ***8-9**, Ponticocythereis manis* Whatley & Titterton, 1981 *8,* Female left valve RT/SIR/882 x 48.6. *9,* Male right valve RT/SIR/883 x 73.5. *10-11, Ponticocythereis pollostus* sp. nov. ***10**,* Female left valve RT/SIR/880 x 63.6. ***11***, Male right valve RT/SIR/881 x 69.4. ***12-13**, Ponticocythereis spinosa* Whatley & Titterton, 1981.*12,* Holotype left valve OS 11750 x 47.9. *13,* Paratype right valve OS 11749 x 52.2. ***14-15**, Ruggeria caryonautes* sp. nov. *14,* Female left valve RT/SIR/664 x 61.4. *15,* Male right valve RT/SIR/668 x 64.8. ***16-17**, Arculacythere polytrematus* sp. nov. *16,* Female left valve RT/SIR/674 x 41.7. *17,* Male right valve RT/SIR/673 x 41.5. ***18-19**, Neomonoceratina entomon* (Brady, 1890) *18,* Left valve RT/SIR/602 x 76.7. *19,* Right valve RT/SIR/601 x 79.1. ***20-21**, Alocopocythere reticulata fultura* subsp. nov. *20,* Left valve RT/SIR/619 x 56.3. *21,* Right valve RT/SIR/620 x 56.1. ***22**, Neomonoceratina koenigswaldi* Keij,1954 right valve RT/SIR/603 x 65.5. ***23**, Australimoosella polypleuron* sp. nov. paratype left valve RT/SIR/204 x 61.4. ***24**, Australimoosella* sp. left valve RT/SIR/413 x 51.5. ***25**, Alocopocythere reticulata perfecta* subsp. nov. female right valve RT/SIR/614 x 55.6.

most at the same position, a strong tubercle is developed. The posterior rib is only developed in the dorsal half of its length, terminating just posterior to a well developed tubercle at mid-height.

3. Small RV and LV, similar in ornament to the second variant but the reticulate ornament is becoming obscured by heavier decalcification. Two carapaces were found in the material, both with similar RV in which the posterior rib and the posteroventral concavity were well developed. However, the LV differed; consequently, the variation seen in the larger valves can not be explained by sexual dimorphism. Nevertheless, it is believed that all the different morphological forms belong to a single species.

Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948
Subfamily TRACHYLEBERIDINAE Sylvester-Bradley, 1948

Genus *Alatahermanites* Whatley and Titterton, 1981

Type species.- Alatahermanites hastatus Whatley and Titterton, 1981.

Alatahermanites hastatus Whatley and Titterton, 1981
(Fig. 5, Nos 1-3; Pl. 3, Figs 1, 3, 4, 8)

1981 *Alatahermanites hastatus* Whatley and Titterton, p.164, Pl. 2, Figs 13-20.
1993 *Alatahermanites beckeri* Jellinek, p.128, Pl. 10, Figs 215-217.

Material.- 16 valves and carapaces, A-2 to adult.

Dimensions.-

	Length	Height	Width
Holotype LV, OS 11762	0.68	0.34	
Paratype C, OS 11763	0.70	0.33	0.50
Paratype RV, OS 11764	0.67	0.33	
LV, RT/SIR/870	0.68	0.34	
LV, RT/SIR/871	0.69	0.34	
RV, RT/SIR/872	0.67	0.33	

Distribution.-Jellinek (1993) encountered the species in reef environments along the coast of Kenya. Present study samples: 15, 29, 57, Guadalcanal.

Remarks.- This enigmatic blind trachyleberidid is discussed by Whatley & Titterton (1981: 64). The material described by Jellinek is so similar to the present species that we have no hesitation in considering it to be conspecific.

Alatahermanites infundibulata (Brady, 1890)
(Fig. 5, No. 4; Pl. 3, Fig. 7)

1890 *Cythere infundibulata* Brady, p. 502, Pl. 2, Figs 15, 16.
1981 *Alatahermanites* sp. Whatley & Titterton, p.165, Pl. 2, Figs 21, 22.

Material.- Adult RV.

Dimensions.-

	Length	Height
RV, OS 11765	0.64	0.32

Distribution.- Brady encountered the species from Fiji. Present study sample: 15, Guadalcanal.

Remarks.- McKenzie (1986: 101) shows *Alatahermanites* sp. of Whatley & Titterton to be the same as Brady'sspecies *Cythere infundibulata* and illustrates the lectotype, a RV (Hancock Museum, Reg. No. B451; pl. 2, fig. 9) and Jellinek (1993: 129) also points this out.

Genus *Cletocythereis* Swain, 1963

Type species.- Cythere rastromarginata Brady, 1880.

Cletocythereis rastromarginata (Brady, 1880)
(Fig. 5, No. 7; Pl. 3, Figs 2, 5, 6, 9)

1880 *Cythere rastromarginata* sp. nov. Brady (pars), p.82, Pl. 16, Fig. 2a-d (non Fig. 1a-d).
2001 *Cletocythereis rastromarginata* (Brady). Titterton *et al.*, p. 39, Pl. 3, Figs 5-9 (*q.v.* for synonymy).

Material - 2 AC, 3 ARV and 1 A-1.

Dimensions.-

	Length	Height	Width
Female C, RT/SIR/621	0.65	0.32	0.28
Female RV, RT/SIR/622	0.65	0.31	
Female RV, RT/SIR/623	0.61	0.32	
Female C, RT/SIR/624	0.65	0.32	0.28
A-1 LV, RT/SIR/625	0.55	0.31	
Female RV, RT/SIR/626	0.60	0.32	

This material is rather smaller than type material in the Natural History Museum, in which a female paralectotype (BMNH no. 1988.383) is 0.68 mm long. The male lectotype is 0.77 mm long (see Titterton *et al.*, 2001).

Distribution.- The species occurs in the Recent of the Hawaiian Islands in sediments dredged off reefs at 40 fathoms (Brady, 1880). It has been recorded at 40 fathoms in the Bass Straits and the eulittoral of the coast of southeast Australia, from the Pleistocene of Midway Island and Subrecent? of the Hawaiian Islands (Holden, 1967). Present study samples: 29, OS5, OS6, Guadalcanal and Shortland islands.

Remarks.- Brady's (1880) type material is illustrated by Titterton *et al.*, 2001 and a full discussion of the synonymy is given and a discussion about the confusion between the two species illustrated by Brady in 1880; *Cythere rastromarginata* and *C. bradyi*. In summary here, *Cythere rastromarginata* is alate and *C. bradyi* is not, although it is very similar in size, shape and ornament.

Genus *Neocaudites* Puri, 1960

Type species.- Neocaudites neviani Puri, 1960.

Neocaudites pacifica Allison and Holden, 1971 *listrotus* sub sp. nov.

(Fig. 5, Nos 5, 6; Pl. 3, Figs 17-21)

Derivatio nominis.- Gr. *λιστροτος - listrotos,* listrotos, levelled, smoothed. With reference to the extent to which celation has smoothed the surface ornament of this subspecies smoothed relative to the nominative subspecies, *N. pacifica pacifica* Allison & Holden, 1971.

Holotype.- Carapace RT/SIR/329. Plate 3, Fig. 17.

Type locality and horizon.- Shortland Island, sample OS6. Exact locality unknown but thought to be from the intertidal zone near a coral reef, on the NE coast of the island, in the vicinity of Rokuai Island. Coarse-grained coral sand. Recent.

Material.- 2 valves and 13 carapaces, all adults.

Diagnosis.- A subspecies of *Neocaudites pacifica* in which celation of the ornament has virtually rendered the lateral surface smooth due to the infilling of the fossae.

Description.- Small to medium. Subrectangular in lateral view; subelliptical in dorsal view valves inflated just ventral to posterior cardinal angle. Anterior margin broadly rounded, with strong denticles extending ventrally; apex at mid-height. Posterior margin subcaudate, with three strong spines postero-ventrally and apex below mid-height. Dorsal margin straight with slight overreach by dorsal rib medianly and sloping posteriorly. Ventral margin with wide, shallow oral concavity. A wide, shallow vertical sulcus occurs just posterior to small glassy eye tubercle. Surface of valves ornamented by ribs, intercostal areas virtually smooth. A broad anterior, occular rib extends from the eye tubercle, continuing around the ventral and posterior margins. Three less well developed ribs radiate from the conspicuous posterodorsal swelling, one subparallel to the dorsal margin to the sulcus; another obliquely and anteriorly to the subcentral tubercle and the third towards the posterior extremity, just failing to connect to the peripheral rib. Npc's few, irregularly distributed, usually in lines parallel to ribs, many as large pore conuli. Inner lamella wide with narrow, crescentic anterior vestibulum. Approximately 34 anterior and 24 posterior rpc's, majority bifurcating distally. Hinge holamphidont, robust and with smooth posteromedian element. Central muscle scars comprise 4 adductor scars, with dorsal scar indistinct, ovate and separate from other 3 scars, ventral scar almost subdivided; almost dumb-bell shaped frontal scar.

Dimensions.-

	Length	Height	Width
Holotype C, RT/SIR/329	0.47	0.26	0.18
Paratype C, RT/SIR/328	0.50	0.26	0.18
Paratype C, RT/SIR/330	0.48	0.24	0.18
Paratype RV, RT/SIR/331	0.50	0.25	
Paratype LV, RT/SIR/332	0.48	0.26	

Distribution.- Samples: 2, OS6 Guadalcanal and Shortland islands.

Remarks.- The subspecies differs from *Neocaudites pacifica pacifica* Allison and Holden, 1971 (Recent, Clipperton Island) in that in the latter the intercostal areas are ornamented by more numerous pits. Watson (1988 MS) describes another subspecies from the Java Sea that differs in that the celation process is incomplete and fossae of the ornament are only partly infilled. The present material possess large pore conuli that are absent in *N. terryi* Holden, 1967 (Neogene, Hawaii) and there is no short rib, just posterior to the anterior ocular rib as in *N. terryi*, although there is a small antero-ventral tubercle in the same area.

Genus *Ponticocythereis* McKenzie, 1967

Type species.- *Cythere militaris* Brady, 1866.

Ponticocythereis manis Whatley & Titterton, 1981
(Fig. 5, Nos 8, 9; Pl. 4, Figs 9-18)

1981 *Ponticocythereis manis* Whatley & Titterton, p.162, Pl.2, Figs.1-12.
1981 *Actinocythereis verrucifera* Hartmann, p. 104, Pl. 4.
1986 *Ponticocythereis manis* Whatley & Titterton. Cabioch *et al*., p. 26, Pl. 9, Figs 1-4.
1996 *Ponticocythereis manis* Whatley & Titterton. Warne & Whatley, p.167, Figs 1A, B, Pl. 1, Figs 1-5, 6a,b, 8a, b.

Material.- 121 valves and carapaces, A-3 to adult.

Dimensions.-

	Length	Height	Width
Holotype female LV, OS 11753	0.72	0.42	0.21
Paratype female C, OS 11754 (open)	0.78	0.45	0.23
Paratype male C, OS 11755 (open)	0.81	0.43	0.21
Paratype female RV, OS 11756	0.72	0.42	0.18
Paratype male LV, OS 11757	0.80	0.43	0.20
Female LV, RT/SIR/882	0.74	0.43	
Male RV, RT/SIR/883	0.74	0.38	

Mean Dimensions.-

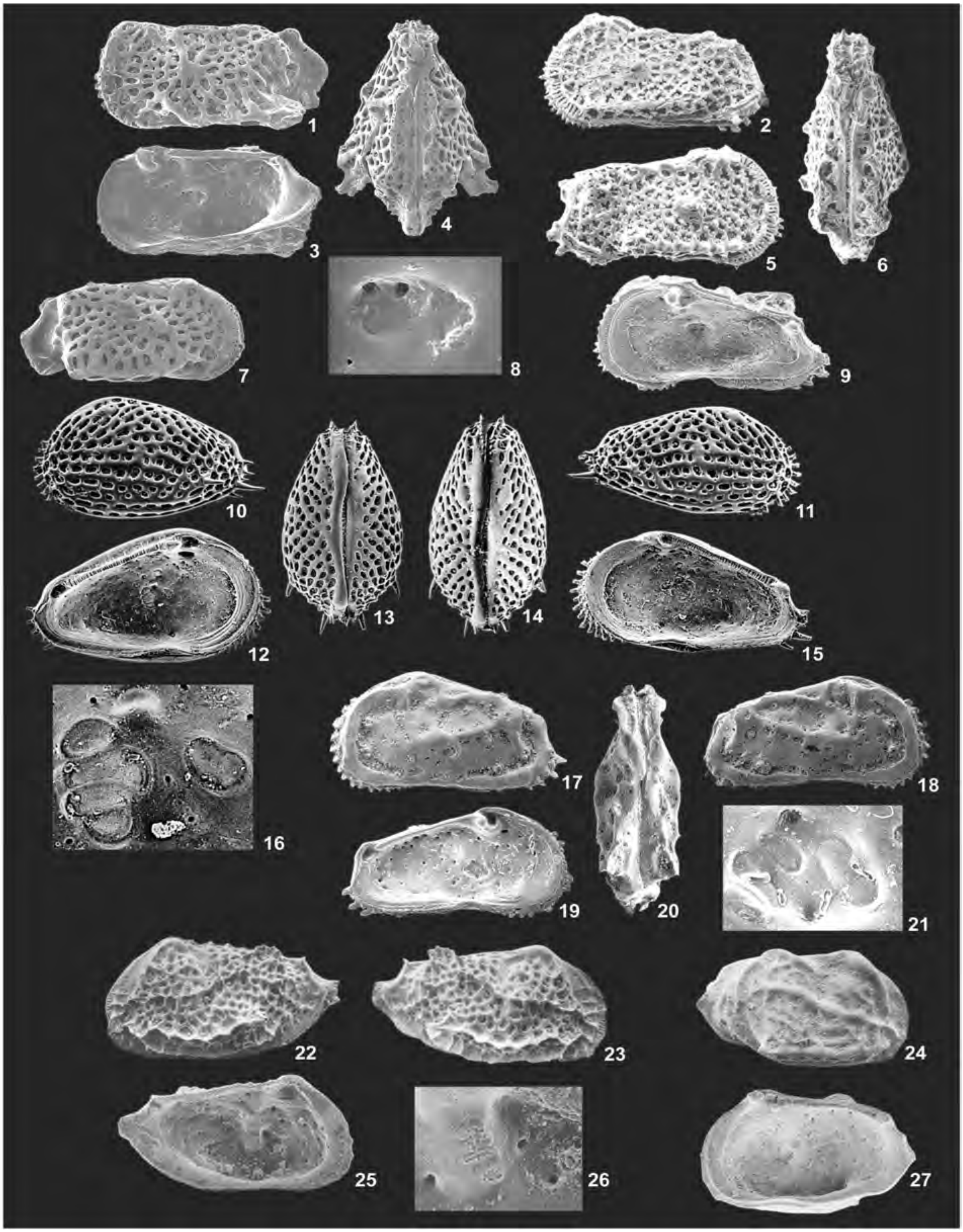
	Length	Height	Width
7 Female C	0.74(0.70-0.76)	0.43(0.41-0.45)	0.41(0.39-0.42)
4 Male LV	0.79(0.78-0.80)	0.43(0.42-0.43)	
16 A-1 LV	0.58(0.56-0.62)	0.35(0.32-0.36)	
13 A-2	0.46(0.44-0.47)	0.27(0.26-0.28)	
5 A-3	0.37(0.36-0.37)	0.22(0.21-0.24)	

Distribution.- Hartmann (1981) found only females living on coral reefs and dead valves from coral sands, Heron Island, NW Australia. Present study sample: OS6 Shortland Island.

Remarks.- Hartmann (1981) placed the present species in *Actinocythereis*. The present authors note that juvenile

Plate 3. ***1, 3, 4, 8,*** *Alatahermanites hastatus* Whatley and Titterton, 1981. *1,* Holotype left valve OS 11762 external lateral view x 60.3. *3, 8,* Paratype right valve OS 11764 *3,* internal view x 59.7, *8,* detail of central muscle scars x 408.6. *4,* Paratype carapace OS 11763 external lateral view of RV x 64.6. ***7,*** *Alatahermanites infundibulata* (Brady, 1890) right valve OS 11765 external lateral view x 58.6. ***2, 5, 6, 9,*** *Cletocythereis rastromarginata* (Brady, 1880) *2,* Female carapace RT/SIR/624 external lateral view of left valve x 61.5. *5,* female right valve RT/SIR/622 external lateral view x 64.6. *6,* Female carapace RT/SIR/621 dorsal view x 88.0. *9,* Female right valve RT/SIR/623 internal view x 68.9. ***10-16,*** *Ruggeria caryonautes* sp. nov. *10,* Holotype female left valve RT/SIR/661 external view x 62.3. *11,* Male right valve RT/SIR/662 external view x 66.7. *12, 16,* Female left valve RT/SIR/664 *12,* internal view x 73.7, *16,* detail of central muscle scars x 401.1. *13,* Paratype female carapace RT/SIR/658 dorsal view x 67.2. *14,* Paratype male carapace RT/SIR/659 dorsal view x 71.9. *15,* Paratype male right valve RT/SIR/665 internal view x 79.2. ***17-21,*** *Neocaudites pacifica* Allison and Holden, 1971 *listrotus* sub sp. nov. *17,* Holotype carapace RT/SIR/329 external lateral view of LV x 89.4. *18,* Paratype carapace RT/SIR/330 external lateral view of RV x 83.3 *19, 21,* Paratype left valve RT/SIR/332 *19,* internal view x 83.3, *21,* detail of central muscle scar x 411.6, *20,* Paratype carapace RT/SIR/328, dorsal view x 86.0. ***22, 23, 25, 26,*** *Neomonoceratina entomon* (Brady, 1890) *22,* Left valve RT/SIR/599 external view x 93.3. *23,* Right valve RT/SIR/600 external view x 95.5. *25, 26,* Left valve RT/SIR/602 *25,* internal view x 95.3, *26,* detail of central muscle scars x 362.7. ***24, 27,*** *Neomonoceratina koenigswaldi* Keij, 1954 right valve RT/SIR/603 *24,* external view x 38.0. *27,* internal view x 38.0.

Plate 3



valves clearly show the species to be *Ponticocythereis*. For a full description and discussion the reader is referred to Whatley & Titterton, 1981, p.162. The males of the present species are relatively more elongate and slimmer than the females.

Ponticocythereis spinosa Whatley & Titterton, 1981
(Fig. 5, Nos 12, 13; Pl. 4, Figs 19-21)

1890 *Cythere militaris*. Brady, p. 504; Pl. 2, Figs 24-26.
?1965 *Trachyleberis militaris* (Brady). McKenzie, p. 448.
1981 *Ponticocythereis spinosa* Whatley & Titterton, p.161, Pl. 1, Figs 14-21.
1981 *Actinocythereis lainensis* Wouters, p. 6, Pl. 2, Figs 1-44, Pl. 3, Figs 2a-f.

Material.- 2 adult and 2 juv. valves.

Dimensions.-

	Length	Height	Width
Holotype LV, OS 11750	0.73	0.41	0.20
Paratype RV, OS 11749	0.69	0.36	0.22

Distribution.- The species has been previously recorded from the Recent of Australia (Brady, 1890 and McKenzie, 1965) from shallow water environments. Wouters (1981) described it from the Recent of Hansa Bay, Papua New Guinea. Present study samples: 17, 30, 32, Guadalcanal.

Remarks.- The authors disagree with McKenzie's (1986: 101) suggestion that this is a junior synonym of *P. quadriserialis* (Brady, 1890). Although the two species have very similar ornament, and we are aware of Brady's note (1890: 504) "A very distinct and remarkable species, no two specimens of which are exactly alike", the size difference is too great for them to be the same. The present adult material is 0.69-0.73mm long, while Brady (1890) records 0.85 mm and McKenzie (1986) 0.80 mm.

Ponticocythereis pollostus sp. nov.
(Fig. 5, Nos 10, 11; Pl. 4, Figs 1-8)

1981 *Ponticocythereis icthyoderma* (Brady). Whatley & Titterton, p. 160, Pl. 1, Figs 1-13.
non 1890 *Cythere icthyoderma* Brady, p. 503, Pl. 2, Figs 22, 23.

Derivatio nominis.- Gr. *πολλοστος* - pollostos, the smallest, least. With reference to the fact that this is the smallest known species of the genus.

Holotype.- Female LV, OS 10910. Plate 4, Fig. 1.

Type locality and horizon.- Honiara Bay, Guadalcanal, sample 2, 500 feet offshore, west of Point Cruz, 1.5 fathoms. Medium-grained, coral sand. Recent.

Material.- 72 valves and carapaces, A-3 to adult.

Diagnosis.- A small to medium (but small for the genus) species of *Ponticocythereis* with ornament of tuberculate to spinose ribs with minutely punctate intercostal areas on which occur large pore conuli.

Description.- Subrectangular in lateral view, subelliptical in dorsal view. Sexually dimorphic with male shorter, proportionally more elongate and more laterally compressed than female. Anterior margin broadly rounded with well developed frill of marginal denticles. These are spatulate and anterodorsally in contact distally, becoming downturned, discrete and more pointed below the extremity at mid-height. Posterior margin sub-caudate, more pointed in male and with 6-8 spinose denticles; extremity above mid-height. Dorsal margin straight, interrupted by spines of dorsal rib. Ventral margin slightly biconvex; not overhung by valve tumidity. Greatest length just above mid-height; greatest height at anterior cardinal angle; greatest width through the sub-central tubercle. Eye tubercle large glassy, hemispherical. Ornament of tuberculate to spinose ribs with minutely punctate intercostal areas on which occur large pore conuli. From the eye tubercle, a spinose rib whose spines are directed dorsally, extend parallel to the anterior margin: anteroventrally the spines become subovate tubercles: the rib extends along the ventro-lateral border, gradually diverging from the ventral margin to its termination at about 1/3 the distance from the posterior extremity. An elevated rib bearing dorsally 6 large posteriorly directed spines extends from the dorsal margin around the posterior and ventral margins to its anteroventral termination. Along the latter margin, it bears strong subovate to spatulate tubercles. A median rib bearing similar tubercles extends diagonally across the valve surface, passing over the sub-central tubercle. Intercostal areas are minutely punctate as are most of the tubercles and spines. Some minute papillae occur around the bases of some spines. Npc's few, large, mostly exiting on conuli and apparently open. Inner lamella strongly developed but rather narrow. Avestibulate, inner margin and outer margin parallel. Rpc's, fairly numerous, straight to slightly sinuous and tending to be paired. On the inner lamella of the RV, just above the posterior extremity, is a distinct striated, shallow oval pit, rather reminiscent of a similar structure in some Tertiary species of *Argentinicytheretta* Rose from Patagonia. Hinge holamphidont, robustly developed. In the LV, a small tooth is developed anterior to anterior terminal socket (rather reminiscent of *Abysocythere* Benson, 1959 and *Alatahermanites hastatus* (Whatley & Titterton, 1981) and the posteromedian denticulate bar is expanded and elevated posteriorly. A shelf-like anti-slip structure occurs below the antero-median hinge element in each valve. Muscle scars as for genus.

Dimensions.-

	Length	Height	Width
Holotype female LV, OS 10910	0.48	0.35	
Paratype male C, OS 10911	0.49	0.28	0.23
Paratype female C, OS 10912	0.55	0.32	0.29
Paratype female RV, OS 10913	0.57	0.32	
Paratype male LV, OS 10914	0.49	0.24	
Paratype male RV, OS 10915	0.48	0.26	
Female LV, RT/SIR/880	0.55	0.32	
Male RV, RT/SIR/881	0.49	0.26	

Mean Dimensions.-

	Length	Height	Width
9 Female C	0.55(0.52-0.57)	0.31(0.29-0.33)	0.28(0.26-0.29)
9 Male C	0.49(0.46-0.52)	0.26(0.25-0.28)	0.23(0.22-0.25)
10 A-1 LV	0.44(0.40-0.47)	0.26(0.23-0.28)	
3 A-2	0.37(0.36-0.38)	0.22(0.21-0.22)	
1 A-3	0.30	0.19	

The longest specimen recorded by Williams (1980 MS) from the Quaternary of the Solomon Islands is 0.59 mm.

Distribution.- The species occurs in Quaternary sediments from offshore Guadalcanal (Williams, 1980 MS). Present study samples: 1, 2, 5, 13, 14, 16, 32, 40-42, 54, 55, 58, 61, 62, Guadalcanal.

Remarks.- Ponticocythereis icthyoderma (Brady) differs from the present species in being substantially larger (L=0.70 Brady, 1890; the lectotype illustrated by McKenzie, 1986, p. 99, pl. 2, fig. 14 is calculated to be 0.72 mm long) and in the former species the intercostal areas are at least partly micropapillate rather than mainly micropunctate; apart from this, the ornament of the two species is very similar. Despite this similarity, the discrepancy in size is too great, exceeding 20% length for them to represent the same contemporary species (see Whatley, 1983, 1985, Whatley *et al.,* 1983). *Ponticocythereis pollostos* differs from *P. militaris* (Brady, 1890) mainly in size and in the tuberculation of the dorsal rib. In the present species (and in *P. icthyoderma*) these tubercles are squamose, while in the former species they are spinose and strongly backward directed. *Ponticocythereis pollostos* sp. nov. seems to be the smallest known species of the genus. An approximate length for the other known species is given below:

- *P. labiata* (Brady, 1890) Brady gives 0.70mm; calculated from McKenzie's (1986) lectotype L= 0.72mm;
- *P. icthyoderma* (Brady, 1890) Brady gives 0.77mm; calculated from McKenzie's (1986) lectotype L= 0.79mm;
- *P. quadriserialis* (Brady, 1890) Brady gives 0.85 mm; calculated from McKenzie's (1986) lectotype L= 0.80mm;
- *P. militaris* (Brady, 1890) Brady gives 0.77-0.79mm; *P. costata* (Hartmann, 1978) from Hartmann, female L=0.63-0.69mm; male L=0.67-0.76mm; from Howe & McKenzie (1989: 41) L= 0.63-0.67mm; *P. cristata* (Brady, 1880) calculated from Warne's (2001) illustration of the lectotype, carapace BM 80.38.121, L= 0.78mm.

Subfamily ARCULACYTHEREINAE Hartmann, 1981

Genus *Arculacythereis* Hartmann, 1981

Type species.- Arculacythereis vacciformis Hartmann, 1981.

Remarks.- Hartmann (1981) noted that Labutis (1977 MS) had named, illustrated and described this family from the Great Barrier Reef, Eastern Australia but that this remained unpublished. Hartmann placed the new subfamily in the Trachyleberididae because of its weak but clearly hemiamphidont hinge. *Arculacythereis* shows some affinities with *Moosella* Hartmann, 1964 and *Angolocythereis* Hartmann, 1974 but differs in being blind.

Arculacythereis polytrematus sp. nov.

(Fig. 5, Nos 16, 17; Pl. 4, Figs 22-28)

Derivatio nominis.- Gr. *πολυς* - many, plus *τρηματος* polytrematos, perforated, many holes. With reference to the secondary ornament of numerous, small but obvious circular puncta within the fossae of the primary reticulum.

Holotype.- Male LV, RT/SIR/675. Plate 4, Fig. 22.

Type locality and horizon.-Shortland Island, sample OS5, from coral reefs to the east of Rokuai Island, off the NE coast of the island. Recent.

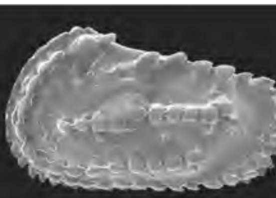
Material.- Twenty-six valves and carapaces, A-2 to adult.

Diagnosis.- A strongly dimorphic species of *Arculacythere*, elongate subrectangular, in lateral view. Characterised by an ornament of polygonal reticulate with rather narrow muri over entire surface, secondary punctation within primary fossae and a third order ornament of fine puncta aligned along some primary muri, especially dorsally.

Description.- Large. Thick-shelled. Opaque. Sexually dimorphic; female larger, more inflated posteriorly and anteriorly thus appearing more constricted medianly than male. Elongate subrectangular in lateral view: sub-elliptical in dorsal view. Anterior margin broadly rounded bearing a frill of small marginal denticles; extremity at mid-height. Posterior margin slightly narrower, bluntly rounded with frill-like marginal denticles; extremity at mid-height. Dorsal margin straight; cardinal angles obtusely rounded, anterior angle the more prominent. Ventral margin gently biconcave with broad oral concavity. Greatest length at mid-height; greatest height just anterior to anterior cardinal angle; greatest width in posterior third. Valves subequal. Eye-tubercle absent. Small, poorly developed subcentral tubercle. Surface of valves strongly reticulate, muri rather narrow, fossae polygonal, irregularly distributed over entire surface. Numerous secondary puncta within primary fossae and a third order ornament of fine puncta aligned along some primary muri, especially dorsally. Inner lamella wide, avestibulate, LOC sinuous, differing between sexes: in male subparallel to outer margin anteriorly and posteriorly and sinuous ventrally, fused area narrowest orally; in female directed towards selvage anterodorsally where the fused area is at its narrowest, sinuous ventrally, curvature posteroventrally more strongly developed than in male, subparallel to outer margin posteriorly. Rpc's moderately numerous; 30-33 anterior canals in male; approximately 24 in female; approximately 14 posterior canals in both sexes, slightly sinuous, some paired, inflated distally. Hinge weakly developed, hemiamphidont; RV anterior terminal element a strong, elongate tooth; median element a long, smooth groove; posterior terminal element a strong, quadrate, quadrilobate bar; LV hinge complementary with dorsal accommodation groove. Both valves with strong platform for muscle attachment below and separate from anterior half of hinge. Central muscle scars comprise 4 small, subovate adductor scars; dorsomedian scar more elongate, on posterior rim of subcentral depression and small v-shaped frontal scar open dorsally on anterior rim.

Plate 4. ***1-8,*** *Ponticocythereis pollostus* sp. nov. *1,* Holotype female left valve OS 10910 external lateral view x 83.3. *2,* Paratype male right valve OS10915 external lateral view x 83.3 *3, 4,* Paratype male left valve OS 10914 *3,* detail of central muscle scars x 256.0, *4,* internal view x 73.3. *5,* Paratype male carapace OS 10911 dorsal view x 81.6. *6,* Paratype female carapace OS 10912, dorsal view x 70.9. *7, 8,* Paratype female right valve OS 10913 *7,* internal view x 81.6, *8,* detail of central muscle scars x 256.0. ***9-18,*** *Ponticocythereis manis* Whatley & Titterton, 1981. *9,* Paratype male left valve OS 11757, external view x 61.8. *10,* Holotype female left valve OS 11753, external view x 55.6. *11,* Paratype female right valve OS 11756, external view x 55.6. *12, 15, 16, 17,* Paratype female carapace OS 11754 *12,* internal view of LV x 52.6, *15,* internal view of RV x 55.1, *16,* detail of central muscle scars of RV x 250.0, *17,* detail of central muscle scars of LV x 251.0. *13, 14, 18,* Paratype male carapace OS 11755 *13,* internal view of LV x 50. 6, *14,* internal view of RV x 51.9, *18,* detail of central muscle scars of right valve x 250.0. ***19-21,*** *Ponticocythereis spinosa* Whatley & Titterton, 1981, *19, 21,* Paratype right valve OS 11749 *19,* detail of central muscle scars x 67.8. *21,* internal view x 66.1. *20,* Holotype left valve OS 11750 external view x 56.2. ***22-28,*** *Arculacythere polytrematus* sp. nov. *22,* Holotype male left valve RT/SIR/675 external lateral view x 48.2. *23,* Paratype male right valve RT/SIR/672 external view x 50.6. *24, 28,* Female right valve RT/SIR/674 *24,* internal view x 42.9, *28,* detail of central muscle scars x 212.8. *25,* Male left valve RT/SIR/673, internal view x 48.8. *26,* Female carapace RT/SIR/670 dorsal view x 49.4. *27,* Paratype female right valve RT/SIR/671, external view x 49.4.

Plate 4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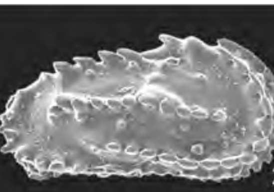
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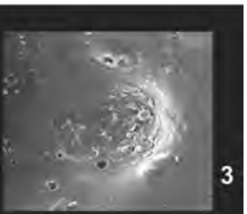
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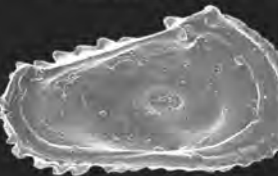
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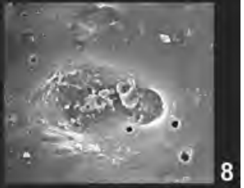
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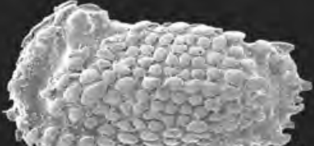
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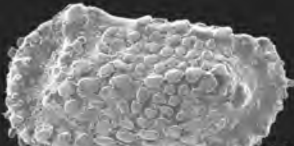
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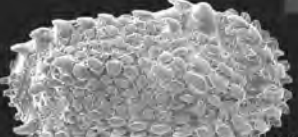
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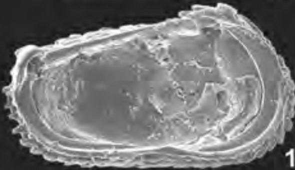
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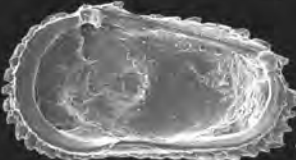
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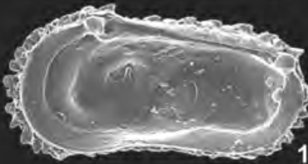
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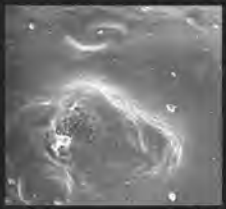
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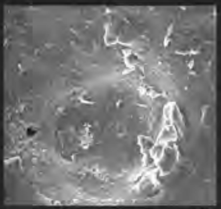
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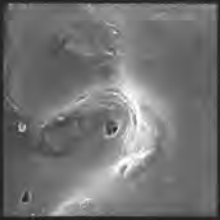
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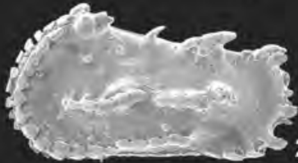
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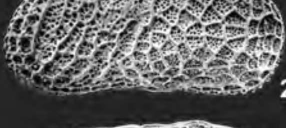
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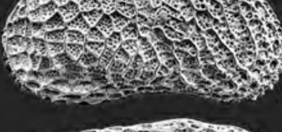
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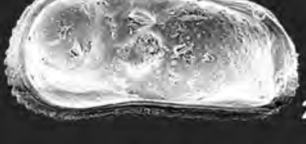
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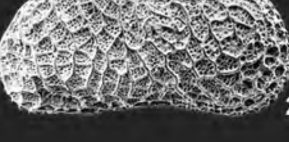
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Dimensions.-

	Length	Height	Width
Holotype male LV, RT/SIR/675	0.83	0.37	
Paratype female C, RT/SIR/670	0.85	0.42	0.38
Paratype female RV, RT/SIR/671	0.85	0.41	
Paratype male RV, RT/SIR/672	0.79	0.38	
Male RV, RT/SIR/673	0.82	0.37	
Female LV, RT/SIR/674	0.84	0.41	
A-1 RV, RT/SIR/676	0.69	0.32	
Female RV, RT/SIR/677	0.84	0.41	

Mean Dimensions.-

	Length	Height
3 Female LV	0.87(0.86-0.88)	0.42(0.41-0.43)
3 Male LV	0.82(0.82-0.83)	0.37
4 A-1 RV	0.68(0.67-0.69)	0.34(0.32-0.35)
3 A-2	0.55(0.53-0.57)	0.29(0.28-0.30)

Distribution.- Samples: OS5, OS6, Shortland Island,

Remarks.- The present species differs from the type *A. vacciformis* Hartmann, 1981 (Recent, NE Australia) in that the reticulae are more complete anteriorly and posteriorly. *Arculacythereis polytrematus* is also similar in size, shape and ornament to *Cythere ovalis* Brady, 1880 (=*Cythere hardingi* nom. nov. Puri and Hulings, 1976) but differs in secondary punctate ornament and a more concave ventral margin. *Arculacythereis* sp. of Howe & McKenzie, 1989 (N Australia) is notably smaller (L=0.68mm), has wider and rounded muri in the reticulum and lacks the secondary punctation.

Subfamily CYTHERETTINAE Triebel, 1952

Genus *Alocopocythere* Siddiqui, 1971

Type species.- *Alocopocythere transcendens* Siddiqui, 1971.

Remarks.- Siddiqui (1971) erected the genus to accommodate seven early Tertiary species from Western Pakistan. He also included *Trachyleberis fossularis* Lubimova & Guha 1960, from the Miocene of Kutch, India. Subsequently, the genus has proved to be an important element of Tertiary to Recent faunas in the Indo-West Pacific area. Gramann (1975, p.16) remarked that *Alocopocythere* closely resembled *Neocytheretta* Morkhoven, 1963 in external morphology and structure of the hinge. However, he argued that, although the latter possesses a *Cytheretta*-like inner margin, as this structure was very deciduous, it may be a junior synonym of *Neocytheretta*. Malz (1980) discussed the differences in hard part morphology between these two genera from the Pliocene-Pleistocene of Taiwan and demonstrated them in tabular form (p.48) and concluded that *Alocopocythere* was a genus distinct from *Neocytheretta* and this has been accepted by most subsequent workers.

Genus *Alocopocythere* Siddiqui, 1971

Alocopocythere reticulata (Hartmann, 1964)

1964 *Bradleya reticulata* Hartmann, p. 108, Figs 269, 274-278, Pls 46, 47, 49.

Alocopocythere reticulata fultura subsp. nov.
(Fig. 5, Nos 20, 21; Pl. 5, Figs 10-15)

Derivatio nominis.- L. *fultus* - to prop up, support, buttress. With reference to the vertically aligned, posteroventral pillar-like rib that appears to buttress the posterolateral spine.

Holotype.- LV, RT/SIR/616. Plate 5, Fig. 10.

Type locality and horizon.- Honiara Bay, Guadalcanal, sample 56, 1,900 feet offshore, east of Point Cruz, very fine grained sand, 15 fathoms. Recent.

Material.- 43 valves and carapaces, A-2 to adult.

Diagnosis.- A reticulate sub-species of *Alocopocythere reticulata*, the reticulation being continuous to the anterior marginal ridge, being "stretched" longitudinally postero- and ventrolaterally and with a vertically aligned posterolateral rib extending ventrally from the postero-lateral spine.

Description.- Medium. Thick-shelled. Opaque. Sexual dimorphism not observed. Subrectangular in lateral view:

subovate, bispinose and flattened mid-laterally in dorsal view. Anterior margin well rounded; 7 or 8 short, strong, regularly spaced marginal denticles anteroventrally; extremity at mid-height. Posterior margin narrower; well rounded in LV, asymmetrical and pointed in RV, with a short concave posterodorsal slope and a long, gently convex posteroventral slope, extremity above mid-height. Dorsal margin straight, slightly overhung by dorsal lateral surface; cardinal angles prominent except posterior angle of RV. Ventral margin almost straight; subparallel to dorsal margin gentle oral concavity in RV. Greatest length well above mid-height; greatest height through anterior cardinal angle; greatest width just anterior to lateral spine. LV > RV. RV posterior cardinal angle over-reached by that of LV. Surface of valves strongly reticulate with a short, backswept posteromedian spine. Reticulae rounded and rather regular and symmetrical anteriorly and dorsally but very angular and "stretched" longitudinally postero- and ventrolaterally. A submarginal rib extends from the eye tubercle, as a rim around the anterior, ventral and posterior margins with a single, peripheral row of reticula encroaching on its proximal flank anteriorly. A vertically aligned rib posteroventrally appears to buttress the posteromedian spine. Eye furrow conspicuous, just posterior to prominent, glassy eye tubercle. Secondary reticulation in solae of juveniles. Npc's numerous, simple, small evenly distributed on muri of reticulum. Inner lamella moderately wide, LOC and inner margin coincident, subparallel to outer margin. Rpc's moderately numerous with approximately 50 anterior and 19 posterior canals, almost straight, anteriorly some bifurcate, some cross, most dorsal pore posteriorly bifurcates. Hinge holamphidont, robust. RV anterior terminal element a slightly bifid tooth; anteromedian element a deep locule; posteromedian element al ong locellate groove; posterior terminal element a rounded boss. Central muscle scars comprise 4 subovate, small adductor scars in vertical row; single, ovate frontal scar. Sexual dimorphism not apparent.

Dimensions.-

	Length	Height	Width
Holotype LV, RT/SIR/616	0.65	0.34	
Paratype C, RT/SIR/615	0.66	0.32	0.27
Paratype RV, RT/SIR/617	0.65	0.33	
Paratype LV, RT/SIR/619	0.64	0.33	
RV, RT/SIR/618	0.65	0.32	
LV, RT/SIR/619	0.64	0.33	
LV, RT/SIR/620	0.66	0.33	
A-1 LV, RT/SIR/621	0.50	0.28	

Mean Dimensions.-

	Length	Height
6 RV	0.65(0.63-0.67)	0.33(0.31-0.35)
14 A-1 LV	0.48(0.47-0.50)	0.27(0.26-0.29)
2 A-2	0.37, 0.39	0.23

Distribution.- Samples: 17, 40, 41, 52, 54-58, Guadalcanal.

Remarks.- The present subspecies differs from *A. reticulata perfecta* subsp. nov. of the present study, in that it possesses a conspicuous vertical rib extending ventrally from the posteroventrolateral spine. *Alocopocythere reticulata indoaustralica* Hartmann, 1978 (Recent, W Australia) also has a posteroventolateral rib but it is not vertically inclined as in the present subspecies, also in the former the reticulation does not extend to the anterior marginal rim. The present subspecies is somewhat similar to *Neocytheretta multilineata* Zhao & Whatley, 1989 (SW Malay Peninsula) but differs in its inner lamella and the details of the reticulocostate ornament; the latter species also lacks the vertical posteroventral buttress to the posteroventrolateral spine.

Alocopocythere reticulata perfecta subsp. nov.

(Fig. 5, No. 25; Pl. 5, Figs 16-26)

1986 *Alocopocythere aff. reticulata indoaustralica* Hartmann. Cabioch *et al.*, p. 26, Pl. 8, Figs 15-19.

Derivatio nominis.- L. *perfectus* - complete, finished, perfect. With reference to the fact that in this subspecies, the reticulate ornament extends onto the extreme anterior of the lateral surface and is complete and quite regular over virtually the entire lateral surface.

Holotype.- Female left valve RT/SIR/606. Plate 5, Fig. 17.

Type locality and horizon.- Honiara Bay, Guadalcana, sample 29, 550 feet offshore, west of Point Cruz. Unconsolidated, fine-grained, coral sand. 19 fathoms. Recent.

Material.- 32 valves and carapaces, A-3 to adult.

Diagnosis.- A dimorphic sub-species *Alocopocythere reticulata*, the reticulation being continuous to the anterior marginal ridge and very regularly distributed over virtually the entire lateral surface.

Description.- Medium. Very thick-shelled. Opaque. Sexual dimorphism conspicuous; male longer, more quadrate and less tumid posteriorly than female. Subquadrate in lateral view; subhastate, bispinose in dorsal view. Anterior margin well rounded; 7-8 short, strong, regularly spaced marginal denticles anteroventrally; extremity at mid-height. Posterior margin narrower; subrounded in LV; asymmetrical in RV with short, concave posterodorsal slope and long, gently curved posteroventral slope; extremity above mid-height. Dorsal margin straight, slightly overhung by posterior tumidity in female. Cardinal angles prominent, posterior angle of RV less so. Ventral margin almost straight, parallel to dorsum in male; more inclined in female very slight oral concavity. Greatest length above mid-height; greatest height through anterior cardinal angle; greatest width just anterior of lateral spine. LV > RV. RV posterior cardinal angle over-reached by that of LV. Surface strongly reticulate, reticulae slightly preferentially orientated in horizontal plane in posterior half and ventrolaterally and extending to anteromarginal ridge. A short, conspicuous backswept spine occurs posteromedianly at about mid-height. Strong anterior marginal rim continues around ventral to posteroventral margin. Lateral reticulae do not cross anterior rim, distal to which is a single row of reticulae. Shallow eye furrow, oblique, just posterior to prominent, glassy eye tubercle. Secondary reticulation in juveniles only. Npc's numerous, small, simple, evenly distributed on muri of reticulum. Inner lamella moderately wide; LOC and inner margin coincident, subparallel to outer margin. Rpc's moderately numerous; approximately 27 anterior and 18 posterior canals, almost straight, anteriorly some bifurcate or trifurcate; dorsal most canal on posterior margin bifurcate. Hinge holamphidont, robust. RV anterior terminal element a weakly bifid tooth; anteromedian element a deep locule; posteromedian element a locellate groove; posterior terminal element a large rounded boss. Central muscle scars comprise 4 small, ovate adductor scars, in compact vertical row; frontal scar ovate.

Dimensions.-

	Length	Height	Width
Holotype female LV, RT/SIR/606	0.59	0.34	
Paratype female C, RT/SIR/604	0.62	0.34	0.33
Paratype male C, RT/SIR/605	0.60	0.31	0.27
Paratype male RV, RT/SIR/609	0.62	0.32	
Female RV, RT/SIR/607	0.61	0.33	
Male LV, RT/SIR/608	0.60	0.32	
A-1 LV, RT/SIR/610	0.48	0.29	
Female RV, RT/SIR/611	0.61	0.34	
Male RV, RT/SIR/612	0.62	0.32	
Female LV, RT/SIR/613	0.60	0.34	
Female RV, RT/SIR/614	0.63	0.32	

Mean Dimensions.-

	Length	Height	Width
3 Female C	0.63(0.62-0.64)	0.35(0.34-0.36)	0.33
7 Male LV	0.62(0.60-0.64)	0.33(0.31-0.34)	
5 A-1 LV	0.47(0.46-0.48)	0.28(0.27-0.30)	
1 A-2	0.43	0.25	
1 A-3	0.36	0.23	

Distribution.- Cabioch *et al.* (1986) encountered the subspecies in New Caledonia. Present study samples: 13, 16, 17, 29, 40, 41, 52, 53-59, 60 Guadalcanal.

Remarks.- The extension of the reticulae to the marginal rim in this subspecies distinguishes it from *A. reticulata indoaustralica* Hartmann, 1978 (Recent, eulittoral W Australia) and from *A. reticulata reticulata* (Hartmann, 1964) (Recent, Red Sea). The reticulae of the present subspecies are also somewhat smaller. *Alocopocythere kendegensis* (Kingma, 1948) (Pliocene to Recent, SE Asia and China) is rather similar in ornament although it is less elongate; it differs mainly in being notable smaller (L= 0.53-0.56). It differs from *A. reticulata* (Hartmann) 1964 morphotype A of Gramann, 1975 (Recent, Burma) in that it does not bear lateral nodes. *Alocopocythere reticulata fulta* subsp. nov. differs from the present sub-species in possessing a distinctive vertical buttress extending ventrally from the posteroventrolateral spine. Hartmann (1981) illustrated an unnamed species, questionably assigned to *Trachyleberis* which, in our opinion, is a species of *Alocopocythere*. It differs, however, from the present subspecies in that the reticulate ornament does not extend to the anterior margin.

Genus *Australimoosella* Hartmann, 1978

Type species.- *Australimoosella exmouthensis* Hartmann, 1978.

Australimoosella polypleuron sp. nov.

(Fig. 5, No. 23; Pl. 5, Figs 27, 28, 31, 35)

Derivatio nominis.- Gr. *πολυς* - poly, many, plus *πλευρον* pleuron ribs, many ribs. With reference to the ornament of numerous horizontal ribs in this species.

Holotype.- LV, RT/SIR/202. Plate 5, Fig. 31.

Type locality and horizon.- Honiara Bay, Guadalcanal, sample 58, 500 feet offshore, east of Point Cruz. 7 fathoms, very fine unconsolidated sand. Recent.

Material.- 19 valves, A-1 to adult.

Diagnosis.- A medium, very elongate species of *Australimoosella* characterised by its numerous longitudinal ribs, separated by single or double rows of circular puncta.

Description.- Small to medium. Moderately thin-shelled. Opaque. Elongate, subrectangular in lateral view, subelliptical in dorsal view. Sexual dimorphism not observed. Anterior margin broadly rounded; extremity well below mid-height. Posterior margin narrower, well rounded, becoming obliquely sloping posteroventrally; extremity above mid-height. Dorsal margin straight: cardinal angles prominent, obtusely rounded. Ventral margin almost straight. Greatest length at mid-height; greatest height through anterior cardinal angle; greatest width medianly. Eye-spot inconspicuous but large. Surface of valves ornamented by some 12 fine, longitudinally aligned ribs with delicate intercostal reticulopunctation in single or double rows between each rib. Anteriorly, 3 broad ribs, subparallel to the margin are developed, with larger reticulae being produced by their interaction with the longitudinal ribs. Posteriorly the longitudinal ribs do not extend to the margin. This area bears delicate puncta and a large pore conulus. Npc's mainly small, moderately numerous, regularly distributed. Inner lamella moderately wide, LOC and inner margin coincident and subparallel to outer margin. Rpc's moderately numerous, about 25 anterior and 14-16 posterior canals, simple, almost straight, some false. Selvage very strongly developed ventrally, becoming peripheral and weakly developed anteriorly. Hinge holamphidont, fairly robust: LV anterior element a deep socket bounded ventrally by a bar; anteromedian element a small ovate tooth and a long denticulate posteromedian bar becoming more strongly dentate posteriorly; posterior terminal element a deep socket open to interior. Salvage, immediately posterior to hinge, with small denticles. Central muscle scars sited anterodorsally around a shallow depression, comprising 4 small, closely spaced, subovate adductor scars on posterior rim of depression and a small v-shaped frontal scar, dorsally, on anterior rim.

Dimensions.-

	Length	Height
Holotype LV, RT/SIR/202	0.54	0.24
Paratype LV, RT/SIR/203	0.51	0.24
Paratype LV, RT/SIR/204	0.57	0.27
Paratype LV, RT/SIR/205	0.54	0.23
Paratype A-1, RV RT/SIR/206	0.40	0.19

Distribution.- Samples: 5, 16, 40, 54, 55, 57, 58, 60, Guadalcanal.

Remarks.- The present species is very similar in size, shape and ornament to *Australimoosella liebaui* Hartmann, 1978 (Recent eulittoral, W Australia) but differs in the detail of the anterior and posterior ornament. *Australimoosella exmouthensis* Hartmann 1978 (W Australia) has fewer, more strongly developed lateral ribs. The present species is more elongate, smaller and less acuminate posteriorly than *Bensonia knysnaensis* (Benson and Maddocks, 1964) (Recent, Knysna Estuary, South Africa) although the ornament is somewhat similar. *Australimoosella rockinghamensis* Hartmann, 1979 differs in its coarser ribs and intercostal ornament and *Australimoosella* (ex *Yassinicythere* Howe & McKenzie, 1989 a junior synonym of *Australimoosella) bassiounii* (Hartmann, 1979) in both shape and ornament.

Australimoosella sp.

(Fig. 5, No. 24; Pl. 5, Figs 29, 30, 32-34)

Description.- Medium to large, thick-shelled. Opaque. Sexual dimorphism not observed. Elongate, subrectangular in lateral view, subhastate in dorsal view. Anterior margin broadly rounded. Posterior margin slightly narrower and bluntly rounded. Dorsal margin almost straight; anterior cardinal angles rounded; posterior angle obtusely rounded. Ventral margin almost straight, gentle, broad oral concavity. Greatest length at mid-height; greatest height through anterior cardinal angle; greatest width at posterior third. Eye tubercle absent. Valves inflated posteriorly but with a narrow rim around posterior margin. A short, deep sulcus just behind anterior cardinal angle, parallel to dorsal margin, reflected internally. Surface of valves strongly ornamented by a series of smooth lateral ribs that extend obliquely anteroventrally to posterodorsally. The ribs do not reach the end margins, being cut off by ribs approximately at right angles, but anteriorly the dorsalmost two lateral ribs curve downwards parallel to the anterior margin and continue laterally and posteriorly. Behind the posterior marginal rib is a broad area ornamented by fine puncta. Intercostal areas elaborately ornamented by very deep often cribrose puncta, which are variously orientated. Npc's, small, on pore conuli posteriorly. Inner lamella broad. Rpc's moderately numerous, approximately 23 anterior and 14 posterior, simple and unbranching. Hinge modified entomodont, robust. Sulcus reflected internally by a strong ridge below anterior part of hinge. Central muscle scars appear to comprise a vertical row of 4 small, ovate adductor scars with a v-shaped frontal scar open dorsally.

Dimensions.-

	Length	Height	Width
LV, RT/SIR/413	0.66	0.32	
C, RT/SIR/414	0.71	0.33	0.33
A-2 LV,RT/SIR/415	0.48	0.25	

Distribution.- Samples: 14, 53, OS6, Guadalcanal and Shortland islands.

Remarks.- The surface ornament of longitudinal ribbing is more characteristic of *Cytheretta* Muller, 1894 but the internal characters are of *Australimoosella*. This species may represent a new genus; therefore, a complete description is given. It is tentatively placed in *Australimoosella*, because of the paucity of material. Cronin, in a preprint sent to the authors on the Ostracoda of some Central Pacific Atolls, has a similar species which he also refers to as *Australimoosella*.

Subfamily RUGGIERIAINAE Warne, Whatley & Blagden, 2006

Genus *Ruggieria* Keij, 1957

Type species.- *Cythere micheliniana* Bosquet, 1852.

Ruggeria caryonautes sp. nov.

(Fig. 5, Nos 14, 15; Pl. 3, Figs 10-16)

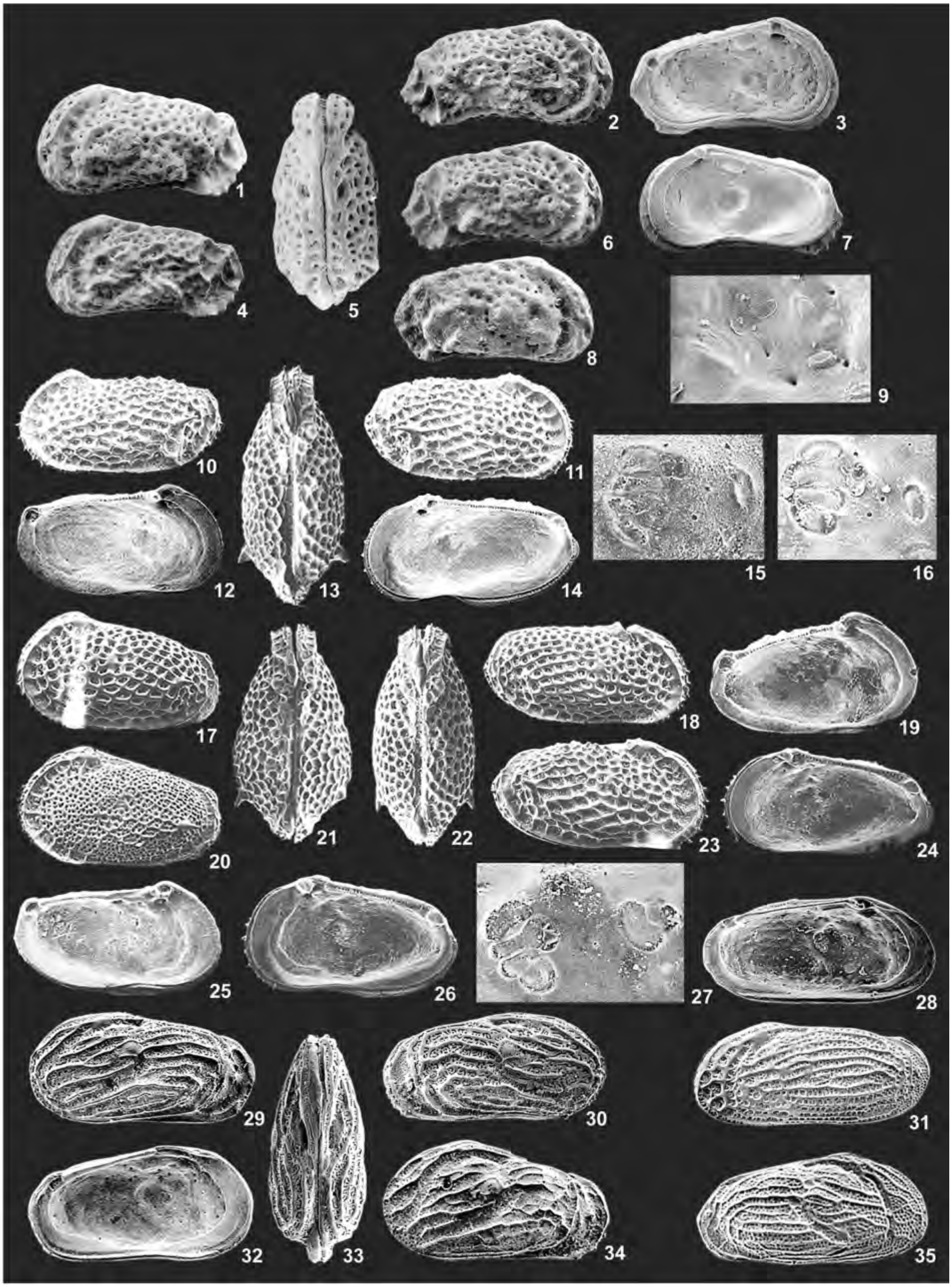
Derivatio nominis.- Gr. *καρυο-ναυτης* one who sails in a nut shell. From the two roots *καρυον* - any kind of nut or kernel and *ναυτης* - a sailor or seaman. With reference to the resemblance of the carapace of the species to a kernel of certain fruits and, therefore, to the condition of the animal it encloses.

Holotype.- Female LV, RT/SIR/661. Plate 3, Fig. 10.

Type locality and horizon.- Honiara Bay, Guadalcanal, sample 60, 2,000 feet offshore east of the Matanikau River. 24 fathoms. Unconsolidated, very fine-grained sand. Recent.

Plate 5. ***1-9,*** *Hypocritecythere polymorphica* gen. et sp. nov. *1,* Holotype left valve RT/SIR/679 external lateral view x 50.0. *2,* Paratype right valve RT/SIR/681 external view x 51.4. *3, 9,* Left valve RT/SIR/685 *3,* internal view x 54.3, *9,* detail of central muscle scars x 365.6. *4,* Paratype left valve RT/SIR/680 external lateral view x 51.4. *5,* Paratype carapace RT/SIR/678 dorsal view x 50.6. *6,* Paratype right valve RT/SIR/682, external lateral view x 52.9. *7,* Right valve RT/SIR/683 internal view x 51.4. *8,* Paratype right valve RT/SIR/688 external lateral view x 55.4. ***10-15,*** *Alocopocythere reticulata fultura* subsp. nov. *10,* Holotype left valve RT/SIR/616, external view x 55.4. *11,* Paratype right valve RT/SIR/617, external view x 58.5. *12, 15,* Paratype left valve RT/SIR/619 *12,* internal view x 57.8. *15,* detail of central muscle scars x 340.0. *13,* Paratype carapace RT/SIR/615, dorsal view x 65.2. *14,* Right valve RT/SIR/618 internal view x 59.4. **16-26,** *Alocopocythere reticulata perfecta* subsp. nov. *16, 25,* Male left valve RT/SIR/608 *16,* detail of central muscle scars x 315.6, *25,* internal view x 62.5. *17,* Holotype female left valve RT/SIR/606 external view x 61.0. *18,* Paratype male right valve RT/SIR/609 external view x 61.3. *19,* Female left valve RT/SIR613 internal view x 58.5. *20,* A-1 left valve valve RT/SIR/610 external view 77.1. *21,* Paratype female carapace RT/SIR/604 dorsal view x 62.9. *22,* Paratype male carapace RT/SIR/605 dorsal view x 62.9. *23,* Female right valve RT/SIR/607 external view x 63.9. *24,* Male right valve RT/SIR/612 internal view x 61.3. *26,* Female right valve RT/SIR/611 internal view x 63.9. ***27, 28, 31, 35,*** *Australimoosella polypleuron* sp. nov. *27, 28,* Paratype left valve RT/SIR/203 *27,* detail of central muscle scars x 340.5, *28,* internal view x 82.4. *31,* Holotype left valve RT/SIR/202 external lateral view x 77.8. *35,* Paratype A-1 right valve RT/SIR/206 external view x 105.0. ***29, 30, 32-34,*** *Australimoosella* sp. *29, 32,* Left valve RT/SIR/413 *29,* external view x 62.1, *32,* internal view x 62.1. *30, 33,* Carapace RT/SIR/414 *30,* external lateral view of RV x 56.3, *33,* dorsal view x 57.7. *34,* A-2 left valve RT/SIR/415 external view x 85.4.

Plate 5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Material.- 235 valves and carapaces, A-2 to adult.

Diagnosis.- A medium species of *Ruggieria* pear-shaped in lateral view, characterised by its surface ornament of longitudinally aligned reticulae. Short, posterolateral spine, posteriorly directed, at about mid-height.

Description.- Medium. Thick-shelled. Adults opaque, juveniles translucent. Sexual dimorphism conspicuous; male considerably smaller, less high and less tumid than female. Pear-shaped in lateral view, subhastate and bispinose in dorsal view. Anterior margin well rounded; anteroventrally bearing 10-12 marginal denticles, extremity at mid-height. Posterior margin acuminate, asymmetrical; with a short, slightly concave posterodorsal slope and a long gently convex posteroventral slope: extremity at about mid-height bearing 4 short, strong marginal spines and 1 longer, robust denticle just ventral of caudal angle: extremity at about mid-height. Dorsal margin straight, inclined towards posterior, cardinal angles obtusely rounded. Ventral margin gently biconvex, overhung by lateral inflation so appearing gently convex in lateral view. Greatest length about mid-height; greatest height through anterior cardinal angle; greatest width just anterior of posterolateral spine. LV> RV, overlap along dorsal margin. Surface of valves strongly reticulate, reticulae aligned longitudinally, particularly anterodorsally. A broad smooth marginal rim parallels the dorsal margin. A short, strong posterolateral, posteriorly directed spine, occurs at about mid-height. Small, inconspicuous eye-tubercle. Npc's numerous, small, simple, distributed on muri, some on small pore conuli posterior to lateral spine. Inner lamella moderately wide, avestibulate, LOC and inner margin coincident, subparallel to outer margin. Rpc's numerous; approximately 40 anterior and 10 posterior canals, closely spaced anteriorly in clusters 2 or 3 associated with marginal spines, all straight, some cross, majority slightly swollen medianly. Hinge pararaphidont, robust. RV anterior terminal element a large dentate tooth with 5 lobes, the anteromedian element is a small socket, the posteromedian element a long locellate groove and the posterior terminal element a large 5 lobed tooth. Central muscle scars comprise 4 small adductor scars in compact vertical row; v-shaped frontal scar open anterodorsally.

Dimensions.-

	Length	Height	Width
Holotype female LV, RT/SIR/661	0.61	0.37	
Paratype female RV, RT/SIR/660	0.58	0.34	
Paratype female C, RT/SIR/658	0.58	0.36	0.34
Paratype male C, RT/SIR/659	0.57	0.31	0.28
Paratype male RV, RT/SIR/665	0.53	0.28	
Male RV, RT/SIR/662	0.57	0.32	
Female LV, RT/SIR/664	0.57	0.32	
Male RV, RT/SIR/668	0.54	0.30	
A-1 LV, RT/SIR/669	0.44	0.26	

Mean Dimensions.-

	Length	Height	Width
7 Female C	0.60(0.58-0.62)	0.36(0.34-0.38)	0.34(0.32-0.37)
6 Male C	0.55(0.52-0.57)	0.31(0.30-0.33)	0.29(0.28-0.29)
20 A-1 LV	0.45(0.41-0.47)	0.28(0.25-0.30)	
20 A-2	0.35(0.33-0.39)	0.22(0.20-0.24)	

Distribution.- Offshore Quaternary, marine, shallow water sediments, Guadalcanal (Williams, 1980 MS). Present study samples: 29, 30, 40-42, 52-56, 58, 60, 61, Guadalcanal.

Remarks.- The present species is very similar to *Ruggeria papuensis* (Brady, 1880) from the Recent of Papua New Guinea but differs in details of the reticulate ornament which in the present species is notably aligned longitudinally.

Subfamily SCHIZOCYTHERINAE Mandelstam, 1960

Genus *Neomonoceratina* Kingma, 1948

Type species.- *Neomonoceratina columbiformis* Kingma, 1948.

Neomonoceratina entomon (Brady, 1890)

(Fig. 5, Nos 18, 19; Pl. 3, Figs 22, 23, 25, 26)

1890 *Cytherura entomon* Brady, p. 509, Pl.3, Figs 26, 27, 27a.

2001 *Neomonoceratina entomon* (Brady). Titterton *et al*., p. 41, Pl. 3, Figs 1-4 (*q.v.* for synonymy).

Material.- 4 adult valves.

Diagnosis.- A species of *Neomonoceratina* with 2 ventral, delicate, sinuous ridges from posteroventral spine to anterior, a median ridge across median sulcus. Intercostate areas strongly reticulate and anteroventral margin with narrow flange. Dimorphic, male more elongate and less inflated with median rather than subdorsal caudal process and less well developed posteroventral spine.

Dimensions.-

	Length	Height
LV, RT/SIR/599	0.45	0.25
RV, RT/SIR/600	0.44	0.24
RV, RT/SIR/601	0.43	0.24
LV, RT/SIR/602	0.43	0.23

Distribution.- The species is of common occurrence in Indonesian waters (Keij, 1954 and Watson, 1988 MS). It also occurs in, New Caledonia and Fiji (Brady, 1890). Present study samples: 53, 60, Guadalcanal.

Remarks.-The present material and that of Watson, 1988 MS (Java Sea) differ slightly from the type material in that they possess a small, crenulate postero-dorsal rib.

Neomonoceratina koenigswaldi Keij,1954
(Fig. 5, No. 22; Pl. 3, Figs 24, 27)

1954 *Paijenborchella (Neomonoceratina) koenigswaldi* Keij, p. 359, T-fig. 1, Pl. 3, Figs 14-18.
1974 *Neomonoceratina koenigswaldi* Keij. Guha, p. 18, Pl. 1, Figs 14, 15.
1978 *Neomonoceratina koenigswaldi* Keij. Hartmann, p. 76, T.-figs 75-84, Pl. 3, Figs 1-8.
1981 *Neomonoceratina koenigswaldi* Keij. Hartmann, p. 101, Pl. 2, Figs 5-8.

Material.- 1 adult and 4 juvenile valves.

Diagnosis.- A species of *Neomonoceratina* ornamented with a series of irregular riblets dominated by a strong lateral oblique rib from anteroventral to posterodorsal across median sulcus and a less dominant single rib along the ventral ridge. Intercostate areas smooth.

Dimensions.-

	Length	Height
RV, RT/SIR/603	0.55	0.31
A-1 LV	0.42	0.24

Distribution.- Lower Miocene, W India (Guha, 1974), Recent, Philippines (Keij, 1954) and the eulittoral of the W and E Australia (Hartmann 1978, 1981). Present study samples: 5, 40, 54, Guadalcanal.

Remarks.- The present species is larger than *N. entomon* and is less strongly ornamented. *Neomonoceratina koenigswaldi* described by Keij (1954) and by Hartmann (1978, 1981) has a more prominent ventral ridge.

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4. REFERENCES

Allison E.C. and Holden, J.C. 1971. Recent ostracodes from Clipperton Island, Eastern Tropical Pacific. *Transactions San Diego Natural History Society,* 16, 165-214.

Baird, W. 1850. Description of several new species of Entomostraca. *Proceedings of the Zoological Society,* 18, 254–257.

Babinot, J-F, & Degaugue-Michalski, F. 1996. Lagoonal to reefal ostracod assemblages from Holocene and Recent deposits, Chesterfield Islands and northern New Caledonia (southwestern Pacific). *Micropalaeontology,* 42 (4), 351-362.

Behrens, P. 1991. Ostracoda (Crustacea) from Lizard Island, northern Great Barrier Reef, Australia II. The family Paradoxostomatidae Brady & Norman, 1889. *Helgoländer Meeresuntersuch,* 45, 143-163.

Benson, R.H. 1959. Ecology of Recent ostracodes of the Todos Santos Bay region, Baja California. *University of Kansas Palaeontological Contributions,* 36 (Arthropoda 6), 1-36.

Benson, R.H. & Maddocks, R.F. 1964. Recent ostracodes from Kynsna Estuary, Cape Province, Union of South Africa. *University of Kansas Palaeontological Contributions*, 34 (Arthropoda 5), 1-39.

Bold**,** W.A. van den. 1957. Oligo-Miocene Ostracoda from southern Trinidad. *Micropaleontology*, 3 (3), 231-254.

Bold, W.A. van den. 1963. Upper Miocene and Pliocene Ostracoda of Trinidad. *Micropalaeontology*, 9 (4), 361-424.

Bold, W.A. van den. 1965. Middle Tertiary Ostracoda from northwestern Puerto Rico. *Micropaleontology,* 11 (4), 381-414.

Bonaduce, G., Masoli, M., Minichelli, G. & Pugliese, N. 1980. Some new benthic marine ostracod species from the Gulf of Aqaba (Red Sea). *Bolletino Societa Paleontologica Italiana,* 19 (1), 143–178.

Bosquet, J.-A.-H. 1852. Description des Entomostraces fossiles des terrains Tertiares de la France et de la Belgique. *Memoiries Couronnes et Memoiries des Savants Etrangers publies par l'Acadamie Royale des Sciences des Lettres et des Beaux-Arts de Belgique,* 24 (1850-1851), 1-142.

Brady, G.S. 1866. On new or imperfectly known species of marina Ostracoda. *Transactions of the Zoological Society of London,* 5 (5), 359-393.

Brady, G.S. 1868. Ostracoda. In De Folin, L. & Perier, L. (Eds). *Les Fonds de la Mer*, Volume 1. Savy, Paris, 49-112.

Brady, G.S. 1880. Report on the Ostracoda. In: *Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873-1886. Zoology,* 1 (3), 184 pp.

Brady, G.S. 1890. On Ostracoda collected by H. B. Brady, Esq. L.L.D., F. R. S., in the South Sea Islands. *Transactions of the Royal Society of Edinburgh,* 35, 489-525.

Brady, G.S. & Norman, A.M. 1889. A Monograph of the marine and freshwater Ostracoda of the North Atlantic and Northwestern Europe. Section 1. Podocopa. *Scientific Transactions of the Royal Dublin Society,* Series 2, 5 (12), 333-374.

Cabioch, G., Anglada, R., & Babinot, J. F. 1986. Microfaunas et paléoenvironments des récifs frangeants quaternaires de mamie et Ricaudy (Nouvelle-Calédonie). *Cahiers de Micropaléontologie,* n.s., 1 (1/2), 5-36.

Coryell, H.N. & Fields, S. 1937. A Gatun ostracode fauna from Cativa, Panama. *American Museum Novitates,* 956, 1-18.

Coryell, H.N. & Fields, S. 1953. In: Puri, H.S. Taxonomic comment on: 'Ostracoda from wells in North Carolina Part 1. Cenozoic Ostracoda' by F. M. Swain. *Journal of Paleontology*, 27 (5), 750-752.

Dewi, K.T. 1997. Ostracoda from the Java Sea, west of Bawean Island, Indonesia. *Marine Geological Institute, Special Publication,* 4, 1-86.

Fischer, S. 1855. Beitrag zur kentniss der Ostracoden. *Abhandlungen der Mathematisch-Physikalischen Klasse der Koeniglich Bayerischen Akadamie der Wissenschaften,* 7, 635-666.

Gou, Y-X. 1990. Recent Ostracoda from Hainan island, South China Sea. *Courier Forschungsinstitut Senckenberg*, 123, 19-36.

Gramman, F. 1975. Ostracoda from Tertiary sediments of Burma with reference to living species. *Geologisches Jahrbuch, Reihe B (Regionale Geologie Ausland),* 14, 1-46.

Guha, D. K. 1974. Marine Ostracoda from Tertiary of Kutch and Gambay. *Publications, Centre of Advanced Study in Geology, Punjab University,* 10, 156-176.

Hanai, T. 1957. Studies on the Ostracoda from Japan: 1. Subfamily Leptocytherinae, new subfamily. *Journal of the Faculty of Science, University of Tokyo,* section 2, 10 (3), 431-468.

Harding, J.P. 1962. *Mungava munda* and four other new species of ostracod crustaceans from fish stomachs. *Nat. Hist. Rennel Island, British Solomon Islands, Copenhagen,* 4, 51-62.

Hartmann, G. 1964. Zur kenntnis der Ostracoden sdes Roten Meeres. *Keiler Meeresforschungen,* 20 (Sonderheft), 35-127.

Hartmann, G. 1974. Die Ostracoden des Untersuchungs Gebiets. In: Zur Kenntnis des Eulittorals der afrikanischen Westkuste zwischen Angola und Kap der Guten Hoffnung und der afrikanischen Ostkuste von Sudafrika und Mozambique unter besonderer Berucksichtigung der Polychaeten und Ostracoden. (Hartmann-Schroder, G. & Hartmann, G.) *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut,* 71, 229-520.

Hartmann. G. 1978. Die Ostracoden der Ordnung Podocopida G. W. Müller, 1894 der tropisch-subtropischen Westküste Australiens (zwischen Derby im Norden und Perth im Süden). In: Zur Kenntnis des Eulittorals der australischen Küsten unter besonderer Berücksichitung der Polychaeten und Ostracoden. Teil 1. (Hartmann-Schroder, G. & Hartmann, G.) *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut,* 75, 63-219.

Hartmann, G. 1979. Ostracoden der Ordnung Podocopida G. W. Müller, 1894 der warmtempereritein und subtropisch-tropischen Kustenabschnitte der Süd- und Südwestküste Australiens (zwischen Perth im Norden und Eucla im Süden). In: Zur Kenntnis des Eulittorals der australischen Küsten unter besonderer Berücksichitung der Polychaeten und Ostracoden. Teil 3. (Hartmann-Schroder, G. & Hartmann, G.). *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut,* 76, 219-301.

Hartmann, G. 1980. Die Ostracoden der Ordnung Podocopida G. W.Müller, 1894 der warmtempereritein und subtropisch-tropischen Kustenabschnitte der Süd- und Südosttküste Australiens (zwischen Ceduna im Westen und Lakes Entrance im Osten). In:. Zur Kenntnis des Eulittorals der australischen Küsten unter besonderer Berücksichitung der Polychaeten und Ostracoden. Teil 4. (Hartmann-Schroder, G. & Hartmann, G.). *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut,* 77, 101–204.

Hartmann, G. 1981. Die Ostracoden der ordnung Podocopida G. W. Müller, 1894, der subtropisch-tropischen Ostküste Australiens (zwischen Eden in süden und Heron Island im norden). *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut,* 78, 97-149.

Holden, J.C. 1967. Late Cenozoic ostracodes from the drowned terraces in the Hawaiian Islands. *Pacific Science*, 24 (1), 1-50.

Howe, H.V. & McKenzie, K.G. 1989. Recent marine Ostracoda (Crustacea) from Darwin and North Western Australia. *Northern Territory Museum of Arts and Sciences, Monograph Series*, 3, 1-50.

Hughes, G.W. 1977 MS. *The Geology and Foraminiferal Micropalaeontology of the Lungaa and Itina Basin Areas of Western Guadalcanal, Solomon Islands*. Unpublished PhD thesis, University of Wales, Aberystwyth, 410 pp.

Ishizaki, K. 1966. Miocene and Pliocene ostracods from the Sendai area, Japan. *Science Reports of the Tokoku University, Sendai* (Series 2, Geology), 37, 131-163.

Jellinek, T. 1993. Zur Ökologie und Systematik rezenter Ostracoden aus dem Bereich des kenianischen Barriere-Riffs. *Senckenbergiana lethaea,* 73 (1), 83-225.

Kajiyama, E. 1913. Ostracoda of Misaki. Part 3: Podocopa. *Zoological Magazine,* 25 (291), 1-16.

Keij, A.J. 1954. Some Recent Ostracoda of Manila (Phillipines). *Proceedings Koninklijke Nederlandse Akademie Wetenschappen*, Amsterdam, series B, 57 (3), 351-363.

Keij, A.J. 1957. Eocene and Oligocene Ostracoda of Belgium. *Memoires Institut Royal des Sciences Naturelles de Belgiqu*e, 136, 1-210.

Kingma, J.Th. 1948. *Contributions to the knowledge of the Young Caenozoic Ostracoda from the Malayan Region*. Published PhD thesis, University of Utrecht, Kemink Printers, Utrecht, 119 pp.

Labutis, V.R., 1977. *Cytheracean Ostracoda from The Great Barrier Reef*. Unpublished MSc thesis, Macquarie University, Sydney, Australia, 258 pp.

Lubimova, P.S. & Guha, D.P. 1960. In: Lubimova, P.S., Guha, D.P. &Mohan, M. On Ostracoda of Jurassic and Tertiary deposits from Kutch and Rajastan (Jaisalmer), India. *Bulletin of the Geological, Mining and Metalurgical Society of India,* 22 (1), 1-61.

Malz, H. 1980. *Cletocythereis* Swain, 1963 (Ostracoda); besondere Merkmale un geographische Verbreitung ihrer Arten. *Senckenbergiana lethaea,* 60 (4/6), 373-379.

Mandelstam, M.I. 1960. In: Lubimova, P.S., Kazmina, T.A. & Reshetnikova, M.A. Ostracoda from Mesozoic and Cenozoic deposits of the West Siberian Lowlands. *Trudy Vsesoyuznogo neftyanogo Nauchno-Issledovatelscogo Geologo-Razvedochnogo Instituta (VNIGRI), novaya seriya.* 160, 1-427. [In Russian].

McKenzie, K.G. 1965. The geological association of an ostracode fauna from Oyster Harbour, a marginal marine environment near Albany, Western Australia. *Pubblicazione della Stazione Zoologica di Napoli*, 33 (supplemento), 421-461.

McKenzie, K.G. 1967. Recent Ostracoda from Port Phillip Bay, Victoria. *Proceedings of the Royal Society of Victoria,* 80, 61-106.

McKenzie, K G. 1986. A comparative study of collections from the S.W. Pacific (Saipan to Tonga), with the description of *Gambiella caudata* (Brady, 1890) and a new species of *Pterobairdia* (Ostracoda). *Journal of Micropalaeontology*, 5 (1), 91-108.

Mohan, S.P., Ravi, G., Hussain, S.M. & Rao, N.R. 2001. Recent Ostracoda from the Bay of Bengal, off Karikkattuppam (near Chennai), South East coast of India. *Journal of the Palaeontological Society of India*, 46, 1-14.

Morkhoven, F.P.C.M. van 1963. *Post-Palaeozoic Ostracoda, their morphology, taxonomy, and economic use.* Volume 2 (generic descriptions). Elsevier, Amsterdam, 478 pp.

Mostafawi, N. 1992. Rezente Ostracoden aus dem mittleren Sunda-Schelf, zwischen der Malaiischen und Borneo. *Senckenbergian Lethaea,* 72, 129-168.

Müller, G.W. 1894. Die Ostracoden des Golfes de Neapel und der angrendzenden Meeres-Abschnitte. *Fauna und flora des Golfes de Neapel und der angrendzenden Meeres-Abschnitte, Herausgegeben von der zoologischen station zu Neapel,* 21, 1-404.

Puri, H.S. 1960. Recent Ostracoda from the West Coast of Florida. *Transactions of the Gulf Coast Association of Geological Societies*, 10, 107-149.

Puri, H.S. & Hulings, N.C. 1976. Designation of lectotypes of some ostracods from the Challenger Expedition. *Bulletin of the British Museum, Natural History*, 29 (5), 251-315.

Ruggieri, G. 1950. Gli ostracodi delle Presiciliano della Peninsola di Crotone. *Giornale di Geologia, Annali del Museo Geologico di Bologna*, serie 2, 20 (1948), 39-62.

Sars, G.O. 1866. Oversigt af Norges marine Ostracoder. *Forhandlinger i Videnskabsselskabet i Kristiania, for 1865,* 1-130.

Sars, G.O. 1928. *An account of the Crustacea of Norway with short descriptions and figures of all the species.* Volume 9 (Ostracoda). Kristiania Alb. Cammermeyer. (Parts 15-16), 241-277.

Scott, A. 1905. Report on the Ostracoda collected by Professor Herdmann at Ceylon, in 1902. *Ceylon Pearl Oyster Fisheries, Supplementary Reports,* 22, 365-385.

Schornikov, E.I. 1974. To the study of ostracods (Crustacea, Ostracoda) from the Intertidal Zone of the Kurile Islands. *Institut Biologii Morya, Dalnevostochnyy NauchnyyTsentre, Akademiya Nauk SSSR,* 1, 137-214.

Schornikov, E.I. 1975. Ostracod fauna of the intertidal zone in the vicinity of the Seto Marine Biological Laboratory. *Publications of the Seto Marine Biological Laboratory,* 22 (1/4), 1-30.

Siddiqui, Q.A. 1971. Early Tertiary Ostracoda of the family Trachyleberididae fom West Pakistan. *Bulletin of the British Museum (Natural History), Geology, Supplements.* 9, 1-98.

Swain, F.M. 1963. Pleistocene Ostracoda from the Gubik Formation, Arctic Coastal Plain, Alaska. *Journal of Paleontology,* 37 (4), 798-834.

Sylvester-Bradley, P.C. 1948. The ostracod genus *Cythereis*. *Journal of Paleontology,* 22 (6), 792-797.

Tabuki, R. & Nohara, T. 1995. Seasonal distribution of intertidal ostracods on gravels from the moat behind a coral reef off Sesoko Island., Ryukyu Islands, Japan. In: Riha, J. (Ed.), *Ostracoda and Biostratigraphy.* Balkema, Rotterdam, 343-349.

Teeter, J.W. 1973. Geographical distribution and dispersal of some Recent shallow-water marine Ostracoda. *Ohio Journal of Science,* 73 (1), 46-54.

Teeter, J.W. 1975. Distribution of Holocene marine Ostracoda from Belize. In: Wantland K. T. & Puseu, W. C. (Eds). Belize shelf carbonate sediments and ecology. *American Association of Petroleum Geologists Studies in Geology,* 527 pp.

Titterton, R. 1984. *The Taxonomy, Ecology and Distribution of Recent Ostracoda from the Solomon Islands*. Unpublished PhD thesis, University of Wales, Aberystwyth, 945 pp.

Titterton, R. & Whatley, R. C. 1988. Recent Bairdiinae (Crustacea, Ostracoda) from the Solomon Islands. *Journal of Micropalaeontology*, 7 (2), 111-142.

Titterton, R. & Whatley, R.C 2005. Recent marine Ostracoda from the Solomon Islands. Part 2: Cytheracea, Xestoleberidae. *Revista Española de Micropaleontología,* 37 (2), 291-313.

Titterton, R. & Whatley, R.C. 2006a. Recent marine Ostracoda from the Solomon Islands. part 1 - Cypridoidea, Platycopina and Cladocopina. *Journal of Micropalaeontology,* 25, 1-22.

Titterton, R. & Whatley, R.C. 2006b. Recent marine Ostracoda from the Solomon Islands. Part 3: Cytheroidea, Bythocytheridae, Cytherideidae, Krithidae, Neocytherideidae, Cytheruridae. *Revista Española de Micropaleontología,* 38 (1), 169-189.

Titterton, R., Whatley, R.C. & Whittaker, J.E. 2001. A review of some key species of mainly Indo-Pacific Ostracoda from the collections of G. S. Brady. *Journal of Micropalaeontology,* 20, 31-44.

Triebel, E. 1952. Ostracoden der Gattung *Cytheretta* aus dem Tertiaer des Mainzer Beckens. *Notizblatt des Hessichen Landesamtes für Bodenforschung,* Serie 6, 3, 15-30.

Warne, M.T. 2001. Observations on *Ponticocythereis tricristata* (Brady, 1880) from the Admiralty Islands, Papua New Guinea and comments on the Quaternary ostracod evolution within the SW Pacific Ocean. *Proceedings of the Royal Society of Victoria*, 113 (2), 229-235.

Warne, M.T. & Whatley, R.C. 1996. The evolutionary significance of scale-like spines on the Australian and S. W. Pacific Cainozoic ostracods *Ponticocythereis manis* Whatley & Titterton, 1981 and *Trachyleberis floridus* sp. nov. *Journal of Micropalaeontology*, 15 (2), 161-168.

Warne, M.T., Whatley, R.C. & Blagden, B. 2006. The Ostracoda of Lee Point on Shoal Bay, Northern Australia: Part 3 - Podocopina, Cytheracea. *Revista Española de Micropaleontología*, 38(1), 103-167.

Watson, K A. 1988. *The taxonomy and distribution of Recent reef Ostacoda from the Palau Seribu, Java Sea*. Unpublished PhD thesis, University of Wales, Aberystwyth, 434 pp.

Whatley, R.C. 1983. Some aspects of the palaeobiology of Tertiary deep-sea Ostracoda from the SW Pacific. *Journal of Micropalaeontology*, 2, 83-104.

Whatley, R.C. 1985. Evolution of the ostracods *Bradleya* and *Poseidonamicus* in the deep sea Cainozoic of the south-west Pacific. *In*: Cope, J. & Skelton, P. (Eds), Evolutionary case histories from the fossil record. *Special papers in Palaeontology,* 33, 103-116.

Whatley, R.C., Harlow, C., Downing, S.E. & Kesler, K. 1983. Some observations on the origin, evolution, dispersion and ecology of the genera *Poseidonamicus* Benson and *Bradleya* Hornibrook. In: Maddocks, R. F. (Ed.) Applications of Ostracoda, Houston Geosciences, 51-77.

Whatley, R.C. Jones, R.L. & Wouters, K. 2000. The Ostracoda of Easter Island. *Revista Española de Micropalaeontologia*, 32 (1), 79-106.

Whatley, R.C., Jones, R.L. & Roberts, R. 2004. The marine Ostracoda of Pitcairn, Oeno and Henderson Islands, southern Pacific. Revista *Española de Micropaleontología,* 36 (3), 493-528.

Whatley, R.C. & Titterton, R. 1981. Some new Recent podocopid Ostracoda from the Solomon Island, South-West Pacific. *Revista Española de Micropaleontología,* 13 (2), 157-170.

Whatley, R.C., Williams, U., Pyne, R. & Titterton, R. (In press). Quaternary marine and brackish water Ostracoda from the Solomon Islands. *Revista Española de Micropaleontología*.

Wouters, K. 1981. Two new marine podocopid species from Hansa bay, Papua New Guinea (Crustacea: Ostracoda). Leopold III Biological station, Laing Island, Contribution No 17. *Bulletin Institut Royale des Sciences Naturelles de Belgique,* 53, 1-12.

Williams, E.U. 1980 MS. *Some Quaternary Ostracoda from the Solomon Islands*. Unpublished Msc thesis, University of Wales, Aberystwyth. 183 pp.

Witte, L. 1993. *Taxonomy and origin of modern West African shallow marine Ostracoda*. Published PhD thesis, Free University, Amsterdam. Academische Pers B. V., Amsterdam, 201 pp.

Witte, L.J. & Van Harten, D. 1991. Polymorphism, biogeography and systematics of *Kotoracythere inconspicua* (Brady, 1880) (Ostracoda: Pectocytheridae). *Journal of Biogeography*, 18, 427-436.

Yassini, I., Jones, B.G. & Jones, M.R. 1993. Ostracods from the Gulf of Carpentaria, northeastern Australia. *Senckenbergiana Lethaea,* 73, 375-406.

Zhao, Q. & Whatley, R.C. 1989. Recent podocopid Ostracoda of the Sedili River and Jason Bay, Southeast Malay Peninsula. *Micropaleontology,* 35, 168-187.

Zhao, Q. 1995. Late Cainozoic ostracod faunas and paleoenvironmental changes at ODP Site 1148, South China Sea. *Marine Micropaleontology,* 54 (1-2), 27-47.

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Evolución del paisaje vegetal durante los últimos 1.680 años BP en el Macizo de Peñalara (Sierra de Guadarrama, Madrid)

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Resumen

El estudio polínico de un depósito higroturboso de origen periglacial localizado en el macizo de Peñalara (Sierra de Guadarrama. Madrid) apoyado en 7 dataciones AMS de ^{14}C, proporciona la primera reconstrucción de alta resolución de la evolución de la vegetación en el área durante los últimos 1689 años. Los resultados obtenidos reflejan la existencia de un paisaje vegetal dominado por el estrato herbáceo, constituido fundamentalmente por Poaceae y *Plantago lanceolata* tipo. La masa forestal está constituida por *Pinus sylvestris* tipo y en menor proporción *Pinus pinaster* tipo y *Quercus*, junto a presencias puntuales de *Betula*. El grupo arbustivo (*Erica arborea*, Rosaceae, cf. *Juniperus* y Cistaceae), está presente a lo largo de toda la secuencia sin llegar a tener un papel importante en la estructura de la vegetación. El análisis de los microfósiles no polínicos (MNPs) ha permitido relacionar las variaciones de la vegetación con la presión pastoral y los cambios tróficos en la turbera. Los valores del pH y de la conductividad del sedimento, constatan los cambios detectados en la vegetación y en los usos del suelo.

Palabras clave: Palinología, vegetación, actividad antrópica, Holoceno Reciente.

Abstract

[*Landscape evolution during the last 1680 years BP in the Peñalara Massif, Guadarrama Range, Madrid*] A study of peat bog from Peñalara (Guadarrama Range, Madrid) supported by 7 ^{14}C AMS dates provides the first high-resolution the vegetacion evolution during the last 1680 years in the area. The landscape is dominated by herbaceous taxa, constituted mainly by Poaceae and *Plantago lanceolata*. Shrubs such as *Erica arborea*, Rosaceae, cf. *Juniperus* and Cistaceae have certain role in the vegetation. Woodlands with *Pinus sylvestris* type, also *P. pinaster*, *Quercus* and *Betula* are also noticeable throughout the sequence. Non-pollen palynomorphs are used to infer the importance of erosive processes and changes in peat bog trophic condition. The information provided by pH and sediment conductivity serves to assess vegetation and land uses changes.

Keywords: Palynology, vegetation, vnthropic activity, Late Holocene.

1. INTRODUCCIÓN

Los lagos constituyen una de las principales fuentes de información en la reconstrucción paleoambiental y paleoclimática del medio continental. En el caso del macizo de Peñalara (Sierra de Guadarrama, Madrid), la actividad glaciar durante la última glaciación (Centeno *et al.*, 1983; Pedraza *et al.*, 2004; Pedraza y Carrasco, 2005; Acaso,

2006) ha propiciado la formación de numerosas cuencas endorreicas de pequeño tamaño, que conservan las claves para la detección de los cambios acaecidos en la vegetación, como respuesta al clima y/o a la actividad antrópica. Bajo esta perspectiva el primer análisis palinológico realizado, en el entorno de la laguna de Peñalara (Alía *et al*., 1957), se llevó a cabo en la turbera "Tremedal de los Hoyos" localizada a 1.900 m.s.n.m, en la denominada Hoya de Peñalara; el análisis de 16 muestras correspondientes a un sondeo de 250 cm de potencia, puso de manifiesto las fluctuaciones en la composición del bosque constituido fundamentalmente por *Pinus, Betula* y *Quercus*, junto con el dominio de las gramíneas en el estrato herbáceo a lo largo del, según los autores, el Holoceno.

Posteriormente, Jiménez Ballesta *et al*. (1985) retomaron las investigaciones palinológicas en el área, comparando la evolución paleoambiental entre algunas turberas de las sierras de Gredos y Guadarrama; en el caso de Peñalara, estudiaron dos muestras procedentes del relleno de la depresión interior del arco morrénico principal, situado a 1.950 m.s.n.m. Los resultados más relevantes se resumen en el dominio del pinar sobre el bosque de quercíneas y en la similaridad de la vegetación fósil con la actual. A partir de 1986, el grupo de Palinología de la Universidad de Alcalá de Henares (Ruiz Zapata *et al*., 1987, 1988) inicia una serie de investigaciones sistemáticas de carácter paleoambiental en la zona, a fin de poder establecer con mayor precisión cronológica la secuencia vegetal y climática del área. El estudio preliminar de siete muestras, procedentes de un sondeo realizado en la Hoya de Peñalara, a 1930 m.s.n.m, situado a 50 m al este de la base del escarpe del Refugio Zabala, reveló la evolución desde paisajes de bosque, relativamente densos hasta la instalación de un paisaje semejante al actual, destacando el papel del estrato arbustivo y la presencia de gramíneas; dichos cambios en la estructura de la vegetación, lo explican como una respuesta tanto a las variaciones en las condiciones climáticas como a la actividad antrópica.

Años más tarde, Bentley (1991), presentó los resultados del análisis polínico de siete muestras procedentes de un perfil de 90 cm (sin ubicación exacta conocida); concluyendo, que la vegetación a escala regional, está caracterizada por la existencia de bosques de *Pinus*, así como mixtos de pinares y quercíneas. Este autor atribuye los descensos de *Betula* y *Quercus*, los cambios en los pinares, y la presencia de fases erosivas, a variaciones en el uso del suelo (clareado y presión pastoral), sin descartar algún tipo de influencia climática en ellos, dada la dificultad para diferenciarlos en el diagrama polínico. Adicionalmente, identifica, a nivel local, pastizales de gramíneas dedicados al ganado, en los cuales varía la presión pastoral en el tiempo.

El análisis de 31 muestras, procedentes de un sondeo de 160 cm en la turbera localizada en la depresión de la lengua glaciar del estadío Würm B, en la Laguna Grande de Peñalara (Vázquez, 1992; Vázquez y Ruiz Zapata, 1992), corrobora las conclusiones de los trabajos previos y aporta, por primera vez, dataciones radiocarbónicas. Así se establece que hacia 4.160 ± 70 BP (Vázquez, 1992), el paisaje local del hoyo de la Laguna Grande de Peñalara corresponde a un medio abierto no forestal con bosques regionales de *Pinus* y *Betula*, que no se encontrarían muy alejados del depósito, mientras que el robledal, también de carácter regional, se situaría a menor cota y aún menor sería el límite altitudinal del encinar. Tras un período de deforestación, que afectaría el pinar y el abedular, aún durante el Subboreal, ambas formaciones forestales muestran una ligera recuperación. Posteriormente, señala una regresión del abedular, relacionada con la mejoría climática del Subatlántico (2.700-2.500 BP), paralela con la expansión de los pinares. A partir de 1.100 ± 60 BP, identifica otra retracción del abedular provocada por condiciones climáticas, aunque la presión antrópica parece afectar también, de manera temporal, a los bosques de *Pinus* y *Quercus*. Con posterioridad a 1.100 BP, identifica el proceso más acusado de degradación antrópica de los bosques, si bien se detectan algunos episodios de recuperación, debido a la disminución de la presión antrópica y quizás por la mejoría climática de los siglos XI-XV d.C. El deterioro climático de la Pequeña Edad del Hielo (siglos XV-principios XVIII d.C.), se detecta a través de una nueva expansión de *Betula* que llega incluso a competir con *Quercus*. Por otro lado, la disminución del pastoreo, como consecuencia de una menor productividad de pastos, favorecería el desarrollo del pinar regional, cuya posterior caída podría estar relacionada con los efectos de las desamortizaciones del siglo XIX d.C. Finalmente, la autora señala que la recuperación de los bosques, en el siglo XX d.C., estaría relacionada con la política proteccionista de los mismos y con la disminución de las prácticas agropecuarias tradicionales.

Gracias a los trabajos palinológicos, antes citados, se ha podido establecer, de un modo general, la evolución de la vegetación en el macizo de Peñalara durante el Holoceno reciente, que se caracterizaría por el tránsito desde formaciones de bosque, fundamentalmente pinares, abedulares y melojares, hasta el desarrollo de espacios abiertos, a través de fluctuaciones entre los taxa arbustivos y herbáceos, cuya dinámica responde a cambios en las condiciones climáticas, así como a una ocupación y usos antrópicos del territorio. Lo expuesto evidencia el interés paleoambiental de la zona, tanto a nivel paleoecológico como paleofitogeográfico, por tratarse de un área de alta montaña sensible tanto a los cambios climáticos holocenos como a los mediados por la actividad humana.

En este sentido el trabajo que se presenta se aborda bajo la perspectiva de un análisis de alta resolución, basado en la identificación de granos de polen y de palinomorfos no polínicos, con el fin de poder relacionar los cambios acaecidos en la vegetación, tanto regional como local; el análisis del pH y la conductividad del sedimento permitirá conocer la respuesta de la propia cuenca de sedimentación, frente a los eventos de carácter climático y/o antrópico.

2. MATERIAL Y MÉTODOS

El testigo analizado (PÑ) se obtuvo con una sonda manual tipo Rusa, alcanzando una profundidad de 154 cm (Fig. 1); el muestreo se realizó cada 2 cm, suponiendo un total de 78 muestras analizadas. Para la extracción de los granos de polen se utilizó la metodología clásica (Coûteaux, 1977; Faegri *et al*., 1989; Moore *et al.*, 1991), consistente en un ataque químico mediante el empleo de ácidos (ClH y FH) y álcalis (NaOH); el residuo fue sometido a técnicas de enriquecimiento, mediante la concentración del polen por flotación en licor denso de Thoulet (Girard and Renault-Miskovsky, 1969; Goeury and Beaulieu, 1979).

La lectura y recuento del contenido polínico se llevo a cabo de acuerdo al método propuesto por Cambon (1981). Para la determinación de los tipos polínicos se tomó como referencia la palinoteca de la Universidad de Alcalá y los manuales de Valdés *et al*. (1987), Moore *et al.* (1991) y Reille (1992). La diferenciación de *Pinus pinaster* tipo se basó en Arobba (1979) y Díaz-Laviada (1989). Los microfósiles no polínicos (MNPs) se han identificado siguiendo la tipología numérica y genérica establecida por la escuela de B. van Geel (van Geel, 1978; van Geel *et al*., 1981, 2003; López Sáez *et al*., 2000, 2005; López Sáez y López Merino, 2007; Riera *et al*., 2006).

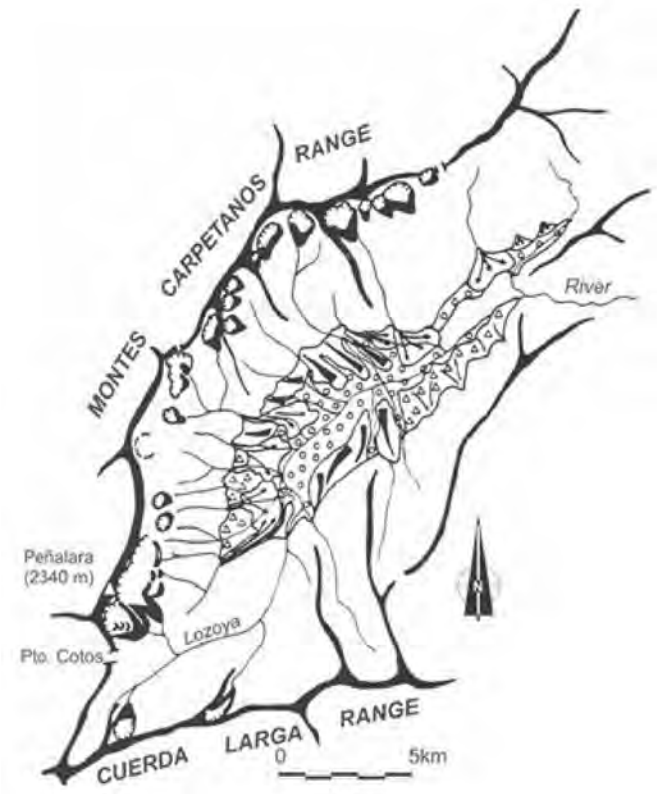

Figura 1. Situación geográfica de la secuencia PÑ.
Figure 1. Geographic location of PÑ sequence.

La representación gráfica de los datos polínicos (Fig. 2) y no polínicos, se expresan en frecuencias relativas, en el denominado Diagrama Polínico, elaborado con el paquete informático TILIA®, TILIA GRAPH® y TGVIEW 1.6.2 (© Eric C. Grimm). Las frecuencias relativas de los taxones arbóreos, arbustivos y herbáceos se calcularon a partir de la suma base, que excluye el polen de la vegetación acuática, las esporas y los MNPs; los porcentajes de estos últimos se han realizado en base a la suma total del contenido en granos de polen y palinomorfos no políni-

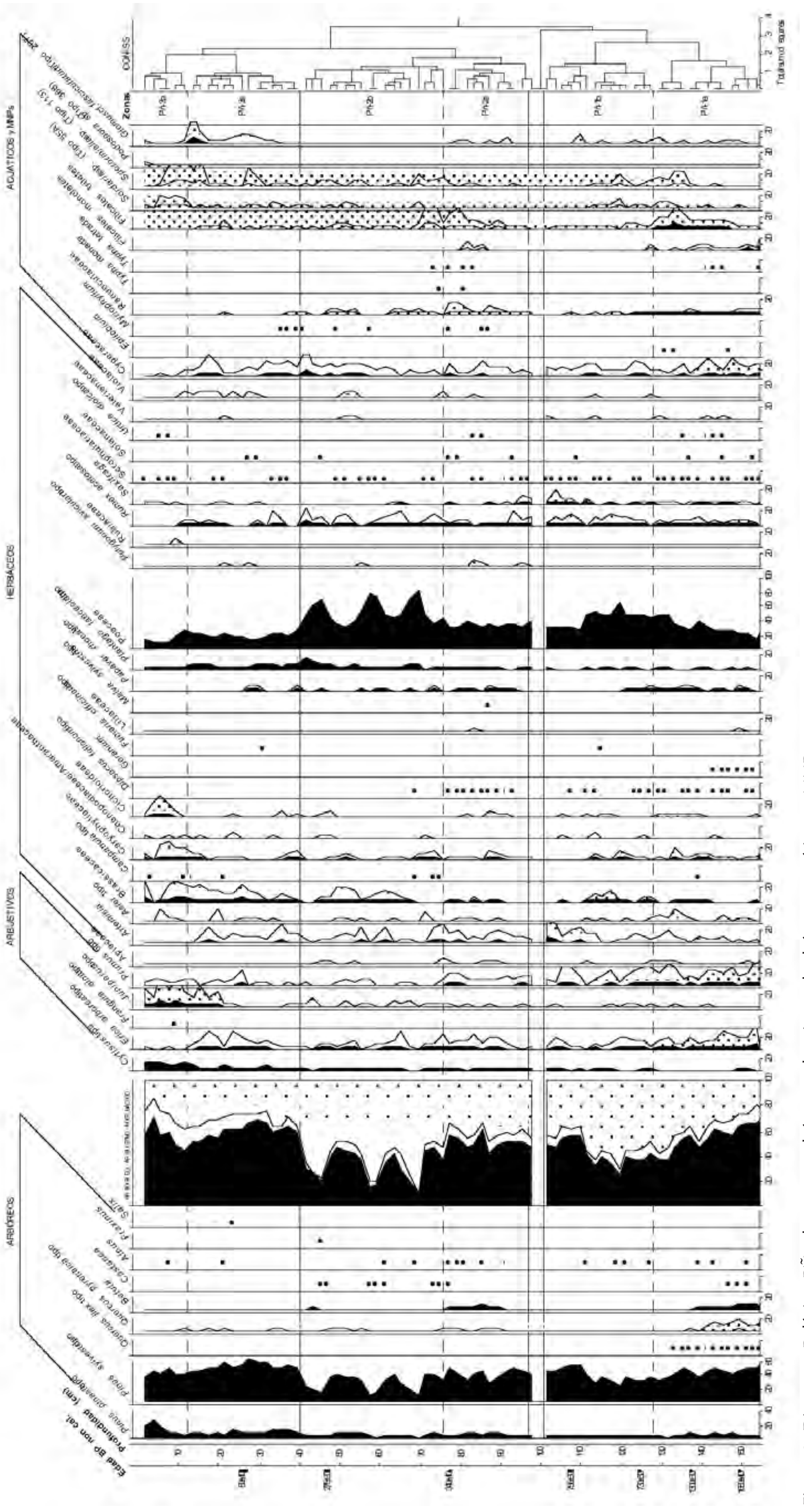

Figura 2. Diagrama Polínico PÑ, elementos arbóreos, arbustivos y herbáceos, acuáticos y MNPs.

Figure 2. PÑ Pollen Diagram, trees, shrubs and herbs, aquatics and MNPs.

cos de cada muestra y su representación (Fig. 3) se combina con el diagrama sintético del contenido en polen. En este diagrama, salvo *Pinus* (que se representa individualmente), se han realizado las siguientes agrupaciones: Bosque perenne (*Quercus ilex* tipo y *Cytisus* tipo), Bosque caduco (*Quercus* tipo y *Prunus* tipo), Bosque ripario (*Alnus*, *Fraxinus* y *Salix*); para los taxones herbáceos se contemplan los grupos de Nitrófilas antropozoógenas (Poaceae, Fabaceae, Caryophyllaceae, Fumariaceae, Brassicaceae, y Apiaceae), Nitrófilas antrópicas (*Aster* tipo, Cichoriaceae, Dipsacaceae, *Papaver rhoeas* tipo, Boraginaceae, *Rumex acetosa* tipo, Solanaceae, Malvaceae, *Ar-*

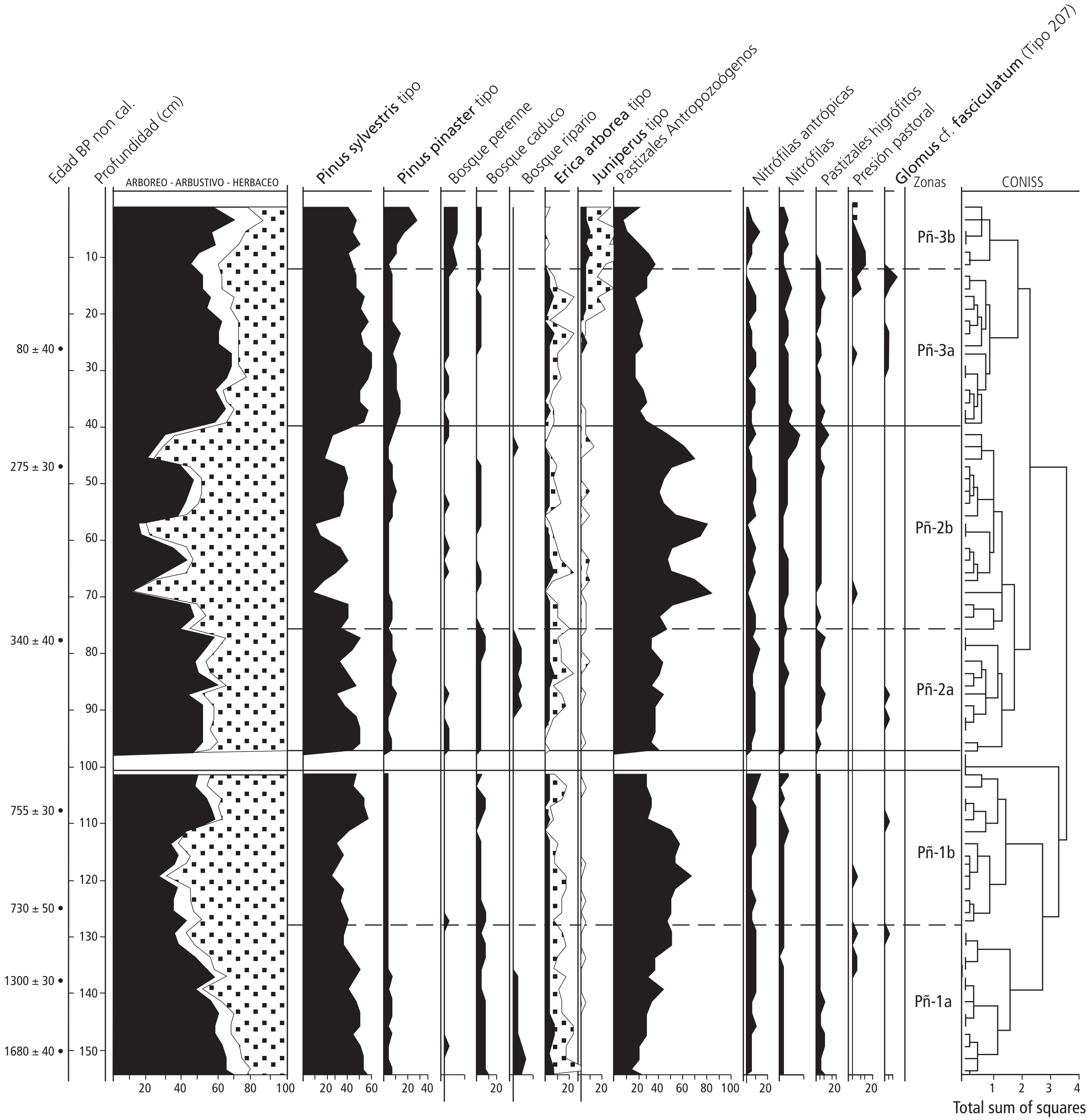

Figura 3. Diagrama Polínico sintético PÑ.

Figure 3. PÑ Synthetic Pollen Diagram.

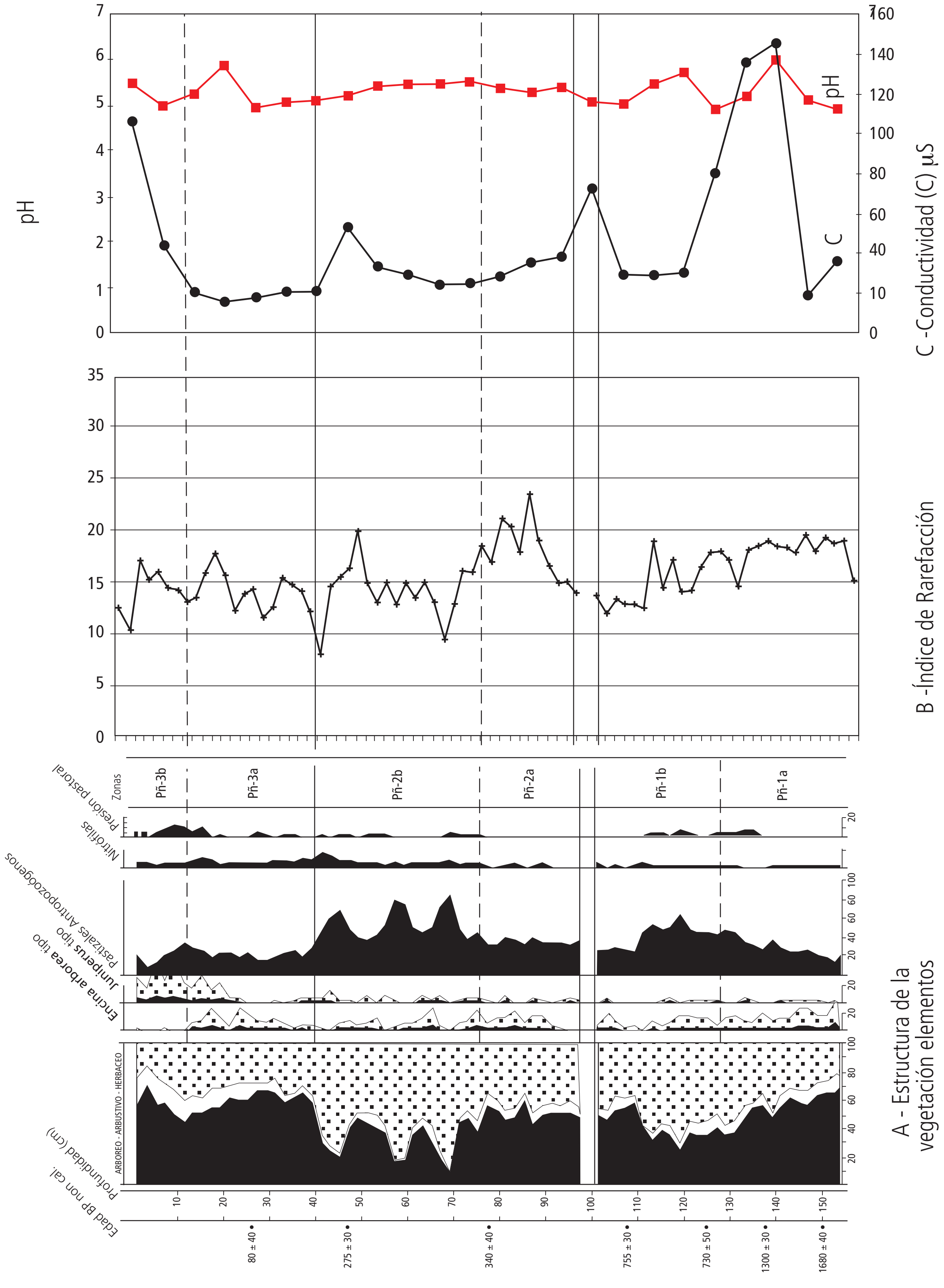

Figura 4. Relación de (A) polen/(B)/Rarefacción/(C) C y pH, en la secuencia PÑ.

Figure 4. Pollen/(A)/Rarefaction (B)/C and pH (C) relation, in PÑ sequence.

temisia), Nitrófilas (*Urtica dioica* tipo, *Plantago lanceolata* tipo, *Polygomun aviculare* tipo, Rubiaceae, Geraniaceae y Chenopodiaceae-Amaranthaceae). Para facilitar la lectura del diagrama se han señalado con presencias aquellos taxones cuyos valores no superan el 5%. Con el fin de evaluar la diversidad biológica del registro y estimar la riqueza polínica (Fig. 4), se ha realizado un análisis de rarefacción (Analytic Rarefaction 1.3; Bronk-Ramsey, 2000).

Las medidas de pH y conductividad (Fig. 4) se llevaron a cabo de acuerdo con la norma ISO 10390:2005; para ello, con las muestras de suelo, secadas al aire y tamizadas, se prepararon suspensiones en agua (1:5) que fueron agitadas vigorosamente durante 10 minutos y a continuación se mantuvieron en reposo para llevar a cabo las medidas de pH y conductividad en el sobrenadante. Dichas medidas se han realizado utilizando un pH-metro Inolab y un conductímetro Crison. En todo momento, la temperatura de trabajo ha sido 25±1° C.

Finalmente, teniendo en cuenta la alta resolución empleado en el análisis polínico, se han llevado a cabo un total de siete dataciones radiocarbónicas AMS (Tabla 1). Las dataciones han sido calibradas a partir de la datación estándar BP y su respectiva desviación típica, sirviéndonos para la calibración del programa OxCal v. 3.5 -©Bronk Ramsey, 2000.

3. RESULTADOS E INTERPRETACIÓN

El análisis polínico llevado a cabo sobre las 78 muestras de la secuencia PÑ, objeto de este trabajo, refleja los cambios acaecidos en la vegetación a partir de los 1680 ± 40 BP. Se han identificado un total de 45 taxones, de los cuales 9 son arbóreos, 5 arbustivos y 25 herbáceos, junto a 6 taxa hidro-higrófitos, 4 MNPs y Filicales monoletes y triletes (Fig. 2).

Desde el punto de vista de la vegetación, los hechos más relevantes se resumen en el dominio de polen herbáceo, representado fundamentalmente por Poaceae y diversos taxa de afinidad nitrófila (Cichorioideae, *Aster* tipo, *Papaver rhoeas* tipo, *Rumex acetosa* tipo, *Urtica dioica* tipo, *Plantago lanceolata* tipo, Chenopodiaceae/Amaranthaceae) y Rubiaceae. El aumento de estos últimos asociado al desarrollo de MNPs de afinidad coprófila, como es el caso de los tipos tipo-55 A (*Sordaria* sp), tipo-113 (*Sporomiella* sp) y el tipo-368 (*Podospora* sp) (van Geel *et al*., 2003; van Geel y Aptroot, 2006; López Sáez y López Merino, 2007), permite definir momentos de mayor presión pastoral. Del componente arbustivo, constituido básicamente por *Erica arborea* tipo, *Prunus* tipo, cf. *Juniperus* y Cistaceae, cabe destacar su presencia constante a lo largo de toda la secuencia así como su expansión hacia el techo de la misma, con posterioridad a los 275±40 BP. En cuanto a la masa forestal, están representados los elementos de carácter regional que se documentan en otros estudios polínicos de la Sierra de Guadarrama (Gil García, 1992; Vázquez, 1992; Franco Múgica, 1995), como es el

MUESTRA	nº Laboratorio	Profundidad cm	^{14}C (BP)		cal. BC/AD (2 σ) 95.4%
Pñ-9	Beta-229289	25-27	80 ± 40	turba	1680 AD – 1740 AD 1800 AD – 1940 AD
Pñ-1	GdA-933	46-48	275 ± 30	turba	1510 AD – 1600 AD 1610 AD – 1670 AD
Pñ-5	Beta-223985	77-78	340 ± 40	turba	1460AD - 1650AD (
Pñ-2	GdA-934	107-108	755 ± 30	turba	1215AD - 1285AD
Pñ-6	Beta-223986	124-125	730 ± 50	turba	1200AD - 1320AD 1350AD - 1400AD
Pñ-3	GdA-935	137-138	1300 ± 30	turba	660 AD – 780 AD
Pñ-7	Beta-229290	149-150	1680 ± 40	turba	240 AD – 440 AD

Tabla 1. Dataciones ^{14}C secuencia PÑ.

Table 1. Radiocarbon dating ^{14}C PÑ sequence.

caso de *Pinus sylvestris* tipo, *P. pinaster* tipo, *Quercus ilex* tipo y *Quercus pyrenaica* tipo, junto a presencias, en porcentajes menores de *Betula, Alnus, Castanea, Salix* y *Fraxinus*. Las fluctuaciones en los valores de los elementos arbóreos, y su ausencia/presencia, marca diversos episodios climáticos que permiten corroborar los retrocesos y avances de la línea superior de bosque (pinar), y la expansión o retroceso de melojares y abedulares en el Valle del Lozoya a cotas altitudinales más bajas (Ruiz Zapata *et al*., 1987, 1988; Vázquez, 1992). Cyperaceae es el taxon acuático dominante y su presencia es constante en todo el perfil, junto a el y de un modo puntual se detectan presencias de *Epilobium, Myriophyllum,* Ranunculaceae, *Typha* monada y *Typha* tetrada y del MNP tipo-207 (*Glomus* cf. f*asciculatum*), indicador de procesos erosivos.

El comportamiento de los granos de polen y de palinomorfos no polínicos a lo largo de la secuencia PÑ, define una sucesión de fases, materializadas en una zonación polínica, realizada con el tratamiento estadístico Coniss (Grimm, 1987). Dicha zonación separa tres grandes unidades, cuyas peculiaridades se exponen a continuación:

Zona Pñ-1: abarca desde los 154 cm hasta los 101 cm del registro sedimentario de PÑ, y está constituido por un lodo orgánico masivo con fragmentos líticos flotantes, de tamaño arena media-gruesa, de cuarzo que pasa gradualmente a una turba poco evolucionada con abundantes restos vegetales de briófitos y raíces. En esta zona se han realizado 4 dataciones: 149-150 cm (1680 ± 30 BP), 137-138 cm (1300 ± 30 BP), 124-125 cm (730 ± 50 BP) y 107-108 cm (755 ± 30 BP).

Domina el estrato herbáceo, constituido fundamentalmente por Poaceae, que llega a alcanzar valores superiores al 30% y *Plantago lanceolata* tipo, y en proporciones menores están presentes Apiaceae, *Artemisia, Aster* tipo, Brassicaceae, Caryophyllaceae, Chenopodiaceae-Amaranthaceae, Cichorioideae, *Papaver rhoeas* tipo, *Polygonum aviculare* tipo, *Rumex acetosa* tipo, *Saxifraga*, Valerianaceae y Violaceae. El grupo arbustivo está constituido por *Erica arborea* tipo y *Prunus* tipo, y, en menor medida, por *Cytisus* tipo y cf. *Juniperus*. Los elementos arbóreos presentes son *Pinus sylvestris* tipo, *Pinus pinaster* tipo, *Quercus pyrenaica* tipo y *Betula*, acompañados por presencias más esporádicas de *Alnus, Castanea* y *Quercus ilex* tipo. El componente arbustivo está constituido por *Prunus* tipo y *Erica arborea* tipo, acompañados por porcentajes menores de cf. *Juniperus*. El taxón hidro-higrófito mejor representado es Cyperaceae y se detecta la permanencia de Ranunculaceae. Están presentes los MNPs tipo-55 A (*Sordaria* sp.), tipo-113 (*Sporomiella* sp.) y el tipo-207 (*Glomus* cf. *fasciculatum*), acompañados de Filicales monoletes y triletes. En esta zona los valores de diversidad polínica oscilan entre 11.9 ± 0.09 y 19.5 ± 0.01 (Fig. 4); los de pH entre 4.92 y 6; y la conductividad entre 18.5 y 145.8 µS cm-1 (Fig. 4).

El comportamiento de los taxones ha permitido diferencias dos subzonas: Pñ-1a, es la inferior y está caracterizada por presentar un mayor desarrollo y diversidad en el componente arbóreo, bajos porcentajes de Poaceae y presencias de *Epilobium* y *Typha* tétrada, así como los valores más altos en la diversidad, entre 15 y 20. En base a las dataciones se puede hablar de una tasa de sedimentación bastante lenta, pues el intervalo de 138-150 cm, representan más de 300 años BP (1680±40-1300±30 BP). En cuanto a la subzona Pñ-1b, presenta un retroceso importante del elemento arbóreo debido tanto a la caída del pinar como a la ausencia de los componentes del bosque caduco y perenne lo que favorece la expansión del grupo herbáceo (Poaceae). El grupo acuático pierde igualmente diversidad, no hay Filicales y si un ligero aumento del MNPs tipo-55 A (*Sordaria* sp.) y en menor medida del tipo-113 (*Sporomiella* sp.) y 207 *Glomus* cf. *Fasciculatum*). Baja el índice de la diversidad, hasta valores próximos a 10. Las dataciones disponibles (730±50 BP y 755±30 BP) permiten estimar una tasa de sedimentación relativamente alta en la turbera, (unos 25 años para los 30 cm existentes entre ambas dataciones).

En líneas generales, los datos expuestos permiten afirmar que la vegetación durante Pñ-1, es decir entre 240-780 cal. AD (1680-755 BP), correspondería a un paisaje que, a nivel regional, se relaciona con un pinar denso y bien desarrollado, en cuyo entorno abundarían especies propias de los matorrales mixtos de la alta montaña guadarrámica como *Cytisus oromediterraneus* y cf. *Juniperus communis*. Los porcentajes relativamente elevados de *Betula*, en la base de la zona, denotan una expansión del abedular, ya que en los datos polínicos de la vegetación actual (Gómez, 2007) este tipo polínico no alcanza nunca valores semejantes. Dicha abundancia podría estar relacionada con la instalación de unas condiciones climáticas de una mayor humedad, que a su vez propició el desarrollo de *Quercus pyrenaica* tipo y las presencias de *Castanea*. La caída, tanto cuantitativa como cualitativa del grupo arbóreo, en la parte superior de esta la zona polínica, puede considerarse como la respuesta a una pérdida tanto de la temperatura como de la humedad, propiciando en zonas de alta montaña el desarrollo de pastos, que asociado al aumento de los MNPs coprófilos permiten inferir que el desarrollo de la vegetación estuvo condicionada por cierto tipo de presión pastoral, probablemente del trasiego de ganados trashumantes provenientes de la zona de fondo de valle, que alcanzarían la laguna de Peñalara y su entorno en el estío.

Respecto al comportamiento de los parámetros físico-químicos analizados, el pH pese a ser ácido, debido al carácter de la roca parental de la que deriva el depósito, presenta ligeras oscilaciones; que contrastan con las fuertes variaciones de los valores altos de conductividad. La presión pastoral, podría ser la responsable del aumento en la cantidad de nitratos y fosfatos disueltos en el medio, hecho que coincide con el incremento de los MNPs indicadores de presión pastoral.

El intervalo de 101 a 97 cm es estéril desde el punto de vista polínico y marca el tránsito entre las zonas Pñ-1 y Pñ-2. No resulta fácil explicar esta falta de información, máxime cuando no se aprecian grandes contrastes en el desarrollo de la vegetación a ambos lados de este nivel, quizá podría estar relacionado con un corto período frío que impidió la conservación de los granos de polen.

La Zona Pñ-2: abarca de los 97 a los 40 cm, y corresponde a una turba poco evolucionada con abundantes restos vegetales de briófitos y raíces. El estrato herbáceo continúa siendo el componente dominante, con porcentajes que oscilan entre el 13% y más del 60% de la suma base polínica. Los hechos más relevantes se resumen en el ligero descenso, respecto a la zona anterior de *Pinus sylvestris* tipo, el suave aumento de *Pinus pinaster* tipo, la reintroducción de *Quercus pyrenaica* tipo, *Betula* y en menor medida *Castanea* y *Alnus*. Poaceae sigue siendo el taxon herbáceo dominante, llegando a superar el 60%, seguidos de *Plantago lanceolata* tipo, y en proporciones menores Apiaceae, *Artemisia, Aster* tipo, Brassicaceae, Caryophyllaceae, Chenopodiaceae-Amaranthaceae, Cichorioideae, *Papaver rhoeas* tipo, *Polygonum aviculare* tipo, *Rumex acetosa* tipo, *Saxifraga,* Valerianaceae y Violaceae, junto a presencias puntuales y discontinuas de *Campanula* tipo, *Dipsacus fullonum* tipo y Scrophulariaceae, entre otros. El estrato arbustivo cuantitativa y cualitativamente es muy similar al de la zona anterior, tan sólo se detecta un ligero aumento de *Cytisus* tipo, así como una menor representación de *Prunus* tipo. Cyperaceae sigue siendo el taxón hidro-higrófito mejor representado, Ranunculaceae aumenta ligeramente y se detectan presencias de Myriophyllum, *Typha* monada y tetrada. La presencia del MNP tipo 133 (*Sporomiella* sp) es más constante a lo largo de la zona que los tipos 55 A (*Sordaria* sp.) y 207 (*Glomus* cf. *fasciculatum*). Los valores de diversidad oscilan entre 8 ± 0.07 y 23.5 ± 0.01 (Fig. 4); el pH entre 4.94 y 5.89; y la conductividad entre 15,3 y 106 µS cm-1 (Fig. 4). Al igual que en el caso anterior tanto el comportamiento de los palinomorfos, y la diversidad nos definen dos subzonas, que a grandes rasgos repite el esquema evolutivo observado en la zona Pñ-1; así en la subzona Pñ-2a, desarrollada con anterioridad a los 340±40 BP, se aprecia un nuevo desarrollo del estrato arbóreo en el que intervienen tanto los dos tipos de *Pinus*, como *Quercus pyrenaica* tipo y *Betula*, en el grupo herbáceo destaca la bajada porcentual de Poaceae; también se detectan presencias de los dos tipos de *Typha* así como el aumento de Ranunculaceae. La diversidad alcanza los valores máximos del perfil. El pH se recupera ligeramente, con respecto a la zona Pñ-1, estabilizándose en valores de 5 y los valores de la conductividad son bajos y con tendencia al retroceso. En cuanto a la subzona Pñ-2b, se define para el intervalo de 40 a 75 cm, acumulados entre 340±40 y 275±30 BP, a lo largo de los cuales vuelve a quedar patente el proceso de retroceso del componente arbóreo, aunque en esta subzona no es tan drástico como en la subzona Pñ-1b. La composición es muy similar a la observada en Pñ-2a; no obstante se detectan presencias de *Castanea* y en menor medida de *Fraxinus*. En el grupo arbustivo, desciende el porcentaje de *Prunus*, y de *Erica arborea* tipo. Se observa un importante incremento de Poaceae, asociado a una pérdida de taxones herbáceos, al igual que ocurre en el grupo acuático, excepto a Cyperaceae. Estos hechos se manifiestan en el descenso general de los valores de la diversidad. En cuanto a los MNPs aumentan tanto el tipo-55 A (*Sordaria* sp.) como el tipo-113 (*Sporomiella* sp.) mientras que el tipo-207 (*Glomus* cf. *fasciculatum*) experimenta una fuerte caída. El pH tiende a descender ligeramente frente a un aumento de la conductividad.

En resumen, la zona Pñ-2 presenta, un comportamiento muy similar al observado en la zona Pñ-1, en cuanto a la estructura y composición de la vegetación, pudiendo ser interpretado como un retorno a unas condiciones de mayor humedad y la pérdida de este factor a lo largo de este intervalo temporal. Respecto a la composición, en la zona Pñ-2b no se detecta la pérdida total de *Quercus pyrenaica* tipo y *Betula,* apreciada en la subzona Pñ-1b, lo que podría ser indicativo de que se trata de un periodo menos drástico que en el ciclo anterior. El aumento de los tipos polínicos *Sordaria* sp. (tipo-55A) y *Sporomiella* sp. (tipo-113), aboga como en el caso anterior, por el aumento de la presión ganadera en los pastos de altura, durante esta etapa más seca, y que origina un aumento de la conductividad del sedimento.

La zona Pñ-3 abarca los primeros 40 cm de la secuencia y cuenta con una datación, a 27 cm, de 80±40 BP. Los aspectos más notables de la misma radican en el dominio del componente arbóreo debido a la expansión tanto de *Pinus sylvestris* tipo, como más discretamente de *Pinus pinaster* tipo y de *Quercus pyrenaica* tipo, así como la ausencia de los taxones de ribera. Aumenta considerablemente la representación del estrato arbustivo, debido al incremento de cf *Juniperus* y en el grupo herbáceo hay un descenso importante de todos sus componentes incluido Poaceae, que sigue siendo el componente principal. El grupo acuático sólo está representado por Cyperaceae. Junto a *Glomus* (tipo-207), *Sordaria* sp. (tipo-55A) y *Sporomiella* sp. (tipo-113) se detectan presencias de *Podospora* sp. (tipo-368). La diversidad, aunque muy fluctuante oscila entre valores similares a los de la subzona Pñ-2b, sin embargo las fluctuaciones del pH y la conductividad definen, al igual que el comportamiento y composición de la vegetación, dos subzonas: Pñ-3a, cuyos rasgos distintivos son la presencia de *Quercus pyrenaica* tipo y muy puntualmente de *Alnus y Salix*, así como el desarrollo de *Glomus cf. fasciculatum*; el pH, muestra una tendencia hacia valores más altos y más bajos en el caso de la conductividad. Sin embargo, en la subzona Pñ-3b aumenta *Pinus pinaster* tipo, desciende *Pinus sylvestris* tipo y no se detecta *Quercus pyrenaica* tipo. Aumentan *Cytisus* tipo y cf. *Juniperus*, asociado a la caída de *Erica arborea* tipo; el grupo herbáceo aparece muy empobrecido. Simultáneamente caen los valores de Cyperaceae, único representante del elemento acuático y aumentan considerablemente los valores de *Sordaria* sp. (tipo-55A) y *Sporomiella* sp. (tipo-113)*,* hay presencias de *Podospora* sp. (tipo-368), y *Glomus cf. fasciculatum* (tipo-207) muestra una fuerte caída porcentual. La diversidad, tras un ligero aumento, tiende a disminuir, disminuyen los valores del pH y se produce un fuerte incremento de la conductividad.

A lo largo de la zona Pñ-3, los pinares montanos de *Pinus sylvestris* tipo aunque mantienen un comportamiento más estable que en las zonas anteriores, presentan la misma tendencia al retroceso, como respuesta a una antropización continuada del entorno, y que en la zona de estudio se fundamenta en una presión pastoral; este hecho favorece la expansión del estrato arbustivo, de cf. *Juniperus* y de *Cytisus* tipo. La caída de los pastizales de Poaceae, responden igualmente a la antropización, materializada en el incremento de los pastizales antrópicos y antropozoógenos y que podría también explicar el aumento de *Pinus pinaster* tipo. Sin embargo el aumento del bosque perennifolio, la ausencia de registro de los taxones riparios, el retroceso de Ericaceae y de los taxones acuáticos, parecen revelar que junto a la actividad antrópica, se instalan unas condiciones más cálidas y secas responsables igualmente, del desarrollo del paisaje vegetal. En cuanto a la diversidad, presenta los valores más bajos de todo el perfil, pero con un intervalo de fluctuación menor; los cambios en el pH son poco representativos en esta zona, al contrario que la conductividad que evoluciona desde los valores más bajos de la secuencia hasta casi alcanzar el valor máximo detectado en la subzona Pñ-1a, abogando por el aumento brusco de iones disueltos en el medio, debido al aumento de la presión pastoral. Así y aunque de un modo más atenuado que en las zonas anteriores, se repite la pauta de pérdida de humedad asociada al aumento de presión ganadera.

El dominio de *Pinus*, a lo largo de los últimos 1.680±40 BP, no impide detectar el desarrollo de los elementos de porte arbóreo, desarrollados a cotas latitudinales más bajas y cuyo comportamiento es capaz de reflejar las fluctuaciones acaecidas desde el punto de vista climático y/o antrópico. Así, en el seno de unas condiciones climáticas de carácter mediterráneo, se han podido inferir variaciones en la temperatura y humedad, fundamentalmente en base al desarrollo de taxones como *Betula*, taxones riparios y acuáticos. Estas variaciones se producen de un modo cíclico, definiendo las tres zonas polínicas identificadas, dentro de las cuales se aprecia el tránsito desde unas condiciones más frescas y húmedas a más templadas y secas, y que a su vez se organizan en una tendencia general a lo largo de la secuencia, hacia la instalación de unas condiciones más cálidas y secas.

Por otro lado, la evolución de los pinares montanos de *Pinus sylvestris* tipo, que muestran dentro de cada zona, un proceso de regresión, puede interpretarse como una respuesta a la antropización continuada del entorno de Peñalara. Esta antropización en la alta montaña guadarrámica, se materializa básicamente en un aumento de la presión pastoral, puesta de manifiesto a través del desarrollo de los MNPs de naturaleza coprófila (*Sordaria* sp. y *Sporormiella* sp.) así como del incremento de los pastizales antrópicos y antropozoógenos, detectadas en la mitad superior de cada zona polínica. Esto puede explicarse como respuesta a la pérdida de humedad, que obliga la búsqueda de pastos en las zonas de alta montaña.

En la parte superior de la secuencia, se acentúa el aumento de temperatura y el descenso de precipitación, asociado a un aumento de la presión pastoral, que llega a provocar el descenso de los pastizales de gramíneas. La expansión de los matorrales de enebros rastreros y piornos podría igualmente explicarse bajo esta óptica dado que la dispersión, al menos los piornos, es zoófila. En las sierras de Gredos y Guadarrama, esta misma coincidencia ha sido también señalada (Bentley, 1991; Gil García, 1992; Vázquez, 1992), aunque puesta en correlación con procesos de incendio antrópico para eliminar el piornal en la búsqueda de claros ávidos al pastoreo. Tales fuegos habrían, a posteriori, provocado una extensión mucho mayor del piornal de la que tenía antes de los incendios, dado su carácter pirófilo. En el caso de la secuencia PÑ esta misma dinámica pudo haber actuado también en fechas recientes, aunque de haber sido así lo lógico hubiera sido documentar microfósiles no polínicos indicativos precisamente de la ocurrencia de tales incendios. Sea como fuere, la relación entre aumento de la presión pastoral, deforestación del pinar y la cobertura arbórea regional, progresión de los pastizales antrópicos y antropozoógenos, y, finalmente, extensión del piornal, parecen bastante evidentes.

Por otro lado, las variaciones observadas en la diversidad polínica, podrían obedecer posiblemente a la respuesta de la vegetación ante las perturbaciones antrópicas discontinuas en el área y por ello, a techo de la secuencia, donde la presión pastoral se acentúa, se detecta un aumento importante de la diversidad. Finalmente, si se atiende a las variaciones de los parámetros físico-químicos, frente a un pH fundamentalmente ácido debido a la naturaleza de la roca parental, la conductividad, interpretada como la medida de la cantidad de nitratos y fosfatos disueltos en el medio, presenta aumentos considerables casi paralelamente al aumento de los MNPs coprófilos, y de los pastizales antropozoógenos y nitrófilos.

4. CONCLUSIONES

El estudio polínico de un depósito higroturboso de origen periglacial localizado en el macizo de Peñalara (Sierra de Guadarrama, Madrid) apoyado en 7 dataciones AMS de ^{14}C, proporciona la primera reconstrucción de alta resolución de la evolución de la vegetación en el área durante los últimos 1.689 años.

Los eventos que se han identificado en el registro, por su posición temporal y ámbito, permiten definir varios períodos, en los que se infieren las variaciones climáticas, los usos del suelo y por ende el impacto antrópico sobre el paisaje de la zona.

El primero de ellos, desde el punto de vista cronocultural, el inicio de la secuencia de Peñalara (parte inferior de Pñ-1a) se correspondería con el imperio romano. Los romanos crearon nuevas vías para el avance militar y para la rápida explotación económica de las tierras conquistadas, desarrollando una nueva ordenación administrativa que favoreciese sus intereses. En el caso de la Sierra de Guadarrama existió una red viaria romana de cierta importancia (Fernández Troyano, 1994), que permitió el trasiego de ganado de corto (trasterminante) y largo recorrido (trashumante) durante la dominación romana en Madrid. Los datos polínicos y de los MNPs del perfil de Peñalara muestran un impacto antrópico sobre el paisaje, observándose una importante deforestación, así como la existencia de presión pastoral local ocasionada por el trasiego ganadero hacia los pastos de la alta montaña guadarrámica en época estival, no descartándose que se viera incrementada por la permanencia del ganado en la zona en periodos algo más largos. Este es el mismo panorama que muestran los datos polínicos de la zona de Guadarrama en época romana, como los de Rascafría (Franco Múgica, 1992), Puertos de Canencia y Morcuera (Gil García, 1992) o Lomas de Peñas Crecientes (Vázquez, 1992). Desde el punto de vista climático, en el seno de este intervalo cronológico se documenta el Periodo Cálido Romano (ca 250 cal BC-450 cal AD) (Desprat *et al*., 2003; Domínguez Castro *et al*., 2006). En nuestra secuencia no resulta fácil detectar este periodo debido a la amplia antropización del territorio, pero una primera aproximación permitiría relacionar cierta recuperación, poco aparente, de la masa arbórea como es la mayor preponderancia de las formaciones de quercíneas perennifolias (encinas en este momento.

Seguidamente tenemos información para el intervalo cronológico que se correspondería a grandes rasgos con la Edad Media (parte superior de Pñ-1a, Pñ-1b y parte inferior de Pñ-2a). La zona superior de Pñ-1a correspondería con la época visigoda donde se aprecia una relativa menor presión pastoral, lo que estaría refrendado por el cambio desde el modo de vida agropecuario en el periodo romano a otro de granja dispersa (Martín, 1999 a y b). Estos datos también quedan reflejados en otras secuencias polínicas como en la del Puerto de Canencia y Pico del Lobo (Gil García, 1992), Hoya de Pepe Hernando (Ruiz *et al*., 1988) y Peñalara (Vázquez, 1992). Desde un punto de vista paleoclimático corresponde a un periodo de deterioro climático denominado Periodo Frío Altomedieval, entre los siglos V-VIII (Desprat *et al*., 2003; Domínguez Castro *et al*., 2006). La desaparición antes mencionada del abedul y el melojo podría ser indicativa de este evento climático, a lo que habría que añadir el aumento porcentual de taxa xerófilos como *Artemisia* o Cichoriodeae que se aprecia en nuestra secuencia.

La información que tenemos para el tránsito entre el mundo islámico y la posterior conquista de los cristianos, es decir entre los siglos X y XV d.C., puede establecerse gracias a las dataciones radiocarbónicas y se correspondería con la zona Pñ-1b y zona inferior de la Pñ-2a. En dichas zonas existen evidencias de la existencia de trasiego de ganado en los aledaños a la turbera por la abundancia de hongos coprófilos de los géneros *Sordaria* sp., *Sporormiella* sp. A esta fuerte presión pastoral, contribuyeron, sin duda, los privilegios que otorgó la Mesta, favoreciendo el incremento de las cabañas ganaderas y las vías de paso de varias cañadas reales por las inmediaciones del depósito. Esta nada despreciable presión pastoral también se observa en las secuencias del Puerto de Morcuera (Gil García, 1992), Peñalara, Lomas de Peñas Crecientes y Hoyos de Pinilla (Vázquez, 1992) y Rascafría (Franco Múgica, 1995). En todas estas secuencias se deduce que las épocas islámica y cristiana fueron claves para el modelado del paisaje natural en la zona, por la intensa actividad ganadera que entonces se produjo y que prácticamente se mantiene de forma más o menos continua aunque con diferente intensidad hasta nuestros días.

A nivel paleoclimático, la dominación musulmana coincidiría con el denominado Periodo Frío Altomedieval, ya comentado. En cuanto a la época cristiana coincidió con un periodo ciertamente benigno, conocido como Periodo Cálido Bajomedieval (Desprat *et al*., 2003; Domínguez Castro *et al*., 2006) entre los siglos X-XIV, que podría relacionarse con la proliferación de abedul y del roble melojo que observamos en la zona Pñ-2a.

En el último intervalo cronológico correspondiente a la Edad Moderna y Contemporánea que queda representado en la parte superior de Pñ-2a, Pñ-2b, Pñ-3a y Pñ-3b se puede ver como la región sufrió in incremento paulatino de la presión ganadera llegando a su máxima expresión en los niveles más superficiales (Pñ-3b). La vocación ganadera de la Sierra de Guadarrama, en época moderna y contemporánea se aprecia con claridad por el importante desarrollo de los MNPs indicativos de presión pastoral. Estos resultados coinciden plenamente con los datos obtenidos en el resto de secuencias polínicas estudiadas en dicha sierra (Franco Múgica, 1995, Gil García, 1992, Vázquez, 1992). Desde el punto de vista climático se ha podido reconocer un evento importante como es el denominado Pequeña Edad de Hielo (PEH) (ca 1400-1850 cal AD) (Desprat *et al*., 2003; Domínguez Castro *et al*., 2006; Gil García *et al*., 2006) que ha sido descrita también en algunas secuencias polínicas de la Sierra de Guadarrama (Gil García, 1992; Vázquez, 1992). En nuestra secuencia, las fechas disponibles de 275±30 BP (zona Pñ-2b) y 80±40 BP (zona Pñ-3a) permiten claramente definir el marco temporal de la PEH entre ambas, que se manifiesta por numerosas fluctuaciones en el porcentaje de

Pinus sylvestris tipo y Poaceae, como respuesta posiblemente a las oscilaciones climáticas. A lo que habría que añadir la relativa abundancia de *Artemisia*, la desaparición del aliso, abedul, castaño y fresno y la reducción del melojo.

El estudio de carácter polínico de alta resolución, llevado a cabo en la secuencia PÑ, procedente de un depósito higroturboso del Macizo de Peñalara, ha permitido inferir algunos hechos relevantes durante los últimos 1.680±40 BP, podemos establecer las siguientes conclusiones:

- El análisis paleopalinológico unido al estudio de los MNPs nos ha permitido establecer con precisión tanto la cronología como la tipología de las actividades antrópicas sobre el paisaje así como su posible relación con eventos climáticos abruptos de corta duración.
- Los principales eventos antrópicos en Peñalara se relacionan con el establecimiento de cabañas ganaderas y la presión pastoral creciente, y, finalmente, con la explotación maderera en épocas más recientes. La antropización continuada ha dejado su huella en la configuración de un paisaje manipulado y transformado por la mano del hombre.
- Ha quedado establecido la importancia de las formaciones de pinos y melojos en la zona, que progresivamente se ha visto diezmadas, debido fundamentalmente a la notable actividad antrópica, pero sin descartar la influencia de las variaciones climáticas detectadas.
- Las variaciones en la diversidad polínica, observadas en el análisis de rarefacción, parecen estar relacionadas con perturbaciones de carácter antrópico como respuesta a la influencia del hombre en el paisaje vegetal
- Las fluctuaciones detectadas en las medidas electroquímicas están directamente relacionadas con los cambios sufridos en la vegetación y en los usos del suelo.
- Se han podido detectar los eventos climáticos del final del Holoceno que son similares a los registrados en otras áreas de la Península Ibérica (Periodo cálido Romano, Periodo Frío Altomedieval, Periodo Cálido Bajomedieval, Pequeña Edad de Hielo). Si bien estas fluctuaciones climáticas han quedado en cierta manera enmascaradas por la interferencia de las actividades antrópicas, puede decirse que se manifiestan de un modo cíclico, con una tendencia general es hacia condiciones cada vez más seco.
- Los datos obtenidos en nuestro estudio ponen de manifiesto que el paisaje actual debe explicarse no sólo por factores climáticos y geográficos (topografía y vegetación), sino también humanos, como evolución de la estructura de la propiedad o los cambios de uso del territorio.

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6. BIBLIOGRAFÍA

Acaso, E. 2006. El circo de las Dos Hermanas (Sierra e Guadarrama, España*). Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)*, 101 (1-4), 79-83.

Alía, M., Menéndez Amor, J. y Vidal, C. 1957. Livre-Guide de l'excursion C3 et C4 Guadarrama, Massif Peñalara et variation El Escorial-Manzanares el Real. En: *V Congres Internacional INQUA. Libro de excursiones,* 28-34.

Arobba, D. 1979. Determinazione di «Pinus halepensis» Miller e «Pinus pinaster» Aiton sulla base di differenze palinologiche. *Archivio Botanico e Biogeografico Italiano*, 55 (3), 83-92.

Bentley, S. 1991. *A vegetational history of Peñalara in Central Spain*. King College, Londres (Informe Inédito).

Bronk-Ramsey, C. 2000. OxCal Version 3.5. *http://www.rlaha.ox.ac.uk/orau/index.htm.*

Cambon, G. 1981. *Relations entre le contenu pollinique de l'atmosphere et le couvert vegetal mediterrannee occidentale a Montpellier (France), Valencia (Espagne) et Oran (Algerie)*. Tesis Doctoral, Université des Sciences et Techniques du Languedoc. (Inédita).

Centeno, J.D., Pedraza, J. y Ortega, I. 1983. Estudio geomorfológico, clasificación del relieve de la Sierra de Guadarrama y nuevas aportaciones sobre su morfología glaciar. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)*, 81 (3-4), 153-171.

Coûteaux, M. 1977. À propos de l'interpretation des analyses polliniques de sédiments minéraux, principalement archéologiques. *Supplément du Bulletin de l'Association française pour l´Etude du Quaternaire*, 47, 259-276.

Desprat, S., Sánchez Goñi, M.F. and Loutre, M.F. 2003. Revealing climatic variability of the last three millennia in northwestern Iberia using pollen infux data. *Earth and Planetary Science*, 213, 63-78.

Díaz-Laviada, T. 1989. *Variabilidad del grano de polen en especies ibéricas del género Pinus*. Tesis Doctoral. Universidad Politécnica, Madrid. (Inédita).

Domínguez Castro, F., Santisteban, J.I., Mediavilla, R., Dean, W., López-Pamo, E., Gil García, M.J. and Ruiz Zapata, M.B. 2006. Environmental and geochemical record of human-induced changes in C storage during the last millennium in a temperate wetland (Las Tablas de Daimiel National Park, central Spain). *Tellus*, 58, 573-585.

Faegri, K. and Iversen, J. 1950. *Text-book of modern pollen analysis*. Ejnar Munksgaard, Copenhagen.

Faegri, K., Kaland, P.E. and Krzywinski, K. 1989. *Textbook of Pollen Analysis* 4nd Ed. John Wiley and Sons, Chichester, 328 pp.

Franco Múgica, F. 1995. *Estudio palinológico de turberas holocenas en el Sistema Central: reconstrucción paisajística y acción antrópica*. Tesis Doctoral, Universidad Autónoma, Madrid. (Inédita).

Gil García, M.J. 1992. *Dinámica de la paleovegetación en el sector oriental del Sistema Central español durante el Holoceno, en base al análisis polínico. Implicaciones climáticas.* Tesis Doctoral, Universidad de Alcalá, Alcalá de Henares. (Inédita).

Gil, M.J., Ruiz Zapata, M.B., Santisteban, J.I., Mediavilla, R., López Pamo, E. and Dabrio, C.J. 2006. Late Holocene environments in Las Tablas de Daimiel (South central Iberian Peninsula, Spain). *Vegetation History and Archaeobotany*, 16 (4), 241-250.

Girard, M. and Renault-Miskovsky, J. 1969. Nouvelles techniques de préparation en palynologie appliquées à trois sédiments du Quaternaire final de l'Abri Cornille (Istres, Bouches du Rhône). *Bulletin de l´Association française pour l´Etude du Quaternaire*, 4, 275-284.

Goeury, C. and Beaulieu, J.L. 1979. À propos de la concentration du pollen à l'aide de la liqueur de Thoulet dans les sédiments minéraux. *Pollen et Spores*, 21, 239-251.

Gómez, C. 2007. *Actividad antrópica y vegetación en el Valle del Lozoya (Madrid) durante el Holoceno reciente*. Tesis Doctoral, Universidad de Alcalá, Alcalá de Henares. (Inédita).

Grimm, E.C. 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences*, 13 (1), 13-35.

Jiménez Ballesta, R., López Martínez, J., López García, P. e Ibáñez, J.J. 1985. Contribución al conocimiento de las formaciones superficiales turbosas en las Sierras de Guadarrama y Ayllón. Análisis polínicos. En: *I Reunião do Quaternario Ibérico*, *Actas,* 213-224.

López Sáez, J.A. and López Merino, L. 2007. Coprophilous fungi as a source of information of anthropic activities during the prehistory in the Amblés valley (Ávila, Spain): the archaeopalynological record. *Revista Española de Micropaleontología*, 38 (1-2), 49-75.

López Sáez, J.A., López Merino, L., Cugny, C. y Galop, D. 2005. Paleoecología de medios húmedos: el aporte de los microfósiles no polínicos. *Nuestra Tierra*, 3, 13-15.

López Sáez, J.A., van Geel, B. y Martín Sánchez, M. 2000. Aplicación de los microfósiles no polínicos en Palinología Arqueológica. En: *3º Congresso de Arqueologia Peninsular, Actas,* 11-20.

Martín, J.L. 1999a. *Historia de España 3. Alta Edad Media. La España visigoda y musulmana (siglos V-XIII)*. Editorial Espasa Calpe, S.A., Madrid.

Martín, J.L. 1999b. *Historia de España 4. Baja Edad Media. De la Reconquista a los Reyes Católicos (siglos XIV-XV)*. Editorial Espasa Calpe, S.A., Madrid.

Moore, P.D., Webb, J.A. and Collinson, M.E. 1991. *Pollen analysis*. Blackwell Scientific Publications, Londres, 217 pp.

Pedraza, J., Carrasco, R.M., Martín-Duque, J.F. y Sanz Santos, M.A. 2004. El Macizo de Peñalara (Sistema Central Español). Morfoestructura y modelado. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)*, 99 (1-4), 185-196

Pedraza, J. y Carrasco, R.M. 2005. El glaciarismo pleistoceno del Sistema Central. *Enseñanza de las Ciencias de la Tierra,* 13, 278-288

Reille, M. 1992. *Pollen et Spores d'Europe et d'Afrique du Nord*. Laboratorie de Botanique Historique et Palynologie, Marseille, 520 pp.

Riera, S., López Sáez, J.A. and Julià, R. 2006. Lake responses to historical land use changes in northern Spain: the contribution of non-pollen palynomorphs in a multiproxy study. *Review of Palaeobotany and Palynology*, 141, 127-137.

Ruiz Zapata, M.B., Acaso Deltell, E., Rebollo, L., Vázquez Gómez, R., Gil, M.J., García Antón, M. y Andrade, A. 1988. Aspectos geomorfológicos y paleoclimáticos del sector oriental de la Sierra de Guadarrama. *Henares Revista Geológica*, 2, 19-28.

Ruiz Zapata, M.B., García Antón, M. y Acaso Deltell, E. 1987. Datos polínicos para el conocimiento de la vegetación en el Macizo de Peñalara (Sierra de Guadarrama). *Acta Salmanticensia*, 65, 351-354.

Valdés, B., Díez, M.J. y Fernández, I. 1987. *Atlas polínico de Andalucía Occidental*. Instituto de Desarrollo Regional nº 43, Universidad de Sevilla, Excma. Diputación de Cádiz, Sevilla, 447 pp.

van Geel, B. 1978. A palaeoecological study of Holocene peat bog sections in Germany and The Netherlands. *Review of Palaeobotany and Palynology*, 25, 1-120.

van Geel, B. and Aptroot, A. 2006. Fossil ascomycetes in Quaternary deposits. *Nova Hedwigia*, 82, 313-329.

van Geel, B., Bohncke, S.J.P. and Dee, H. 1981. A palaeoecological study of an Upper Late Glacial and Holocene sequence from 'De Borchert', The Netherlands. *Review of Palaeobotany and Palynology*, 31, 367-448.

van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroop, A., van Reenen, G. and Hakbijl, T. 2003. Environmental reconstruction of a Roman Period settlement site in Uitgeest (The Netherlands), with special reference to coprophilous fungi. *Journal of Archaeological Science*, 30, 873-883.

Vázquez, R. 1992. *Evolución del paisaje vegetal durante el Cuaternario reciente en la zona central y oriental de la Sierra de Guadarrama a* *partir del análisis palinológico*. Tesis Doctoral, Universidad de Alcalá, Alcalá de Henares. (Inédita).

Vázquez, R. y Ruiz Zapata, M.B. 1992. Contribución al conocimiento de la historia de la vegetación durante los últimos 2.000 años en la zona oriental de la Sierra de Guadarrama (Sistema Central Español), a través del análisis polínico. *Boletín de la Real Sociedad Española de Historia Natural (Sección Biológica)*, 88 (1-4), 235-250.

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Evolución de la vegetación en la Sierra de Gata (Cáceres-Salamanca, España) durante el Holoceno reciente. Implicaciones biogeográficas

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Resumen

Se presentan los resultados preliminares del análisis palinológico de la turbera de El Payo (Salamanca, España), situada en el sector occidental del Sistema Central en la Península Ibérica. La datación obtenida para la base es de 3.825 cal BP. La vegetación dominante hasta fechas muy recientes es el abedular de *Betula alba*, lo que supone una clara transición entre los robledales más húmedos de la Serra da Estrela y los pinares-abedulares más continentales de la Sierra de Béjar. Se describe el impacto de las actividades humanas y se discute la presencia de especies relictas eurosiberianas como el castaño, el roble carballo, el tejo o el olmo, y otras mencionadas en el área como el haya, el tilo o el carpe.

Palabras clave: Paleopalinología, Holoceno, Paleofitogeografía, Sierra de Gata, Cáceres, Salamanca, España.

Abstract

[*Vegetation changes in Sierra de Gata (Cáceres-Salamanca, Spain) over Late Holocene. Biogeographic implications*] Preliminary results are presented on the pollen analysis of El Payo mire (Salamanca, Spain), located in the western sector of the Central System of the Iberian Peninsula. The date obtained at the base is 3825 cal BP. Vegetation until recent times has been dominated by birch (*Betula alba*) forest, which shows a clear transition between more humid oak forests from Serra da Estrela and more continental pine-birch forests from Béjar mountain range. The impact of human activities is described and the presence of eurosiberian relic species in the pollen diagram like sweet chestnut, pedunculate oak, yew or elm, and in the area like beech, lime and hornbeam is discussed.

Keywords: Palaeopalynology, Holocene, Palaeophytogeography, Gata Range, Cáceres, Salamanca, Spain.

1. INTRODUCCIÓN

Los trabajos paleopalinológicos realizados en el sector occidental del Sistema Central de la Península Ibérica son numerosos, aunque se han centrado sobre todo en la Serra da Estrela, en Portugal (Janssen & Woldringh, 1981; van den Brink & Janssen, 1985; van der Knapp & van Leeuwen, 1994, 1995, 1997) y en la Sierra de Béjar (Atienza, 1983). También se han estudiado un buen número de depósitos en la Sierra de Gredos (*e.g.* Dorado, 1993; Andrade, 1994; Franco Múgica, 1995), en la Sierra de Guadarrama (*e.g.* Gil García, 1992; Vázquez, 1992; Ruiz del Castillo, 1993; Franco Múgica, 1995) y en la Sierra de Ayllón (Gil García, 1992; Franco Múgica, 1995; Franco Múgica *et al*., 2001). Sin embargo, son escasos los estudios tanto en la vertiente meridional del Sistema Central (López Sáez *et al*., 1997) como en extensas áreas occidentales, especialmente en la Sierra de Francia (Atienza, 1993; López Jiménez & López Sáez, 2005), y, más concretamente, en la Sierra de Gata, en la que hasta la fecha no se ha acometido ningún trabajo.

La situación de la turbera de El Payo (Fig. 1), junto al Puerto de Santa Clara, que separa ambas vertientes de la Sierra de Gata, y la localización de esta sierra entre las Sierras da Estrela al oeste y la de Béjar-Francia al este, proporcionan un interesante marco de estudio para una mejor comprensión del gradiente oceanidad-continentalidad que, de occidente a oriente, determina la fisonomía de los bosques del Sistema Central (Peinado Lorca & Rivas-Martínez, 1987; Franco Múgica, 1995; Costa Tenorio *et al*., 1997). De este modo, en el período Subboreal, dominan los robledales en la Serra da Estrela, se observa la codominancia de pinos y abedules en la Sierra de Béjar, el dominio de los pinos en las Sierras de Gredos y Guadarrama (Franco Múgica, 1995) y, en el sector más oriental, la Sierra de Ayllón, se da una codominancia entre el pinar y el melojar (Gil García, 1992).

El área de estudio añade a este importante interés biogeográfico la presencia actual de especies relictas, situadas en el límite de su área de distribución. El interés es aún mayor cuando en las sierras aledañas, como la Serra da Estrela y la Sierra de Béjar, se han encontrado en el registro paleopalinológico holoceno especies desaparecidas en la región como *Fagus*, *Carpinus* o *Tilia* (van den Brink & Janssen, 1985; Atienza, 1993; Pulido *et al.,* 2007), o por la explicación de antiguas citas en la zona sobre la presencia de *Fagus sylvatica* (Rivas Mateos, 1898).

2. MARCO GEOGRÁFICO Y FÍSICO

La turbera de El Payo (Fig.1) se encuentra muy próxima al Puerto de Santa Clara, que separa las provincias de Cáceres y Salamanca (UTM: 29TPE 689552/4458271), en el sector salmantino de la Sierra de Gata, a 1.000 m de altitud, junto al cauce del Arroyo del Mostajo, que, junto con otros cauces de pequeña entidad, forman el río de Payo,

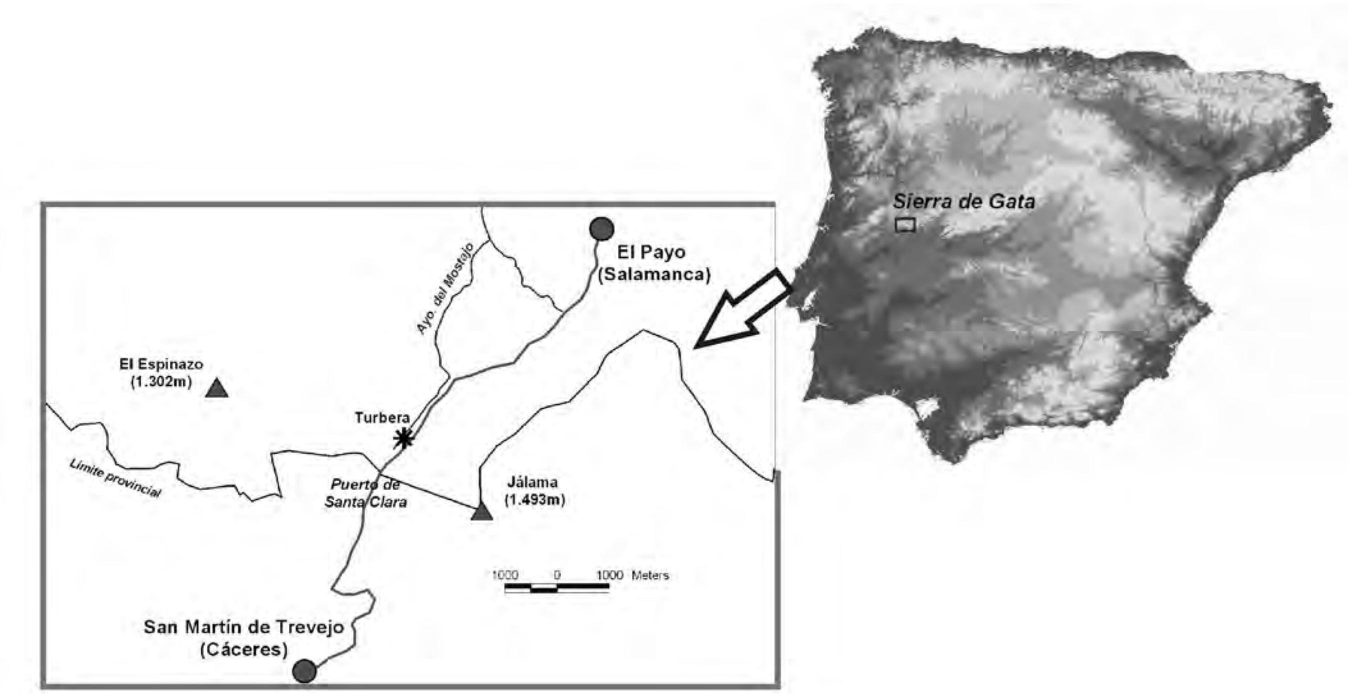

Figura 1. Situación del área de estudio.
Figure 1. Location of study area.

tributario del río Agueda que, tras pasar por Ciudad Rodrigo (Salamanca), desemboca en el río Duero.

La Sierra de Gata se encuentra en el sector occidental del Sistema Central, entre la Sierra de la Peña de Francia y la Serra da Estrela, ya en Portugal, que constituye el macizo más occidental de la cordillera. Supone el límite administrativo entre las provincias de Salamanca y Cáceres, entre España y Portugal, y, como el resto del Sistema Central, la divisoria de las cuencas del Duero y del Tajo.

Los materiales geológicos dominantes son los granitos y las pizarras precámbricas, dispuestos en bandas paralelas de orientación NO-SE, que se fracturan en dirección NE-SO facilitando la formación de las diversas cuencas que vierten a uno u otro lado del macizo (IGME, 1982; Sánchez del Corral, 1994). Comparte con el resto del Sistema Central la diferente altitud del nivel de base en sus vertientes septentrional y meridional, aunque presenta una menor media altitudinal, situada aproximadamente en 1.000 m, con cotas máximas de 1.523 m (Bolla Grande) y de 1.493 m (Jálama).

La estación meteorológica más próxima al área de estudio, Navasfrías, en la provincia de Salamanca, situada a 902 m de altitud, señala una temperatura media anual de 11,3ºC y una precipitación anual de 1.263 mm anuales, lo que situaría el área de estudio en el piso bioclimático supramediterráneo inferior con un ombroclima húmedo (Peinado Lorca & Rivas-Martínez, 1987). El régimen de los vientos ábregos hace que se produzca un notable incremento de la precipitación en las áreas más orientales y occidentales del Sistema Central, por lo que la Sierra de Gata se sitúa entre las áreas más húmedas de la cordillera.

El carácter fronterizo de la Sierra de Gata se refleja claramente en su vegetación, ya que se sitúa en el límite de las provincias corológicas Carpetano-Ibérico Leonesa y Luso-Extremadurense, y se enriquece con numerosos elementos atlánticos resultado de la influencia oceánica que supone su situación geográfica (Peinado Lorca & Rivas-Martínez, 1987).

La vegetación potencial está constituida por melojares húmedos de la *Holco mollis-Quercetum pyrenaicae* (Peinado Lorca & Rivas-Martínez, 1987), característicos de este piso en el sector más occidental del Sistema Central, que se sitúan, en las vertientes meridionales, por encima de los melojares subhúmedos luso-extremadurenses de la *Arbuto unedonis-Quercetum pyrenaicae*, y en las septentrionales, por encima de los melojares subhúmedos carpetano-leoneses de la *Genisto falcatae-Quercetum pyrenaicae*. Es característica la presencia de elementos atlánticos como *Linaria triornitophora, Erythronium dens-canis, Physospermum cornubiense, Omphalodes nitida, Simethis planifolia*, etc., que se añaden a los procedentes de las formaciones de cada una de las provincias corológicas citadas. Las orlas arbustivas están dominadas por *Genista florida* y *Cytisus striatus* o, sobre suelos con menor capacidad de retención hídrica, por *Cytisus multiflorus* y *Echinospartum ibericum*. En los brezales seriales la especie principal es *Erica australis*.

En la actualidad el área de estudio se encuentra dentro de un melojar degradado por la actividad ganadera, próximo a recientes repoblaciones de *Pinus sylvestris*. En las zonas de mayor altitud el paisaje está dominado por el matorral, en el que destacan las distintas formaciones de *Echinospartum ibericum, Cytisus oromediterraneus, C. striatus* y *Erica australis*. Junto a los cauces se desarrollan alisedas abiertas entre las que aún podemos observar ejemplares aislados de *Betula alba*, quizá vestigios de antiguos abedulares que cubrirían amplias extensiones de la Sierra de Gata.

En la vertiente meridional del Puerto de Santa Clara se encuentra el célebre castañar de O´Soitu, que alberga otras especies leñosas como *Quercus robur, Ilex aquifolium, Sorbus latifolia, Ulmus glabra* y una enorme variedad de herbáceas que pueden considerarse relictos de carácter eurosiberiano (Pulido *et al.,* 2007), junto a elementos luso-extremadurenses como *Arbutus unedo, Viburnum tinus, Cytisus multiflorus,* etc.

3. MATERIAL Y MÉTODOS

El sondeo de la turbera de El Payo se realizó mediante una sonda rusa de 5 cm de diámetro, con la que se obtuvo un testigo sedimentario de 100 cm de profundidad, por debajo de la cual aparecían niveles de arenas y gravas. Las muestras para análisis polínico se estudiaron con un grado de resolución de 5 cm, por lo que se sometieron a análisis polínico 20 muestras en dicha turbera.

Se ha efectuado una caracterización de la turbera de El Payo (Fig. 2) en función del tipo de sedimentos presentes en la muestra, con el fin de aclarar determinados acontecimientos relevantes en su formación y, por ende, en la evolución del paisaje de su entorno, para lo que se ha utilizado el sistema de Aaby & Berglund (1986), en el que se describen las turberas en función de las propiedades físicas, el grado de humificación y la naturaleza de los depósitos.

En este estudio preliminar de la turbera de El Payo se ha realizado, por el momento, una sola datación radiocarbónica (AMS) en la base del testigo (100 cm.) para la que se ha obtenido una fecha de 3.560 ± 40 BP (Beta-230841), la cual, una vez calibrada por el propio laboratorio mediante la curva INTCAL04 (Reimer *et al.,* 2004), ofrece una fecha media, en el intervalo de mayor probabilidad, de 3.825 cal BP (1875 cal BC) a 2 σ (cal BP 3.970 a 3.810 y cal BP 3.800 a 3.720).

El método químico utilizado para la extracción de polen, esporas y microfósiles no polínicos de las muestras ha sido el clásico para este tipo de sedimentos (Faegry & Iversen, 1989; Moore *et al.,* 1991), utilizando licor de Thoulet para la separación densimétrica de los microfósiles polínicos y no polínicos (Goeury & Beaulieu, 1979). Además, al comienzo de cada tratamiento se añadió a cada muestra una pastilla de *Lycopodium*, elemento exógeno usualmente empleado para poder estimar la concentración polínica (Stockmarr, 1971). El tratamiento de datos y representación gráfica se ha realizado con ayuda de los programas TILIA y TGView (Grimm, 1992, 2004). Para la zonación polínica se ha realizado una clasificación divisiva con el programa CONISS (Grimm, 1987) incluido en el paquete TILIA.

Para la elaboración del diagrama polínico (Fig. 3) se han excluido de la suma base (500 granos) los taxa hidro-higrófitos y los microfósiles no polínicos, considerados de carácter local o extra-local, por lo que suelen estar sobrerrepresentados (Wright & Patten, 1963), aunque su porcentaje relativo se ha calculado respecto a aquella. También se incluye un diagrama de concentración polínica (Fig. 4) simplificado de los distintos palinomorfos y

Figura 2. Esquema estratigráfico de la turbera de El Payo.
Figure 2. El Payo peat bog sedimentation graphic.

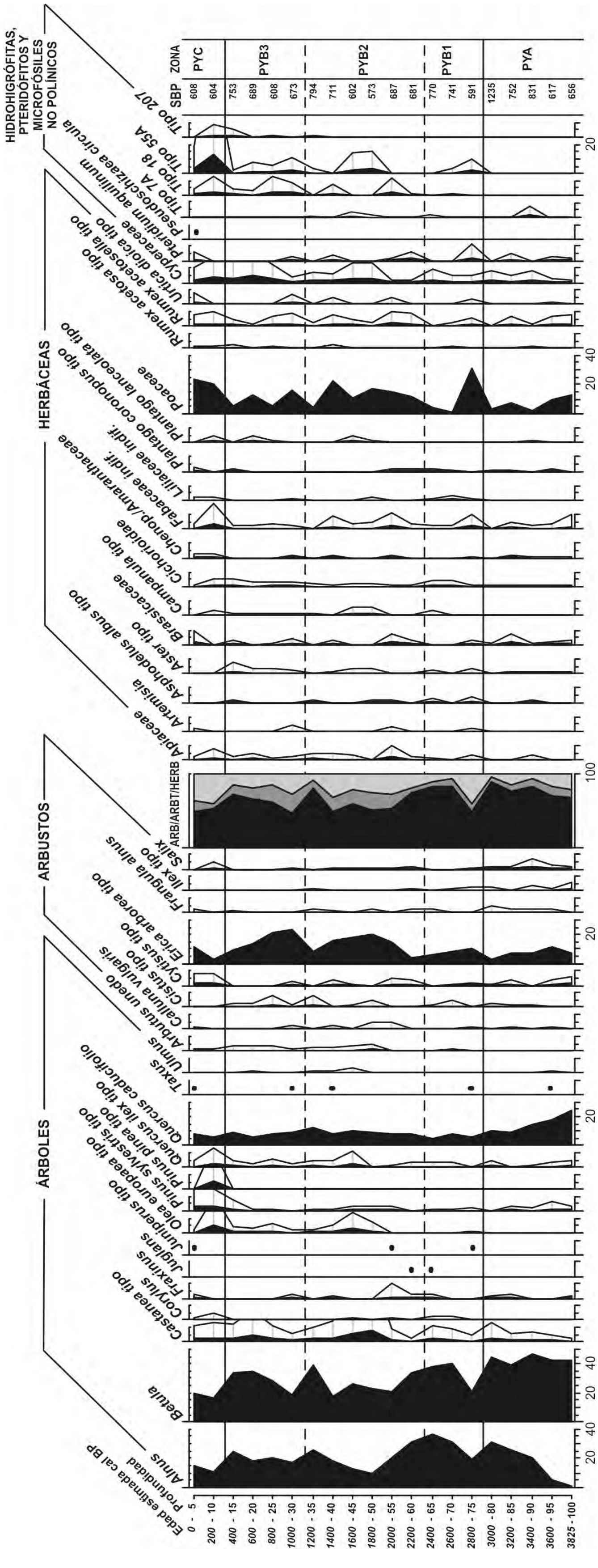

Figura 3. Diagrama polínico sintético de la turbera de El Payo.
Figure 3. El Payo peat bog synthetic pollen diagram.

microfósiles no polínicos para facilitar la interpretación de los resultados.

4. RESULTADOS

Según la datación obtenida se puede afirmar que la turbera de El Payo se formó hace unos 3.825 años. En la gráfica de sedimentación (Fig. 2) se observa la formación continua de turba desde la base del perfil, excepto en una corta sección de la columna, entre 62 y 72 cm., en la que no aparece turba, sino limos.

En el diagrama polínico de la turbera (Fig. 3), mediante la ayuda del programa CONISS, se han separado las siguientes zonas:

4.1. Zona PYA (100-78 cm)

En esta zona el porcentaje de polen arbóreo es el más alto de todo el perfil, llegando incluso al 95% a 80 cm. El taxón dominante es *Betula* (40%) acompañado en la base por *Quercus* caducifolio (24%), que experimenta una fuerte regresión hasta el 10%; y hacia el final de la zona por *Alnus*, que aparece en la base para alcanzar el 31 % final. Conviene destacar la notable presencia en esta subzona de *Castanea* tipo, que llega a alcanzar un 2,6%; de *Pinus sylvestris* tipo (1%) y de *Quercus ilex* tipo (<1%), así como la aparición puntual de *Corylus, Fraxinus, Taxus* y *Ulmus*. Entre las especies arbustivas destaca *Erica arborea* tipo, que llega a alcanzar el 11%, junto a *Cytisus* tipo (1%). También superan el 1% en esta subzona *Ilex* tipo y *Salix*, mientras que, de manera más puntual, aparecen *Frangula alnus y Cistus* tipo. Entre las herbáceas domina Poaceae, que desciende desde el 12% inicial hasta el 2%, acompañada de Fabaceae, Brassicaceae, *Rumex acetosella* tipo y Apiaceae, con porcentajes en torno al 1%, y, en menor medida, de otros taxa antropozoógenos como *Urtica dioica* tipo, Cichorioidae, *Aster* tipo y *Plantago* sp. Cyperaceae mantiene bajos niveles (1%) entre las hidrohigrófitas y *Pteridium aquilinum* (<1%) entre los helechos. No aparecen microfósiles no polínicos, a excepción del tipo 7A (*Chaetomium*).

4.2. Zona PYB (78-13 cm)

A lo largo de esta zona se producen hasta tres abruptos descensos de los niveles de polen arbóreo, con posteriores recuperaciones hasta llegar a un 84% final.

4.2.1. Subzona PYB1 (78-63 cm)

La curva de esta subzona se inicia con el primer gran descenso de polen arbóreo, que desciende hasta el 60%. *Betula* reduce su presencia a la mitad, al igual que *Quercus* caducifolio, mientras *Alnus* pasa del 31 al 19%. La curva del resto de arbóreas no sufre alteraciones significativas. Conviene destacar la presencia puntual de *Taxus* y *Juniperus* tipo. Las especies arbustivas, por el contrario, aumentan su representación gracias a la expansión de *Erica arborea* tipo, que alcanza el 10%. El resto de taxa mantiene sus niveles o los reduce significativamente como ocurre con *Ilex* tipo y *Salix*. Dentro del espectacular crecimiento de los niveles de polen no arbóreo, Poaceae alcanza el 31%, acompañado de Fabaceae (2%) y *Rumex acetosella* tipo (1%). El resto de taxa mantienen sus niveles, mientras que cabe destacar la aparición de *Artemisia*, Liliaceae y de *Asphodelus albus* tipo. Cyperaceae mantiene sus niveles, mientras que *Pteridium aquilinum* experimenta cierta expansión (2,4%). Entre los microfósiles no polínicos hay que destacar la aparición del tipo 55A (Sordariaceae).

4.2.2. Subzona PYB2 (63-33 cm)

Tras una fase de recuperación hasta los niveles previos al acusado descenso de prácticamente todos los taxa, se produce un nuevo y abrupto declive del polen arbóreo (90-71%) entre 60 y 55 cm de profundidad. *Betula* reduce significativamente sus porcentajes (33-18%) y aún más *Alnus* (36-10%). Por el contrario, *Quercus* caducifolio recupera sus porcentajes hasta el 10% al igual que lo hacen, en menor medida, *Quercus ilex* tipo (2%) y *Pinus sylvestris* tipo (1%). En esta subzona se inicia la curva continua de *Olea europaea* tipo*,* mientras que *Castanea* tipo alcanza sus máximos (7,5%). Puntualmente aparecen *Juglans* y *Juniperus* tipo y, hacia el final de esta fase, *Taxus* y *Ulmus*. *Erica arborea* tipo aumenta sus valores hasta el 20%, acompañada por *Cytisus* tipo, *Calluna vulgaris* y, de forma más esporádica, por *Cistus* tipo, todos ellos con porcentajes en torno al 1%. Comienza la curva continua

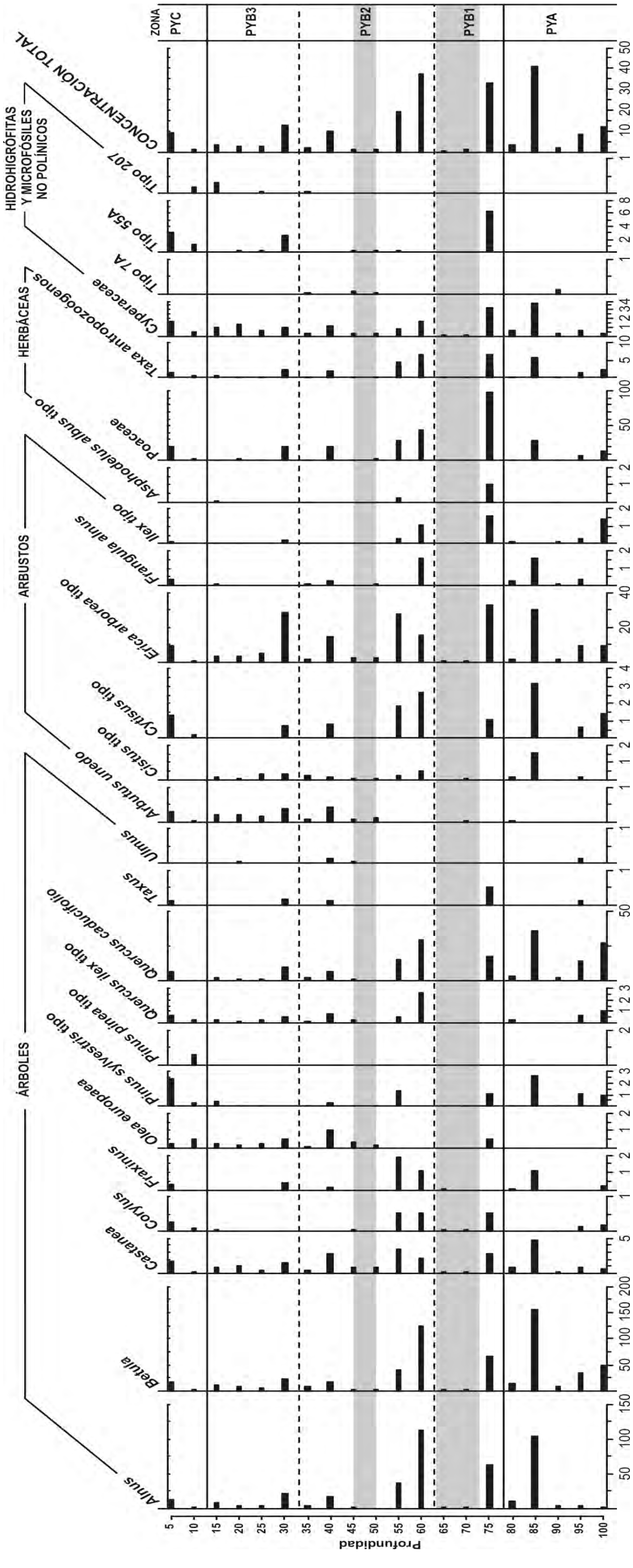

Figura 4. Diagrama sintético de concentración polínica. Se muestran sombreadas las zonas de mínima concentración polínica.

Figure 4. El Payo peat bog synthetic pollen concentration diagram. Areas of minimum pollen concentration are shady shown.

de *Arbutus unedo* y la desaparición progresiva de *Ilex* tipo. En cuanto a las herbáceas, Poaceae experimenta un gran desarrollo (hasta el 22%), acompañada fundamentalmente por Fabaceae y *Rumex acetosella* tipo, con aproximadamente el 2%. Cyperaceae experimenta un fuerte descenso inicial (0,4%) y se va recuperando progresivamente (2%), mientras que *Pteridium aquilinum* aparece de forma cada vez más puntual. Entre los microfósiles no polínicos, el tipo 7A (*Chaetomium*) aparece esporádicamente mientras se inician las curvas continuas del tipo 55A (Sordariaceae) y del tipo 18.

Se produce una nueva y espectacular recuperación del polen arbóreo (92%) protagonizada por *Betula* (40%), *Alnus* (25%) y *Quercus* caducifolio (12%), frente a una acusado descenso de *Erica arborea* tipo (8%), Poaceae (4%), y de prácticamente todos los taxa asociados a la actividad ganadera.

4.2.3. Subzona PYB3 (33-13 cm)

Tras este episodio puntual de recuperación arbórea vuelve a producirse un nuevo evento de deforestación acusada. Descienden los porcentajes de *Betula* (19%) y, en menor medida, los de *Alnus* (18%) y *Quercus* caducifolio (9%). También se reduce la presencia del resto de taxa arbóreos: *Castanea* tipo, *Olea europaea* tipo, *Pinus sylvestris* tipo (que llega a desaparecer) y *Quercus ilex* tipo. Aparecen, de forma muy puntual, *Ulmus* y *Taxus*. Por el contrario, *Erica arborea* tipo alcanza sus máximos (24%). El resto de especies arbustivas mantienen sus niveles con significativa presencia de *Cistus* tipo, *Calluna vulgaris* y *Arbutus unedo*. En la misma línea, Poaceae vuelve a recuperar altos valores (16,5%) junto al resto de taxa antropozoógenos. Cyperaceae prácticamente desaparece mientras se da la puntual aparición de *Pteridium aquilinum*. Entre los microfósiles no polínicos, el tipo 55A retoma los valores que había alcanzado en la fase anterior.

La subzona finaliza con una última recuperación del nivel de polen arbóreo (hasta el 84%) liderada por *Betula* (33%), *Alnus* (25%) y *Quercus* caducifolio (9%), con la pequeña aportación de *Castanea* tipo (2,5%), *Olea europaea* tipo, *Pinus sylvestris* tipo y *Quercus ilex tipo* (en torno al 1%). Todas las especies arbustivas reducen su presencia, especialmente *Erica arborea* tipo (10%), excepto *Arbutus unedo*, que se mantiene en bajos niveles (<1%). También decae Poaceae, con varios altibajos hasta situarse en el 5%, junto al resto de herbáceas. En esta fase se producen los máximos de Cyperaceae (5%) y se hace continua la curva del tipo 207 (*Glomus* cf. *fasciculatum*).

4.3. Zona PYC (13-0 cm)

En esta zona se igualan los valores más bajos de polen arbóreo (60%) que se produjeron al inicio de la subzona anterior. *Betula* (19%) y *Alnus* (15%) siguen siendo las protagonistas entre las especies arbóreas, seguidas de *Quercus* caducifolio (8%). Además, se observan los máximos de *Olea europaea* tipo (5%), *Pinus sylvestris* tipo (3%), y *Quercus ilex* tipo (2,6%). También aparece *Pinus pinea* tipo (5,6%) mientras que *Castanea* tipo se mantiene en bajos niveles (2,6%) y *Corylus* alcanza el 1%. En la muestra más superficial aparece *Taxus*. Entre las especies arbustivas se produce cierta expansión final de *Erica arborea* tipo (11%) y de *Cytisus* tipo (1,7%), con bajos porcentajes de *Arbutus unedo* y *Salix* (en torno al 1%). Poaceae experimenta un fuerte crecimiento (24%), acompañada de Fabaceae, Apiaceae, Brassicaceae, Cichorioidae, *Rumex acetosella* tipo y *Urtica dioica* tipo, que superan el 1%. Cyperaceae reduce sus porcentajes (2%), mientras crecen los de *Pteridium aquilinum* (>1%). En esta subzona se dan los máximos del tipo 55A y del tipo 207, así como la aparición de *Pseudoschizaea circula*.

Respecto al diagrama de concentración polínica (Fig. 4), se observa un notable acontecimiento entre 72 y 62 cm en el que se producen los mínimos de concentración polínica de todo el perfil. Se registra, además, un nuevo mínimo entre 50 y 45 cm.

5. DISCUSIÓN

5.1. El inicio de la formación de la turbera y la documentación de relictos eurosiberianos

La turbera de El Payo comenzó a formarse hacia 3.825 cal BP, es decir, en la segunda mitad del período Subboreal, fecha muy reciente en comparación con la época de formación del resto de turberas del sector occidental del Sistema Central (Franco Múgica, 1995). La práctica totalidad de las turberas estudiadas en la Serra da Estrela tienen su origen en el período Boreal y en los inicios del Atlántico, mientras que en la Sierra de Béjar comenzaron a desarrollarse algo más tarde, a finales del período Boreal y en pleno período Atlántico. Según nos desplazamos hacia el este el inicio de la formación de las turberas del Sistema Central va siendo más reciente, salvo contadas excepciones. De este modo, la turbera de El Payo comenzaría a formarse en épocas similares a las de un buen número de turberas de las vertientes septentrionales de la Sierra de Gredos, fase que parece coincidir con un período neoglacial de carácter global (Font Tullot, 1988). La escasa antigüedad de la turbera estudiada puede explicarse por la menor altitud del área de estudio respecto al resto de las turberas occidentales, aunque no debe descartarse que la acumulación de turba en El Payo se haya debido a las modificaciones hidrológicas (aumento de la escorrentía y el encharcamiento superficial) inducidas por el aclarado de los bosques producto de las actividades humanas en la zona (Franco Múgica, 1995).

El paisaje estaba dominado en esas fechas por los abedulares, gracias a las condiciones frías de ese período (Font Tullot, 1988; López García, 1997; Jalut *et al., 2000)* y a la influencia de la humedad derivada de su proximidad al océano Atlántico. En la Serra da Estrela (Portugal) se producen en esta época los mínimos de *Betula alba* en el depósito de Charco da Candeira (Van der Knaap & van der Leeuwen, 1995), mientras mantiene porcentajes similares a los del área de estudio en Lagoa Comprida (Janssen & Woldringh, 1981). En la Sierra de Candelario el abedul no supera el 6% bajo el dominio de *Pinus*, mientras en la Sierra de Béjar también domina *Betula*, que inicia su declive en favor de *Pinus* (Atienza, 1993)

El aumento de las temperaturas en las últimas fases del período Subboreal (Font Tullot, 1988) habría favorecido la potente expansión del aliso en los numerosos cauces y vaguadas del área, que pasa de estar ausente a alcanzar un 31 % de presencia en el diagrama polínico, fenómeno que, a menor escala, también se produce en la misma época en el registro de Charco da Candeira en la Serra da Estrela (van der Knaap & van der Leeuwen, 1995). Este fulgurante desarrollo de las alisedas discurre paralelo al intenso declive de los robledales, en los que la participación de *Quercus robur* debió ser, sin duda, mucho más importante que en la actualidad. Apoya esta afirmación la presencia de otros elementos atlánticos como el acebo, el tejo, el castaño, el avellano, el olmo o el arraclán, asociados en la actualidad a los bosques de roble carballo (Costa Tenorio *et al*., 1997).

Los reducidos niveles de *Pinus sylvestris* tipo y de *Quercus ilex* tipo no permiten pensar en su presencia local. Los pinares presentes en el Subboreal en la Sierra de Béjar (Atienza, 1993) y los encinares de las zonas llanas meridionales parecen las áreas de distribución más probables de una y otra especie.

El territorio ya sufría en esta época los primeros síntomas de deforestación, en detrimento sobre todo de los robledales, pero también de los abedulares, para la apertura de pastizales sobre los que se desarrolla la incipiente ganadería, mediante el uso del fuego, como atestigua la presencia del microfósil no polínico de ecología carbonícola *Chaetomium* (tipo 7A) (van Geel, 1978; Kuhry, 1985). El impacto de esta actividad es moderado, lo que permite pensar en una ganadería no estante, sino de tipo estival o temporal, como corresponde al tipo de uso de la transición del Calcolítico a la Edad del Bronce (Stevenson & Harrison, 1992; López Jiménez & López Sáez, 2005; Gil-Romera, *et al*., 2008). En estas fechas el paisaje del Charco da Candeira en la vecina Serra da Estrela (Portugal) entra dentro de una dinámica de "bosque antropogénico" (van der Knaap & van der Leeuwen, 1995).

La presencia del castaño se observa desde la base de la turbera de El Payo. Además, aparece en Lagoa Comprida (Serra da Estrela) hacia 5770 cal BP (van der Brink & Janssen, 1985) y en épocas prerromanas en la dehesa de Candelario, en la Sierra de Béjar (Atienza, 1993) o en la Sierra de Francia (López Jiménez *&* López Sáez*,* 2005), lo que permite pensar en áreas de refugio en la zona occidental del Sistema Central para esta especie, aparte de las propuestas por Krebs *et al.* (2004) y como corroboran otros trabajos (Conedera *et al.,* 2004; Benito Garzón *et al.,* 2007; García-Amorena *et al.,* 2007).

No se ha encontrado polen de *Fagus, Carpinus* y *Tilia* en la turbera de El Payo. En el caso del haya, la cuestión es clara dada su ausencia en zonas más occidentales, a pesar de las citas contemporáneas de la especie en la Sierra de Gata (Rivas Mateos, 1898) y de su localización en el registro polínico de la turbera de La Garganta (Sierra de Béjar, Cáceres) (Pulido *et al.,* 2007). Parece ser que, a pesar de su rápida expansión por la Península Ibérica durante el Holoceno Medio (Costa Tenorio *et al*. 1990; Martínez Atienza & Morla Juaristi, 1992; Ramil-Rego *et al.*, 2000; López-Merino *et al.,* 2008), no llegó a alcanzar estas zonas occidentales del Sistema Central antes de que el intenso impacto de las actividades humanas dificultase su extensión (Costa Tenorio *et al*., 1997). No ocurre lo mismo con el carpe, cuyo polen se ha localizado tanto en la Sierra de Béjar entre 6000 y 4525 cal BP (Atienza, 1993) como en la Serra da Estrela entre 4940 y 3515 cal BP (Van den Brink & Janssen, 1985). Las áridas y frías condiciones climáticas del evento 4,0 ka BP (4.500-4.100 cal BP), que provocaron el declive de los taxa mesófilos (Jalut *et al.,* 2000; Carrión, 2002; Arroyo *et al*., 2004) acabaron con su presencia en la Sierra de Béjar. Su carácter termófilo y pionero (Gardner & Willis, 1999; Willis *et al.,* 2000) permitieron una presencia más dilatada en el tiempo en la Serra da Estrela, gracias a una mayor influencia oceánica.

El tilo aparece en el período Subboreal en la Serra da Estrela (Janssen & Woldringh, 1981), y en el período Subatlántico en la Sierra de Béjar (Atienza, 1993), aunque siempre de forma testimonial. Un estudio de mayor resolución en la secuencia de la turbera de El Payo podría facilitar su localización en el área, ya que su presencia suele ser esporádica y muy puntual en los diagramas polínicos debido a su dispersión zoófila y a su baja producción polínica (Turner, 1962; Bueno *et al*., 1993).

Tampoco se ha encontrado polen de cereal en la secuencia, lo que parece indicar cierta lejanía de las zonas aptas para su cultivo, ya que, en cambio, aparece de forma continua desde el período Atlántico en la Serra da Estrela (van der Knaap & van der Leeuwen, 1995), desde los inicios del Subatlántico en la Sierra de Francia (López Jiménez & López Sáez*,* 2005), y de forma esporádica desde Época Romana en la Sierra de Béjar (Atienza, 1993).

De este modo, nos encontramos en esta primera fase de desarrollo de la turbera, en la segunda mitad del período Subboreal, durante la Edad del Bronce, con un paisaje de transición entre unas condiciones más suaves y húmedas en la Serra da Estrela, que favorecieron el desarrollo de los robledales, y otras más continentales en la Sierra de Béjar que permitieron el dominio de los pinares sobre el abedular, siguiendo el gradiente de mayor continentalidad hacia el este del Sistema Central (Franco Múgica, 1995; Costa Tenorio *et al*., 1997). La antropización en las cercanías de El Payo es moderada, consistiendo únicamente en una baja presión pastoral no continuada.

5.2. El evento 2.800 cal BP y la mayor huella antrópica durante la Edad del Hierro, la Época Romana y la Edad Media

La siguiente zona viene determinada por el inicio de un nuevo período, el Subatlántico, marcado por un abrupto evento climático ocurrido a escala planetaria, definido por unas repentinas condiciones más frías y húmedas, que se sitúa en torno a 2.800 cal BP (Van Geel *et al.,* 2004), período en el que se datan numerosos eventos extremos, en especial, crecidas e inundaciones en la Península Ibérica (Benito, 2006). En la turbera parece detectarse este acontecimiento a pesar de la ausencia de dataciones radiocarbónicas.

En este período se produce el mínimo de concentración polínica del diagrama, junto con un significativo cambio en la sedimentación de la turbera que pasa de acumular turba a un nivel de limos humificados, probable consecuencia de la inundación de la turbera y la deposición de materiales de arrastre erosionados de la cuenca.

Los abedulares y el resto de formaciones arbóreas reducen notablemente su extensión, permitiendo una gran expansión de los brezales y un incremento de los pastizales. Esta apertura de claros muestra, además, una clara influencia antrópica, ya que se produce una intensificación de los usos ganaderos, como señalan los aumentos en los niveles de *Artemisia*, *Rumex acetosella* tipo o del microfósil no polínico de ecología coprófila tipo 55A (Sordariaceae) (van Geel, 1978; van Geel *et al*., 2003), que indicaría el establecimiento de las cabañas ganaderas *in situ* (López Sáez *et al*., 2000; López Sáez & López Merino, 2007). En el mismo sentido, el de la apertura del paisaje, hablan la presencia de ciertos tipos relacionados con el uso del fuego, tales como *Asphodelus albus* tipo y el aumento de Liliaceae. Por lo tanto, asistimos en esta época a la extensión de los pastizales mediante el uso del fuego, que favorece la instalación de nuevas comunidades humanas en la zona, en un período marcado por una gran inestabilidad climática (Font Tullot, 1988; Desprat *et al.*, 2003).

En estos inicios del período Subatlántico la Serra da Estrela ya había sufrido una intensa deforestación, ya que aparecen los primeros síntomas de sobrepastoreo y los brezales ocupan amplios espacios del paisaje (van der Knaap & van der Leeuwen, 1995). En la Sierra de Béjar, la deforestación permite un postrero desarrollo de los abedulares en detrimento de los pinares en las zonas altas y de los robledales en zonas medias (Atienza, 1993).

Tras esta fase de ocupación del territorio se produce una intensa recuperación del arbolado, favorecida por unas condiciones más húmedas, tal y como indica la presencia desde entonces del microfósil no polínico correspondiente a ascósporas fúngicas tipo 18 (van Geel, 1978), relacionado con un aumento de la humedad (Mighall *et al.*, 2006), y por el abandono de la actividad ganadera, ya que desaparece el tipo 55A.

La llegada de la cultura romana cambia de nuevo la fisonomía del paisaje del área de estudio. La introducción de nuevos cultivos arbóreos como el castaño y el olivo, y la intensificación de la actividad ganadera, tras el corto período de abandono, fueron acompañadas por una nueva deforestación, más prolongada en el tiempo que la anterior, que afectó sobre todo a los abedulares y a las alisedas. Se extendieron los brezales y los pastos graminoides, que llegaron a constituir entre ambos la mitad de la suma base polínica en este período.

A este intenso impacto antrópico en Época Romana hay que añadir el aumento de las temperaturas (López García, 1997; Desprat *et al.*, 2003). Estos dos factores unidos provocan la sustitución progresiva de los robledales atlánticos, probablemente con mayor presencia de *Quercus robur*, y con presencia de *Ilex aquifolium* en el sotobosque, por melojares de *Quercus pyrenaica*, en los que se data a partir de estas fechas la presencia continua del madroño, más adaptados al fuego y a la acción antrópica. Este hecho de cambio en la composición del sotobosque es una información muy valiosa a tal respecto, puesto que, desafortunadamente, el polen de las especies caducifolias de *Quercus* no puede diferenciarse. También se ven favorecidas durante este período más cálido otras especies como la encina e incluso el pino silvestre, que aumenta ligeramente su presencia en las zonas altas vecinas de la Sierra de Béjar (Atienza, 1993). También el matorral va cambiando su composición, lo que indica una creciente degradación de los suelos, con una mayor presencia de brecina, jaras y jaguarzos y una probable sustitución de *Erica arborea* por *Erica australis*.

La actividad ganadera es más continua y sostenida en el tiempo, como indica la continuidad de la curva de Sordariaceae (tipo 55), lo que favoreció la extensión de pastos. Así lo señala el incremento y la continuidad de las curvas de prácticamente todos los taxa antropozoógenos asociados a tal actividad, además de la utilización, también reiterada, del fuego, como indica *Chaetomium* (tipo 7A). Se trata de un cambio sincrónico en todas las secuencias limítrofes al área de estudio, aunque varía la intensidad de la acción antrópica en cada una de ellas. En Serra da Estrela las formaciones arbóreas se sitúan por debajo del 30%, con una extensión de los brezales de hasta el 35% (van der Knaap & van der Leeuwen, 1995), mientras que la intensidad deforestadora es menor en las Sierras de Béjar y Francia (Atienza, 1993) donde el arbolado nunca retrocede por debajo del 50%, al igual que ocurre en la Sierra de Gata.

Tras una nueva etapa de regeneración del arbolado como consecuencia del abandono de las actividades agroganaderas y de unas condiciones más frías e inestables, correspondientes al Episodio Frío Altomedieval (Font Tullot, 1988) o "Dark Ages" (Desprat *et al.*, 2003), en la que aparecen de forma puntual olmos y tejos, se produce un nuevo evento deforestador que coincide, con toda probabilidad, con la época de las repoblaciones-colonizaciones de los reinos cristianos en el inicio del II milenio AD, favorecidas por las óptimas condiciones climáticas del Episodio Cálido Medieval (Desprat *et al.*, 2003). Esta fase se corresponde con la destrucción del bosque en Serra da Estrela (van der Knaap & van der Leeuwen, 1995) y con el Segundo Período Agrícola en la Sierra de Béjar (Atienza, 1993). Ambas tienen en común un acusado declive de las formaciones arbóreas y la extensión de brezales y pastizales.

En nuestra zona de estudio se reduce el área de todas las formaciones arbóreas hasta los niveles de deforestación que se alcanzaron en Época Romana, por lo que se sigue manteniendo una mayor cobertura arbórea que en las sierras adyacentes. Sin embargo, hay que destacar el espectacular avance de los brezales y, en menor medida, de los jarales, y no tanto de los pastizales, probablemente debido al uso como estivaderos de las zonas aledañas a la turbera. Apoyando los indicios de esta mayor huella antrópica durante la Edad Media, se observa también en esta fase un incremento de los cultivos de castaño y olivo.

Tras esta fase de deforestación se produce una nueva etapa de regeneración arbórea, protagonizada casi en exclusiva por el carácter pionero (David & Barbero, 1995) y la gran capacidad de regeneración frente a los incendios del abedul (Costa Tenorio *et al*., 1997), que recupera terreno frente a los brezales, favorecido quizá por las condiciones más frías de la Pequeña Edad del Hielo (Manrique & Fernández-Cancio, 2000; Mauquoy *et al*., 2002).

5.3. Las características del paisaje subactual y la intensificación del impacto humano

La zona más superficial de la turbera se caracteriza por nuevos mínimos en la cobertura arbórea, a pesar de las repoblaciones realizadas con pinos y la expansión de la encina y de los cultivos del olivo y, en menor medida, del castaño.

Tanto el abedul como el aliso registran sus mínimos porcentuales en todo el diagrama. En el caso del abedul podemos afirmar que es en esta fase más reciente cuando se da el paso de formaciones boscosas de abedular hacia comunidades de carácter más ripario en compañía del aliso, el sauce, el avellano o el fresno, tal y como podemos observar en la actualidad. Conviene recordar que esta situación se da hacia el final del período Subboreal tanto en la Serra da Estrela (Van der Brink & Janssen, 1985; Janssen & Woldringh, 1981) como en la Sierra de Béjar (Atienza, 1993), por lo que la pervivencia de los abedulares en la Sierra de Gata es muy posterior.

Las repoblaciones de pino se realizaron a costa de los extensos brezales que, si bien reducen su área inicialmente, vuelven a recuperar sus niveles junto con una notable expansión de los escobonales, favorecidos por la apertura de claros en los bosques. Queda patente también la intensa erosión provocada por las tareas de repoblación a gran escala, como atestiguan los indicadores de procesos erosivos *Pseudoschizaea circula* y *Glomus* cf. *fasciculatum* (van Geel *et al*., 1989; Pantaleón-Cano *et al*., 1996), así como la desaparición de los madroños en la composición del matorral. También en esta última zona polínica, los pastizales alcanzan su máximo desarrollo, así como los indicadores de actividad ganadera anteriormente comentados y los taxa asociados a esta actividad, lo que denota una ganadería de tipo estante en las inmediaciones de la turbera, tal como ocurre en la actualidad

6. CONCLUSIONES

– La turbera de El Payo comenzó a formarse en la segunda mitad del período Subboreal, *ca*. 3.825 cal BP, época en la que ya se observa cierta actividad antrópica basada en la ganadería.

– La formación vegetal dominante hasta épocas muy recientes ha sido el abedular, mientras que los robledales de *Quercus robur* debieron ser más abundantes que en la actualidad, aunque desempeñaron un papel secundario. En la actualidad los abedules sólo aparecen aislados asociados a enclaves húmedos. Pinares y encinares tuvieron un carácter regional, hasta el desarrollo de las repoblaciones contemporáneas.

– A lo largo del perfil de la turbera pueden datarse, de forma relativa, acontecimientos climáticos extremos como el evento 2.800 cal BP e intensos impactos antrópicos, especialmente los producidos en cronología romana y la época de expansión de los reinos cristianos en el medioevo. Todos ellos han dejado su huella en el registro fósil en forma de deforestación, sobre todo mediante el uso del fuego para la apertura de claros que permitieron el desarrollo de los pastizales y la instalación de cultivos, principalmente castaños y olivos.

– La mayor intensidad de las actividades humanas ha ocurrido en los últimos siglos, en los que el bosque se encuentra completamente aclarado y el matorral domina en las zonas altas.

– La Sierra de Gata supone un área de transición entre la

Serra da Estrela y las Sierras de Béjar y Francia en el gradiente de oceanidad-continentalidad de oeste a este que presenta el Sistema Central, con unas características de alta humedad y baja temperatura que favorecen el desarrollo de los abedules, frente a la mayor termicidad estrellense que permite la expansión de los robledales, y la mayor aridez bejarana que facilita el establecimiento de los pinares montanos.

- Aunque no puede diferenciarse la morfología del grano de polen de las distintas especies de roble, a lo largo de la secuencia parece producirse la sustitución de los robledales más atlánticos de roble carballo, acompañados de acebo, por melojares acompañados de madroño, favorecida por el ascenso de las temperaturas durante el Período Cálido Romano y por el uso del fuego asociado secularmente a las actividades humanas.

- No se han encontrado muestras de polen de *Fagus, Carpinus* o *Tilia* en la secuencia, por lo que se emprenderá un estudio de mayor resolución para aclarar esta situación. Otros taxa como *Ulmus, Corylus* o *Taxus* presentan un carácter testimonial.

- La presencia de polen de castaño previa a la ocupación romana en esta turbera, así como en depósitos próximos, permite pensar en la posibilidad de un área de refugio para esta especie en el sector occidental del Sistema Central.

7. BIBLIOGRAFÍA

Aaby, B. y Berglund, B.E. 1986. Characterization of peat and lake deposits. En: Berglund, B.E. (Ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*, John Wiley & Sons Ltd., Chichester, 231-246.

Andrade, A. 1994. *Dinámica de la vegetación durante los últimos 3.000 BP en las Sierras de la Paramera, La Serrota y Villafranca (Ávila) a partir del análisis polínico*. Tesis Doctoral, Universidad de Alcalá de Henares, Alcalá de Henares.

Arroyo, J., Carrión, J.S., Hampe, A. y Jordano, P. 2004. La distribución de las especies a diferentes escalas espacio-temporales. En: Valladares, F. (Ed.), *Ecología del bosque mediterráneo en un mundo cambiante*. Ministerio de Medio Ambiente, Madrid**,** 27-67.

Atienza Ballano, M. 1993. *Evolución del paisaje vegetal en las Sierras de Béjar y Francia durante el Holoceno, a partir del análisis polínico.* Tesis Doctoral, Universidad de Alcalá de Henares, Alcalá de Henares.

Benito, G. 2006. Riesgos de inundaciones: tendencias históricas y perspectivas de acuerdo con el cambio climático. *Cuaternario y Geomorfología,* 20(3-4), 29-44.

Benito Garzón, M., Sánchez de Dios, R. y Sáinz Ollero, H. 2007. Predictive modelling of tree species distributions on the Iberian Peninsula during the Last Glacial Maximum and Mid-Holocene. *Ecography,* 30, 120-134.

Bueno, A., Vera, M.L. y Fernández, M.A. 1993. Estudio palinológico del género *Tilia* L. (Tiliaceae) en la Cornisa Cantábrica. *Anales de la Asociación de Palinólogos de Lengua Española,* 6, 51-57.

Carrión, J. S. 2002. Patterns and processes of Late Quaternary environmental change in a montane region of southwestern Europe. *Quaternary Science Reviews,* 21, 2047-2066.

Conedera, M., Krebs, P., Tinner, W., Pradella, M. y Torriani, D. 2004. The cultivation of *Castanea sativa* (Mill.) in Europe, from its origin to its difusión on a continental scale. *Vegetation History and Archeobotany,* 13, 161-179.

Costa Tenorio, M., García Antón, M., Morla Juaristi, C. y Saínz Ollero, H. 1990. La evolución de los bosques de la Península Ibérica: una interpretación basada en datos paleobiogeográficos. *Ecología,* Fuera de serie, 1, 31-58.

Costa Tenorio, M., Morla Juaristi, C. y Sainz Ollero, H. (Eds.) 1997. *Los bosques ibéricos. Una interpretación geobotánica*. Planeta, Barcelona.

David, F. y Barbero, M. 1995. De l'histoire du genre Betula dans les Alpes Françaises du Nord. *Review of Palaeobotany and Palynology,* 89, 455-467.

Desprat, S., Sánchez Goñi, M.F. y Loutre, M.F. 2003. Revealing climatic variability of the last three millennia in northwestern Iberia using pollen influx data. *Earth and Planetary Science Letters,* 213, 63-78.

Dorado, M. 1993. *Evolución de la vegetación durante el Holoceno en el Valle de Amblés (Ávila)*. Tesis Doctoral, Universidad de Alcalá de Henares, Alcalá de Henares.

Faegri, K. e Iversen, J. 1989. *Textbook of Pollen Analysis. 4th Edn*. John Wiley & Sons, Chichester.

Font Tullot, I. 1988. *Historia del clima de España. Cambios climáticos y sus causas*. Instituto Nacional de Meteorología, Madrid.

Franco Múgica, F. 1995. *Estudio palinológico de turberas holocenas en el Sistema Central: reconstrucción paisajística y acción antrópica*. Tesis Doctoral, Universidad Autónoma, Madrid.

Franco Múgica, F., García Antón, M., Maldonado Ruiz, J., Morla Juaristi, C. y Sainz Ollero, H. 2001. Evolución de la vegetación en el sector septentrional del Macizo de Ayllón (Sistema Central). Análisis polínico de la turbera de Pelagallinas. *Anales del Jardín Botánico de Madrid,* 59 (1), 113-124.

García Amorena, I., Gómez Manzaneque, F., Rubiales, J.M., Granja, H.M., Soares de Carvalho, G. y Morla, C. 2007. The Late Quaternary coastal forests of western Iberia: A study of their macroremains. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 254, 448-461.

Gardner, A. R. y Willis, K.J. 1999. Prehistoric farming and the postglacial expansion of beech and hornbeam: a comment on Küster. *The Holocene,* 9(1), 119-122.

Gil García, M.J. 1992. *Dinámica de la paleovegetación en el sector oriental del Sistema Central español durante el Holoceno, en base al* *análisis polínico. Implicaciones climáticas*. Tesis Doctoral, Universidad de Alcalá de Henares, Alcalá de Henares.

Gil Romera, G., García Antón, M. y Calleja, J.A. 2008. The late Holocene palaeoecological sequence of Serranía de las Villuercas (southern Meseta, western Spain). *Vegetation History and Archaeobotany*, 17, 653-666.

Goeury, C. y Beaulieu, J. L. de 1979. À propos de la concentration du pollen à l'aide de la liqueur de Thoulet dans les sédiments minéraux. *Pollen et Spores,* 21, 239-251.

Grimm, E.C. 1987. Coniss: a Fortran 77 program for stratigraphically constrained cluster análisis by the method of incremental sum of squares. *Computers & Geosciences*, 13 (1), 13-35.

Grimm, E.C. 1992. *Tilia, version 2*. Springfield. IL 62703. USA: Illinois State Museum. Research and Collection Center.

Grimm, E.C. 2004. *TGView*. Illinois State Museum, Springfield.

IGME, 1982. Plasencia. *Mapa Geológico de España*, E. 1:200.000. Ministerio de Industria, Servicio de Publicaciones, Madrid.

Jalut, G., Amat, A.E., Bonnet, L., Gauquelin, T. & Fontugne, M. 2000. Holocene climatic changes in theWestern Mediterranean, from south-east France to south-east Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 160, 255-290.

Janssen, C. y Woldringh, R.E. 1981. A preliminary radiocarbon dated pollen sequence from the Serra da Estrela, Portugal. *Finisterra*, 16 (32), 299-309.

Krebs, P., Conedera, M., Pradella, M., Torriani, M., Felber, D. y Tinner, W. 2004. Quaternary refugia of the sweet chesnut (*Castanea sativa* Mill.): an extended palynological approach. *Vegetation History and Archeobotany,* 13, 145-160.

Kuhry, P. 1985. Transgression of a raised bog across a coversand ridge originally covered with an oak-lime forest. Palaeoecological study of a Middle Holocene local vegetational succession in the Amstven (northwest Germany). *Review of Palaeobotany and Palynology*, 44, 303-353.

López García, P. (Ed.) 1997. *El Paisaje Vegetal de la Comunidad de Madrid durante el Holoceno Final*. Serie Arqueología, Paleontología y Etnografía, Monográfico 5, Consejería de Educación y Cultura de la Comunidad de Madrid, Madrid.

López Jiménez, O. y López Sáez, J.A. 2005. Paleoambiente y formación de los paisajes antiguos de la comarca de la Sierra de Francia (Salamanca, España): de la estructura social a la creación del paisaje. *Conímbriga,* 44, 5-24.

López-Merino, L., López Sáez, J.A., Ruiz Zapata, M.B. y Gil García, M.J. 2008. Reconstructing the history of beech (*Fagus sylvatica* L.) in the north-western Iberian Range (Spain): From Late-Glacial refugia to the Holocene anthropic-induced forests. *Review of Palaeobotany and Palynology,* 152, 58-65.

López Sáez, J.A., López García, P. y Macías Rosado, R. 1997. Acción antrópica y reconstrucción de la vegetación durante el Holoceno reciente en el valle del Tiétar, Sierra de Gredos (Ávila). *Cuaternario y Geomorfología*, 11, 43-54.

López Sáez, J.A. y López Merino, L. 2007. Coprophilous fungi as a source of information of anthropic activities during the Prehistory in the Amblés Valley (Ávila, Spain): the archaeopalynological record. *Revista Española de Micropaleontología*, 39 (1-2), 103-116.

López Sáez, J.A., van Geel, B. y Martín Sánchez, M. 2000. Aplicación de los microfósiles no polínicos en Palinología Arqueológica. En: Oliveira Jorge, V. (Ed.), *Contributos das Ciências e das Technologias para a Arqueologia da Península Ibérica*, Actas 3º Congresso de Arqueología Peninsular, vol. IX. Adecap, Oporto, 11-20.

Manrique, E. y Fernández-Cancio, A. 2000. Extreme climatic events in dendroclimatic reconstructions from Spain. *Climatic Change,* 44, 123–138,

Martínez Atienza, F. y Morla Juaristi, C. 1992. Aproximación a la Paleocorologia Holocena de *Fagus* en la Península Ibérica a través de datos paleopolínicos. *Investigaciones Agrarias,* Fuera de serie, 1, 135-145.

Mauquoy, D., van Geel, B., Blaauw, M. y van der Plicht, J. 2002. Evidence from northwest European bogs shows 'Little Ice Age' climatic changes driven by variations in solar activity. *The Holocene,* 12 (1), 1–6

Mighall, T., Martínez Cortizas, A., Biester, H. y Turner, S.E. 2005. Proxy climate and vegetation changes during the last five millennia in NW Iberia: pollen ad non-pollen palynomorph data from two ombrotrophic peat bogs in the North Western Iberian Peninsula. *Review of Palaeobotany and Palynology,* 141, 203-223.

Moore, P. D., Webb, J. A. y Collinson, M. E. 1991. *Pollen analysis.* Blackwell Scientific Publications, Londres.

Pantaleón-Cano, L., Pérez-Obiol, R., Yll, E.I. y Roure, J.M. 1996. Significado de *Pseudoschizaea* en secuencias sedimentarías de la vertiente mediterránea de la Península Ibérica e islas Baleares. En: Ruiz Zapata, M.B. *et al*. (Eds.), *Estudios Palinológicos, XI Simposio de palinología (A.P.L.E.)*. Universidad de Alcalá de Henares, Alcalá de Henares, 101-105.

Peinado Lorca, M. y Rivas-Martínez, S. (Eds.). 1987. *La vegetación de España*. Colección Aula Abierta, Universidad de Alcalá de Henares, Alcalá de Henares.

Pulido, F., Sanz, R., Abel, D., Ezquerra, J., Gil, A., González, G., Hernández, A., Moreno, G., Pérez, J.J., y Vázquez, F. 2007. *Los bosques de Extremadura, evolución,ecología y conservación*. Junta de Extremadura. Mérida.

Ramil-Rego, P., Rodríguez Guitián, M.A., Muñoz Sobrino, C. y Gomez-Orellana, L. 2000. Some considerations about the postglacial history and recent distribution of *Fagus sylvatica* in the NW Iberian Peninsula. *Folia Geobotanica*, 35, 241-271.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Bertrand, C.J.H., Blackwell, P.G., Buck, C.E., Burr, G.S., Cutler, K.B., Damon, P.E., Edwards, R.L., Fairbanks, R.G., Friedrich, M., Guilderson, T.P., Hogg, A.G., Hughen, K.A., Kromer, B., McCormac, G., Manning, S., Ramsey, C.B., Reimer, R.W., Remmele, S., Southon, J.R., Stuiver, M., Talamo, S., Taylor, F.W., van der Plicht, J. y Weyhenmeyer, C.E. 2004. IntCal04 Terrestrial Radiocarbon Age Calibration, 0 to 26 cal Kyr BP. *Radiocarbon,* 46, 1029-1058.

Rivas Mateos, M. 1898. Flora de la provincia de Cáceres. *Anales Instituto Botánico A.J. Cavanilles*, 30, 235-255

Ruiz del Castillo, J. 1993. *Análisis palinológico de nueve perfiles turbosos cuaternarios en el sector oriental del Sistema Central Español.* Tesis Doctoral, Universidad Complutense, Madrid.

Sánchez del Corral Jiménez, A. 1994. El contacto montaña-superficies inferiores en la vertiente Sur de la Sierra de Gata (Sistema Central español, Cáceres). *Cuaternario y Geomorfología,* 8(1-2), 45-55.

Stevenson, A. C. y Harrison, R.J. 1992. Ancient forests in Spain: a model for land-use and dry forest management in South-west Spain from 4000 BC to 1900 AD. *Proceedings of the Prehistoric Society,* 58, 227-247.

Stockmarr, J. 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores*, 13, 614-621.

Turner, J. 1962. The *Tilia* decline: an anthropogenic interpretation. *New Phytologist*, 61, 328-341.

van den Brink, L. M. y Janssen, C.R. 1985. The effect of human activities during culrural phases on the development of montane vegetation in the Serra da Estrela, Portugal. *Review of Palaeobotany and Palynology,* 44, 193-215.

van der Knaap, W.O. y van Leeuwen, J.F.N. 1994. Holocene vegetation, human impact, and climatic change in Serra da Estrela, Portugal. *Dissertationes Botanicae*, 234, 497-535.

van der Knaap, W.O. y van Leeuwen, J.F.N. 1995. Holocene vegetation and degradation as responses to climatic change and human activity in the Serra da Estrela, Portugal. *Review of Palaeobotany and Palynology*, 89, 153-211.

van der Knaap, W.O. y van Leeuwen, J.F.N. 1997. Late Glacial and early Holocene vegetation sucession, altitudinal vegetation zonation, and climatic change in the Serra da Estrela, Portugal. *Review of Palaeobotany and Palynology*, 97 (3/4), 239-285.

van Geel, B. 1978. A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. *Review of Palaeobotany and Palynology*, 25, 1-120.

van Geel, B., Coope, G.R. y Hammen, T. van der. 1989. Palaeoecology and stratigraphy of the Late-glacial type section al Usselo (The Netherlands). *Review of Palaeobotany and Palynology*, 60, 25-129.

van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroot; A., van Reenen, G. y Hakbijl, T. 2003. Environmental reconstruction of a Roman Period settlement site in Uitgeest (The Netherlands), with special reference to coprophilous fungi. *Journal of Archaeological Science*, 30, 873-883.

van Geel, B., Bokovenko, N.A., Burova, N.D., Chugunov,K.V., Dergachev, V.A., Dirksen, V.G., Kulkova, M., Nagler, A., Parzinger, H., Van der Plicht, J., Vasiliev, S.S. y Zaitseva, G.I. 2004. Climate change and the expansion of the Scythian culture after 850 BC: a hypothesis. *Journal of Archaeological Science,* 31, 1735-1742.

Vázquez, R. 1992. *Evolución del paisaje vegetal durante el Cuaternario reciente en la zona central y oriental de la Sierra de Guadarrama a partir del análisis palinológico.* Tesis Doctoral, Universidad de Alcalá de Henares, Alcalá de Henares.

Willis, K., Rudner, E. y Sümegi, P. 2000. The Full-Glacial Forests of Central and Southeastern Europe. *Quaternary Research,* 53, 203-213.

Wright, H. E. y Patten, H. J. 1963. The pollen sum. *Pollen et Spores,* 5 (2), 445-450.

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On the origins of Superfamily Heterohelicacea Cushman, 1927 and the polyphyletic nature of planktic foraminifera

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Resumen

Un nuevo grupo de foraminíferos bentónicos pertenecientes a la superfamilia Praeplanctoniacea nov., que se originó a partir del género *Pleurostomella* Reuss 1860, se describe en los sedimentos del Albiense superior de la Meseta de Blake (oeste del Atlántico Norte). La citada superfamilia está integrada por dos familias: Praeplanctonidae nov. y Archaeoguembelitriidae nov. La familia Praeplanctonidae incluye dos géneros bentónicos: *Praeplanctonia* nov. gen. y *Haigella* nov. gen. *Praeplanctonia* incluye dos especies con cámaras globulares: *P. globifera* nov. sp. y *P. quasiplanctonica* nov. sp. El género *Haigella* se propone para una línea de foraminíferos en la cual las proyecciones de las cámaras están orientadas hacia atrás y donde se incluyen las especies: *H. intermedia* nov. sp. y *H. haigi* nov. sp. La familia Archaeoguembelitriidae está integrada por un solo género (*Archaeoguembelitria* nov. gen.) y dos especies: *A. cenomana* (Keller 1935) y *A. harrisi* (Tappan 1940). *Archaeoguembelitria* caracteriza a nivel genérico una línea de foraminíferos triseriadas en la cual *A. cenomana* (Albiense tardío) es una especie bentónica con la superficie de las cámaras no ornamentada y *A. harrisi* es una especie planctónica que tiene la superficie de las cámaras ornamentada con montículos porados. *Praeplanctonia globifera* nov. gen., nov. sp.es el antecessor de *Haigella* nov. gen., *Archaeoguembelitria* nov. gen. and *"Heterohelix" washitensis* (Tappan, 1940). La existencia de una relación filogenética entre el foraminífero bentónico *Praeplanctonia globifera* nov. gen., como antecesor, y "*Heterohelix*" *washitensis*, especie más antigua, planctónica y biseriada, como descendiente, demuestra que el grupo de los foraminíferos planctónicos es polifilético. Se revisan otros dos géneros: *Guembelitriella* Tappan 1940, que se reasigna a la Superfamilia Turrilinacea Cushman 1927 y *Guembelitria* Cushman 1933, que se restringe a test triseriados de edad Santoniense tardío-Paleoceno temprano. Los tests triseriados del Albiense tardío-Turoniense incluyen al género *Archaeoguembelitria* nov. gen. Los primeros ejemplares triseriados del intervalo Aptiense superior-Albiense superior bajo se incluyen en el género *Koutsoukosia* nov. gen., que tiene como especie tipo a *K. sergipensis* (Koutsoukos, 1994). *Koutsoukosia* está asignado a la familia Globuligerinidae Loeblich & Tappan 1984.

Palabras clave: Foraminíferos bentónicos, foraminíferos planctónicos, Cretácico, nuevos taxones, foraminíferos planctónicos polifiléticos.

Abstract

A new group of benthic foraminifera is described from the upper Albian sediments of the Blake Plateau (western North Atlantic), superfamily Praeplanctoniacea nov., which originated from the genus *Pleurostomella* Reuss, 1860. Superfamily Praeplanctoniacea comprises two families: Family Praeplanctonidae nov. and Family Archaeoguembelitriidae nov. Family Praeplanctonidae includes two benthic genera: *Praeplanctonia* nov. gen. and *Haigella* nov. gen. *Praeplanctonia* consists of species with globular chambers, *P. globifera* nov. sp. and *P. quasiplanctonica* nov. sp. *Haigella* is proposed for a lineage in which backward oriented chamber projections are gradually developed: *H. intermedia* nov. sp. and *H. haigi* nov. sp. A single genus is included in Family Archaeoguembelitriidae: *Archaeoguembelitria* nov. gen., which consists of two species, namely *A. cenomana* (Keller, 1935) and *A. harrisi* (Tappan, 1940). *Archaeoguembelitria* formalizes at the genus level a lineage of triserial foraminifera in which *A. cenomana* (late Albian) is a benthic species with smooth chamber surface and *A. harrisi* is a planktic species that has the chamber surface ornamented with pore mounds. *Praeplanctonia globifera* nov. gen., nov. sp. is the ancestral species for *Haigella* nov. gen., *Archaeoguembelitria* nov. gen. and *"Heterohelix" washitensis* (Tappan, 1940). The existence of a phylogenetic relationship between the benthic foraminifer *Praeplanctonia globifera* nov. gen., nov. sp., as ancestor and the oldest biserial planktic foraminiferal species, "*Heterohelix*" *washitensis* as descendant, demonstrates that the planktic foraminiferal group is polyphyletic. Two other genera are reviewed: *Guembelitriella* Tappan, 1940, which is reassigned to Superfamily Turrilinacea Cushman, 1927 and *Guembelitria* Cushman, 1933, which is restricted to triserial tests of the late Santonian-early Paleocene. The late Albian-Turonian triserial tests are included within *Archaeoguembelitria* nov. gen. The earliest triserials of the upper Aptian to lowermost upper Albian are included within *Koutsoukosia* nov. gen., which has *K. sergipensis* (Koutsoukos, 1994) as type species. *Koutsoukosia* is assigned to the Family Globuligerinidae Loeblich & Tappan, 1984.

Keywords: Benthic foraminifera, planktic foraminifera, Cretaceous, new taxa, polyphyletic planktic foraminifera.

1. INTRODUCTION

Mesozoic planktic foraminifera have been traditionally regarded as representing a branching and monophyletic group. This view is shared by many researches, such as Caron (1983, 1985), Hart (1999) and Hart *et al.* (2002). The origin of Cenozoic planktic foraminifera from Cretaceous taxa were outlined by Liu & Olsson (1992) and Olsson *et al.* (1999) and the recovery from the end-Cretaceous cataclysmic event further demonstrate the vitality and diversification potential of the group.

A different view was advocated by Darling *et al.* (1996, 1997) through molecular rDNA studies on some Cenozoic species, such as *Neogloboquadrina dutertrei* (d'Orbigny, 1839), *Globigerinelloides conglobatus* (Brady, 1879), *G. ruber* (d'Orbigny, 1839), etc. suggesting that the group is polyphyletic. This conclusion was based on the discovery of rDNA sequences of benthic foraminifera in that of planktic species. Darling *et al.* (1997, p. 251) concluded that "Our phylogenetic analysis shows that the planktic foraminifera are polyphyletic in origin, not evolving solely from a single 'globigerinid-like' lineage in the Mid-Jurassic, but derived from at least two ancestral benthic lines." Despite the conclusions of Darling *et al.* (1997) and in the absence of any supporting paleontological evidence, the uncertainty as to whether or not the planktic foraminifera represent a monophyletic or polyphyletic group still persists.

Extensive study on the upper Albian-lower Cenomanian benthic and planktic foraminifera showed that the earliest biserial and triserial planktics commenced their evolution during the Late Albian (*Pseudothalmanninella ticinensis* Biozone). The earliest representatives of this group have twisted and asymmetrical tests as well as asymmetrically developed periapertural structures [e.g., "*Heterohelix*" *washitensis*]. This observation is highly significant as it rules out the possibility of finding the ancestor of the biserial and triserial planktic foraminifera among the upper Albian contemporaneous planktic foraminiferal taxa. The latter are represented mainly by trochospiral (e.g., *Hedbergella*, *Ticinella* and *Clavihedbergella*) and planispiral (e.g., *Globigerinelloides* and *Planomalina*) species and the earliest biserial planktic taxa lack an early trochospiral or planispiral stage. The other potential ancestor could be the triserial species *Guembelitria cenomana* (Keller, 1935), which has a benthic appearance. A potential phylogenetic relationship between *G. cenomana* and "*H.*" *washitensis* cannot be taken in consideration due to relatively narrow variability of the former species, which presents only triserial tests without any trend to develop biserial chamber arrangement.

A new benthic foraminiferal group of the upper Albian, with twisted tests and high morphological variability is described. Three lineages are recognized within the new group, each of them formalized at the genus level, *Praeplanctonia* nov. gen., *Haigella* nov. gen. and *Archaeoguembelitria* nov. gen. The group is formalized as Superfamily Praeplanctoniacea nov. The origins of the praeplanctonids apparently can be traced from representatives of the Superfamily Pleurostomellacea Reuss, 1860. Consequently, the biserial planktic foraminifera, which were traditionally regarded as members of the Superfamily Heterohelicacea Cushman, 1927 are removed from Suborder Globigerinina Delage & Hérouard, 1896 and included within Suborder Rotaliina Delage & Hérouard, 1896, in order to accommodate the newly inferred phylogenetic relationships.

2. A HISTORY OF CONCEPTS ON HETEROHELICID ORIGINS

The origins of the Cretaceous serial planktic foraminifera have been rarely studied (Cushman, 1950; Fuchs, 1973, 1975; Loeblich & Tappan, 1974; Hart, 1999, 2006; Hart *et al.,* 2002). Throughout these studies, the planktics with serial chamber arrangement were considered related to the other major groups of planktic foraminifera, namely those with planispiral and trochospiral coil.

The first account on the origins of the heterohelicids was by Cushman (1950). In the fourth edition of his Treatise, Cushman (1950, p. 252) noted: "Derived from a planispiral ancestry, this is held in the early stages of all the most primitive genera, at least in the microspheric forms. There is no evidence that the group was derived from the specialized pelagic Globigerinidae, although the genus *Gümbelina* may have been pelagic."

Contrasting phylogenies were proposed by Fuchs (1973) who considered that *Heterohelix* and *Guembelitria* evolved from different ancestors. According to this author, the genus *Heterohelix* is the end member of the *Woletzina*-*Eoheterohelix*-*Heterohelix* lineage. By contrast, *Guembelitria* Cushman, 1933 evolved from *Conoglobigerina* Morozova, 1961. Therefore, *Heterohelix* and *Guembelitria*, the two genera around which the taxonomy of the Cretaceous serial planktic foraminifera is centered (Loeblich & Tappan, 1987), were considered phylogenetically unrelated. This idea was not further developed and a couple of years later Fuchs (1975, p. 220) postulated the existence of a different evolutionary sequence, at suprageneric levels: Oberhauserellidae – Guembelitriinae – Heterohelicinae. The phylogenetic relationship between Oberhauserellidae (ancestor) and Heterohelicidae (descendant) was considered valid by Loeblich & Tappan (1974).

Evolution and diversity of the early planktic foraminifera was extensively studied by Hart (1999, 2006) and Hart *et al*. (2002). According to these studies, a phylogenetic relationship could have existed between the planispirally coiled planktic foraminifera, as ancestor and *Heterohelix* as descendant (Hart, 1999, fig. 2; Hart *et al*., 2002, fig. 2).

This historical presentation shows that there is no clear view on the origins of the Cretaceous serial planktics, despite the existence of a number of hypothesized phylogenetic relationships between various genera, subfamilies and families. All of these phylogenetic relationships are postulated exclusively based on the gross test architecture. Moreover, data on the stratigraphic and paleobiogeographic distribution played, at best, a secondary role in interpreting the proposed phylogenies.

3. STUDIED MATERIAL

Most of the material analyzed came from a succession of sixty-nine samples obtained from upper Albian-lower Cenomanian sediments of the ODP Hole 1050C (Blake Plateau, western North Atlantic). Spot samples were studied from two other wells drilled in its proximity, namely ODP Holes 1052E and 1049B (Fig. 1). The first biostratigraphic zonation of the upper Albian-middle Cenomanian sediments drilled during Leg 171B was provided by Bellier & Moullade (2002). In total, over one thousand SEM micrographs were taken and specimens from throughout the stratigraphic range of the various benthic and planktic species were investigated.

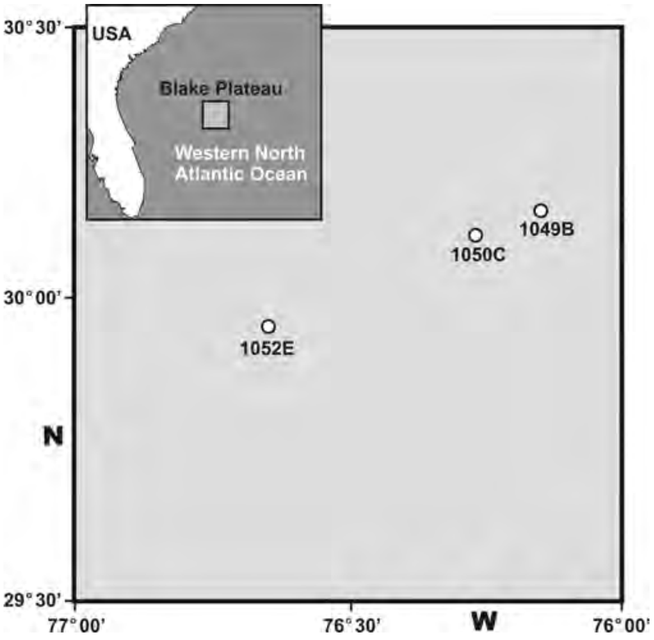

Figure 1. Location of the ODP Holes 1049B, 1050C and 1052E, which yielded most of the fossil material analyzed in this study.

The holotypes of the following species were examined at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.: *Gümbelina washitensis* (USNM 299328, USNM 307987 and USNM 307988), *Gümbelitria harrisi* (USMN 307994 and USNM 307995), *Gümbelitriella graysonensis* (USNM299329, USNM 299330, USNM 307998 and USNM 307999), *Bulimina nannina* (USNM 298868, USNM 303520 and USNM 303521) and *Neobulimina minima* (USNM 299596, USNM 311438, USNM 311439 and USNM 311440), all of them described by (Tappan, 1940) from the Grayson Bluff, Texas, USA and *Neobulimina irregularis* Cushman & Parker, 1936 from the Ector tongue of the Austin Chalk, Grayson County, Texas, USA (USNM 311431, USNM 311432, USNM 311433, USNM 311434 and USNM 311435). Topotypes of the following species deposited in the Loeblich and Tappan Topotype Collection (NMNH, Washington D.C.) could be examined and SEM photographed: *G. graysonensis* (USNM 473114) and *Gümbelitria cretacea* (Cushman, 1933), the latter from the Navarro Formation, Guadelupe County, Texas, USA (USNM 473112). Species names are given according to the labels in the Cushman Collection (NMNH).

The type material (holotype and paratypes) together with a number of topotypes of *Koutsoukosia sergipensis* (Koutsoukos, 1994) from the well 1-CA-1-SE (proximity of the city of Aracaju, Sergipe Basin, eastern Brazil) could be examined at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. We could also examine specimens of *Archaeoguembelitria harrisi* (Tappan, 1940) from the Bass River Formation (New Jersey coastal plain subsurface) and deposited at Rutgers, The State University of New Jersey.

All the type material of the new taxa described in this article is deposited in the Willi Karl Braun Micropaleontological Collection at the University of Calgary (Calgary, Alberta, Canada). They are referred in text as “WKB”, followed by the inventory number.

4. TAXONOMIC CONCEPTS

A major difficulty in recognizing phylogenetic relationships at generic and suprageneric level among Cretaceous foraminifera is due to the present-day classification, which is fundamentally typological. The basis of typological classification is represented by morphological resemblances between various entities (e.g., individuals within a species, species within a genus, genera within a family, etc.). This procedure is extremely rigid and prone to grouping entities, which although morphologically close, are the result of iterative evolution from phylogenetically distant groups, as shown by Steineck & Fleisher (1978) for the Cenozoic planktic foraminifera. The problem is further complicated by the large-scale use of the typological species and genus concepts in current micropaleontological practice. These two concepts are major impediments in recognizing evolutionary trends and phylogenetic relationships. The use of the typological species concept has the disadvantage of considering the species morphologically homogeneous entities, often centered on the holotype (Masters, 1977). Another recent development in the use of the typological species was the practice to define species with the aid of a small number of features, which resulted in extensive lumping (Nederbragt *et al.*, 1998). Similarly, the typological genus concept can lead to the definition of trans-lineage taxonomic units that lack any significance in a phylogenetic classification.

All these difficulties of taxonomical nature had to be overcome in searching for the origins of the serial Cretaceous planktic foraminifera. For this reason, the well-documented paleontological species concept (Georgescu & Huber, 2007) and the concept of genus-lineage were used.

4.1. Species concept

The transition between the optical microscope-based observations to those in which the morphological data are mostly collected with the aid of a scanning electron microscope (SEM) resulted in a significant improvement of the observation detail. Accordingly, the species variability can be better described and used for taxonomic and phylogenetic purposes. Recent studies carried out on Late Cretaceous species of stellate and strongly ornamented planktic foraminifera showed that the species variability is much higher than previously considered. For example, Georgescu & Huber (2008) demonstrated that in *Hastigerinoides alexanderi* (Cushman, 1931), a planktic foraminifer with stellate outline from the Santonian (Late Cretaceous), can be recognized two test varieties according to the chamber arrangement: planispiral and very low trochospiral. This wide range of morphological variability comes in contradiction with the widely accepted classification of Loeblich & Tappan (1987), in which such differences in the coiling mode are regarded as valid taxonomic criteria at superfamily level.

The concept of well-documented paleontological species was proposed by Georgescu & Huber (2007, p. 158) to accommodate the wide morphological variability present in most of the Cretaceous planktic foraminiferal species: "A well-documented paleontological species is the basic unit with taxonomic significance in the fossil record, and has the following characteristics: (i) it is monophyletic; (ii) it has a distinct range of morphological variability, showing relative stability over a definable period of time and presenting relatively discrete evolutionary changes; (iii) it is a morphologically heterogeneous and discontinuous entity, consisting of one or (mostly) more morphological and/or paleoecological varieties; (iv) it has its own developmental history traceable in space and time; and (v) its existence and integrity can be tested not only by comparative morphological distinctiveness, but also by its response to paleoenvironmental and geological factors (e.g., paleoclimatic changes, sea-level fluctuations, etc.), as inferred from paleontology and related geological disciplines". It was applied with excellent results by Georgescu (2007a, 2007b), Georgescu & Abramovich (2008), Georgescu & Huber (2008) and Lipson-Benitah (2008).

This way to define the paleontological species is the only one that proved functional in the case of the upper Albian-Cenomanian benthic and serial planktic foraminifera of the ODP Hole 1050C (Blake Plateau). As an example, extreme morphological variability was observed in the case of three species: *Praeplanctonia globifera* nov. sp., *P. quasiplanctonica* nov. sp. and *Haigella intermedia* nov. sp. Notably, all of them have twisted axis of test growth. These species present two different kinds of chamber arrangement: biserial throughout and triserial in the early stage and biserial when adult. Most of the specimens have a biserial chamber arrangement throughout and consistently represent more than 95% of the total specimens examined for all of the three species. The specimens with early triserial stage and biserial chamber arrangement in the adult are less numerous and consequently occur rarely and in scattered occurrences. Noteworthy, the tests of the two varieties are otherwise identical, having a similar number of chambers, aperture size, position and periapertural structures, sutures, etc. Moreover, the stratigraphical ranges of the two varieties of each species are identical and specimens with intermediate morphological features are present throughout their stratigraphic ranges. This record shows clearly that despite the significant morphological differences between these varieties, they should be considered as parts of the same species. In this situation, the chamber arrangement cannot be successfully used in typological sense as taxonomic criterion at species or genus level.

4.2. Genus concept

The genus concept used in planktic foraminifera has been rarely treated in detail. The vast majority of the Cretaceous planktic foraminiferal genera are defined only according to the morphological similarities between component species. This way of defining them does not take into account two factors: morphological resemblances between members of distant lineages due to iterative evolution and monophyletic nature not only of a genus, but of any supraspecific category.

A more elaborate way to define genera for the serial and planispiral planktic foraminifera was developed by Georgescu (2007a, 2007b), Georgescu & Abramovich (2008) and Georgescu & Huber (2008). They demonstrated that a genus can be defined to accommodate a lineage in which most, if not all, of the morphological features change through time. The phylogenetic relationships, if well documented, can be successfully used to include morphologically distant species within a genus. This concept of "genus-lineage" is followed herein.

5. SYSTEMATIC PALEONTOLOGY

Suprageneric classification largely follows that of Loeblich & Tappan (1987), whereas the species concept is that of Georgescu & Huber (2007).

Suborder GLOBIGERININA Delage & Hérouard, 1896
Superfamily ROTALIPORACEA Sigal, 1958
Family GLOBULIGERINIDAE Loeblich & Tappan, 1984
Genus *Koutsoukosia* nov. gen.

Type species.- *Guembelitria sergipensis* Koutsoukos, 1994.

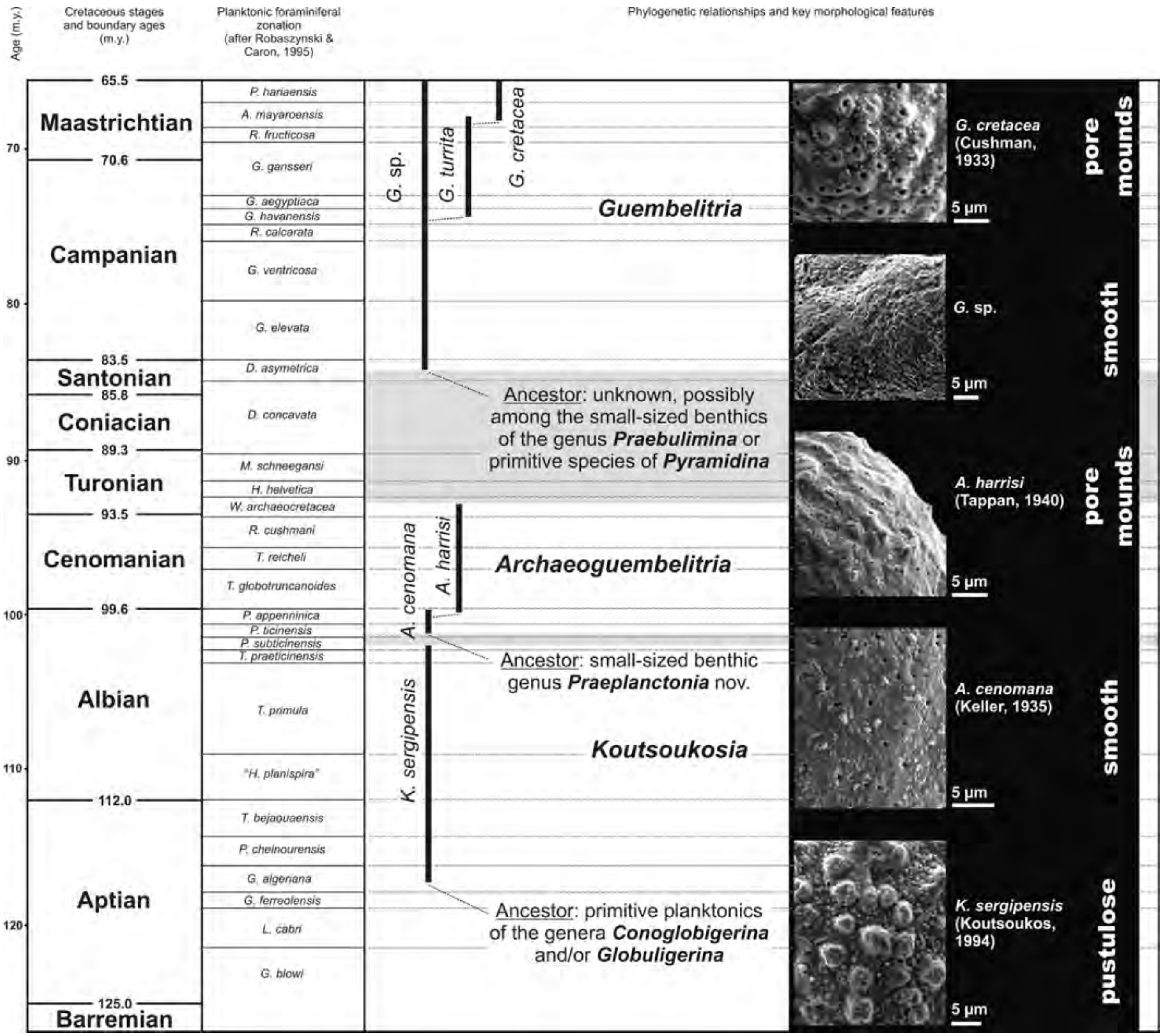

Figure 2. Diagram showing the three Cretaceous genera of triserial planktic foraminifera and diagnostic test ornamentation. The gray areas indicate the stratigraphical intervals without triserial planktics. Ages after Gradstein *et al.* (2004).

Diagnosis.– Test triserial with strong and blunt pustules on all of the chambers.

Description.– Test with triserial chamber arrangement; chambers are globular and increase gradually in size as added. Sutures are distinct and depressed. Aperture is large, in the shape of a high arch. Chamber surface is ornamented with large-sized, blunt pustules. Test wall is calcitic, microperforate.

Remarks.– *Koutsoukosia* differs from all other triserial genera of the Cretaceous by having the test ornamentation consisting of blunt pustules (Fig. 2; Pl. 1, Fig. 2). The pore mounds mentioned in the original description of the type species are probably the result of diagenesis, which affected the original ornamentation on the chamber surface. Overall, the ornamentation of *Koutsoukosia* is similar to that of the primitive planktic foraminifera of the Family Globuligerinidae (Riegraf, 1987; Simmons *et al.*, 1997).

Etymology.– Genus dedicated to Dr. E. A. M. Koutsoukos (University of Rio de Janeiro, Brazil).

Stratigraphic range.– Upper Aptian to lower part of upper Albian (from the *G. algeriana* Biozone throughout the lower part of *P. subticinensis* Biozone).

Geographic distribution.– South America (Sergipe Basin, eastern Brazil).

Koutsoukosia sergipensis (Koutsoukos, 1994)
(Pl. 1, Figs 1-2)

1994 *Guembelitria sergipensis* Koutsoukos, p. 288, pl. 1, figs 1-16, pl. 2, figs 1-12.

Description.– Test triserial throughout consisting of 10 to 15 globular chambers, which increase gradually and rapidly in size as added (Pl. 1, Fig. 1). Sutures are distinct, straight to slightly curved and depressed. Aperture is simple and arch-shaped, situated at the base of the apertural face of the last-formed chamber. Chamber surface is ornamented with large-sized blunt pustules, up to 10 μm in the maximum dimension and with an average height of 6 μm (Pl. 1, Figs 1-2). Test wall is calcareous, hyaline and with small circular pores, 0.4 to 0.8 μm in diameter.

Remarks.– *Koutsoukosia sergipensis* was originally described as having irregular pore mounds. The pore mound-like structures present in the original figuration (Koutsoukos, 1994, pl. 1, figs 3, 10, 11, 14, 16, pl. 2, figs 5, 7, 9, 10) are not constant ornamentation features. They are completely absent in the topotypes investigated for the present study. Moreover, they present a general different appearance when compared with the pore mounds from other Upper Cretaceous planktic foraminifera, such as *Laeviheterohelix pulchra* (Brotzen, 1936) and *Guembelitria cretacea* (Cushman, 1933). Accordingly, the pore mound-like structures are considered to be the result of imperfections in specimen preservation.

Stratigraphic range.– Upper Aptian to lower part of the upper Albian (from the *G. algeriana* Biozone throughout the lower part of *P. subticinensis* Biozone).

Geographic distribution.– South America (Sergipe Basin, eastern Brazil).

Suborder ROTALIINA Delage & Hérouard, 1896
Superfamily HETEROHELICACEA Cushman, 1927
Family HETEROHELICIDAE Cushman, 1927
Genus *Heterohelix* Ehrenberg, 1843

Type species.- *Textilaria americana* Ehrenberg, 1843.

Description.– Test with or without early incipient planispiral coil and with chambers biserially arranged in the adult stage. The earliest species has twisted tests, asymmetrical in edge view, whereas the evolved species has symmetrical tests (i.e., with lose rotation of the twisting axis) when observed in edge view. Chambers are globular to slightly laterally compressed and increase gradually in size as added. Aperture is situated at the base of the last-formed chamber and is bordered by rims or flanges. Chamber surface is smooth to coarsely costate. Test wall is calcitic, hyaline, nannoperforate to finely perforate.

Remarks.– The report of twisted, asymmetrical tests with asymmetrical apertures and periapertural structures in the upper Albian, Cenomanian and Turonian further adds to the significant morphological variability of the genus *Heterohelix*. The taxonomical review of this genus will be the subject of a number of forthcoming articles. The term 'nannoperforate' is defined for the test wall with pore diameter between 0.1 and 0.5 μm. Accordingly, the 'finely perforate' term is used in restricted sense, namely for the test wall with pore diameter between 0.5 and 1.0 μm.

Stratigraphic range.– Upper Albian-Maastrichtian (from the *P. ticinensis* Biozone throughout *P. hariaensis* Biozone).

Geographic distribution.– Cosmopolitan.

"Heterohelix" washitensis Tappan, 1940
(Pl. 1, Figs 3-13)

1940 *Gümbelina washitensis* Tappan, p. 115, pl. 19, fig. 1.
1975 *Heterohelix moremani* (Cushman, 1938), North & Caldwell, pl. 4, fig. 9.
1977 *Heterohelix moremani* (Cushman, 1938), Masters, pl. 2, fig. 1.
1989 *Heterohelix moremani* (Cushman, 1938), Hart *et al.*, p. 346, pl. 7.16, fig. 9.
2006 *Laeviheterohelix* sp. Petrizzo & Huber, pl. 1, fig. 2.

Emended description.– Test twisted, biserial throughout (Pl. 1, Figs 3, 5, 13), with globular chambers that increase gradually in size as added. Sutures are distinct, straight to slightly curved and depressed. Test periphery is broadly rounded, without peripheral structures. Aperture is medium high and asymmetrical, situated at the base of the last formed chamber (Pl. 1, Figs 4, 6-11). It is bordered by asymmetrical periapertural structures, a thin rim on one side and a ridge on the opposite side and provided with a relict toothplate (Pl. 1, Figs 4, 7-11). Chamber surface is smooth (Pl. 1, Figs 3-13). Test wall calcitic, hyaline and nannoperforate to microperforate; pores are circular, with diameter between 0.4 and 0.7 µm.

Remarks.– "*Heterohelix*" *washitensis* is the earliest member of the Superfamily Heterohelicacea Cushman, 1927 (Fig. 3). Careful observations over a large number of specimens (holotype, paratypes, topotypes and over 100 hypotypes) of "*H.*" *washitensis* from the Late Albian and Cenomanian revealed that the chamber surface is smooth, as mentioned in the original description by Tappan (1940, p. 115). Our data also confirm the observations by Thomas (1927, p. 137) and Thomas & Rice (1927, p. 141) that the costate ornamentation is later developed in the heterohelicid evolution and the earlier representatives of the group are smooth. Moreover, it is observed, for the first time, that the test of "*H.*" *washitensis* is slightly twisted and with an asymmetrical aperture and periapertural structures. The twisted and asymmetrical tests and asymmetrical apertures and periapertural structures indicate that, most likely, the ancestor of the group is a taxon with an asymmetrical test.

Stratigraphic range.– Upper Albian-lower Turonian (from the *P. ticinensis* Biozone throughout the *H. helvetica* Biozone).

Geographic distribution.– USA (Texas), Canada (Saskatchewan and Manitoba), western North Atlantic Ocean (Blake Plateau) and northwestern Europe (North Sea).

Superfamily TURRILINACEA Cushman, 1927
Family TURRILINIDAE Cushman, 1927
Genus *Guembelitriella* Tappan, 1940

Type species.- *Gümbelitriella graysonensis* Tappan, 1940.

1940 *Gümbelitriella* Tappan, p. 115.
1957 *Guembelitriella* Tappan, 1940, Montanaro Gallitelli, p. 137.
1964 *Guembelitriella* Tappan, 1940, Loeblich & Tappan, p. C652.
1975 *Guembelitriella* Tappan, 1940, Fuchs, p. 229.
1987 *Guembelitriella* Tappan, 1940, Loeblich & Tappan, p. 453.

Emended description.– Test trochospiral throughout, with earlier chambers globular and those in the adult stage strongly overlapping. Sutures are distinct and depressed. Aperture is in the shape of a low to medium arch, situated at the base of the last formed chamber and bordered by a thin, imperforate rim. Chamber surface is smooth or with scattered small-sized pustules. Test wall is calcitic, hyaline and microperforate.

Remarks.– The understanding of the systematic position of the genus *Guembelitriella* was strongly biased by its original description. This taxon was described as presenting serial chamber arrangement and this definition was followed by Loeblich & Tappan (1964, 1987). A different view on its morphology was given by Longoria (1974, p. 50) who considered the genus "…trochoid and has an extraumbilical-umbilical aperture." Observations made on topotypes from the Loeblich and Tappan Topotype Collection and new material from ODP Site 1050C confirm without doubt that *Guembelitriella* has a trochospirally coiled test and therefore is morphologically closer to *Praebulimina* than *Guembelitria*. A different interpretation was given by Kroon & Nederbragt (1990) who considered that the test ornamentation is not a taxonomic criterion that can be used at generic level. As a result, *Guembelitriella* and its type species, *G. graysonensis*, were considered as representing gerontic stages of *Guembelitria cenomana* (Keller, 1935) but no data was presented to support their interpretation. This opinion is inconsistent with the test morphology, stratigraphic and geographic distribution of the two taxa. Apparently Kroon & Nederbragt (1990, p. 33) were not aware of the observations of Longoria (1974) who described and figured well preserved *Guembelitria graysonensis* specimens from the Aptian of Mexico, France and Spain. However, the synonymization of *Guembelitriella* under *Guembelitria* was mentioned but apparently

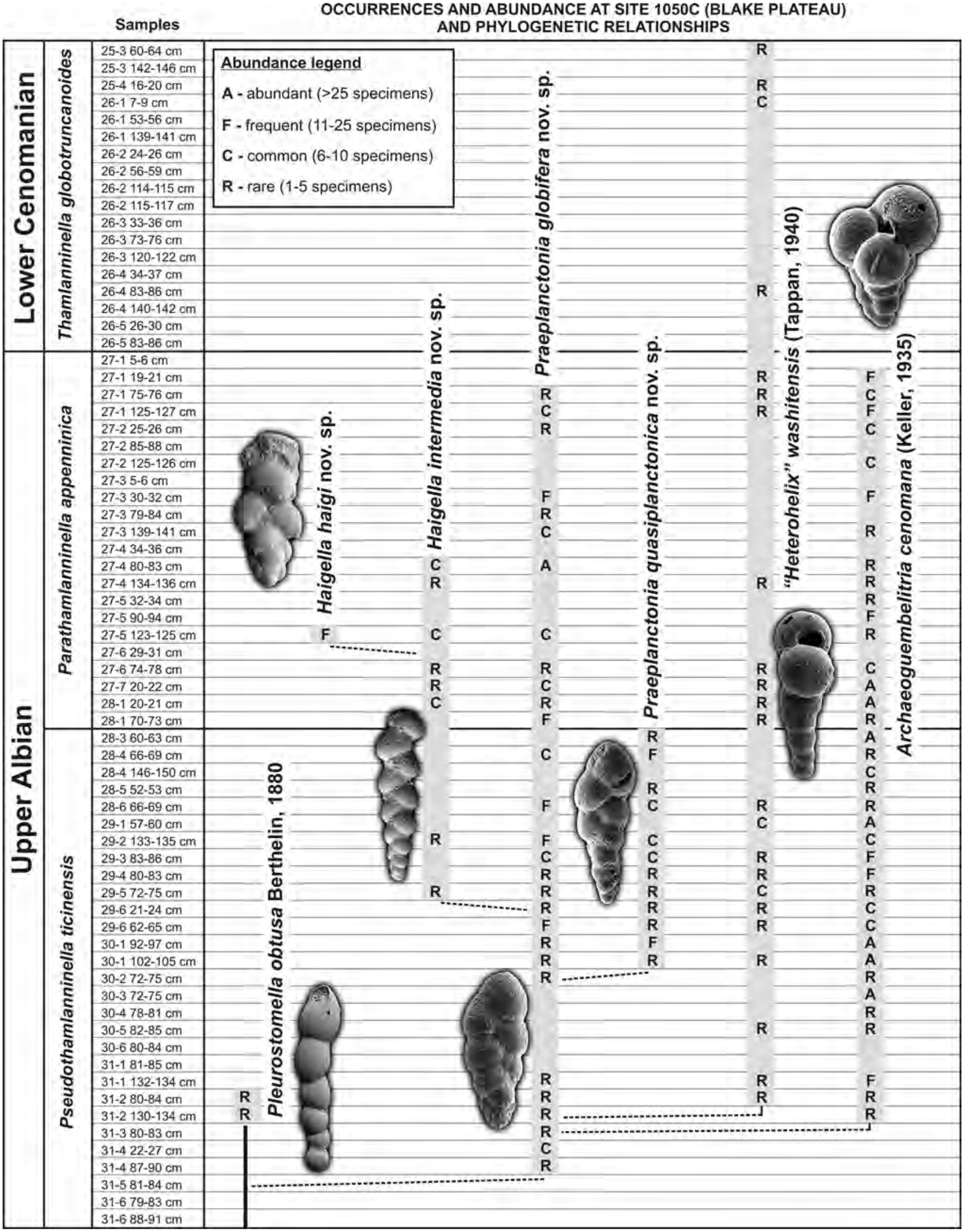

Figure 3. Stratigraphic record, abundance and inferred phylogenetic relationships at ODP Hole 1050C (Blake Plateau, western North Atlantic). Planktic foraminiferal zonation after Petrizzo & Huber (2006).

not accepted by de Klasz *et al*. (1995). However, the examination of the holotype of *Guembelitria graysonensis* in the Cushman Collection (NMNH, Washington, D.C.) confirmed that the test is trochospirally coiled throughout.

Stratigraphic range.– Aptian throughout lower Cenomanian (from the *L. cabri* Biozone throughout *T. globotruncanoides* Biozone).

Geographic distribution.– USA (Texas), Caribbean (Trinidad), Atlantic Ocean (Blake Plateau, offshore Florida and Mazagan Plateau, offshore Morocco) and equatorial Pacific Ocean (Shatsky Rise).

Guembelitriella graysonensis Tappan, 1940
(Pl. 2, Figs 1-5)

1940 *Gümbelitriella graysonensis* Tappan, p. 116, pl. 19, fig. 3.
1959 *Globigerina graysonensis* Tappan, 1940, Bolli, p. 270, pl. 23, figs 1-2.
1972 *Guembelitriella graysonensis* Tappan, 1940, Michael, p. 208, pl. 1, figs 1-3.
1974 *Gubkinella graysonensis* (Tappan, 1940), Longoria, 1974, p. 50, pl. 1, figs 1-12.
1975 *Gubkinella* (?) *graysonensis* (Tappan, 1940), Luterbacher, 1975, pl. 2, figs. 4-8.
1984 *Gubkinella graysonensis* (Tappan, 1940), Leckie, p. 593, pl. 1, figs 2-3.

Description.– Test is medium to high trochospirally coiled throughout (Pl. 2, Figs 1-4). Chambers are globular, those of the final whorls strongly overlapping. There are three to four chambers in the last whorl. Sutures are distinct and depressed, more incised between the chambers of the last whorl; they are straight to slightly curved. Aperture is a low to medium-high arch situated at the base of the last formed chamber (Pl. 2, Figs 1, 2, 4). It is bordered by a thin and imperforate apertural rim (Pl. 2, Figs 1, 2, 4). Chamber surface is smooth or with scattered pustules on the earlier part of the test. Test wall is calcareous, hyaline and nannoperforate to microperforate; pore diameter is between 0.4 and 0.6 μm.

Remarks.– *Guembelitriella graysonensis* differs from *G*. sp. in having more elongate aperture and better developed chamber overlapping.

Local occurrence.– Lower Cenomanian (*T. globotruncanoides* Biozone).

Stratigraphic range.– Aptian throughout lower Cenomanian (from the *L. cabri* Biozone throughout *T. globotruncanoides* Biozone).

Geographic distribution.– USA (Texas), Caribbean (Trinidad) and Atlantic Ocean (Blake Plateau, offshore Florida and Mazagan Plateau, offshore Morocco) and equatorial Pacific Ocean (Shatsky Rise).

Guembelitriella sp.
(Pl. 2, Fig. 6)

(?) 1969 *Gubkinella californica* Church, p. 573, pl. 7, fig. 8.

Description.– Test is high trochospiral (Pl. 2, Fig. 6). Chambers are globular throughout and increase gradually and slowly in size. Sutures are distinct and depressed, straight to slightly curved, joining the previous whorl at acute angles. Aperture is a low arch, situated in the base of the apertural face and is bordered by a narrow and imperforate rim (Pl. 2, Fig. 6). Chamber surface is smooth. Test wall is calcitic, hyaline and nannoperforate to microper-

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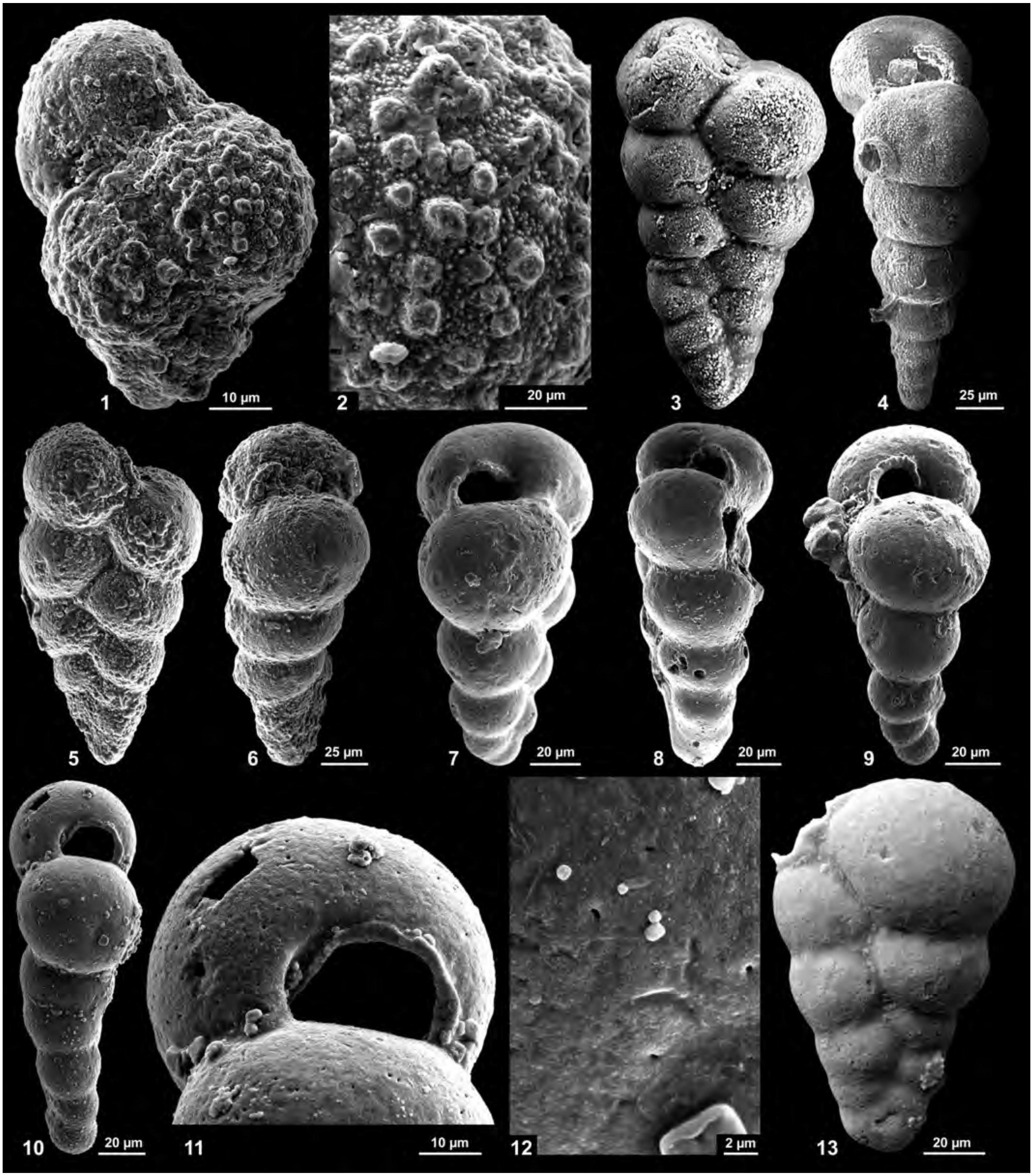
Plate 1. *Koutsoukosia sergipensis* (Koutsoukos, 1994) and "*Heterohelix*" *washitensis* (Tappan, 1940). ***1-2.*** Topotypes of *K. sergipensis* from well 1-CA-1-SE, 855-870 m (proximity of the city of Aracaju, Sergipe Basin, eastern Brazil); note the chamber surface ornamented with large-sized pustules and the absence of the pore mounds. The specimen was made available to me by Dr. E. A. M. Koutsoukos (University of Rio de Janeiro). ***3-4.*** Holotype of "*H.*" *washitensis* originally described and figured as *Gümbelina washitensis* from the Grayson Bluff, Texas, USA; USNM 307987; note the twisted test and asymmetrical aperture and periapertural structures. ***5-6***. Topotype of "*H.*" *washitensis* from the Loeblich and Tappan Topotype Collection (NMNH, Loeblich sample 6024, USNM 473118). ***7-9***. Three hypotypes of "*H.*" *washitensis* from the uppermost Albian (upper part of the *P. appenninica* Biozone) of the western North Atlantic Ocean (Blake Plateau), Sample 171B-1052E-40-2, 118-121 cm; note the asymmetrical apertures and periapertural structures. ***10-12***. Hypotype of "*H.*" *washitensis* from the uppermost Albian (upper part of the *P. appenninica* Biozone) of the western North Atlantic Ocean (Blake Plateau), Sample 171B-1052E-40-3, 71-75 cm; note the well developed asymmetrical periapertural structures consisting of a ridge to the left and an imperforate thin rim to the right (11) and the simple, microperforate test wall (12). ***13.*** Hypotype of "*H.*" *washitensis* (Tappan, 1940) from the upper Albian (lower part of the *P. ticinensis* Biozone) of the western North Atlantic Ocean (Blake Plateau), Sample 171B-1050C-31-2, 80-84 cm; this specimen is the oldest known of its species and documents its first evolutionary occurrence. Photographs were taken with the SEM (1-2, 5-12), ESEM (3-4) and Microprobe (13).

Plate 1


1
10 µm
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20 µm
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10 µm
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2 µm
13
20 µm

forate, with pore diameter ranging between 0.4 and 0.8 µm.

Stratigraphic range.– Lower Albian (equivalent of the *T. primula* Biozone).

Geographic distribution.– Western North Atlantic Ocean (Blake Plateau).

Superfamily PRAEPLANCTONIACEA nov. superfam.

Description.– Test biserial, triserial or triserial in the early stage and biserial when adult; aperture is subterminal and provided with a toothplate; relict suture between the aperture base and the suture between the last formed chamber and penultimate one is developed in the primitive representatives; evolved taxa with the aperture at the base of the last-formed chamber; test wall nannoperforate to microperforate, smooth or ornamented with pore mounds.

Stratigraphic range.– Upper Albian-lower Turonian (from the *P. ticinensis* Biozone to the *W. archaeocretacea* Biozone).

Family PRAEPLANCTONIDAE nov. fam.

Description.– Test biserial, triserial or triserial in the early stage and biserial when adult; aperture subterminal and provided with a toothplate; relict suture between the aperture base and the suture between the last formed chamber and penultimate one; test wall is nannoperforate, with a combination of elongate and circular pores.

Stratigraphic range.– Upper Albian (from the *P. ticinensis* Biozone to the *P. appenninica* Biozone).

Genus *Praeplanctonia* nov. gen.

Type species.- *Praeplanctonia globifera* nov. sp.

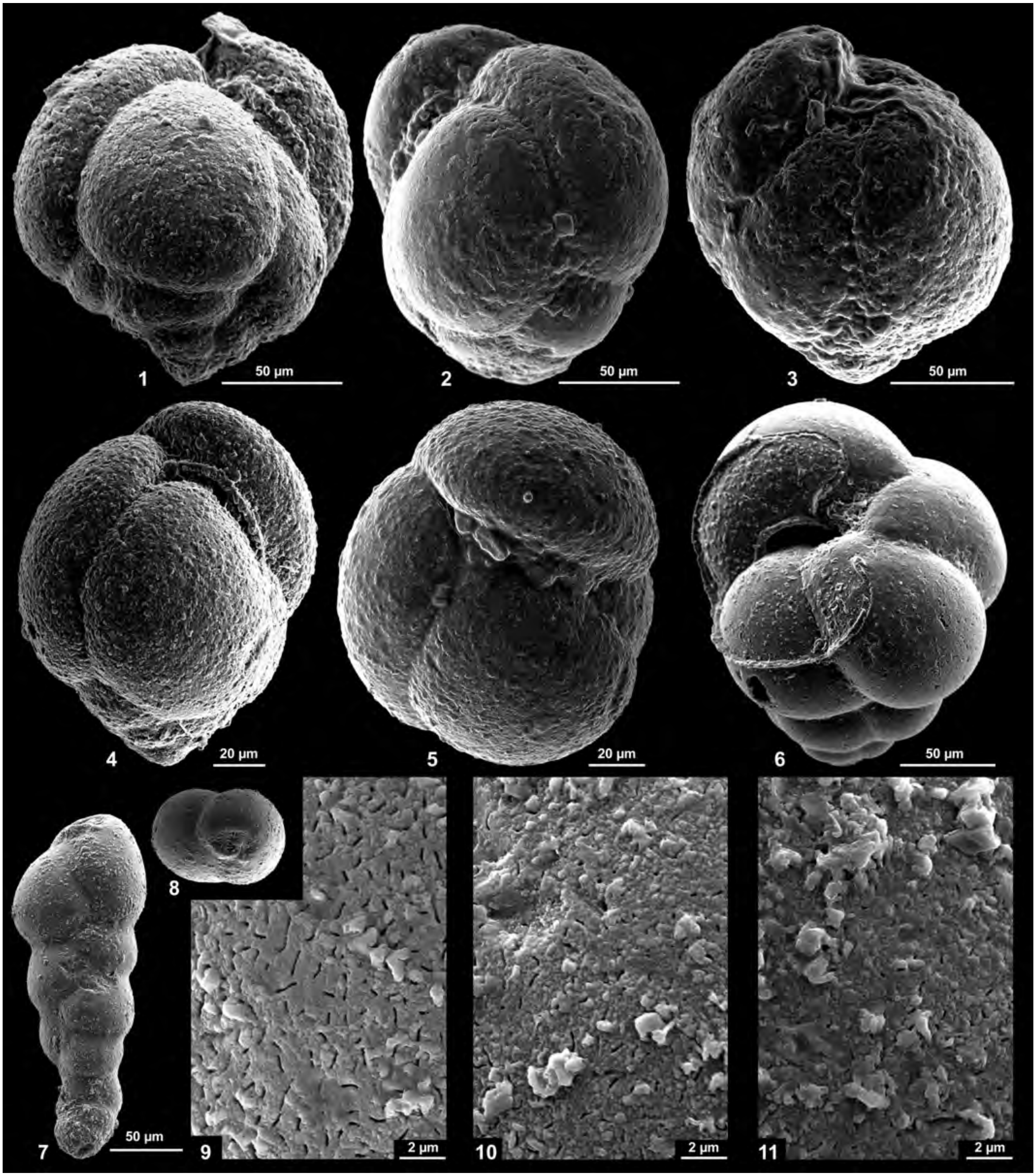
Diagnosis.– Test biserial throughout or with a short triserial juvenile stage and biserial in the adult; aperture subterminal bordered by a short rim and provided with a toothplate; apertural face with supplementary suture; chamber surface smooth.

Description.– Test twisted, biserial throughout or with an early triserial stage and biserial in the adult. Chambers are globular to subglobular, overlapping at various rates. Sutures are distinct and depressed. Aperture subcircular and subterminal in position and bears a toothplate and is bordered by an asymmetrical rim. A supplementary suture is present on the apertural face, which connects the aperture base with the suture between the penultimate and last-formed chamber. Chamber surface is smooth. Test wall is calcitic, hyaline and nannoperforate; pore shape is elongate to circular.

Remarks.– *Praeplanctonia* nov. gen. is characterized by high variability of the morphological features. The test may have an early triserial stage, becoming biserial when adult or is biserial throughout; the triserial-biserial tests present general resemblances with some *Neobulimina* Cushman & Wickenden, 1928 species of the late Albian, such as *N. irregularis* (Cushman & Parker, 1936), *N. numerosa* (Vasilenko, 1961), *N. vridhachalensis* (Rasheed & Govindan, 1968) and *N. canadensis* var. *beta* (Mello, 1969). By contrast to *Neobulimina*, has twisted tests and therefore can be considered morphologically closer to *Cassidella* Hofker, 1951 and *Fursenkoina* Loeblich & Tappan, 1961. *Praeplanctonia* differs from these two in having an early triserial stage, which is occasionally developed, subterminal aperture rather than situated at the base of the last-formed chamber and the presence of the supplementary suture on the apertural face.

Plate 2. Scanning electron microscope photographs of *Guembelitriella graysonensis* (Tappan, 1940), *Guembelitriella* sp. and *Praeplanctonia globifera* nov. gen., nov. sp. ***1-3***. Lateral views of three topotypes of *G. graysonensis* from the Cenomanian of the Grayson Formation, Grayson Bluff on Denton Creek, Denton County, Texas, USA; specimens from the Loeblich and Tappan Topotype Collection (NMNH, USNM 473114); note the test trochospiral coil and the strongly overlapping last whorl; topotypes of the same species were previously figured by Longoria (1974, pl. 1, figs 7-12). ***4-5.*** Hypotype of *G. graysonensis* from the lower Cenomanian (upper part of the *T. globotruncanoides* Biozone) from the western North Atlantic (Blake Plateau), Sample 171B-1050C-25-2, 87-89 cm; notice the four chambers in the last whorls, which are visible in the top view (5). **6.** *Guembelitriella* sp. from the lower Albian (equivalent of the *T. primula* Biozone) sediments of the western North Atlantic (Blake Plateau), Sample 171B-1049B-12-2, 84-89 cm; biostratigraphical framework at this site was kindly made available to me by Dr. B. T. Huber (National Museum of Natural History, Washington, D.C.); note the loose trochospiral coil when compared to the tight one in *G. graysonensis*. **7-11**. Holotype of *P. globifera* from the upper Albian sediments (upper part of the *P. ticinensis* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-28-4, 66-69 cm; note the circular and nearly circular pores, which are visible despite the moderate diagenesis (10-11); the elongate pores (9) are enigmatical and their evolutionary and taxonomic significance is unknown yet.

Plate 2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Etymology.– The name suggests that this genus is ancestral to the planktic foraminifera with serial chamber arrangement.

Stratigraphic range.– Upper Albian (from the *P. ticinensis* Biozone throughout the *P. appenninica* Biozone).

Geographic distribution.– Western North Atlantic Ocean (Blake Plateau), Eastern North Atlantic Ocean (offshore Cape Bojador, Spanish Sahara) and Caribbean region (Trinidad).

Praeplanctonia globifera nov. sp.
(Pl. 2, Figs 7-11, Pl. 3, Figs 1-13, Pl. 4, Figs 1-8)

1994 *Neobulimina irregularis* Cushman & Parker, 1932. Bolli *et al*., p. 131, fig. 35:16 (only).

Holotype.– Specimen WKB 010010.

Dimensions of the holotype.– Length: L = 0.241 mm; width: W = 0.093 mm; W/L = 0.386; thickness: T = 0.067 mm; T/L = 0.278; proloculus diameter: PD = 0.035 mm.

Paratypes.– Seven specimens, WKB 010011.

Dimensions.– L = 0.182-0.244 mm; W = 0.076-0.093 mm; T = 0.058-0.068 mm. Measurements taken on 12 specimens (holotype, paratypes and topotypes).

Type location.– Western North Atlantic Ocean (Blake Plateau), ODP Leg 171B, Site 1050C. Geographical coordinates: 30º 05′ N, 76º 14′ W.

Type level.– Upper Albian (upper part of the *P. ticinensis* Biozone), Sample 28-4, 66-69 cm.

Material.– Over 300 specimens.

Etymology.– The species name reflects the globular to subglobular shape of the chambers.

Diagnosis.– Species of *Praeplanctonia* with large proloculus and globular chambers, which increase slowly in size.

Description.– Test biserial throughout (Pl. 2, Fig. 7, Pl. 3, Figs 1, 2, 5, 6, 8, 10, Pl. 4, Figs 7, 8) or, occasionally, with a very short early triserial stage (Pl. 3, Fig. 12, Pl. 4, Fig. 1). The test is twisted along the axis of growth at least in the earlier part. Proloculus is large, its maximum dimension ranging between 28 and 44 µm. Chambers are globular to subglobular, with little overlapping and slow and gradual increase in size. Aperture is elliptical and subterminal in position; it is bordered by an asymmetrical imperforate rim (Pl. 2, Fig. 8, Pl. 4, Figs 1, 2, 3, 6, 7) and provided with a toothplate. A supplementary suture is present on the apertural face of the last-formed chamber and it extends from the aperture base to the suture between the last-formed two chambers (Pl. 3, Fig. 2, Pl. 4, Figs 1-4, 6, 7). Chamber surface is smooth. Test wall is calcitic, hyaline, nannoperforate; pores are elongate to circular in shape, their size ranging between 0.2 and 0.5 µm.

Remarks.– *Praeplanctonia globifera* differs from *P. quasiplanctonica* nov. sp. by having larger proloculus and lower rate of increase in chamber size during the ontogenetic development.

Stratigraphic range.– Upper Albian (from the *P. ticinensis* Biozone throughout the *P. appenninica* Biozone).

Geographic distribution.– Western North Atlantic Ocean (Blake Plateau) and Caribbean (Trinidad).

Praeplanctonia quasiplanctonica nov. sp.
(Pl. 4, Figs 9-20)

1984 *Neobulimina minima* Tappan, 1940. Moullade, pl. 3, fig. 23.

Holotype.– Specimen WKB 010015.

Dimensions of the holotype.– Length: L = 0.224 mm; width: W = 0.095 mm; W/L = 0.424; thickness: T = 0.079 mm; T/L = 0.353; proloculus diameter: PD = 0.012 mm.

Paratypes.– Five specimens, WKB 010016.

Dimensions.– L = 0.162-0.227 mm; W = 0.49-0.095 mm; T = 0.042-0.079 mm. Measurements taken on 12 specimens (holotype, paratypes and topotypes).

Type location.– Western North Atlantic Ocean (Blake Plateau), ODP Leg 171B, Site 1050C. Geographical coordinates: 30º 05 N′, 76º 14′ W.

Plate 3

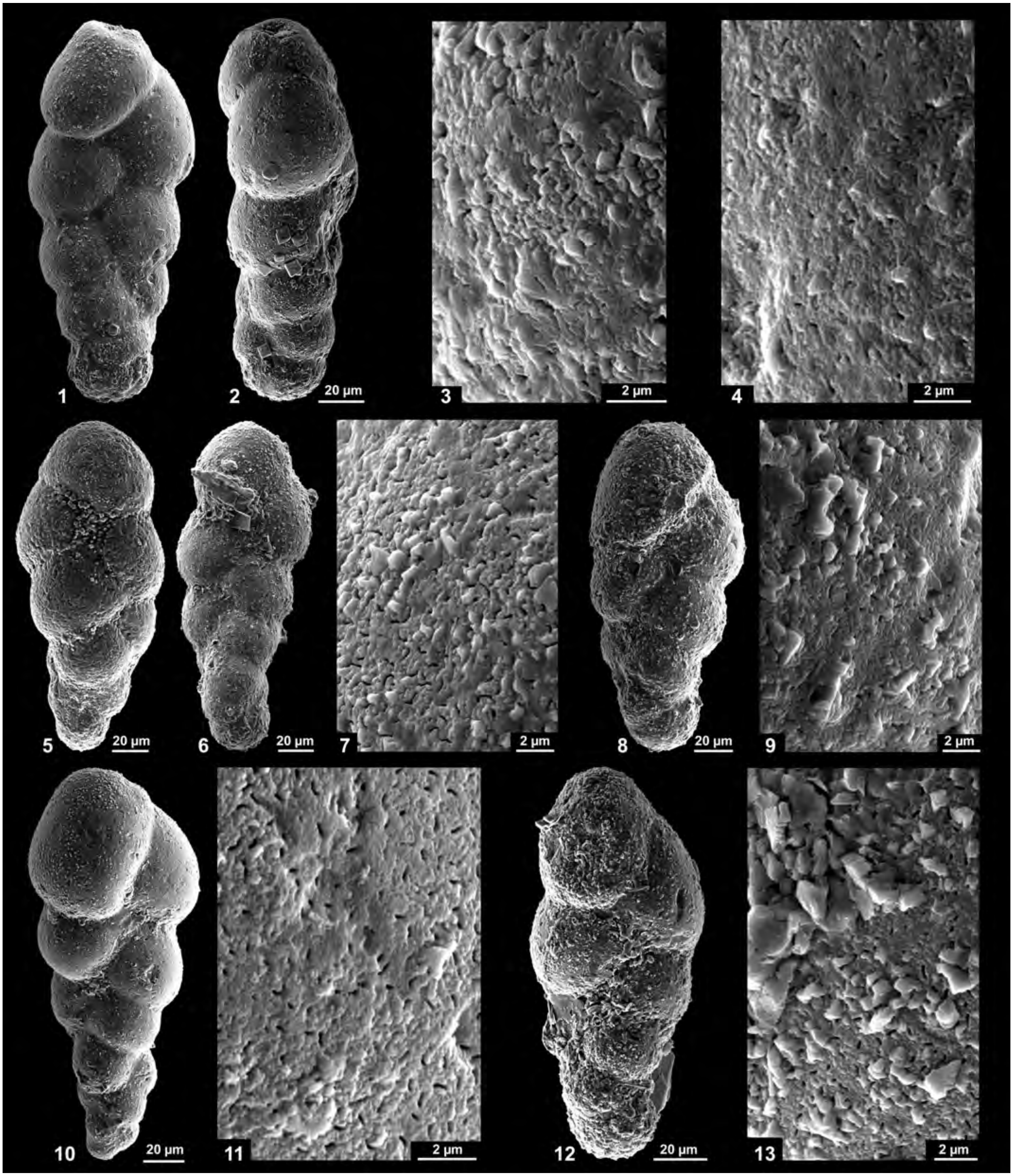


Plate 3. Scanning electron microscope photographs of paratypes of *Praeplanctonia globifera* nov. gen., nov. sp. ***1-13.*** Specimens from the upper Albian (upper part of the *P. ticinensis* Biozone) western North Atlantic (Blake Plateau), Sample 171B-1050C-28-4, 66-69 cm; note the microperforate test wall (3, 4, 7, 9, 11 and 13) and the elongate pore (7, 11).

Type level.– Upper Albian (upper part of the *P. ticinensis* Biozone), Sample 28-4, 66-69 cm.

Etymology.– The name suggests the quasi-planktic appearance of this species.

Material.– Over one hundred specimens.

Diagnosis.– Species of *Praeplanctonia* nov. gen. with relatively smaller proloculus and lower rate of chamber increase in size.

Description.–Test twisted, small-sized with biserial chambers arrangement throughout (Pl. 4, Figs 14, 19, 20) or sometimes with a short triserial stage in the earlier part of the test (Pl. 4, Figs 9, 12, 13, 16, 17). Proloculus is relatively small, its diameter being between 11 and 14 µm. Chambers are globular in the earlier part of the test, subglobular in the adult and increase slowly in size as added. Sutures are distinct, depressed and straight to slightly curved. Aperture is elliptical in shape and subterminal in position; it is bordered by an asymmetrical and imperforate rim (Pl. 4, Fig. 10) and bears a toothplate (Pl. 4, Figs 16-20). Chamber surface is smooth. Test wall is calcitic, hyaline, nannoperforate with elongate to circular pores, pore dimension ranging between 0.2 and 0.5 µm (Pl. 4, Fig. 11).

Remarks.– *Praeplanctonia quasiplanctonica* differs from any species of serial planktic foraminifera in the position of the aperture, which is subterminal and not interiomarginal and by having the aperture provided with a well-developed toothplate, which is absent in the planktics with serial chamber arrangement.

Stratigraphic range.– Upper Albian (upper part of the *P. ticinensis* Biozone throughout the upper part of *T. appenninica* Biozone).

Geographic distribution.– Western North Atlantic Ocean (Blake Plateau) and Eastern North Atlantic Ocean (offshore Cape Bojador, Spanish Sahara).

Genus *Haigella* nov. gen.

Type species.- *Haigella haigi* nov. sp.

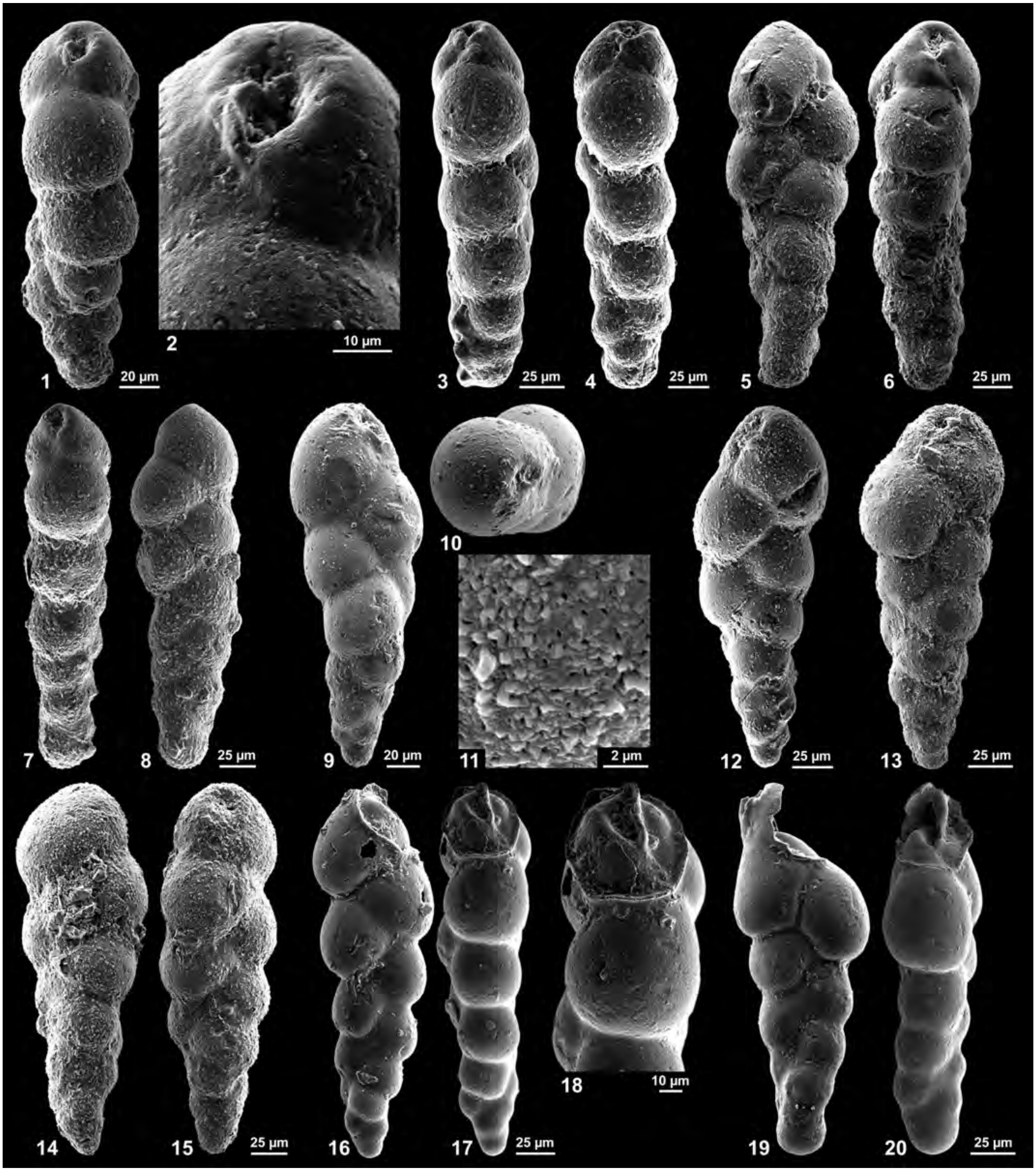
Diagnosis.– Test triserial throughout or with an adult biserial stage; chambers with backward-oriented peripheral projections; aperture subterminal bearing a toothplate.

Description.– Test with serial chamber arrangement, with a short triserial stage followed by a biserial one, approximately two times longer in the primitive species and triserial throughout in the adult one. Earlier chambers are globular, those in the adult stage of the evolved species subangular and with lateral projections. Sutures are deeply incised and distinct. Aperture is subcircular in shape and subterminal in position. A supplementary suture is present on the apertural face between the aperture and suture between the last-formed two chambers. Chamber surface is smooth. Test wall is calcitic, hyaline and nannoperforate.

Remarks.– *Haigella* is proposed to accommodate a distinct lineage that evolved from *Praeplanctonia* and is confined to upper Albian sediments. The life span of *Haigella* is of approximately 900,000 years according to the depthage model for the upper Albian sediments at ODP Site 1050C (Huber *in* Petrizzo & Huber, 2006). This genus differs from *Archaeoguembelitria* nov. gen. by the presence

Plate 4. Scanning electron microscope photographs of *Praeplanctonia globifera* nov. gen., nov. sp. and *P. quasiplanctonica* nov. gen., nov. sp. ***1-2***. Topotype of *P. globifera* from the upper Albian (middle part of the *P. appenninica* Biozone) western North Atlantic (Blake Plateau), Sample 171B-1050C-27-3, 139-141 cm; note the subterminal and asymmetrical aperture, suggesting the torsion process, which resulted in the formation of the periapertural rim (2); note the short triserial stage visible in edge view (1). ***3-4.*** Edge views of two topotypes of *P. globifera* from the upper Albian sediments (middle part of the *P. appenninica* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-27-4, 80-83 cm; note the distinct supplementary suture on the apertural face of the last formed chamber, which runs from the aperture to the suture between the last formed chamber and the penultimate one. ***5-6***. Topotype of *P. globifera* from the upper Albian sediments (middle part of the *P. appenninica* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-27-4, 80-83 cm; note the oblique supplementary suture and the asymmetrical aperture resulting from the torsion of the last formed chamber around the growth axis (6). ***7-8***. Topotype with numerous chambers of *P. globifera* from the upper Albian sediments (middle part of the *P. appenninica* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-27-4, 80-83 cm. ***9-11***. Holotype of *P. quasiplanctonica* from the upper Albian (uppermost part of the *P. ticinensis* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-28-4, 66-69 cm; notice the microperforate test wall (11). ***12-15.*** Three paratypes of *P. quasiplanctonica* from the upper Albian (uppermost part of the *P. ticinensis* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-28-4, 66-69 cm; note the short early triserial stage (12). ***16-20***. Two hypotypes of *P. quasiplanctonica* from the upper Albian (upper part of the *P. appenninica* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1052-40-3, 71-75 cm; note the exposed toothplate (17, 18 and 20).

Plate 4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of the chamber peripheral projections in the evolved species and the presence of the elongate biserial adult stage of the primitive one. Noteworthy, a supplementary suture on the apertural face is known also in *Pyramidina* Brotzen, 1948 of the Upper Cretaceous (Santonian)-Eocene. This genus exhibits substantial variability with respect to the position of the aperture, which is situated at the base of the last-formed chamber and becomes subterminal due to the symmetrical extensions of the test wall near the base of the aperture (Brotzen, 1948; Hofker, 1957). Accordingly, *Haigella* and *Pyramidina* appear to have evolved separately and there is no phylogenetic relationship between them.

Etymology.– The genus is named after Dr. D. Haig (The University of Western Australia) as recognition for his contributions in the study of foraminifera.

Stratigraphic range.– Upper Albian (from the upper part of the *P. ticinensis* Biozone throughout the lower part of the *P. appenninica* Biozone).

Geographic distribution.– Western North Atlantic Ocean (Blake Plateau).

Haigella haigi nov. sp.
(Pl. 5, Figs 7-14, Pl. 7, Fig. 2)

Holotype.– Specimen WKB 010017.

Dimensions of the holotype.– Length: L = 0.405 mm; width: W = 0.177 mm; W/L = 0.437; proloculus diameter: PD = 0.031 mm.

Paratypes.– Seven specimens, WKB 010018.

Dimensions.– L = 0.215-0.405 mm. This range is based on measurements taken on eight specimens (holotype included). Test width could not be measured due to the fact that all of the *Haigella haigi* nov. sp. specimens display poorly preserved terminal part of the test.

Type location.– Western North Atlantic Ocean (Blake Plateau), ODP Leg 171B, Site 1050C. Geographical coordinates: 30º 05' N, 76º 14' W.

Type level.– Upper Albian (lower part of the *P. appenninica* Biozone), Sample 27-5, 123-125 cm.

Material.– Approximately 20 specimens.

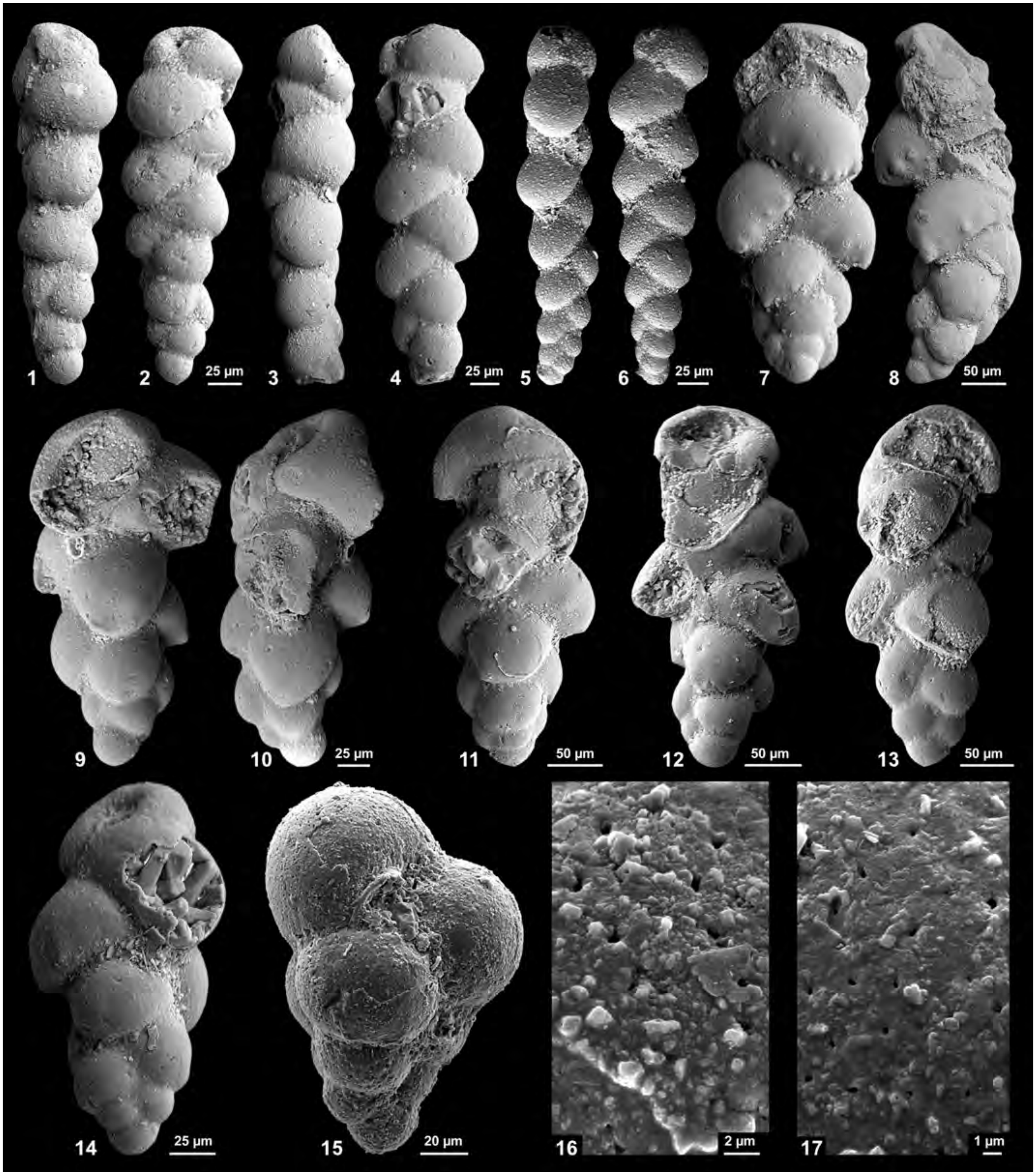
Etymology.– As for the genus.

Diagnosis.– *Haigella* with triserial test and chambers of the adult stage with lateral projections.

Description.– Test with curved growth axis and triserial chamber arrangement. Earlier chambers are globular, those of the adult stage present short, backward oriented lateral projections (Pl. 5, Figs 7-14). A line of tubercles lines up the chamber projections in the adult stage (Pl. 5, Figs 7, 8, Pl. 7, Fig. 2). Earlier part of the test with rounded periphery; the chambers of the adult portion of the test present subacute to acute periphery due to the development of backward oriented chamber projections. Sutures are distinct, deeply incised, straight or slightly curved. Aperture is single, elliptical in shape and subterminal in position (Pl. 5, Figs 10, 14). It is bordered by an asymmetrically developed imperforate rim. A supplementary suture is present on the apertural face, between the base of the aperture and the suture between the last-formed and penultimate chamber (Pl. 5, Figs 10, 14). Chamber surface is smooth. Test wall is calcitic, hyaline and nannoperforate, with pore diameter ranging between 0.2 and 0.5 µm (Pl. 7, Fig. 2).

Plate 5. *Haigella intermedia* nov. gen., nov. sp., *Haigella haigi* nov. gen., nov. sp. and *Archaeoguembelitria cenomana* (Keller, 1935). ***1-2.*** Holotype of *H. intermedia* from the upper Albian (lower part of the *P. appenninica* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-27-5, 123-125 cm; note the early triserial stage (2) and supplementary suture on the last formed chamber (2). ***3-4.*** Paratype of *H. intermedia* from the upper Albian (lower part of the *P. appenninica* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-27-5, 123-125 cm; note the incipient backward oriented chamber projections (4). ***5-6***. Topotype of *H. intermedia* from the upper Albian (lower part of *P. appenninica* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-28-1, 20-21 cm; note the higher number of chambers when compared to the holotype. ***7-8.*** Holotype of *H. haigi* from the upper Albian (lower part of the *P. appenninica* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-27-5, 123-125 cm; note the small tubercles bordering the acute periphery of the backward oriented chamber projections. ***9-14***. Five paratypes of *H. haigi* from the upper Albian (lower part of the *P. appenninica* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-27-5, 123-125 cm; note the consistently crushed last formed chamber(s) due to the very thin test wall in the distal portion of the test; note the supplementary suture in a paratype with relatively better preservation of the last formed chamber (14). ***15-17***. Hypotype of *A. cenomana* from the upper Albian (upper part of *P. ticinensis* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-28-4, 80-83 cm; note the microperforate test wall (16 and 17). Photographs were taken with the Microprobe (1-14) and SEM (15-17).

Plate 5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Remarks.– *Haigella haigi* differs from *H. intermedia* by being completely triserial and bearing well developed backward-oriented chamber projections in the adult stage. The specimens with relatively similar gross test architecture reported from the lower Turonian (offshore Ghana, equatorial Atlantic Ocean) and assigned to *Praebulimina* sp. 1 by Holbourn & Kuhnt (1998, p. 363, pl. 3, figs 1-2) cannot be included within *Haigella*. They present chamber projections without lined peripheral tubercles and aperture situated at the base of the apertural face, without relict suture.

Stratigraphic range.– Upper Albian (lower part of the *P. appenninica* Biozone).

Geographic distribution.– Western North Atlantic Ocean (Blake Plateau).

Haigella intermedia nov. sp.
(Pl. 5, Figs 1-6, Pl. 7, Fig. 1)

Holotype.– Specimen WKB 010019.

Dimensions of the holotype.– Length: L = 0.264 mm; width: W = 0.080 mm; W/L = 0.303; length of the early triserial stage: LET = 0.086 mm; LET/L = 0.326; proloculus diameter: PD = 0.029 mm.

Paratypes.– Two specimens, WKB 010020.

Dimensions.– L = 0.289-0.337 mm; W = 0.080-0.106 mm; W/L = 0.280-0.314. Measurements based on five specimens (holotype included).

Type location.– Western North Atlantic Ocean (Blake Plateau), ODP Leg 171B, Site 1050C. Geographical coordinates: 30º 05 N’, 76º 14’ W.

Type level.– Upper Albian (lower part of the *P. appenninica* Biozone), Sample 27-5, 123-125 cm.

Etymology.– The name of the species suggests it is intermediate between *Praeplanctonia globifera* and *Haigella haigi*.

Material.– Approximately 40 specimens.

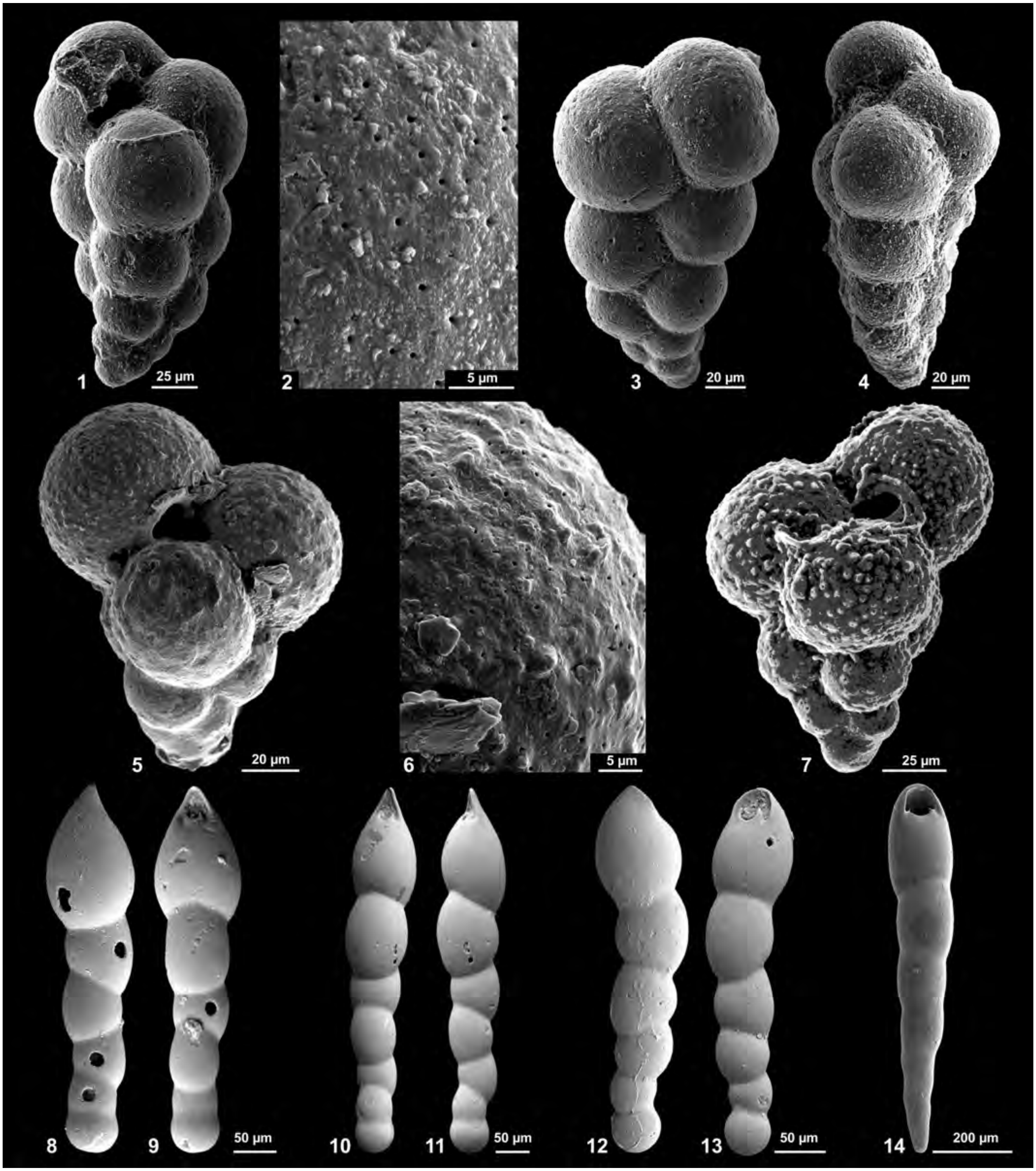
Diagnosis.– *Haigella* with occasionally developed early triserial stage and biserial in the adult.

Description.– Test with biserial chamber arrangement throughout (Pl. 5, Figs 5, 6) or with an early triserial stage (Pl. 5, Figs 1, 2). Earlier chambers are globular, those of the adult stage subglobular and with a slight backward elongation, resulting in a strongly lobate outline in lateral view (Pl. 5, Figs 2, 4, 5, 6, Pl. 7, Fig. 1). Sutures are deeply incised, straight to slightly curved. Aperture is small, elliptical in shape and subterminal in position (Pl. 5, Figs 1, 2); it is bordered by an asymmetrically developed imperforate rim (Pl. 5, Fig. 2). A supplementary suture is developed between the aperture and the suture between the last and penultimate chambers (Pl. 5, Figs 2, 4). Chamber surface is smooth. Test wall is calcitic, hyaline and nannoperforate; pore diameters range between 0.2 and 0.5 µm (Pl. 7, Fig. 1).

Remarks.– Specimens of *Haigella intermedia* differ from its ancestor, *Praeplanctonia globifera*, by having backward-oriented incipient chamber elongations in the adult stage and the strongly lobate outline. This is a rare species

Plate 6**.** *Archaeoguembelitria cenomana* (Keller, 1935), *Archaeoguembelitria harrisi* (Tappan, 1940) and *Pleurostomella obtusa* Berthelin, 1880. ***1-3.*** Hypotype of *A. cenomana* from the upper Albian (middle part of *P. ticinensis* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-29-5, 72-75 cm; note the numerous chambers of the test (1) and microperforate test wall (2). ***4***. Hypotype of *A. cenomana* from the upper Albian (upper part of *P. ticinensis* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-28-4, 66-69 cm; note the numerous chambers of the test. ***5-6.*** Specimen with intermediate features of chamber ornamentation between *A. cenomana* and *A. harrisi* from the upper Albian (upper part of the *T. appenninica* Biozone) of the western North Atlantic Ocean (Blake Plateau), Sample 171B-1052E-40-3, 51-53 cm; note the incipient pore mounds (6). ***7***. Hypotype of *Archaeoguembelitria harrisi* (Tappan, 1940) from the New Jersey Coastal Plain subsurface, Bass River Formation (Cenomanian-lower Turonian); the specimen could be examined courtesy to Dr. R. K. Olsson (Rutgers, The State University of New Jersey); note the well-developed pore mounds on the test surface. ***8-11***. Two hypotypes of *P. obtusa* Berthelin, 1880 from the upper Albian (lower part of the *P. ticinensis* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-31-2, 80-84 cm; note the two triangular teeth united by a ridge (9 and 10), structure similar to that illustrated by Holbourn *et al.* (2001, pl. 3, figs 5-6). ***12-13***. Hypotype of *P. obtusa* Berthelin, 1880 from the upper Albian (lower part of the *P. ticinensis* Biozone) of the western North Atlantic (Blake Plateau), Sample 171B-1050C-31-2, 130-134 cm. ***14.*** *P.* sp. from the lower Campanian (*Archaeoglobigerina cretacea* Biozone) of the South Atlantic Ocean (Falkland Plateau), Sample 79-511-32-1, 19-22 cm; specimen illustrated to show the triangular teeth, which are independent and therefore quite different of those recorded in the Aptian-Albian representatives of the genus *Pleurostomella*; planktic foraminiferal zonation after Huber (1992) and Huber *et al.* (1995). Photographs were taken with the SEM (1-7, 14) and Microprobe (8-13).

Plate 6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and only a few specimens of it were recorded in most of the samples where it occurs.

Stratigraphic range.– Upper Albian (from the upper part of the *P. ticinensis* Biozone throughout lower part of the *T. appenninica* Biozone).

Geographic distribution.– Western North Atlantic Ocean (Blake Plateau).

Family ARCHAEOGUEMBELITRIIDAE nov. fam.

Description.– Test is triserial throughout with globular chambers; aperture is semicircular, situated at the base of the last formed chamber; test wall is calcareous, smooth to ornamented with pore mounds, microperforate.

Stratigraphic range.– Upper Albian-lowermost Turonian (from the *P. ticinensis* Biozone to the *W. archaeocretacea* Biozone).

Genus *Archaeoguembelitria* nov. gen.

Type species.- *Gümbelitria harrisi* Tappan, 1940, p. 115, pl. 19, fig. 2.

Diagnosis.– Test triserial with chamber surface exhibiting the transition from completely smooth to pore mounds.

Description.– Test triserial throughout, twisted or not. Chambers are globular and increase gradually in size as added. Sutures are distinct and depressed. Aperture is umbilical in position, large, a high arch situated at the base of the last formed chamber. A thin and delicate lip borders the aperture. Chamber surface is smooth in the earlier species and with pore mounds in the evolved ones. Test wall is calcitic, hyaline, microperforate.

Remarks.– *Archaeoguembelitria* is proposed for a lineage of upper Albian to lowermost Turonian age, which consists of triserial foraminifera and were previously included within *Guembelitria* (Fig. 2). The test surface shows gradual transition between the earlier, smooth *A. cenomana* (Keller, 1935) and the evolved species, which bears pore mounds on the test surface, namely *A. harrisi* (Tappan, 1940). This sequence in the development of test ornamentation from smooth to pore mounds is relatively similar to the late Santonian-earliest Paleocene *Guembelitria*, namely *G.* sp. (smooth surface)-*G. turrita* (pustulose)-*G. cretacea* (pore mounds).

Etymology.– The prefix "archaeo-" (ancient, old) is added to the pre-existent genus name *Guembelitria*.

Stratigraphic range.– Upper Albian to lowermost Turonian (from the *P. ticinensis* Biozone throughout the lower part of the *W. archaeocretacea* Biozone).

Geographic distribution.– Cosmopolitan.

Archaeoguembelitria harrisi (Tappan, 1940) - emended
(Pl. 6, Fig. 7)

1940 *Gümbelitria harrisi* Tappan, p. 115, pl. 19, fig. 2.
1970 *Guembelitria harrisi* (Tappan, 1940). Eicher & Worstell, p. 296, pl. 8, figs 1-2.
1973 *Guembelitria harrisi* (Tappan, 1940). Smith & Pessagno, pl. 2, figs 1-3.
1977 *Guembelitria harrisi* Tappan, 1940. Petters, pl. 1, fig. 1.
1983 *Guembelitria harrisi* Tappan, 1940. Petters, pl. 1, fig. 1.
1985 *Guembelitria cenomana* (Keller, 1935). Caron, p. 57, figs 24:3-4.
1990 *Guembelitria cenomana* (Keller, 1935). Kroon & Nederbragt, p. 33, pl. 2, figs 8-9.

Emended description.– Test triserial throughout, rarely twisted or with curved axis of growth. Chambers are globular throughout and increase gradually in size; the last three chambers form approximately one third of the test. Proloculus is subspherical and with the maximum dimension between 12 and 19 µm. Sutures are deeply incised, straight to slightly curved. Aperture is situated at the base of the last-formed chamber and has a semicircular shape with variable height. It is bordered by an asymmetrically developed, thin and imperforate lip and provided with a relict, small toothplate. Chamber surface is smooth in the earlier part of the test and with pore mounds over the last-formed chambers of the test (Pl. 6, Fig. 7). Test wall is calcitic, hyaline and microperforate; pore diameter ranges between 0.5 and 0.7 µm.

Remarks.– This species is emended to include only the specimens with pore mounds. There are significant morphological resemblances between *A. harrisi* and *Guembelitria cretacea* Cushman, 1933 mainly with respect to the chamber surface ornamented with pore mounds (Fig. 2) and the aperture bordered by a narrow imperforate lip provided with a small toothplate. Such similar structures were achieved in distinct lineages and there are no records of similar tests in the Turonian-middle Campanian stratigraphic interval.

Stratigraphic range.– Uppermost Albian-lowermost Turonian (from the uppermost part of the *P. appenninica* Biozone to the lower part of *W. archaeocretacea* Biozone).

Geographic distribution.– USA (Texas, Wyoming, Colorado, South Dakota, Nebraska, Kansas, New Jersey), western North Atlantic Ocean (Blake Plateau), northern Africa (Tunisia), Gulf of Guinea and South-East Asia (Indonesia).

Archaeoguembelitria cenomana (Keller, 1935)
(Pl. 5, Figs 15-17, Pl. 6, Figs 1-4)

1935 *Gümbelina cenomana* Keller, p. 557, pl. 3, figs 13-14.
1967 *Guembelitria harrisi* (Tappan, 1940). Pessagno, p. 258, pl. 48, figs 12-13.
1972 *Guembelitria harrisi* (Tappan, 1940). Michael, p. 207, pl. 6, fig. 7.
1984 *Guembelitria cenomana* (Keller, 1935). Leckie, p. 593, pl. 11, fig. 12.
2006 *Guembelitria cenomana* (Keller, 1935). Petrizzo & Huber, pl. 1, fig. 1.

Description.– Test triserial throughout, twisted and often with curved axis of growth (Pl. 5, Fig. 15, Pl. 6, Figs 1, 3, 4). Chambers are globular, increase gradually in size and overlap at various rates. Proloculus is subspherical in shape and with a maximum dimension ranging between 14.8 and 22 µm. Sutures are distinct, depressed and straight to slightly curved. Aperture is situated at the base of the last-formed chamber; it is slightly asymmetrical, semicircular in shape, bordered by a narrow and imperforate lip and provided with a small toothplate. Chamber surface is smooth. Test wall is calcitic, hyaline and nannoperforate to microperforate; pore diameter ranges between 0.3 and 0.7 µm (Pl. 5, Figs 16, 17, Pl. 6, Figs 2, 6).

Remarks.– *Archaeoglobigerina cenomana* differs from *A. harrisi* in having smooth chamber surface, less incised sutures and smaller apertural opening.

Stratigraphic range.– Upper Albian (from the *P. ticinensis* Biozone to the *T. appenninica* Biozone).

Geographic distribution.– USA (Texas), Northern Atlantic Ocean (Blake Plateau and Mazagan Plateau), Tethys Realm (southwest Russia) and northern Africa (Tunisia).

Superfamily PLEUROSTOMELLACEA Reuss, 1860
Family PLEUROSTOMELLIDAE Reuss, 1860
Subfamily PLEUROSTOMELLINAE Reuss, 1860
Genus *Pleurostomella* Reuss, 1860

Type species: *Dentalina subnodosa* Reuss, 1851, p. 24.

1860 *Pleurostomella* Reuss, p. 203.
1911 *Pleurostomellina* Schubert, p. 58.
1928 *Ellipsonodosaria* (*Ellipsodentalina*) Franke, p. 54.
1967 *Clarella* Fuchs, p. 333.
1987 *Pleurostomella* Reuss, 1860, Loeblich & Tappan, p. 538.

Diagnosis.– Test loose biserial throughout with terminal aperture with projecting hood and provided with two symmetrically positioned triangular teeth.

Description.– Test loose biserial throughout. Chambers are globular to elongate and separated by depressed sutures. Aperture is large, with a projecting hood and with two symmetrically developed triangular teeth. Chamber surface is smooth. Test wall is calcareous, hyaline and nannoperforate.

Remarks.– *Pleurostomella* Reuss, 1860 is a genus with significant morphological variability. The species from the Aptian and Albian have in general a slightly elongate chamber in the biserial stage and low rate of chamber size increase in the adult. *Pleurostomella mirabilis* Bukalova (1960, p. 230, pl. 1, fig. 6) from the upper Albian of the Caucasus is not congeneric and should be probably transferred to *Bandyella* Loeblich & Tappan, 1962.

Stratigraphic range.– Aptian throughout the Holocene.

Geographic distribution.– Cosmopolitan.

Pleurostomella obtusa Berthelin, 1880
(Pl. 6, Figs 8-13, Pl. 7, Figs 3-4)

1880 *Pleurostomella obtusa* Berthelin, p. 29, pl. 1, fig. 9.
1954 *Pleurostomella obtusa* Berthelin, 1880. Bartenstein, p. 41.
1965 *Pleurostomella obtusa* Berthelin, 1880. Neagu, p. 29, pl. 7, figs 29-32.
1977 *Pleurostomella obtusa* Berthelin, 1880. Sliter, pl. 6, fig. 6.
1979 *Pleurostomella* (*Clarella*) *bulbosa* (Ten Dam, 1950). Sigal, pl. 4, figs 12-13.

Description.– Test with chambers in a loose biserial arrangement. Chambers are subglobular, the last formed ones being slightly elongate in the direction of test growth. Proloculus is large, its maximum dimension being between 42 and 55 µm. Sutures are deeply incised, slightly curved and oblique to the long axis of the test when seen in edge view. Aperture large and with a projecting hood and two short triangular teeth, which are united by a bridge-like plate (Pl. 6, Figs 9, 10, 13, Pl. 7, Figs 3-4). Chamber surface is smooth. Test wall is calcitic, hyaline and nannoperforate; pore diameter ranges between 0.10 and 0.16 µm (Pl. 6, Figs 8-13, Pl. 7, Figs 3-4).

Remarks.– *Pleurostomella obtusa* differs from *P. subnodosa* Reuss, 1860 in having a larger proloculus and lower rate of chamber increase in size. *Pleurostomella copiosa* Bukalova (1960, p. 229, pl. 1, fig. 8) described from the upper Albian of northwestern Caucasus, has the chambers of the adult stage with a very low rate of size increase, which results in a nearly tubular appearance in the adult portion. The differences in the rate of chamber increase in size, which is higher in *P. obtusa*, warrants the distinction of the two species, in which *P. obtusa* is the ancestor and *P. copiosa* its descendant. This species is recorded at Site 1050C only in the sediments from the lower part of the *P. ticinensis* Biozone. However, the first evolutionary occurrence of this species is well documented in the middle Albian of the Romanian sector of the Moesian Platform (Neagu, 1965, p. 2).

Stratigraphic range.– Middle-upper Albian (from the *T. primula* Biozone to *P. ticinensis* Biozone).

Geographic distribution.– Europe (France, Romania, Germany), North Atlantic (Blake Plateau, southern Vigo Seamount) and western South Atlantic (São Paolo Plateau).

Superfamily UNCERTAIN
Family GUEMBELITRIIDAE Montanaro Gallitelli, 1957
Genus *Guembelitria* Cushman, 1933

Type species.- *Guembelitria cretacea* Cushman, 1933, p. 37, pl. 4, fig. 12.

1933 *Guembelitria* Cushman, p. 37.
1957 *Guembelitria* Cushman, 1933, Montanaro Gallitelli, p. 136.
1964 *Guembelitria* Cushman, 1933, Loeblich & Tappan, p. C652.
1987 *Guembelitria* Cushman, 1933, Loeblich & Tappan, p. 453.
1990 *Guembelitria* Cushman, 1933, Kroon & Nederbragt, p. 33.
1999 *Guembelitria* Cushman, 1933, Olsson *et al*., p. 79.

Diagnosis.– Test triserial, with test surface smooth, pustulose or ornamented with pore mounds.

Description.– Test is triserial. Chambers are globular, increasing in size as added. Sutures are straight or slightly curved, distinct and depressed. The aperture is in the shape of a medium or high arch. It is bordered by a slightly asymmetrical lip and is provided with a relict toothplate. Chamber surface is variable, ranging from smooth to pustulose or with pore mounds (Fig. 3). Test wall is calcitic, hyaline and microperforate.

Remarks.– The genus *Guembelitria* was defined based on the triserial chamber arrangement (Cushman, 1933) and this definition was followed with few changes since then (Loeblich & Tappan, 1964, 1987; Kroon & Nederbragt, 1990; Koutsoukos, 1994; Olsson *et al*., 1999). The most significant advances in our knowledge of the morphology of *Guembelitria* are the descriptions of different ornamentation patterns in various species of the genus. Pore mounds on the chamber surface are well-known in *G. cre-*

Plate 7

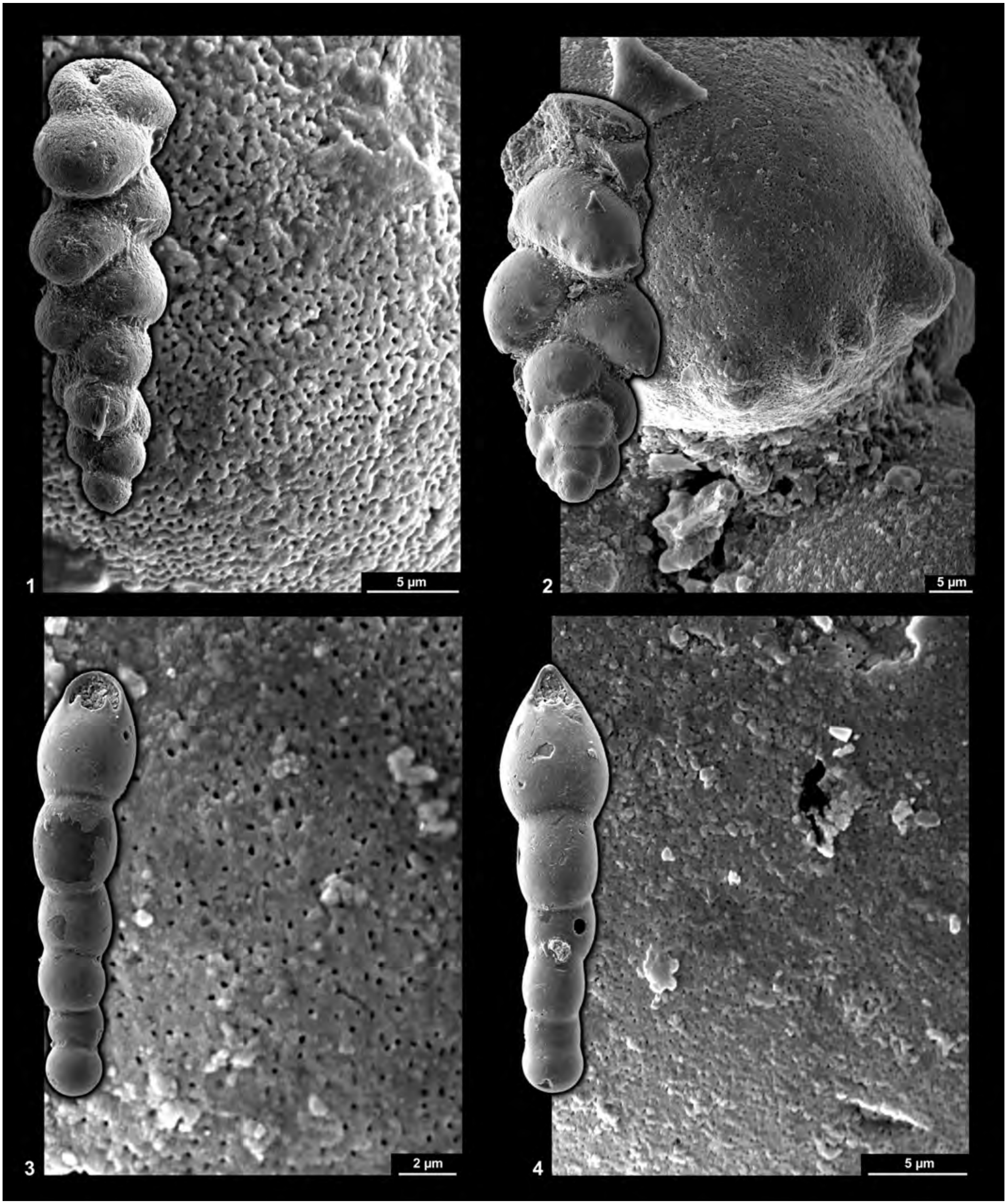

Plate 7. High magnification scanning electron microscope micrographs of *Haigella* nov. gen. and *Pleurostomella* Reuss, 1860 from the upper Albian sediments of ODP Site 1050C, illustrating the nannoporous test wall. ***1.*** Edge view of the holotype of holotype of *H. intermedia* nov. sp. (specimen figured in Pl. 5, figs 1-2). ***2***. Holotype of *H. haigi* nov. sp. (specimen figured in Pl. 5, figs 7-8). ***3***. Hypotype of *P. obtusa* (specimen figured in Pl. 6, figs 12-13). ***4***. Hypotype of *P. obtusa* (specimen figured in Pl. 6, figs 8-9).

tacea (Olsson, 1970; Smith & Pessagno, 1973; Keller, 1989; Liu & Olsson, 1992; Olsson *et al.*, 1999) (Fig. 2). *Guembelitria turrita*, which was described by Kroon & Nederbragt (1990) from the sediments adjacent to the Campanian-Maastrichtian boundary from the Grand Banks (North Atlantic Ocean, offshore Canada) exhibits ornamentation consisting of small-sized, scattered pustules on the earlier chambers of the test. Triserial tests with completely smooth surface are also known from the Late Cretaceous (late Santonian-Maastrichtian). These tests seemingly occur only in the Eastern Hemisphere. Excellently preserved material from the Maastrichtian of Madagascar was recently shown to the author by Dr. S. Abramovich (Ben Gurion University of the Negev, Israel). This guembelitriid species differs from *G. turrita* in having the test completely smooth. Its taxonomic status will be the subject of a forthcoming article. Accordingly, *Guembelitria* Cushman, 1933 *s. s.* appears to be restricted to the late Santonian-early Paleocene and it includes a lineage that initiates with smooth tests (*G.* sp.), continued with tests with pustulose chamber surface (*G. turrita*) and the end member bears pore mounds (*G. cretacea*). A distinct lineage from the upper Cenomanian and Turonian sediments of the Western Interior of Canada and USA consists of two species described by Stelck & Wall (1954, 1955). These were originally reported as *G. cretacea* Cushman var. *albertensis* Stelck & Wall (1954, p. 23, pl. 2, fig 19) and *G. cretacea* Cushman var. *spiritensis* Stelck & Wall (1955, p. 44, pl. 2, fig. 11). The former is characterized by a test consisting of two stages, triserial in the earlier portion of the test and biserial in the adult and the latter is triserial throughout. The two species were considered synonyms and included within *Neobulimina* by Eicher (1966, p. 26) and this taxonomic solution was followed by Eicher & Worstell (1970, p. 290) and McNeil & Caldwell (1981, p. 218). The excellent illustrations given by Eicher & Worstell (1970, pl. 4, figs 2-4) and McNeil & Caldwell (1981, pl. 18, figs 2-3) show clearly that these are benthic tests and therefore cannot be assigned to *Guembelitria*. Triserial tests are known at lower stratigraphical levels. For example, Wall (1960, p. 109, pl. 1, figs 23-24) reported *Gümbelitria* sp. from the Shaunavon Formation (Bathonian) of Saskatchewan (Canada). The illustrations given by Wall (1960) show clearly tests with guembelitriid appearance. Notably, no additional occurrences were discovered in the course of a more recent study by Brooke & Braun (1972). This report needs further documentation to demonstrate the occurrence of truly guembelitriid tests below the Jurassic/Cretaceous boundary.

Stratigraphic range.– Late Santonian-early Paleocene (from the *D. asymetrica* Biozone throughout the Paleocene planktic foraminiferal Biozone P1b). Paleocene biozonation is after Olsson *et al*. (1999).

Geographic distribution.– Cosmopolitan.

Guembelitria cretacea Cushman, 1933
(Fig. 4)

1933 *Gümbelitria cretacea* Cushman, p. 37, pl. 4, fig. 12.
1967 *Guembelitria cretacea* Cushman, 1933. Pessagno, p. 258, pl. 87, figs 1-3.
1973 *Guembelitria cretacea* Cushman, 1933. Smith & Pessagno, p. 15, pl. 1, figs 1-8.
1990 *Guembelitria cretacea* Cushman, 1933. Huber, p. 502, pl. 1, fig. 1.
1992 *Guembelitria cretacea* Cushman, 1933. Liu & Olsson, p. 341, pl. 1, figs 1-2.
1999 *Guembelitria cretacea* Cushman, 1933. Olsson *et al.*, p. 79, pl. 8, figs 1-3, pl. 13, fig. 3, pl. 63, figs 1-12.
2003 *Guembelitria cretacea* Cushman, 1933. Abramovich *et al.*, pl. 1, fig. 1.

Description.– Test is triserial. Chambers are globular and increase gradually in size. Sutures are straight or slightly curved, distinct and depressed. Aperture is large and bordered by an asymmetrical imperforate rim and provided with a poorly developed toothplate. Chamber surface is ornamented with pore mounds or a mixture of pore mounds and scattered pustules. Test wall is calcitic, hyaline and nannoperforate to microperforate; pores are circular in shape, with diameter between 0.4 and 0.8 µm.

Remarks.– *Guembelitria cretacea* differs from any other Late Cretaceous triserial planktic foraminifer by the chamber surface covered with pore mounds or a combination of pores and pore mounds. Morphologically it is similar to *Archaeoguembelitria harrisi* of the Cenomanian-early Turonian. Such similarity in test morphology appears the result of convergent evolution in two distant lineages.

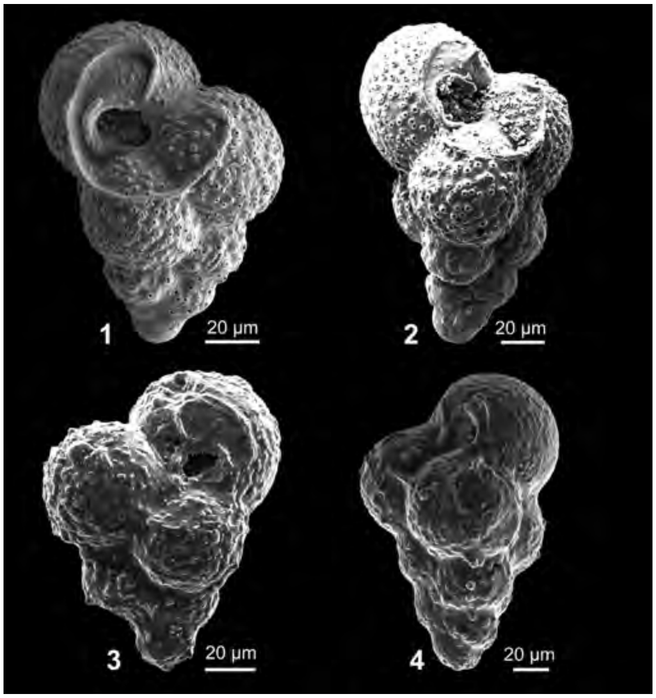

Figure 4. Specimens of *Guembelitria cretacea* Cushman, 1933. *1-2.* Two hypotypes from the Maastrichtian sediments of Madagascar with well-developed pore mounds on the test surface. The photographs were kindly made available by Dr. Sigal Abramovich (Ben Gurion University of the Negev, Israel). *3-4.*Topotypes from the Navarro Formation (upper Maastrichtian) of Texas; specimens from the Loeblich and Tappan Topotype Collection (USNM 473122).

Stratigraphic range.– Maastrichtian to early Paleocene (from the *A. mayaroensis* Biozone throughout the Paleocene planktic foraminiferal Biozone P1b).

Geographic distribution.– Cosmopolitan.

6. DISCUSSION AND CONCLUSIONS

New detailed data on the general test morphology, test wall ultrastructure and porosity and stratigraphic distribution apparently indicate that the ancestor of the biserial planktic foraminifera (Superfamily Heterohelicacea Cushman, 1927) was among the small sized benthics with a serial chamber arrangement. The evolutionary process through which a small group of benthic foraminifera with serial chamber arrangement was extremely complex, involving major changes in chamber arrangement, aperture size and shape, periapertural structures and test porosity.

A most interesting and new benthic foraminiferal group from the upper Albian sediments fills in the gap between the benthic and planktic foraminifera with serial chamber arrangement (Fig. 5). Superfamily Praeplanctoniacea includes Family Praeplanctonidae nov. and Family Archaeoguembelitriidae nov. The former consists entirely of benthic taxa and the latter of species that document the gradual transition from the benthic to planktic way of life. The newly described Superfamily Praeplanctoniacea is geographically restricted to the southern North Atlantic (Blake Plateau and offshore Cape Bojador, Spanish Sahara) and Caribbean region (Trinidad), an area that covers in part that of the earliest planktic foraminifera [Caribbean region, southern North Atlantic, Western Interior Seaway (USA and Canada) and North Sea].

6.1. *Praeplanctonia* – the key genus in the quest for heterohelicid ancestors

Praeplanctonia occurs in the upper Albian (*P. ticinensis* Biozone and *P. appenninica* Biozone) sediments at Blake Nose. It consists of two species, *P. globifera* and *P. quasiplanctonica*. This genus exhibits a serial chamber arrangement, which can be either biserial throughout or with a short earlier triserial stage and biserial when adult. This kind of variability with respect to the chamber arrangement shows remarkable consistency in the two species and is therefore considered a characteristic at genus level.

The two species of *Praeplanctonia* have different size of proloculus, which is larger in *P. globifera* (28-44 µm in maximum dimension) and smaller in *P. quasiplanctonica* (11-14 µm). The evolutionary trend is towards the development of small proloculus from a more primitive, larger one as shown in the record of the two species at ODP Site 1050C, where only *P. globifera* occurs in the lower part of the *P. ticinensis* Biozone. This trend can be observed in all the four lineages, which were initiated from *P. globifera* throughout the *P. ticinensis* Biozone: (i) *P. globifera* (28-44 µm) – *Archaeoguembelitria cenomana* (14.8-22 µm), (ii) *P. globifera* (28-44 µm) – *"Heterohelix" washitensis* (3-1 µm), (iii) *P. globifera* (28-44 µm) – *P. quasiplanctonica* (11-14 µm) and (iv) *P. globifera* (28-44 µm) – *Haigella intermedia* (19-24 µm).

Another feature which proved of taxonomically significant is the supplementary suture on the apertural face of the

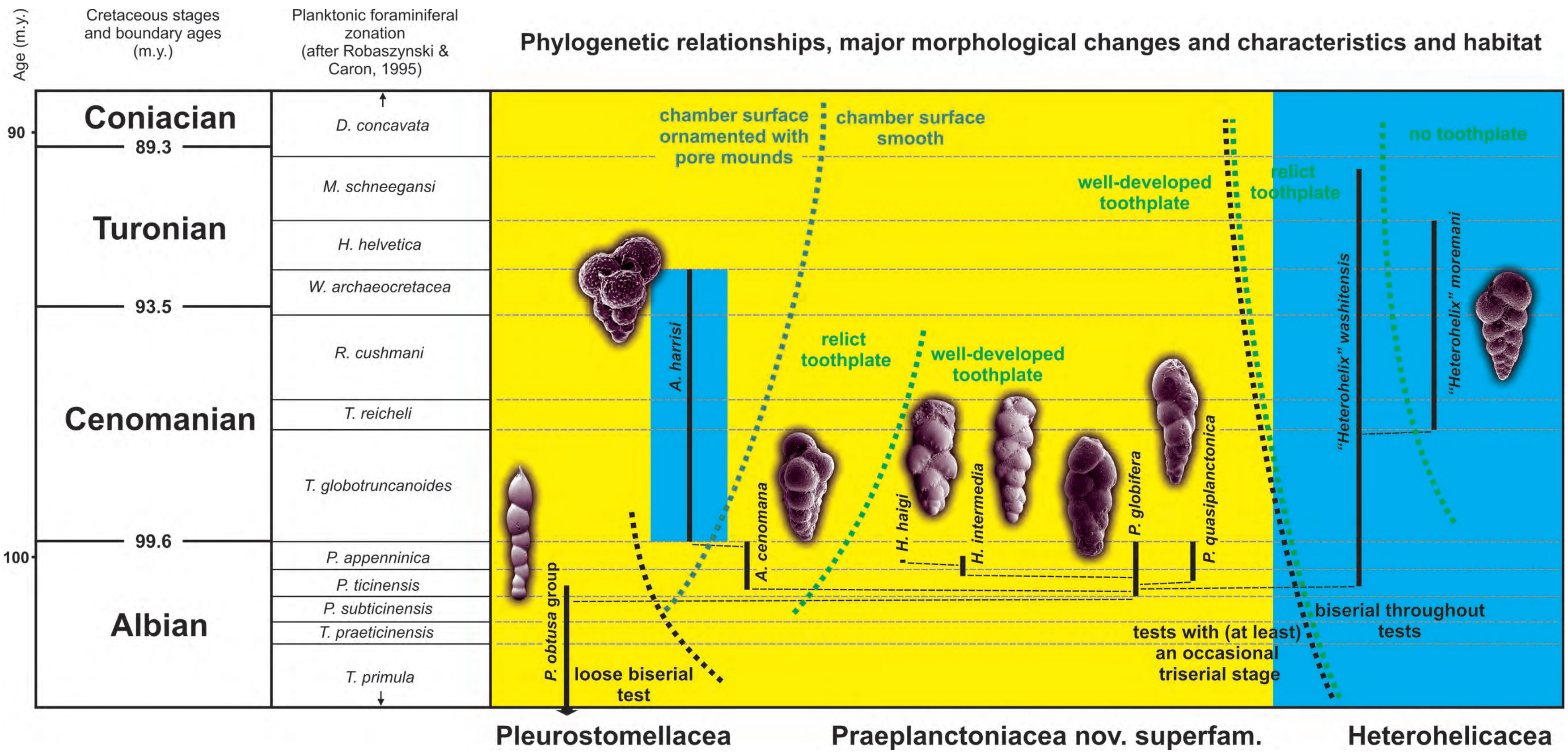

Figure 5. Inferred phylogenetic relationships demonstrating that the serial planktic foraminifera evolved from serial benthics and therefore, the planktic foraminifers are polyphyletic. Benthic taxa are shown on yellow background, the planktic ones on blue background. Ages after Gradstein *et al.* (2004).

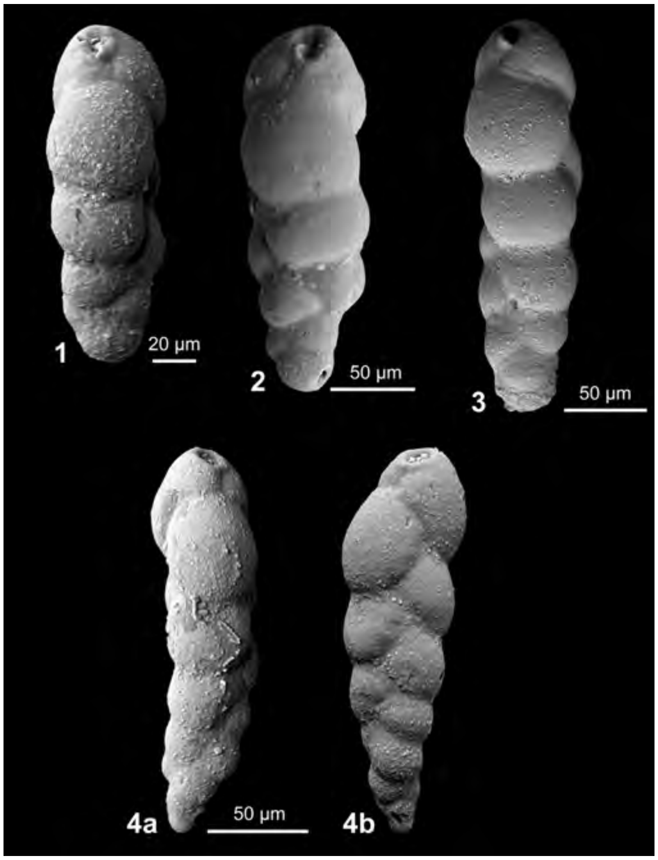

Figure 6. Microprobe photographs of *Praeplanctonia globifera* nov. gen., nov. sp. (1-3) and *P. quasiplanctonica* nov. gen., nov. sp. (4) showing the supplementary suture and periapertural rim or lip, which demonstrates that the aperture "wrapping" process can be either dextral or sinistral. 1: Sample 171B-1050C-31-1, 102-105 cm; 2: Sample 171B-1050C-31-1, 132-134 cm; 3: Sample 171B-1050C-27-4, 80-83 cm; 4: Sample 171B-1050C-28-6, 66-69 cm.

last-formed chamber (Fig. 6, 1-4). This additional suture is consistently present in the specimens of *Praeplanctonia* and it connects the aperture base and the last suture namely that between the last formed and penultimate chambers. In some specimens the supplementary suture is situated within a depression on the apertural face. Noteworthy, the supplementary suture is always oblique both to the test last suture and test axis of growth. A relatively similar structure was previously described from the type species of *Pyramidina*, namely *P. curvisuturata* (Brotzen, 1940). The formation of this structure was explained by Brotzen (1940, p. 17) as follows: "The aperture in the initial stage is elongate at the base of the apertural face as in *Bulimina*. In the following stage the apertural opening will be contracted near the base and the apertural opening acquires a more terminal position. In this stage a distinct suture is visible between the base and the apertural opening." As a result, the supplementary suture in *P. curvisuturata* is straight and this appearance contrasts to that known in the *Praeplanctonia* species, which is oblique. Detail SEM micrographs show that the supplementary suture of *Praeplanctonia* is the result of a "wrapping" process of the adjacent test wall over the apertural area (Pl. 4, Fig. 2).

6.2. The origin of *Praeplanctonia; Pleurostomella – Praeplanctonia* lineage

The "wrapped" test wall in the proximity of the aperture in *Praeplanctonia globifera* and *P. quasiplanctonica* suggests that the ancestor of this genus probably had a wider apertural opening, which was situated at the base of the last chamber of the test. There is a single genus in the upper Albian, which has such a large apertural opening, namely *Pleurostomella*. Very few data are known about the evolutionary trends, ancestor and possible descendants of this genus. The only account on this subject was given by Loeblich & Tappan (1974, p. 46). These authors noted that Family Pleurostomellidae Reuss, 1860 might have been evolved from the members of the Family Glandulinidae Reuss, 1860 based on the similarities in the test wall structures but no further details were given. The stratigraphic range of *Pleurostomella* was considered Cretaceous (Aptian) throughout Recent by Loeblich & Tappan (1987, p. 538).

The species of *Pleurostomella* are characterized in general by significant morphological variability with respect to the proloculus size, chamber increase in size, test wall perforations and position of the apertural teeth. Moreover, it seems that some of these features are consistent with the stratigraphical distribution of certain groups of species and therefore, a possible polyphyletic nature of *Pleurostomella* cannot be *a priori* excluded. However, the Aptian-Albian group of species, which includes the type species *P. subnodosa* (Reuss, 1851) is characterized by large proloculus (48-57 μm maximum dimension), nannoperforate test wall, relatively low rate of chamber size increase and apertural teeth connected by a bridge-like calcareous plate.

There are two common morphological features in the earliest representatives of *Praeplanctonia globifera* and the

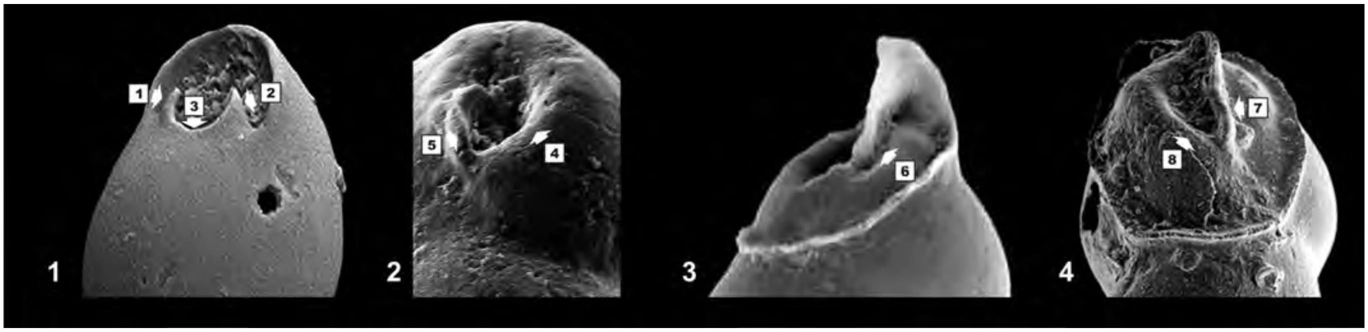

Figure 7. Periapertural structures and toothplate in *Pleurostomella* (1) and *Praeplanctonia* (2-4). 1. *P. obtusa* Berthelin, 1880 – 1 and 2: apertural teeth, 3: bridge-like calcareous plate. 2. *P. globifera* nov. sp. – 4: prolongation of the periapertural test wall, 5: periapertural rim resulted from the merging and migration of the pleurostomellid periapertural structures. 3. *P. quasiplanctonica* nov. sp. – 6: toothplate. 4. *P. quasiplanctonica* nov. sp. – 7: toothplate, 8: toothplate branch.

specimens from the last occurrences of *Pleurostomella obtusa* at ODP Hole 1050C: generally large-size proloculus, 42-55 µm in the latter when compared to 28-44 µm in the former and similar rate of chamber increase in size. There are other taxa with a large proloculus in the Albian, such as *Dentalina soluta* Reuss, 1851, *D. distincta* Reuss, 1860, *D. guttifera* d'Orbigny, 1846, etc. but all of them belong to Suborder Lagenina Delage & Hérouard, 1896 and therefore have a cribrate aperture (Neagu, 1965; Bartenstein *et al.*, 1966; Bartenstein & Bolli, 1973). Consequently, a phylogenetic relationship between these lagenid species and *P. globifera* cannot be taken in consideration. The chamber rate of increase in size can be only qualitatively estimated, due to the twisted tests of *P. globifera*, which occasionally have early triserial stage. However, the similarities in rate of chamber increase in size between *P. obtusa* and *P. globifera* are evident in all the examined specimens. There are contradictory data in the record at ODP Hole 1050C, where the occurrences of *P. obtusa* are above the first evolutionary appearance of *P. globifera*. Lower stratigraphical occurrences of *P. obtusa* are well documented in the Romanian sector of the Moesian Platform, where they occur in middle Albian, in foraminiferal assemblages associated with the ammonite *Anahoplites intermedius* Biozone (Neagu, 1965).

A distinct evolutionary trend in the development of the apertural structures is recognized in this study. The two apertural triangular teeth of *Pleurostomella* are symmetrically developed and with the same ultrastructure as the test wall in the earliest member of the genus, *P. prima* Bettenstaedt & Spiegler, 1982 (upper Aptian-lower Albian). In the late representatives of the Aptian-Albian pleurostomellid stock, the teeth are united by a thin calcareous, bridge-like plate (Fig. 7, 1). This feature is observed in *P. subnodosa* Reuss, 1860 and *P. gracillis* Bettenstaedt & Spiegler, 1982, the latter being considered here a junior synonym of *P. copiosa* (Bukalova, 1960). This newly observed structure in *P. obtusa* is of particular importance in identifying the evolutionary trends in the *Pleurostomella*-*Praeplanctonia* lineage, as it most likely represents the ancestor structure of the periapertural rim of *Praeplanctonia globifera*. The transition of the pleurostomellid aperture to that of *P. globifera* can be explained through the torsion of the test wall around the chamber longitudinal axis. This process results in the overlapping of the test wall at the base of the aperture, which is no longer situated at the base of the chamber in *P. globifera* when compared with its ancestor, *P. obtusa*. Test wall overlapping leads to the formation of the supplementary suture and in the case of specimens with a thinner test wall a triangular depression area is present. The complex apertural structures consisting of the two teeth connected by the calcareous bridge-like structure apparently migrate towards the lateral sides of the modified aperture. This migration is accompanied by the anastomosing of the three components (i.e., the two teeth and thin bridge-like structure between them), which result in the formation of the periapertural rim (Fig. 7, 2). Tests documenting this process are extremely rare, but one of them was figured by Bettenstaedt & Spiegler (1982, pl. 7.3-4, fig. 8) and originally assigned to *P. elongata*. Test wall torsion can be either dextral or sinistral (Fig. 6), which is demonstrated by the presence of the newly formed periapertural rim on either side of the aperture in *P. globifera*.

Apertures with a toothplate have not been reported in any *Pleurostomella* species of the Aptian and Albian (Bettenstaedt & Spiegler, 1982; Holbourn *et al*., 2001; this study). Two broken specimens of *P. obtusa* from the Blake Plateau (ODP Hole 1050C) did not reveal any additional information due to chamber infill. The earliest occurrences of tube-like structures connecting the successive foramina in representative of this genus are from *P. nitida* Morrow, 1934 of the upper Cenomanian-Turonian (Eicher & Worstell, 1970, pl. 4, figs 8-9) and *P. articulata* (Brotzen, 1936) of the lower Senonian (Brotzen, 1936). We can only conclude that the toothplate in *Praeplanctonia* is the result of the test wall torsion process (Fig. 7, 3-4), which may have produced significant changes in the pleurostomellid aperture and periapertural structures. This conclusion is also supported by the fact that the toothplate, whenever observed, is always present on the opposite side of the test than the periapertural rim.

Another major evolutionary trend in the *Pleurostomella-Praeplanctonia* lineage is the increase in pore diameter in the latter genus. The Aptian-Albian representatives of the genus *Pleurostomella* have small sized pores (nannopores), their diameter being between 0.10 and 0.16 µm. Over 20 *P. globifera* specimens were studied in detail in SEM micrographs and demonstrated, without exception, that the test wall of the specimens of this species is thoroughly nannoperforate, but the pore diameter varies between 0.2 and 0.5 µm. It can also be concluded that the increase in pore size could be related to the reduction in the surface of the apertural opening, in order to maintain the communication between the test interior and surrounding environment.

6.3. Development of backward oriented chamber projections in *Praeplanctonia globifera-Haigella* lineage

P. globifera-Haigella lineage resulted in the development of chambers with backward oriented prolongations in the adult stage. *Haigella* nov. gen. consists of two species, *H. intermedia* nov. sp. and *H. haigi* nov. sp. It is a very short lineage, recorded in the ODP Hole 1050C only in the upper part of the *P. ticinensis* Biozone and the lower part of the *P. appenninica* Biozone. Both species have an early initial stage resembling that of *P. globifera* and a subterminal aperture with supplementary suture on the apertural face. By contrast, *Haigella haigi*, which is the end member of the lineage, has a triserial chamber arrangement throughout. Its ancestor, *Haigella intermedia* has an occasional early triserial stage, resembling thus the variability of the ancestral species, *P. globifera*. A detailed study of the tests in the *P. globifera-H. intermedia-H. haigi* lineage shows that the tests of the intermediate species are more elongate [i.e., thickness/length ratio (T/L)] than those of the ancestral species and the end member of the genus. This demonstrates that, the intermediate taxa can differ in some features from their ancestors and descendants, the latter being similar, and some features or parameters may show a reversible pattern along a lineage. The stratigraphic range of *Haigella* indicates that this taxon is rather a local offshoot. Its evolutionary history contrasts with that of *Gabonella* de Klasz, Marie & Meijer, 1960, an Upper Cretaceous genus also with chamber projections, but which shows significant species proliferation (de Klasz *et al*., 1960; de Klasz *et al*., 1961; de Klasz & Rerat, 1963; Roveda, 1964).

6.4. Planktic adaptive radiations originating from *Praeplanctonia globifera*

Our study could not substantiate an ancestor-descendant relationship between the biserial and triserial planktic foraminifera of the upper Albian-middle Cenomanian sediments of the ODP Hole 1050C (Blake Plateau). The earliest biserial and triserial tests make their first evolutionary occurrence approximately at the same time (samples 171B-1050C-31-2, 130-134 cm and 171B-1050C-31-2, 80-84 cm respectively) at this site (Fig. 3).

There are a number of morphological features in the earliest triserial and biserial foraminifera, *A. cenomana* and "*H.*" *washitensis* respectively, which require special attention. Probably the most important of them is that both species have a quite stable chamber arrangement, being either completely triserial or completely biserial and specimens with intermediate morphology between the two species have not been reported ever. The apertures and periapertural structures are remarkably similar in the shape and size, presence of an imperforate lip or rim and relict toothplate. The test wall in the two species is microperforate and has nearly identical pore size, 0.5-0.7

µm in *A. cenomana* and 0.4-0.7 µm in "*H.*" *washitensis*. Together, these features suggest that *A. cenomana* and "*H.*" *washitensis* emerged rather through divergent evolution than forming a distinct lineage, with one of them being the ancestor of the other.

A better explanation of the evolutionary process that resulted in the appearance of the triserial *A. cenomana* and the biserial with twisted test "*H.*" *washitensis* can be provided if it is taken into consideration the highly variable and morphologically heterogeneous *Praeplanctonia globifera*. The latter has two distinct test varieties with respect to the chamber arrangement, namely biserial throughout and/or with an early triserial stage, becoming biserial when adult. The significant morphological resemblances between *A. cenomana* and "*Heterohelix*" *washitensis* as well as the lack of tests with intermediate features can be easily explained through divergent evolution from the two varieties of *P. globifera*. Accordingly, the biserial with twisted tests "*H.*" *washitensis* evolved from the biserial throughout variety of *P. globifera* and the triserial throughout *A. cenomana* from that variety of *P. globifera* with an early triserial test, through the development of the triserial stage simultaneously with the reduction of the biserial one (Fig. 8). Divergent evolution from *P. globifera*, not only provides a clear explanation for the morphological resemblances between *A. cenomana* and "*H.*" *washitensis*, but it also explains the change to planktic habitat achieved in both *Archaeoguembelitria* lineage and biserial planktics in a relatively short time interval.

A major difficulty in documenting the divergent evolution from *P. globifera* to *Archaeoguembelitria* and "*Heterohelix*" respectively, are the sharp differences between the apertures and in the presumed ancestor and descendants. The small aperture of *P. globifera* was formed through the reduction in size when compared with that of its pleurostomellid ancestor. This is the result of the wrapping around of the periapertural test walls, which shifted the anastomosing apertural triangular teeth and bridge-like calcareous plate into a lateral position (Fig. 9). This kind of aperture is only known in *Praeplanctonia* and *Haigella*, two genera with short stratigraphic ranges (upper Albian) and herein included within Family Praeplanctonidae nov. Only a vestige of the periapertural test wall prolongation is present in "*H.*" *washitensis* as the periapertural ridge, which occurs on the lateral side of the aperture, opposed to the imperforate lip or rim. This suggests that the periapertural test wall prolongations reduced in the process of achieving a planktic habitat.

<u>*Praeplanctonia globifera-Archaeoguembelitria* lineage</u> initiated its evolution in the upper Albian (*P. ticinensis* Biozone), just before the first evolutionary occurrence of the biserial planktic foraminifera, as indicated by the stratigraphic record at ODP Hole 1050C. It is a lineage with major developments in the test ornamentation (Fig. 10). The earliest species, *A. cenomana* has smooth chamber surfaces and general appearance of a benthic species. Its descendant, *A. harrisi* has the chamber surface ornamented with pore mounds and consequently, a planktic habitat is inferred from this kind of ornamentation. The transition from the benthic mode of life to the planktic one happened in the proximity of the Albian/Cenomanian boundary as indicated by the occurrence of tests with incipient pore mounds.

<u>*Praeplanctonia globifera*- "*Heterohelix*" *washitensis* lineage</u> commenced its evolution in the upper Albian (*P. ticinensis* Biozone) and is the first adaptive radiation originating from *Praeplanctonia globifera*, namely from the biserial throughout variety of the ancestral species. The biserial planktics (Superfamily Heterohelicacea Cushman, 1927) underwent a rapid evolution, the earliest representatives of the group being planktic in habitat (Fig. 10). This lineage gave rise to the biserial planktics included within Superfamily Heterohelicacea Cushman, 1927. The earliest species of the group, "*H.*" *washitensis*, is characterized by asymmetrical tests, asymmetrical periapertural structures, vestiges of the periapertural chamber prolongations as a ridge on a lateral side of the aperture and relict toothplate. Symmetrical tests and periapertural structures in the heterohelicid history are developed in the middle Cenomanian (*T. reicheli* Biozone) in "*H.*" *moremani* (Cushman, 1938). Based on the newly documented phylogenetic relationships, Superfamily Heterohelicacea Cushman, 1927 is removed from Suborder Globigerinina Delage & Hérouard, 1896 and included within Suborder Rotaliina Delage & Hérouard, 1896.

The genus *Guembelitria* Cushman, 1933 in which all the planktic foraminifera with triserial chamber arrangement were included is now reviewed. The upper Aptian-lowermost part of the upper Albian tests with pustulose cham-

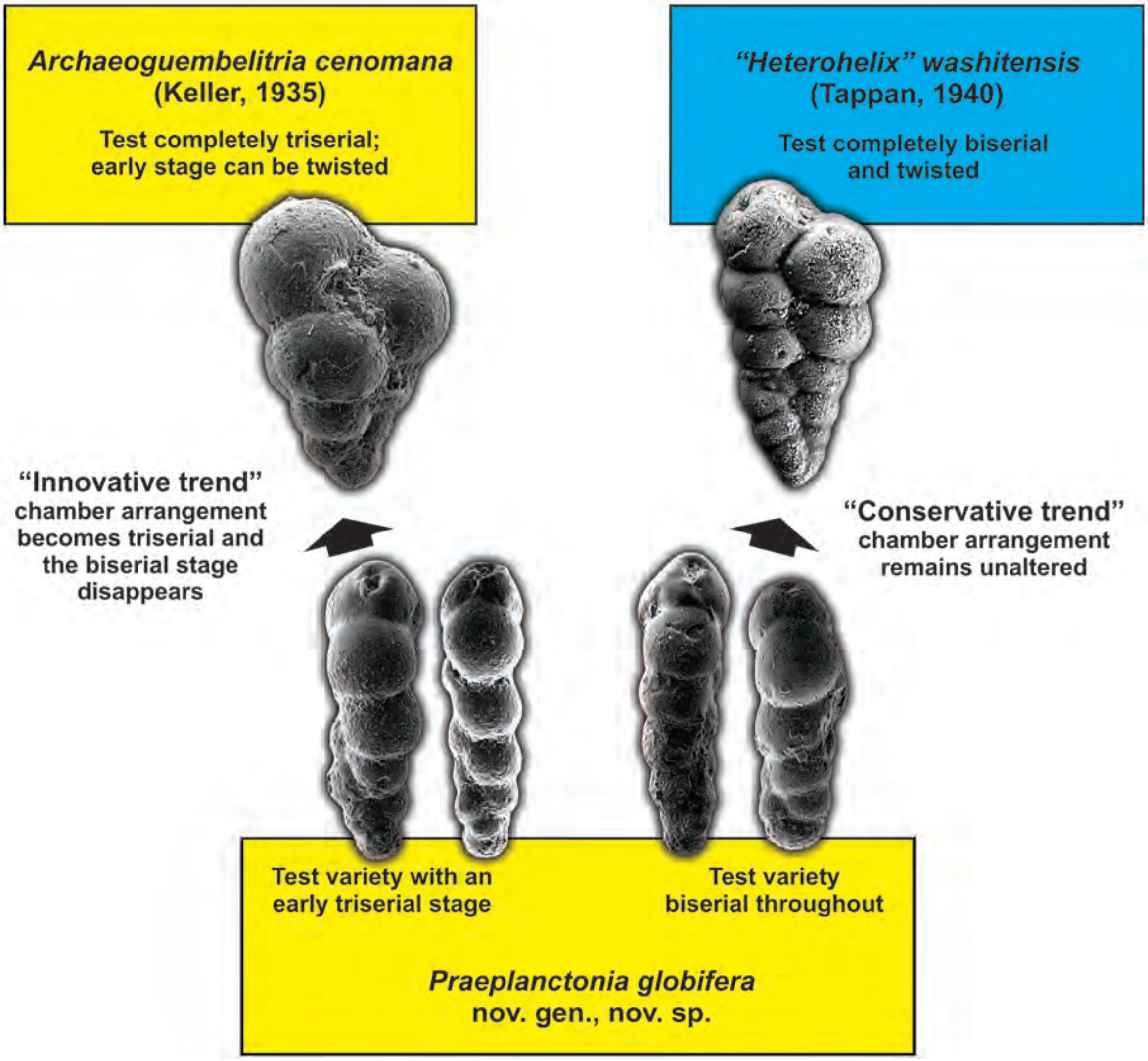

Figure 8. Diagram presenting the major morphological changes in the chamber arrangement during the divergent evolutionary processes, which resulted in the emergence of the planktic foraminifera with serial chamber arrangement. According to the Blake Nose ODP Hole 1050C data the *Archaeoguembelitria* lineage initiated just before the "*Heterohelix*" lineage. Benthic taxa are shown with yellow background, the planktic ones on blue background.

ber surface are included in the genus *Koutsoukosia* nov. gen. (Family Globuligerinidae Loeblich & Tappan, 1984) based on the test ornamentation which is similar to that of the primitive planktic foraminifera of the Middle Jurassic-Early Cretaceous. *Koutsoukosia* probably evolved from the primitive planktic foraminifera with high trochospire and pustulose chamber surface of *Conoglobigerina* Morozova, 1961 as postulated by Koutsoukos (1994, p. 293). The stratigraphic ranges of the two genera do not overlap, the extinction of *Conoglobigerina* is in the lower Valanginian (Simmons *et al.*, 1997) and the first occurrence of *Koutsoukosia* is upper Aptian. Therefore, there is gap spanning the upper Valanginian-middle Aptian without records of either of the two genera or tests with intermediate test morphology. The origin from a different, presumably globular-chambered and trochospiral ancestor should not be ruled out *a priori*. In this case, the developments of test ornamentation consisting of blunt pustules in species of *Conoglobigerina*, *Globuligerina* and *Koutsoukosia*, respectively, would be the result of the iterative evolutionary process.

The upper Albian-lower Turonian triserials are included within *Archaeoguembelitria* nov. gen. (Family Archaeoguembelitriidae nov. fam.). *Guembelitria* Cushman, 1933 is restricted to the tests of the upper Santonian-lowermost Paleocene and the test ornamentation shows grad-

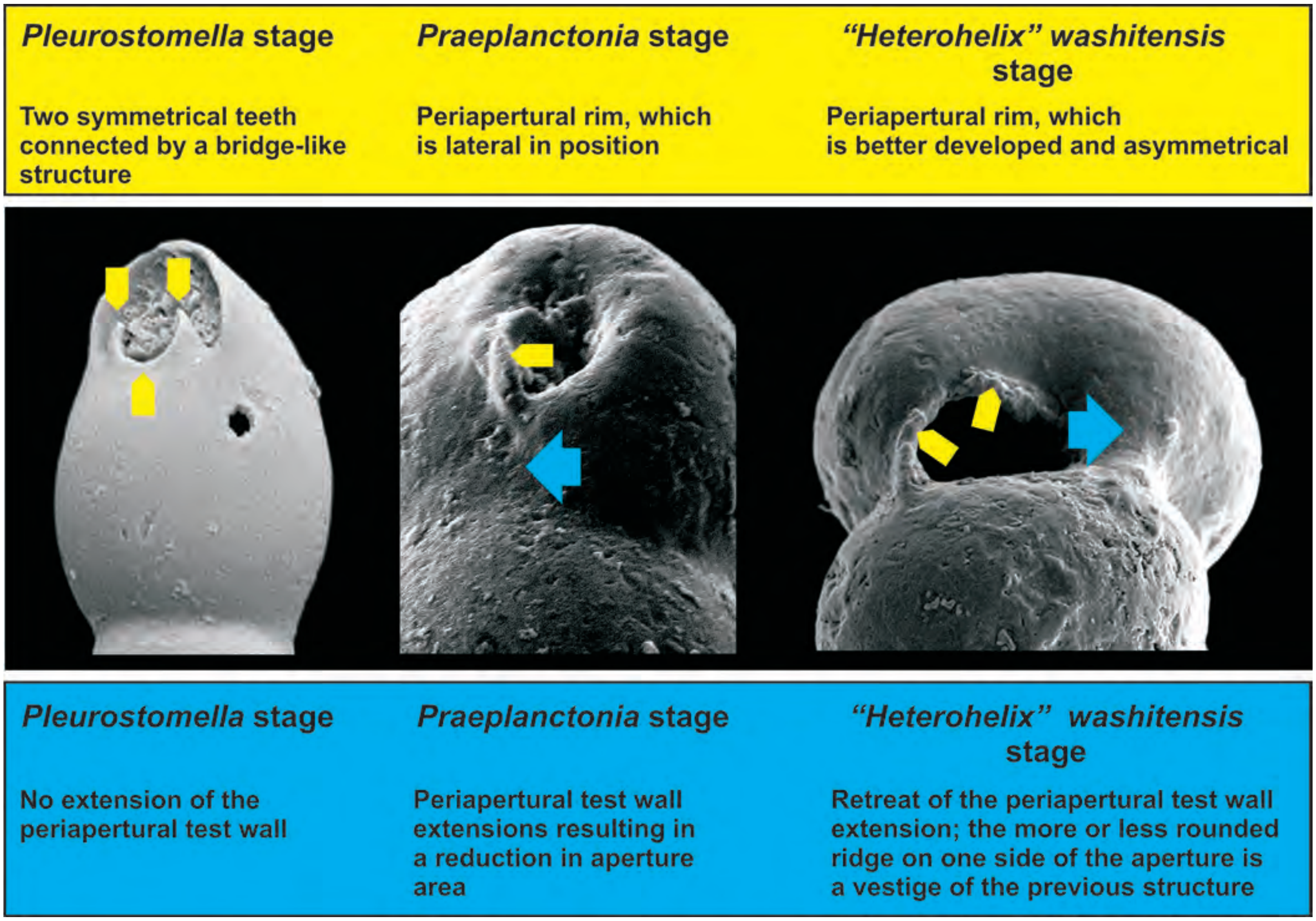

Figure 9. Diagram synthetically showing the major morphological changes in the aperture and periapertural structures in the *Pleurostomella obtusa*-*Praeplanctonia globifera* “*Heterohelix*” *washitensis* lineage. The extension of the periapertural test wall (blue) is a reversible process, in contrast to the periapertural structures (yellow). This structure is reduced in “*Heterohelix*” *washitensis*, its vestige being the ridge situated on one side of the aperture and indicated in the right hand figure by the blue arrow.

ual change from smooth to pustulose and with pore mounds in the end member of the lineage, namely *Guembelitria cretacea* Cushman, 1933, which is also the type species of the genus.

Guembelitriella Tappan, 1940 is reviewed and considered benthic in habitat. Accordingly, it is removed from Family Guembelitriidae Montanaro Gallitelli, 1957 (Superfamily Heterohelicacea Cushman, 1927) and included within Family Turrilinidae Cushman, 1927 (Superfamily Turrilinacea Cushman, 1927).

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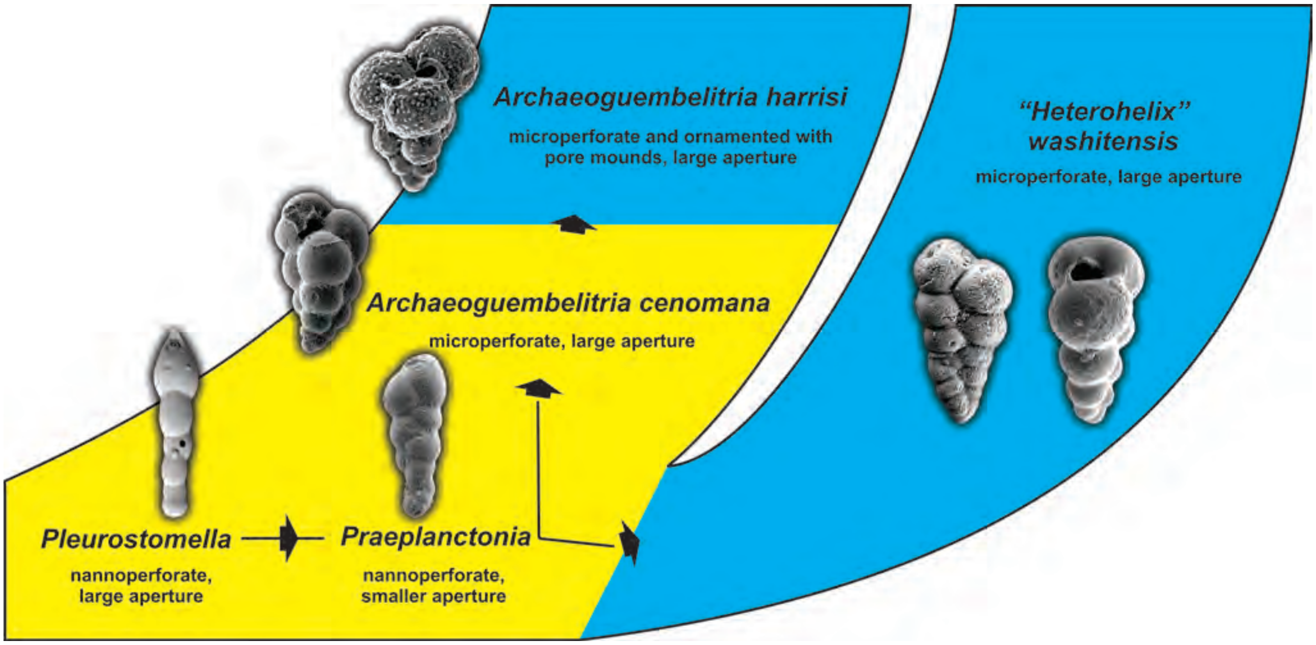

Figure 10. Diagram presenting the major morphological changes in the chamber arrangement, aperture and periapertural structures and pore size in the process of evolution of the serial planktic foraminifera.

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8. REFERENCES

Abramovich, S., Keller, G., Stüben, D. and Berner, Z. 2003. Characterization of late Campanian and Maastrichtian planktic foraminiferal depth habitats and vital activities based on stable isotopes. *Palaeogeography, Palaeclimatology, Palaeoecology*, 202, 1-29.

Bartenstein, H. 1954. Revision von Berthelin's Mémoire 1880 über die Alb-Foraminiferen von Montcley. *Senckenbergiana*, 35, 37-50.

Bartenstein, H., Bettenstaedt, F. and Bolli, H.M. 1966. Die Foraminiferen der Unterkreide von Trinidad, W. I. *Eclogae Geologiae Helvetiae*, 59, 129-177.

Bartenstein, H. and Bolli, H.M. 1973. Die Foraminiferen der Unterkreide von Trinidad, W. I. Dritter Teil: Maridaleformation (Co-Typlocalität). *Eclogae Geologiae Helvetiae*, 66, 389-418.

Bellier, J.-P. and Moullade, M. 2002. Lower Cretaceous planktonic foraminiferal biostratigraphy of the western North Atlantic (ODP Leg 171B) and taxonomic clarification of key index species. *Revue de Micropaléontologie*, 45, 9-26.

Berthelin, G. 1880. Mémoire sur les foraminifères fossils de l'étage Albien de Montcley (Doubs). *Mémoires de la Societé Géologique de France*, 1(5), 1-84.

Bettenstaedt, F. and Spiegler, D. 1982. *Pleurostomella* (Foram.) in der Unterkreide Nordwestdeutschlands. *Geologisches Jahrbuch*, A65, 445-479.

Bolli, H. M. 1959. Planktic foraminifera from the Cretaceous of Trinidad, B. W. I. *Bulletins of American Paleontology*, 39(179), 255-277.

Bolli, H.M., Beckmann, J.P. and Saunders, J.B. 1994. *Benthic foraminiferal biostratigraphy in the south Caribbean region*. Cambridge University Press, Cambridge, 408 pp.

Brooke, M.M. and Braun, W.K. 1972. Biostratigraphy and microfaunas of the Jurassic System of Saskatchewan. *Department of Mineral Resources Report, Geological Sciences Branch, Sedimentary Geology Division*, 161, 1-83.

Brotzen, F. 1936. Foraminiferen aus dem schwedischen unterer Senon von Eriksdal in Schonen. *Sveriges Geologiska Undersökning*, ser. C, 396(30), 1-69.

Brotzen, F. 1940. Flintrännans och Trindelträmnans geologi (Öresund). *Sveriges Geologiska Untersökning*, ser. C, 435(34-5), 1-33.

Brotzen, F. 1948. The Swedish Paleocene and its foraminiferal fauna. *Sveriges Geologiska Untersökning*, ser. C, 493(42), 1-140.

Bukalova, T.V. 1960. Buliminids and ellipsoidinids of the Albian outcrops from Beloi and Kuban (northern Great Caucasus). *Trudy VNIGRI, 16, Paleontologiceski Sbornik*, 3, 225-234 [in Russian].

Caron, M. 1983. La spéciation chez les foraminifères planctoniques: une réponse adaptée aux contraintes de l'environment. *Zitteliana*, 10, 671-676.

Caron, M. 1985. Cretaceous planktic foraminifera. In: *Plankton Stratigraphy* (Eds. H. M. Bolli, J. B. Saunders and K. Perch-Nielsen), Cambridge, Cambridge University Press, 17-86.

Church, C.C. 1968. Lower Cretaceous foraminifera of the Orchard Peak-Devils Den area, California. *Proceedings of the California Academy of Sciences*, 32, 523-580.

Cushman, J.A. 1933. Some new foraminiferal genera. *Contributions from the Cushman Laboratory for Foraminiferal Research*, 9, 32-38.

Cushman, J.A. 1950. *Foraminifera. Their Classification and Economic Use*. Harvard University Press, Cambridge, Massachusetts, 605 pp.

Darling, K.F., Kroon, D., Wade, C.M. and Leigh Brown, A.J. 1996. Molecular evolution of planktic foraminifera. *Journal of Foraminiferal Research*, 26, 324-330.

Darling, K.F., Wade, C.M., Kroon, D., Leigh Brown, A.J. 1997. Planktic foraminiferal molecular evolution and their polyphyletic origins from benthic taxa. *Marine Micropaleontology*, 30, 251-266.

Ehrenberg, C.G. 1843. Verbreitung und Einfluss des mikrosckopischen Lebens in Süd-und Nord America. *Abhandlungen der königlichen preussischen Akademie der Wiessenschaften zu Berlin (1841)*, 1, 291-446.

Eicher, D.L. 1966. Foraminifera of the Cretaceous Charlie Shale of Colorado. *Contributions from the Cushman Foundation for Foraminiferal Research*, 17, 16-31.

Eicher, D.L. and Worstell, P. 1970. Cenomanian and Turonian foraminifera from the Great Plains, United States. *Micropaleontology*, 16, 269-324.

Franke, A. 1928. Die Forfaminiferen der oberen Kreide Nord- und Mitteldeutschlands. *Preussiche Geologische Landesanstalt Abhandlungen*, 111, 1-208.

Fuchs, W. 1967. Die Foraminiferenfauna eines Kernes des höheren Mittel-Alb der Tiefbohrung Delft 2 - Niederlande. *Jahrbuch der Geologischen Bundesanstalt*, 110, 255-341.

Fuchs, W. 1973. Ein beitrag zur Kenntis der Jura-"Globigerinen" und verwandter Formen an Hand polnischen Materials des Callovien und Oxfordien. *Verhandlungen der Geologischen Bundesanstalt*, 3, 445-487.

Fuchs, W. 1975. Zur Stammesgeschichte der Planktonforaminiferen und verwandter Formen im Mesozoikum. *Jahrbuch der Geologischen Bundesanstalt*, 118, 193-246.

Georgescu, M.D. 2007a. Taxonomic re-evaluation of the Late Cretaceous serial planktic foraminifer *Gümbelina punctulata* Cushman, 1938 and related species. *Revista Española de Micropaleontología*, 39, 155-167.

Georgescu, M.D. 2007b. A new planktic heterohelicid foraminiferal genus from the Upper Cretaceous (Turonian). *Micropaleontology*, 53, 212-220.

Georgescu, M.D. and Abramovich, S. 2008. Taxonomic revision and phylogenetic classification of the Late Cretaceous (upper Santonian-Maastrichtian) serial planktic foraminifera (Family Heterohelicidae Cushman 1927) with peripheral test wall flexure. *Revista Española de Micropaleontología*, 40, TBC.

Georgescu, M.D. and Huber, B.T. 2007. Taxonomic revision of the late Campanian-Maastrichtian (Late Cretaceous) planktic foraminiferal genus *Rugotruncana* Brönnimann and Brown, 1956, and a new species concept for planktic foraminifera. *Journal of Foraminiferal Research*, 37, 150-159.

Georgescu, M.D. and Huber, B.T. 2008. Taxonomic re-evaluation and phylogeny of the stellate planktic foraminiferal genus *Hastigerinoides* Brönnimann, 1952. *Journal of Foraminiferal Research*, 38, 52-58.

Gradstein, F.M., Ogg, J.G., Smith, A.G., Agterberg, F.P., Bleeker, W., Cooper, R. A., Davydov, V., Gibbard, P., Hinnov, L. A., House, M. R., Lourens, L., Luterbacher, H.P., McArthur, J., Melchin, M.J., Robb, L.J., Shergpold, J., Villeneuve, M., Wardlaw, B.R., Ali, J., Brinkhuis, H., Hilgen, F.J., Hooker, J., Hoewath, R.J., Knoll, A.H., Laskar., J., Monechi, S., Plumb, K. A., Powell, J., Raffi. I., Röhl, U., Sadler, P., Sanfilippo, A., Schmitz, B., Schackelton, N.J., Shields, G.A., Strauss, H., Van Dam, J., van Kolfschoten, T., and Wilson, D. 2004. *A Geologic Time Scale 2004*. Cambridge University Press, 1-589.

Hart, M.B. 1999. The evolution and biodiversity of Cretaceous planktic Foraminiferida. *Geobios*, 32, 247-255.

Hart, M.B. 2006. The origin and evolution of planktic foraminifera. In: *Forams 2006* (Ed., I. de Souza Carvalho), Rio de Janeiro, *Anuário do Instituto de Geociências*, 29, 167.

Hart, M.B., Bailey, H.W., Crittenden, S., Fletcher, B.N., Price, R.J., and Swiecicki, A. 1989. Cretaceous. In: *Stratigraphical Atlas of Fossil Foraminifera, second edition* (Eds. D.G. Jenkins and J.W. Murray), Chichester, *Ellis Horwood Press*, 273-371.

Hart, M.B., Oxford, M.J. and Hudson, W. 2002. The early evolution and paleobiogeography of Mesozoic planktic foraminifera. In: *Palaeobiogeography and Biodiversity Change: the Ordovician and Mesozoic-Cenozoic Radiations* (Eds. J.A. Crame and A.W. Owen), London, *The Geological Society of London Special Publications*, 194, 115-125.

Hofker, J. 1957. Foraminiferen der Oberkreide von Nordwestdeutschland und Holland. *Beihefte zum Geologischen Jahrbuch*, 27, 1-464.

Holbourn, A.E.L. and Kuhnt, W. 1998. Turonian-Santonian benthic foraminifer assemblages from Site 959D (Côte d'Ivoire-Ghana transform margin, equatorial Atlantic): indication of a Late Cretaceous oxygen minimum zone. In: *Proceedings of the Ocean Drilling Program, Scientific Results, v. 159* (Eds. J. Mascle, G.P. Lohmann and M. Moullade), Washington, D. C., United States Government Printing Office, 159, 375-387.

Holbourn, A.E.L., Kuhnt, W. and Erbacher, J. 2001. Benthic foraminifers from Lower Albian black shales (Site 1049, ODP leg 171): evidence for a non "uniformitarian" record. *Journal of Foraminiferal Research*, 31, 60-74.

Huber, B.T. 1990. Maestrichtian plamktonic foraminifer biostratigraphy of the Maud Rise (Weddell Sea, Antarctica): ODP Leg 113 Holes 689B and 690C. In: *Initial Reports of the Deep Sea Drilling Project, v. 113* (Eds. P. F. Baker, J. P. Kennett *et al*.), Washington, D. C., United States Government Printing Office, 113, 489-513.

Huber, B.T. 1992. Upper Cretaceous planktic foraminiferal biozonation for the Austral Realm. *Marine Micropaleontology*, 20, 107-128.

Huber, B.T. Hodell, D.A. and Hamilton, C.P. 1995. Middle-Late Cretaceous climate of the southern high latitudes: Stable isotopic evidence for minimal equator-to-pole thermal gradients. *Geological Society of America Bulletin*, 107, 1164-1191.

Keller, B.M. 1935. Microfauna of the Upper Cretaceous in the Dnjepr-Donets valley and some other adjacent regions. *Byiulletin Moskovskovo Ovacestva Prirodii (Geologii)*, 43 (13), 522-558 [in Russian].

Keller, G. 1989. Extended Cretaceous/Tertiary Boundary Extinctions and Delayed population Change in Planktic Foraminifera from Brazos River, Texas. *Paleoceanography*, 4, 287-332.

Klasz, I. de, Marie, P. and Meijer, M. 1960. *Gabonella* nov. gen., un nouveau genre de foraminifères du Crétacé supérieur et du Tertiaire basal de l'Afrrique Occidentale. *Revue de Micropaléontologie*, 3, 167-182.

Klasz, I. de, Marie, P. and Rerat, D. 1961. Deux nouvelles espèces du genre *Gabonella* (foraminifère) du Crétacé du Gabon (Afrique équatoriale). *Revue de Micropaléontologie*, 4, 77-79.

Klasz, I. de and Rerat, D. 1963. The stratigraphic range of the foraminiferal genus *Gabonella* in the Upper Cretaceous of Gabon (Equatorial Africa). *Micropaleontology*, 9, 325-326.

Klasz, I. de, Klasz, S. de and Saint-Marc, P. 1995. Heterohelicids from the Turonian of Senegal (West Africa) with particular emphasis on *Heterohelix americana*. *Micropaleontology*, 41, 359-368.

Koutsoukos, E.A.M. 1994. Early stratigraphic record and phylogeny of the planktic genus *Guembelitria* Cushman, 1933. *Journal of Foraminiferal Research*, 24, 288-295.

Kroon, D. and Nederbragt, A. J. 1990. Ecology and Paleoecology of Triserial Planktic Foraminifera. *Marine Micropaleontology*, 16, 25-38.

Leckie, R. M. 1984. Mid-Cretaceous planktic foraminiferal biostratigraphy off central Morocco, Deep Sea Drilling Project Leg 79, Sites 545 and 547. In: *Initial Reports of the Deep Sea Drilling Project, v. 79* (Eds. K. Hinz, E. L. Winterer *et al*.), Washington, D. C., United States Government Printing Office, 79, 579-620.

Lipson-Benitah, S. 2008. Phylogeny of the Middle Cretaceous (late Albian-late Cenomanian) planktic foraminiferal genera *Parathalmanninella* nov. gen. and *Thalmanninella*. *Journal of Foraminiferal Research*, 38, 183-189.

Liu, C. and Olsson, R.K. 1992. Evolutionary adaptive radiation of microperforate Planktic Foraminifera following the K/T mass extinction event. *Journal of Foraminiferal Research*, 22, 328-346.

Loeblich, A.R.Jr. and Tappan, H. 1964. Sarcodina Chiefly "Thecamoebians" and Foraminifera. In: *Treatise on Invertebrate Paleontology* (Ed. R.C. Moore), The University of Kansas Press and The Geological Society of America, Boulder, Part C, 1-900.

Loeblich, A.R.Jr. and Tappan, H. 1974. Recent Advances in the Classification of the Foraminiferida. In: *Foraminifera* (Eds. R.H. Hedley & C.G. Adams), Academic Press, London and New York, 1-53.

Loeblich, A.R.Jr. and Tappan, H. 1987. *Foraminiferal Genera and Their Classification*. Van Nostrand Reinhold Company, New York, 970 pp.

Longoria, J.F. 1974. Stratigraphic, morphologic and taxonomic studies of Aptian planktic foraminifera. *Revista Española de Micropaleontología, número extraordinario*, 11-107.

Luterbacher, H. 1975. Early Cretaceous foraminifera from the northwestern Pacific: Leg 32 of the Deep Sea Drilling Project. In: *Initial Reports of the Deep Sea Drilling Project, v. 32* (Eds. L.R. Larson, R. Moberly *et al*.), Washington, D. C., United States Government Printing Office, 32, 703-718.

Masters, B.A., 1977, Mesozoic Planktic Foraminifera: a world-wide review and analysis. In: *Oceanic Micropaleontology* (Ed. A. T. S. Ramsay), Academic Press, New York, 1, 301-733.

McNeil, D.H. and Caldwell, W.G.E. 1981. Cretaceous Rocks and Their Foraminifera in the Manitoba Escarpment. *The Geological Association of Canada Special Paper*, 21, 1-439.

Michael, F.Y. 1972. Planktic foraminifera from the Comanchean Series (Cretaceous) of Texas. *Journal of Foraminiferal Research*, 2, 200-220.

Montanaro Gallitelli, E. 1957. A Revision of the Foraminiferal Family Heterohelicidae. In: *Studies in Foraminifera* (Ed. A.R.Jr. Loeblich), *United States National Museum Bulletin*, 215, 133-154.

Moullade, M. 1984. Intérêt des petits foraminifères benthiques "profonds" pour la biostratigraphie et l'analyse des paleoenvironments océaniques Mésozoïques. In: *Benthos '83. Second International Symposium on Benthic Foraminifera (Pau, 1983)* (Ed. H.J. Oertli), Pau et Bordeaux, 429-464.

Neagu, T. 1965. Albian foraminifera of the Rumanian Plain. *Micropaleontology*, 11, 1-38.

Nederbragt, A.J., Erlich, R.N., Fouke, B.W., and Ganssen, G.M. 1998. Paleoecology of the biserial planktic foraminifer *Heterohelix moremani* (Cushman) in the late Albian to middle Turonian circum-North Atlantic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 144, 115-133.

North, B.R., and Caldwell, W.G.E. 1975. Illustrations of Canadian Fossils: Cretaceous Foraminifera from Saskatchewan and Manitoba. *Geological Survey of Canada*, 74-38, 1-35.

Olsson, R.K. 1970. Planktic Foraminifera from Base of Tertiary, Millers Ferry, Alabama. *Journal of Paleontology*, 44, 598-604.

Olsson, R.K., Hemleben, C., Berggren, W.A. and Huber, B.T. 1999. Atlas of Paleocene Foraminifera. *Smithsonian Contributions to Paleobiology*, 85, 1-252.

Pessagno, E.A.Jr. 1967. Upper Cretaceous planktic foraminifera from the western Gulf Coastal Plain. *Palaeontographica Americana*, 5(37), 245-445.

Petrizzo, M.R. and Huber, B.T. 2006. Biostratigraphy and taxonomy of Late Albian planktic foraminifera from ODP Leg 171B (western North Atlantic Ocean). *Journal of Foraminiferal Research*, 36, 166-190.

Petters, S.W. 1977. Upper Cretaceous planktic foraminifera from the subsurface of the Atlantic Coastal Plain of New Jersey. *Journal of Foraminiferal Research*, 7, 165-187.

Petters, S.W. 1983. Gulf of Guinea planktic foraminiferal biochronology and geological history of the South Atlantic. *Journal of Foraminiferal Research*, 13, 32-59.

Reuss, A.E. 1851. Die Foraminiferen und Entomostraceen der Kreidemergels von Lemberg. *Haidinger's Naturwissenschaftlische Abhandlungen, Wien*, 4, 17-52.

Reuss, A.E. 1860. Die Foraminiferen der westphalishen Kreideformation. *Königlich Akademie der Wissenschaften Wien, Mathematik-Naturwissenschaften Classe*, 40, 147-238.

Riegraf, W. 1987. Planktic foraminifera (Globuligerinidae) from the Callovian (Middle Jurassic) of southwest Germany. *Journal of Foraminiferal Research*, 17, 190-211.

Robaszynski, F. and Caron, M. 1995. Foraminifères planctoniques du Crétacé: commentaire de la zonation Europe-Mèditerranée. *Bulletin de la Société Géologique de France*, 6, 681-692.

Roveda, V. 1964. Découverte de *Gabonella* dans le Crétacé supérieur du Sahara Espagnol. *Revue de Micropaléontologie*, 7, 195-204.

Schubert, R.J. 1911. Die fossilien Foraminiferen des Bismarckarchipels und einiger angrenzender Inseln. *Abhandlungen der Geologischen Reichsanstaldt*, 20, 1-130.

Sigal, J. 1979. Chronostratigraphy and ecostratigraphy of Cretaceous formations recovered on DSDP Leg 47B, Site 398. In: *Initial Reports of the Deep Sea Drilling Project, v. 47* (Eds., F. H. Laughter and E. M. Fagerberg), Washington, D. C., United States Government Printing Office, 47, 287-326.

Simmons, M.D., BouDagher-Fadel, M.K., Banner, F.T. and Whittaker, J.E. 1997. The Jurassic Favusellacea, the earliest Globigerinina. In: *The Early Evolutionary History of Planktic Foraminifera* (Eds., M. K. BouDagher-Fadel, F. T. Banner & J. E. Whittaker), London, Chapman and Hall, 17-50.

Sliter, W.V. 1977. Cretaceous benthic foraminifers from the western South Atlantic Leg 39, Deep Sea Drilling Project. In: *Initial Reports of the Deep Sea Drilling Project, v. 39* (Eds., P. R. Supko, K. Perch-Nielsen *et al.*), Washington, D. C., United States Government Printing Office, 39, 657-697.

Smith, C.C. and Pessagno, E.A.Jr. 1973. Planktic foraminifera and stratigraphy of the Corsicana Formation (Maestrichtian) north-central Texas. *Cushman Foundation for Foraminiferal Research, Special Publication*, 12, 1-68.

Steineck, P.L. and Fleisher, R.L. 1978. Towards the classical evolutionary reclassification of Cenozoic Globigerinacea (Foraminiferida). *Journal of Paleontology*, 52, 618-635.

Stelck, C.R. and Wall, J.H. 1954. Kaskapau Foraminifera from Peace River area and western Canada. *Research Council of Alberta*, 68, 1-38.

Stelck, C.R. and Wall, J.H. 1955. Foraminifera of the Cenomanian *Dunveganoceras* Zone from Peace River area of western Canada. *Research Council of Alberta*, 70, 1-81.

Tappan, H. 1940. Foraminifera from the Grayson Formation of northern Texas. *Journal of Paleontology*, 14, 93-126.

Thomas, N.L. 1927. The use of evolutionary changes in geologic correlation. *Journal of Paleontology*, 1, 135-140.

Thomas, N.L. and Rice, E.M. 1927. Changing characters in some Texas species of Guembelina. *Journal of Paleontology*, 1, 141-145.

Wall, J.H. 1960. Jurassic Microfaunas from Saskatchewan. *Department of Mineral Resources Reports*, *Petroleum and Natural gas Branch*, 53, 1-229.

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Implications for high latitude gondwanide palaeozoogeographical studies of some new Upper Cretaceous marine ostracod faunas from New Zealand and the Antarctic Peninsula

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Resumen

Se han identificado sesenta especies de ostrácodos en sedimentos cenomanienses, santonienses y maastrichtienses de Nueva Zelanda, y en sedimentos del Campaniense tardío de las islas Snow Hill y James Ross (Península Antártica). Las dos principales localidades neozelandesas estudiadas tienen una edad maastrichtiense que contrasta con sus regímenes térmicos – facies de plataforma cálida en Waiparaa, y de plataforma externa/parte superior de vertiente fría en Pukehou. A partir de nuevos datos se clarifica en Gondwana durante el tránsito K/T la historia paleozoogeográfica de varios taxones significativos: *Rostrocytheridea* sobrevivió en Pukehou hasta unos pocos metros antes del K/T, mientras que *Majungaella* ha sido hallado en Waipara aproximadamente a medio metro del techo del Maastrichtiense. Las adaptaciones retrotérmicas conocidas previamente de *Majungaella* se confirman en el Maastrichtiense de Pukehou, en donde se observaron adaptaciones similares en *Rostrocytheridea* y, posiblemente, en *Krithe*. Los primeros dos géneros se extinguieron en Australasia a lo largo del límite Mesozoic/Terciario, mientras que en la región que abarca la Patagonia y la Península Antártica, el género *Majungaella* sobrevivió y colonizó gran parte del litoral antártico. Probablemente en esta región *Rostrocytheridea* no sobrevivió durante el Paleógeno. El género actual *Ameghinocythere* se conoce desde el Campaniense tardío en la isla de Snow Hill y el Maastrichtiense de Nueva Zelanda. Los primeros registros del *Apateloschizocythere*, que es un género gondwánico ampliamente distribuido, proceden probablemente del Cenomaniense de Coverham (Nueva Zelanda). En este trabajo se describen por primera un género (*Parahystricocythere*) y nueve especies de ostrácodos: *Ameghinocythere lutheri*, *A. eagari*, *Apateloschizocythere*? *colleni*, *Limburgina postaurora*, *Majungaella wilsoni*, *M. waiparaensis*, *Parahystricocythere ericea*, *Rayneria*? *punctata*, *Rostrocytheridea pukehouensis* y *Trachyleberis hornibrooki*.

Palabras clave: Ostrácodos, Nueva Zelanda, Península Antártica, Cretácico Superior, límite K/T, adaptación retrotérmica.

Abstract

Sixty species of Ostracoda have been recovered from Cenomanian, Santonian and Maastrichtian strata in New Zealand, and late Campanian sediments on Snow Hill and James Ross islands in the Antarctic Peninsula. The two main New Zealand sites are in latest Maastrichtian strata, but in contrasting thermal regimes - warm, shelfal facies at Waipara, and cool, outer shelf/upper slope at Pukehou. The palaeozoogeographical history of several important taxa across the K/T boundary in Gondwanaland is clarified by the new data: *Rostrocytheridea* survived at Pukehou to within a few metres of the K/T, while *Majungaella* was found ~0.5 m from the top of the Maastrichtian at Waipara. The previously-known retrothermal propensities of *Majungaella* can be traced to the Maastrichtian at Pukehou, where a similar adaptation is observed in *Rostrocytheridea,* and possibly in *Krithe*. The first two genera became extinct across Mesozoic/Tertiary boundary in Australasia, while in the Patagonia-Antarctic Peninsula region, *Majungaella* survived and colonised much of the Antarctic seaboard, but *Rostrocytheridea* probably did not survive into the Palaeogene. The extant genus *Ameghinocythere* is now known from late Campanian of Snow Hill Island, and also occurs in the late Maastrichtian in New Zealand. The earliest record of the widely distributed Gondwanide genus *Apateloschizocythere* is probably from the Cenomanian at Coverham, New Zealand. Nine new species are described: *Ameghinocythere lutheri*, *A. eagari*, *Apateloschizocythere*? *colleni*, *Limburgina postaurora*, *Majungaella wilsoni*, *M. waiparaensis*, *Parahystricocythere ericea*, *Rayneria*? *punctata*, *Rostrocytheridea pukehouensis* and *Trachyleberis hornibrooki*. The genus *Parahystricocythere* is new.

Keywords: Ostracoda, New Zealand, Antarctic Peninsula, Upper Cretaceous, K/T transition, retrothermal.

1. INTRODUCTION

Regional relationships between high latitude Gondwanide ostracod faunas of latest Mesozoic-early Tertiary age have been difficult to assess, particularly phylogenies across the K/T boundary and faunal changes presaging the onset of Palaeogene glaciation. This was primarily because of a dearth of data from Australasia.

Previous studies by Bertels (1975, 1977), Rossi de García & Proserpio (1980), Ballent *et al.* (1998), Fauth *et al.* (2003) and Ballent & Whatley (2007), have established a good corpus of data for the late Cretaceous faunas of Patagonia and the Antarctic Peninsula, although there had been less progress with understanding relationships between Patagonia and the relatively well-known Antarctic Palaeogene faunas (Błaszyk, 1987; Szczechura, 2001; Dingle & Majoran, 2001). For Australasia, the only relevant data have been from the Santonian/Campanian faunas in Western Australia (Bate, 1972; Neale, 1975).

The dataset herein allows me to extend the work of Fauth *et al.* (2003) to higher levels in the late Campanian of the Antarctic Peninsula, and to describe for the first time Cenomanian, Santonian and Maastrichtian ostracods from New Zealand. As a consequence it is now possible to assess the palaeozoogeographical relationships between these three now widely-separated areas, prior to their final dislocations in southern Gondwanaland[1]. In particular further insights are presented of the long-term association of the distinctive warm-water Gonwanide generic trio of *Majungaella* Grekoff, *Rostrocytheridea* Dingle and *Cytherelloidea* Alexander, and the initiation in Campanian time of retrothermal[2] tendencies in the first two.

In addition, Cenomanian samples from New Zealand suggest that the genus *Apateloschizocythere* Bate has a longer history in Australasia than previously realised, and allow a first comparison with the middle Cretaceous faunas of Queensland (Krömmelbein 1975).

A list of the ostracod species recovered from Antarctica and New Zealand is given in Table 1.

	NZ Cen.	NZ San.	Ant Cam.	NZ Maas.
Ameghinocythere lutheri sp. nov.			x	
Ameghinocythere eagari sp. nov.				x
Ameghinocythere? sp. 5078				x
Apateloschizocythere? *colleni* sp. nov.	x			
Argilloecia? sp. 2 F&S			x	
Bairdoppilata sp. 5052				x
**Bairdoppilata*? sp. 5092			x	
Bairdoppilata cf. *B. austracretacea* (B)				x
Bythocypris cf. *B. chapmani* N				x
Bythocypris cf. *B. sudaustralis* MRR	x			
Cythereis cf. *C. brevicostata* B				x
Cytherella sp. 5086				x
**Cytherella* sp. 1a				x
Cytherella sp. 5063	x			
Cytherella sp. 2 F&S			x	

Table 1. Upper Cretaceous ostracods from Antarctica and New Zealand. F&S = Fauth & Selling (2003); B = Bate (1972); Bert. = Bertels (1973); MRR = McKenzie, Reyment & Reyment (1991); N = Neale (1975); R = Rossi de García & Proserpio (1980); K = Krömmelbein (1975). Ant = Antarctica; NZ = New Zealand. Cen. = Cenomanian; Sant = Santonian; Camp. = Campanian; Maas. = Maastrichtian. ***,** not illustrated.

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[1] I prefer the original term coined by Suess for the geographic entity, instead of Gondwana, which refers to rock units or biogeographic realms (e.g. the notional Gondwana System).

[2] A descriptor I coin for the propensity of adapting through time to progressively cooler-water habitats, by adapting to climate change, by occupying deeper water or by colonising higher latitudes

	NZ Cen.	**NZ San.**	**Ant Cam.**	**NZ Maas.**
Cytherella cf. *C.* sp. 5051				x
Cytherella sp. 5051				x
Cytherelloidea spirocostata Bert.			x	
Cytherelloidea cf. *C. westaustaliensis* B				x
Cytheropteron sp. 5034			x	
**Krithe* sp. 631.1			x	
Krithe sp. 5055				x
Krithe sp. 5056				x
Krithe sp. 5079				x
Limburgina postaurora sp. nov.				x
Maddocksella sp. 5047				x
Majungaella wilsoni sp. nov.				x
Majungaella australis? R			x	
Majungaella waiparaensis sp. nov.				x
Majungaella sp. 4978				x
Mandelstamia antarctica F&S			x	
Paracypris sp. Bert.			x	
Paracypris? sp. 5080				x
Paracypris sp. 5040				x
Parahystricocythere sp. 5070		x		
Parahystricocythere ericea sp. nov.				x
Pelecocythere sp. 5042				x
Platella sp. 5048				x
Platella sp. 5071				x
Rayneria? *punctata* sp. nov.				x
Rostrocytheridea hamiltonensis F&S			x	
Rostrocytheridea pukehouensis sp. nov.				x
Rostrocytheridea cf *R. allaruensis*? K	x			
Rostrocytheridea? sp. 4992				x
Scepticocythereis cf. *S. ornata* B				x
Scepticocythereis? sp. 5044				x
Trachyleberis hornibrooki sp. nov.				x
Indet sp 5082				x
Indet sp 5083				x
Indet sp. 5081				x
Indet sp 5085				x
Indet sp 5084				x
Indet.sp. 5087				x
Indet. sp. 5089			x	
Indet sp. 5060			x	
*Indet sp. 633.29			x	
*Indet sp. 633.15/22			x	
*Indet sp. 628.32			x	
*Indet sp. 5092			x	
*Indet sp. 5091			x	

Table 1. (Continued) Upper Cretaceous ostracods from Antarctica and New Zealand. F&S = Fauth & Selling (2003); B = Bate (1972); Bert. = Bertels (1973); MRR = McKenzie, Reyment & Reyment (1991); N = Neale (1975); R = Rossi de García & Proserpio (1980); K = Krömmelbein (1975). Ant = Antarctica; NZ = New Zealand. Cen. = Cenomanian; Sant = Santonian; Camp. = Campanian; Maas. = Maastrichtian. ***,** not illustrated.

2. MATERIAL

2.1. Antarctica (Figures 1 & 2, Table 2)

Campanian and Maastrichtian marine sediments crop out at several localities around Admiralty Sound in the northern Antarctic Peninsula (see Pirrie *et al.,* 1997a for regional stratigraphy), and early to late Campanian ostracod faunas have been described previously from James Ross Island by Fauth *et al.* (2003). In the present publication I document ostracods from later Campanian sequences on Snow Hill Island, as well as from two new Campanian horizons on James Ross Island.

All material in the present study (except one sample from Hamilton Point) was collected by the author during the British Antarctic Survey 1994-95 (December-January) field season, and details of measured sections and locality numbers are given in Dingle (1995). The locality of the Hamilton Point sample is described by Pirrie (1995). All Antarctic sample numbers have a DJ. prefix.

Snow Hill Island: Snow Hill Island Formation (late Campanian to early Maastrichtian). The lower part of the formation, as exposed in the Second Ice Gulley, has a relatively high sulphur content (see Dingle & Lavelle 1998a, 2000, and personal, unpublished data).

Second Ice Gulley. 64.3633º S, 56.995º W, south of Nordenskjöld=s hut[3] See Figure 2.1-3. Sample prefixes DJ633. Eight samples up a 0-95m section: 633.31 (0m), .5 (15m), .1 (40m), .29 (52m), .15 (55m), .12 (81m),and .22 (95m). Sulphur-rich clays and limestones: mean S (n=7) 3898 ppm, max. 5056, min 2631. This was the most ostracod-rich sequence within the Snow Hill Island Formation.

Haslam Crag. 64.36º S, 56.9817º W, cliff section, northeast of Nordenskjöld's hut. Overlies Second Ice Gulley

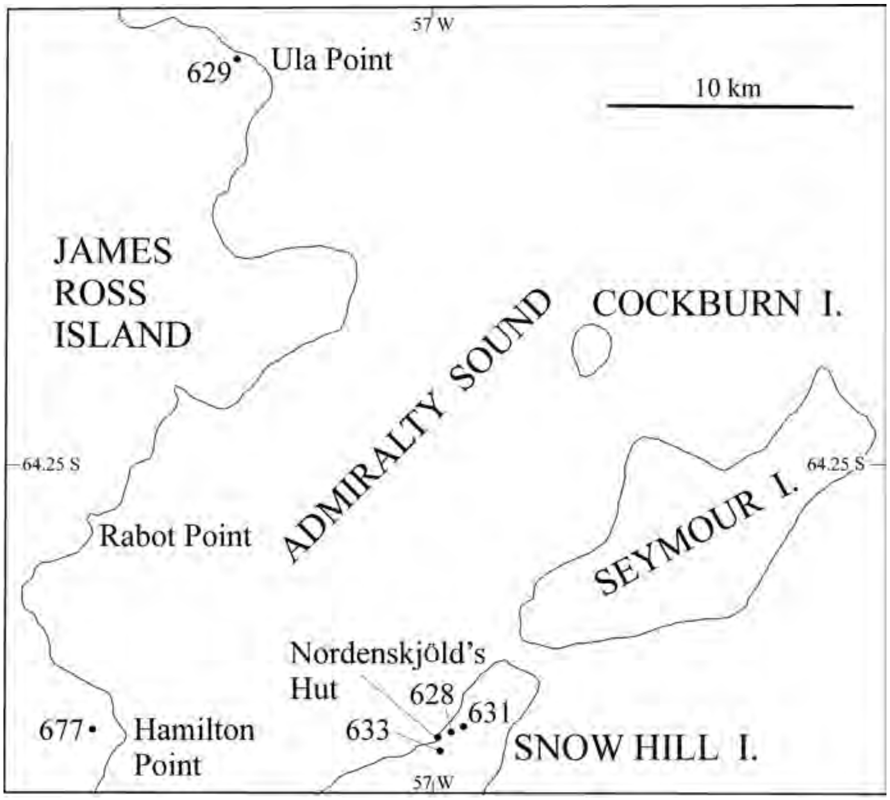

Figure 1. Sampling localities for Campanian sediments in the Admiralty Sound region on James Ross and Snow Hill islands. British Antarctic Site numbers carry a DJ prefix. Details of localities are given in Dingle (1995: sites 628-633), and Pirrie (1995: site 677). Location of these sites is shown on Fig. 5 as the James Ross Basin.

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[3] Otto Nordenskjöld, geologist, leader of the 1901-1904 Swedish South Polar Expedition, who established his prefabricated hut on Snow Hill Island, 9th February 1902 - it still stands.

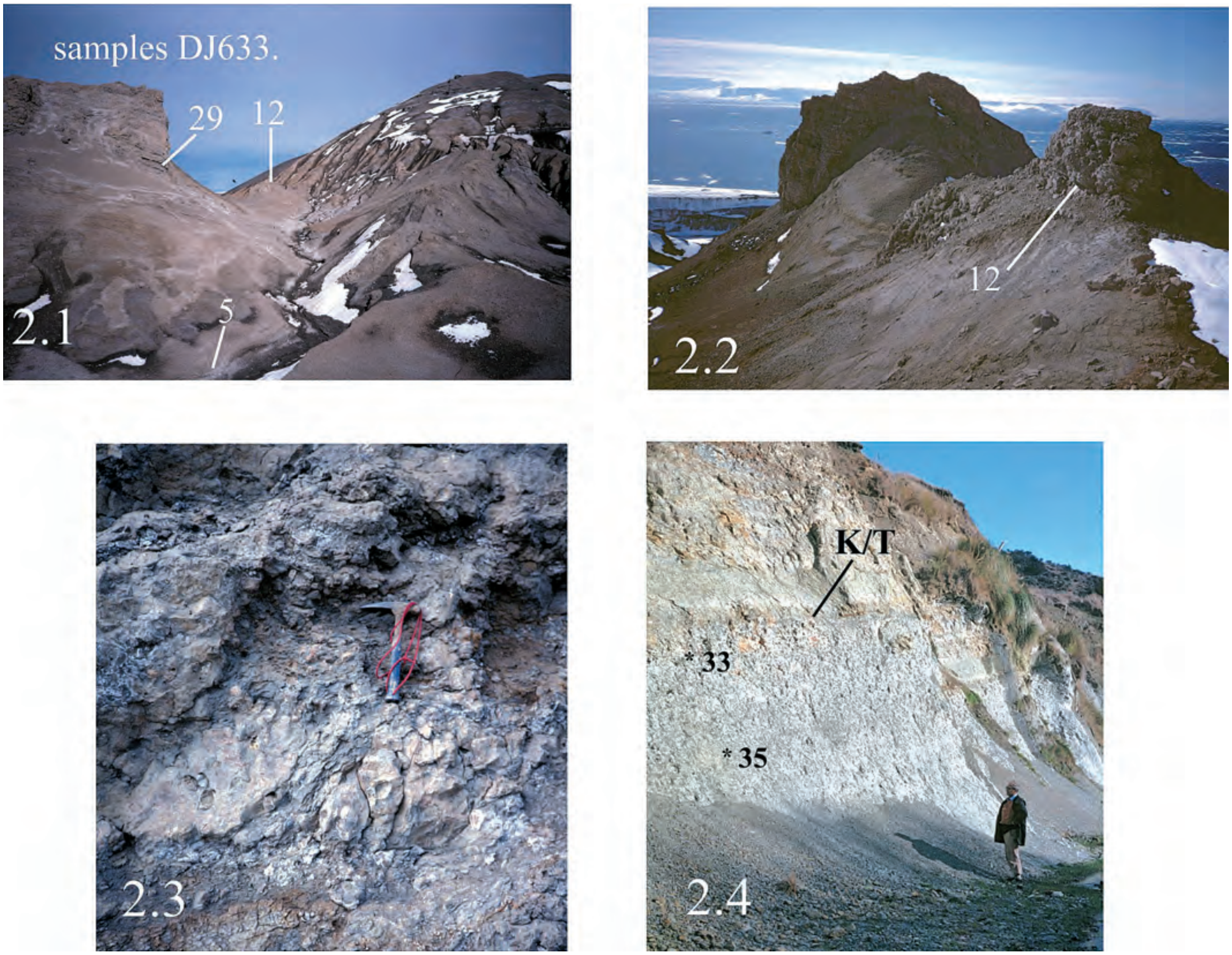

Figure 2. Photographs of sampling localities on Snow Hill Island and in Waipara Gorge.
2.1 - 2.3. Sampling sites (DJ633.) in Second Ice Gulley, Snow Hill Island, Antarctica. 2.1: General view of gulley looking approximately ESE in Snow Hill Island Formation sediments. Samples 29 and 12 are argillites within *Thyasira* limestones on the west side of the gulley. Most other samples in this section were taken close to and on west side of the central thalweg. Base of section lies below lower edge of photograph (which extends to ~15 m). 2.2: Small *Thyasira* limestone/argillite bluff near top of the gulley from which sample DJ633.12 (81 m) was collected. Argillites are sulphurous (S = ~4000 ppm). View looking approximately west, with James Ross Island visible across Admiralty Sound (~13 km distant). 2.3: Sample DJ633.29 (52m) taken at hammer tip from within a tectonically- incorporated sulphur-rich argillite inter-bed (S = 5056 ppm) at the base of the large allochthonous limestone buttress shown on the left side (west) of Fig. 2.1. 2.4: Upper Laidmore Formation sediments with K/T boundary section on south side of Waipara Gorge, South Island, New Zealand. The boundary is marked by the rusty horizon. Samples # 33 and #35 were collected 50cm and 2m below it, respectively, between the photographer and figure of the late Dr Derek D. Wilson. All photographs taken by the author (2.1-2.3 January 1996; 2.4 May 1981).

section. Three samples spanning 5-135m in type section of Haslam Crag Member (Samples DJ628.18-41). Mean S content (ppm, n=12) 1970, max. 3281, min. 937.

Cross Island Traverse. 64.3617° S, 56.9783° W. One sample at start of an approximately W-E traverse across the central plateau of the island (Sample DJ631.1) Overlies Haslam Crag section. Mean S content (ppm, n=10) 1204, max. 2249, min. 272.

James Ross Island: Santa Marta Formation (early-late Campanian).

Hamilton Point. 64.3617° S, 57.33° W. One sample, originally described by Pirrie (1995) as a clay intercalation from within the “Hobbs Glacier Formation” on Hamilton Point (Sample DJ677.3). The type section of the Hobbs Glacier Formation is at Rabot Point, approximately 8 km to the north (Pirrie *et al*,. 1997b), which has been dated

		Section	**Second Ice Gulley**							**Cross Island Traverse**	**Haslam Crag**			**Ula Point**	**Hamilton Point**
		Formation	**Snow Hill Island Formation**											**Santa Marta Fm.**	**Hobbs Glacier Fm.**
		Sample No.	633.31	633.5	633.1	633.29	633.15	633.12	633.22	631.1	628.18	628.32	628.41	629.2	677.3
		height	0m	15m	40m	52m	55m	81m	95m	0m	5m	102m	135m		
Genus	**Species**	**Author**													
Cytherella	sp. 2	F&S				1c									
Cytherelloidea	*spirocostata*	Bertels, 1973													1c
Bairdoppilata	sp.									2c					
Argilloecia	sp. 2	F&S		1v	2c	2c									
Paracypris	sp.	Bertels, 1973				1v 9c		3c	4c						
Krithe	sp.									1c					
Cytheropteron	sp. 5034									2c					
Majungaella	*australis*	R&P										1v			
Rostrocytheridea	*hamiltonensis*	F&S	1v	2v 3c		2c			2c		2c				2c
Mandelstamia	*antarctica*	F&S	1c										1c	1c	2v 4c
Ameghinocythere	*lutheri*	sp. nov.		1c				1c							
Indet.	sp. 5091														1c
Indet.	sp. 633.5b			1c											
Indet.	sp. 633.5c			1c											
Indet.	sp. 633.29					1c									
Indet.	sp. 633.15						1c		1c						
Indet.	sp. 628.32											1v			
Indet.	sp. 5092									1c					
Indet.	sp. 631.1b									1c					

Table 2. Antarctica: Snow Hill Island & James Ross Island ostracods. c = carapace, v = valve. R&P = Rossi de García & Proserpio (1980); F&S = Fauth & Seeling (2003).

using Sr isotope ratios as Miocene (9.9Ma, Dingle & Lavelle, 1998b).

Ula Point. 64.067° S, 57.167° W. One sample in a stream gulley on the coastal plain (Sample 629.2, see Dingle 1995 for location map).

2.2. New Zealand (Figure 3, Table 3)

Upper Cretaceous ostracod faunas were recovered from twelve samples at seven localities in New Zealand. Nine of these were Maastrichtian in age (Mid-Waipara, Woodside Creek, Rewa Stream, Mangatarata Road, Te Wainohu Point and Pukehou) and have been referred to the local Haumurian (Maastrichtian) stage by Wilson (1963), Kingma (1971), and Webb (1971) on the basis of their molluscan and foraminiferal faunas. One sample from Te Wainohu Point is Santonian (Kingma, 1971), while two samples (Coverham and Rewa Stream) have been referred to the Ngaterian (Cenomanian) stage by Hall (1963) and Henderson (1973).

The material was collected by the author during May-June 1981. Figure 3 shows sampling localities. Locations cit-

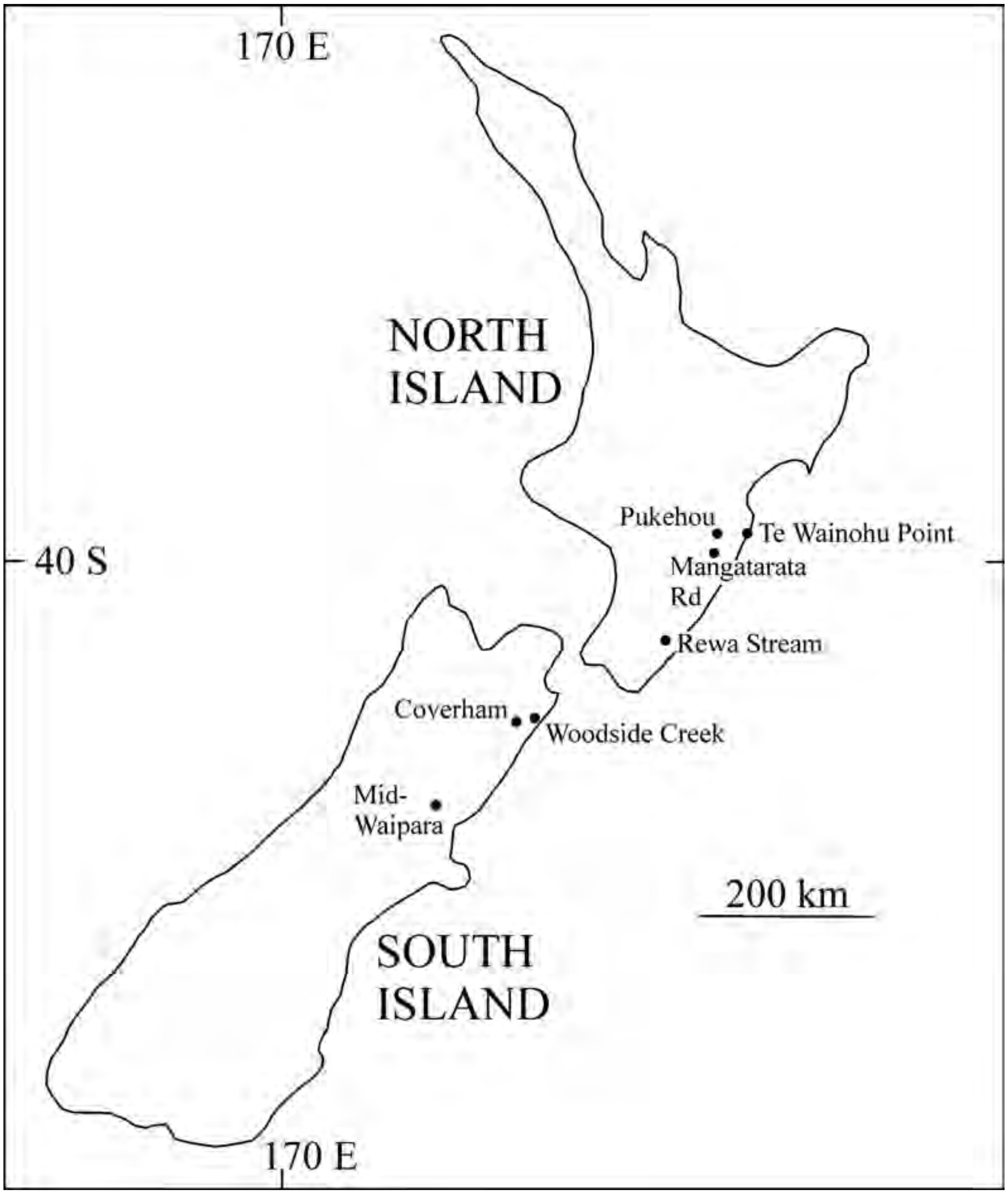

Figure 3. Sampling localities for Upper Cretaceous sediments in New Zealand.

		Locality	**Woodside Creek**	**Coverham**	**Mid-Waipara**				**Rewa Stream**			**Mangatarata Road**	**Pukehou**				**Te Wainohu Point**	
		Sample No.	3	9	33		35		50	47	48	66	68		71		75	76
		age	Maas.	Cen.	Maas.		Maas.		Cen.	Maas.	Maas.	Maas	Maas.		Maas.		Sant.	Maas.
		author			valves	%	valves	%					valves	%	valves	%		
Ameghinocythere	*eageri*	sp nov.											4	0,4	50	20,2		
Ameghinocythere?	sp. 5078												2					
Apateloschizocythere?	*colleni*	sp nov.		18														
Bairdoppilata	cf. austracretacea	Bate 1972			3	1,6	25	11,7					7	0,7	1	0,4		
Bairdoppilata	sp. 5052						1	0,5			1		4	0,4	2	0,8		
Bythocypris	cf. chapmani	Neale 1975	1		2	1,1	2	0,9					1	0,1				
Bythocypris	cf. sudaustraliensis	McKenzie et al. 1991 (in Ayress 1996)	1										2	0,2	5	2,0		
Cythereis	cf. brevicostata	Bate 1972	1								.		1	0,8				
Cytherella	sp. 5086		15															
Cytherella	sp. 1a							1	0,5									
Cytherella	sp. 5063			4														
Cytherella	sp. 5051												2	0,2				
Platella	sp. 5048				1	0,5	5	2,3										
Platella	sp. 5071									2								2
Cytherelloidea	cf. westaustraliensis	Bate 1972			12	6,4	5	2,3										
Krithe	sp. 5055						1	0,5					3	0,3				
Krithe	sp. 5056				4	2,1	2	0,9					19	1,8	10	4,0		
Krithe	sp. 5079											14						
Limburgina	*postaurora*	sp. nov.			30	16,0	55	25,8										
Maddocksella	sp. 5047				2	1,1												
Majungaella	sp. 4978														2	0,8		
Majungaella	*waiparaensis*	sp. nov.			4	2,1	47	22,1										
Majungaella	*wilsoni*	sp. nov.			4	2,1	34	16,0										
Paracypris	sp. 5080											2						
Paracypris	sp. 5040														5	2,0		
Parahystricocythere	*ericea*	sp. nov.			69	36,7	3	1,4										
Parahystricocythere	sp. 5070																1	
Pelecocythere	sp. 5042				1	0,5									1	0,4		
Rayneria?	*punctata*	sp. nov.			2	1,1	11	5,2					11	0,9				
Rostrocytheridea	*pukehouensis*	sp. nov.											851	82,2	143	57,7		
Rostrocytheridea?	sp 4992						1	0,5										
Rostrocytheridea?	cf. *allaruensis*	Krommelbein, 1975							2									
Scepticocythereis	cf. *ornata*	Bate, 1972	3		6	3,2	1	0,5					124	12,0	29	11,7		
Scepticocythereis?	sp. 5044						5	2,3			2							
Trachyleberis	*hornibrooki*	sp. nov.			48	25,5	15	7,0										
Indet.	sp. 5082											2						
Indet.	sp. 5085		1															
Indet.	sp, 5081											2						
Indet.	sp. 5083											2						
Indet.	sp. 5084		1															
Indet.	sp. 5089												8	0,9				
Indet. fragments											2							
		Total valves	23	22	188		214		2	2	3	24	1035		248		1	2

Table 3. Upper Cretaceous ostracods from New Zealand.

ing latitude and longitude have been taken from the Google Earth interactive website, while national grid values are taken from various maps of the New Zealand Geological Survey.

Mid-Waipara River Gorge (South Island, Fig. 2.4), Upper Laidmore Formation (Haumurian = Uppermost Maastrichtian). This section contains the K/T boundary (Wilson 1963). Three samples were collected from the cliff section illustrated by Strong (1984 fig. 2) on the south side of the river at 43.0607º S, 172.5815º E (S68/964135). Strong (1984 fig. 1) and Hollis & Strong (2003 fig. 2) located the Maastrichtian/Danian boundary at the heavily iron-stained "rusty" band. Sample # 34 (50cm above the boundary) was barren (from Strong's 1984 non-calcareous glauconitic sandstone), while # 33 (50cm below boundary) and #35 (2m below boundary) from the underlying grey, glauconitic, calcareous clay were ostracod-rich.

Woodside Creek (South Island), Mead Hill Formation, Uppermost Maastrichtian. Sample #3 was a hard grey calcareous argillite, 3.5m below the horizon from which Strong (1977, Fig. 1) collected his sample f28 at the Cretaceous/Tertiary boundary in the Woodside Creek gorge (41.9297º S, 174.0737º E, S36/331477).

Coverham (South Island), Saw Pit Mudstone (Hall 1963, 1964), (Ngaterian = Cenomanian). Sample #9 is a greyish brown mudstone with iron-staining, from a cliff on the eastern bank of Nidd Stream at 41.9444º S, 173.8766º E.

Rewa Stream (North Island), two sites.

1. Te Mai Formation (Haumurian = late Maastrichtian) from upper Rewa Stream (Johnston 1980). Sample #47 was a medium grey clayey silt from 40.8442º S, 176.03347º E (N159/494757), and #48 was a green sandy clay with abundant belemnite and *Inoceramus* fragments from 40.84378º S, 176.0345º E (N159/492757, 20m upstream, i.e. stratigraphically below, #47).

2. Springhill Formation from upper Rewa Stream (Johnston 1980 p. 17) (uppermost part of Ngaterian Stage = Cenomanian according to Henderson 1973). Sample #50 was a light grey, glauconitic mudstone ~40m downstream from a small waterfall (40.8430º S, 176.0286º E, N159/489758).

Pukehou (North Island), Whangai Formation (Upper Haumurian = Uppermost Maastrichtian) on the eastern limb of the Otane Anticline. The area was mapped by Kingma (1971), and the two ostracod-rich samples described herein are from the locality where Kingma (1971 p. 35) collected his sample N141/507. Sample #68 (39.8422º S, 176.6267º E; N141/ 0564971), is a soft, light grey shale from a stream section ~1km south of Pukehou village, just below the waterfall, while sample #71 (39.8475º S, 176.6245º E; N141/051965), a slightly harder grey shale is from a second stream ~400m south of #68. Both sections lie to the west of the main road and are a few metres below the K/T boundary, but the precise distance is not known. These samples are probably from a slightly lower stratigraphical level (i.e. older) within the Maastrichtian than those from Waipara.

Mangatarata Road (North Island), Whangai Formation (Upper Haumurian = Upper Maastrichtian) from the core of the New Rangitoto Anticline (Kingma 1971, section H-H' figs 39, 41). Sample #66 is a light grey shale (waterlain rhyolitic tuff) at 39.9930º S, 176.6036º E (N146/030789), in a small cut, on the south side of the road.

Te Wainohu Point (North Island). Two sites in close proximity, south of the Point. Sample #75 is a grey sandy silt/clay from the cliff at 39.8464º S, 176.9944º E (N142/399960), from where Kingma (1971, p. 30, Tab. 4) collected his sample N142/547, which was referred to the Teratan Stage (= Santonian) on the basis of *Inoceramus opetius* Wellman. Sample #76 was from a mudstone slab on the beach beneath the cliff of Haumurian glauconitic argillites (=Maastrichtian, Kingma 1971, fig. 8) at 39.8444º S, 176.9944º E (N142/399963).

3. SYSTEMATIC DESCRIPTIONS

All the materials are deposited in the collections of the Natural History Museum, London (= NHM). Reference numbers all have the prefix NHM PM - OSXXXXX. RVD#XXXX are SEM number in author's collection to be deposited at the NHM.

Abbreviations: LV = left valve, RV = right valve, C = carapace, RPC = radial pore canals, NPC = normal pore canals, AM = anterior margin, VM = ventral margin, PM = posterior margin, DM = dorsal margin, MS = muscle scars, ATE = anterior terminal element, PTE=posterior terminal element, ME=median element, AMA = anterior marginal area, PMA = posterior marginal area, SCT = sub-central tubercle, l/h = length/height. Measurements are in microns (1 micron, μ = 0.001 mm).

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PLATYCOPINA Sars, 1866
Family CYTHERELLIDAE Sars, 1866

Genus *Platella* Coryell & Fields, 1937

Remarks.- Although some authors consider *Platella* to be a junior synonym of *Cytherella* (e.g. van Morkhoven 1963), I will follow the Treatise (Moore 1961) and Bate (1972) in retaining its status within the family as a taxon with distinct punctuation/reticulation overall.

Platella sp. 5048
(Pl. 1, Figs.1-2)

Material.- Two valves, two carapaces.

Illustrated specimens.- OS16596, RVD#5048. C, sample #35, Waipara.

OS16597, RVD#5050. RV, sample #33, Waipara.

Other comparative material.- OS16598, RVD#5049. C, sample #35, Waipara.

Occurrence.- Present only in small numbers at Mid-Waipara.

Remarks.- This species is similar to *Platella* sp. Bate, 1972 from the Campanian of Western Australia, but *P.* sp. 5048 is more narrowly rounded at AM in LV and has smaller, less strongly developed reticulae. The LV is also considerably larger (680-700 μ vs 410-450 μ) (although Bate surmised that his specimens were juveniles). The species is also reminiscent of *Cytherella* cf. *C. hemipuncta* Swanson (as illustrated by Ayress, 1995, Fig. 12.7) from the late Eocene of South Canterbury, but *Platella* sp. 5048 is reticulate, in contrast to being punctate.

Platella sp. 5071
(Pl. 1, Fig. 3)

Material.- Two carapaces.

Illustrated specimen.- OS16600, RVD#5071. C, Te Wainohu Point (#76), Maastrichtian.

Occurrence.- Also found in the Maastrichtian of Rewa Stream (sample #47).

Remarks.- This species is more elongate than *P.* sp. 5048 (l/h ratio: 1.95 vs 1.77), and has a denser pattern of reticulation. There is also a distinct concavity of the VM outline.

Genus *Cytherella* Jones, 1849

Cytherella sp. 5051
(Pl. 1, Fig. 4)

Material.- Two valves.

Illustrated specimen.- OS16602, RVD# 5051. LV, sample 68, Pukehou.

Other comparative material.- OS16603.

Plate 1. ***1,*** *Platella* sp. 5048, LV, Waipara #35, Maastrichtian, OS16596, RVD5048. ***2,*** *Platella* sp. 5048, RV, Waipara #33, Maastrichtian, OS16597, RVD5050. ***3,*** *Platella* sp. 5071, LV, Te Wainohu Point #76, Maastrichtian, OS16600, RVD5071. ***4,*** *Cytherella* sp. 5051, LV, Pukehou #68, Maastrichtian, OS16602, RVD5051. ***5,*** *Cytherella* sp. 5063, RV, Coverham #9, Cenomanian, OS16604, RVD5063. ***6,*** *Cytherella* sp. 5086, LV, Woodside Creek #3 Maastrichtian, OS16606, RVD5086. ***7,*** *Cytherella* sp. 2 Fauth & Seeling 2003, LV, Snow Hill Island DJ633.29, Campanian, OS16609, RVD5037. ***8,*** *Cytherelloidea* cf. *C. westaustraliensis* Bate 1972, LV, Waipara #33, OS16611, RVD5003. ***9,*** *Cytherelloidea spirocostata* Bertels 1973, RV, James Ross Island DJ677.3, Campanian, OS16613, RVD5004. ***10,*** *Bairdoppilata* cf. *B. austracretacea* (Bate 1972), RV, Pukehou #68, Maastrichtian, OS16614, RVD5053. ***11,*** *Bairdoppilata* sp. 5052, RV, Pukehou #68, Maastrichtian, OS16617, RVD5052. ***12,*** *Bairdoppilata*? sp. 5092, RV, Snow Hill Island DJ631.1, Campanian, OS16619, RVD5092. ***13***, *Bythocypris* cf. *B. sudaustralis* McKenzie, Reyment & Reyment 1991, RV, Pukehou #71, Maastrichtian, OS16620, RVD4981. ***14,*** *Bythocypris* cf. *B. chapmani* Neale 1975, RV, Waipara #35, Maastrichtian, OS16624, RVD5043. ***15,*** *Argilloecia*? sp. 2 Fauth & Seeling 2003, RV, Snow Hill Island DJ633.29, Campanian, OS16626, RVD5061. ***16,*** *Paracypris* sp. 5040, RV, Pukehou #71, Maastrichtian, OS16631, RVD5040. ***17,*** *Paracypris*? sp. 5080, LV, Mangatarata Road #66, Maastrichtian, OS16633, RVD5080. ***18,*** *Paracypris* sp. Bertels 1973, RV, Snow Hill Island DJ633.29, Campanian, OS16634, RVD5038. Scales, μ: 300- 4, 5, 7, 13, 14, 15, 16, 18; 250- 1, 3, 6, 8, 10, 11; 200- 2, 17; 150- 9; 100- 12.

Plate 1

1


2


3


4


5


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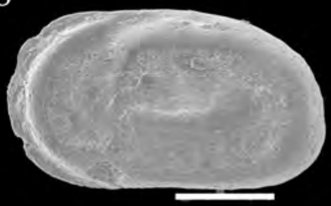
8


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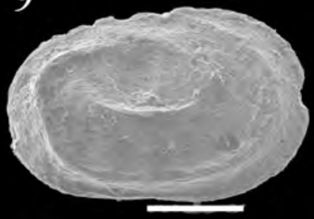

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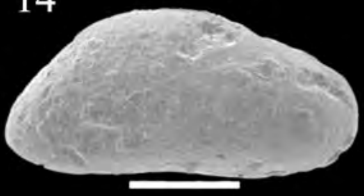

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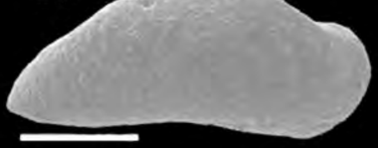
16


17


18


Occurrence.- Found only in sample 68 at Pukehou, Maastrichtian.

Remarks.- Elongate LVs with straight, sub-parallel DM and VM. There is a weak AM rim. The species is similar in shape, but more elongate than *Cytherella* sp. B Bate from the Santonian of Western Australia.

Cytherella sp. 5063
(Pl. 1, Fig. 5)

Material.- Two slightly damaged carapaces.

Illustrated specimen.- OS16604, RVD#5063. C, sample 9, Coverham.

Other comparative material.- OS16605.

Occurrence.- Found only in the Cenomanian at Coverham (#9).

Remarks.- A slender ovate species with a narrowly rounded AM outline.

Cytherella sp. 5086
(Pl. 1, Fig. 6)

Material.- 14 valves and one carapace.

Illustrated specimen.- OS16606, RVD#5086. LV, Woodside Creek, sample 3.

Other comparative material.- OS16607.

Occurrence.- Found only in sample 3 from Woodside Creek, Maastrichtian.

Remarks.- This species has a distinctively compressed anterior valve area with a very broadly rounded AM outline and a narrow rim. DM and VM converge posteriorly.

Cytherella sp. 1a
(not illustrated)

Material.- One broken RV. OS16608.

Occurrence.- Restricted to sample #35, Waipara Gorge, Maastrichtian

Remarks.- Species with distinctive, ovate outline.

Cytherella sp. 2 Fauth & Seeling 2003
(Pl. 1, Fig. 7)

2003 *Cytherella* sp. 2; Fauth & Seeling in Fauth *et al.*, 96, pl. 1, figs 3-4.

Material.- One carapace.

Illustrated specimen.- OS16609, RVD#5037.

Occurrence.- Restricted to sample DJ633.29 (52m) from Second Ice Gulley on Snow Hill Island.

Remarks.- The RV overlaps the LV along the entire perimeter of the carapace. Fauth *et al.* (2003) recorded this species only from locality DJ703 on Hamilton Point, James Ross Island.

Genus *Cytherelloidea* Alexander, 1929

Cytherelloidea cf. *C. westaustraliensis* Bate, 1972
(Pl. 1, Fig. 8)

1917 *Cytherella williamsoniana* Jones; Chapman 57, pl. XIV, fig. 20.
1917 *Cytherella williamsoniana* var. *stricta* Jones & Hinde; Chapman, 58, pl. XIV, fig. 21.
1917 *Cytherella chapmani* Jones & Hinde, Chapman, 58. Pl. XIV, fig. 22.
1972 *Cytherelloidea westaustraliensis* Bate,10, pl.1, figs 1-6; pl. 3 fig. 3; text-figs 5A-E.
1975 *Cytherelloidea westaustraliensis* Bate; Neale, 7, pl. 1, figs. 2, 4, 5; pl. 4, fig. 7.

Material.- 15 valves, one carapace.

Illustrated specimen.- OS16611, RVD#5003. LV, sample 33 Waipara, Maastrichtian.

Other comparative material.- OS16610, RVD# 5002. RV. sample 33 Waipara, Maastrichtian.

Occurrence.- Restricted to the latest Maastrichtian sediments in Waipara Gorge, where it is a minor component of the fauna (#35,2% - #33, 6%).

Remarks.- Specimens from New Zealand have the characteristic central loop, which is detached from the curved dorso-lateral rib. However, they are somewhat smaller than Bate's specimens: ~730 µ vs ~900 µ. Originally found in the Santonian-Campanian chalk of Western Australia by Chapman (1917), where it occurs as a minor component (5-8%), and subsequently recorded by Bate (1972) and Neale (1975).

Cytherelloidea spirocostata Bertels, 1973
(Pl. 1, Fig. 9)

1973 *Cytherelloidea spirocostata* Bertels, 1973, 313, pl. 1, figs 5a-c.
2003 *Cytherelloidea megaspirocostata* Majoran & Widmark, 1998; Fauth & Seeling in Fauth *et al.*, 97, pl.1, figs 5-7.

Material.- One carapace.

Illustrated specimen.- OS16613, RVD#5004. DJ677, Campanian.

Occurrence.- Found only in Pirrie's (1995) sample DJ677.3 from the clay within his Hobbs Glacier Formation on Hamilton Point, James Ross Island.

Remarks.- Fauth *et al.* (2003) identified this species as the deep-water form *C. megaspirocostata* Majoran & Widmark from the late Cretaceous at ODP site 689 on the Maud Rise off East Antarctica. I believe that my material (DJ677), as well as theirs from sites DJ702, 703 and 704 on James Ross Island is conspecific with Bertel's species from the Danian of Patagonia.

This species is very similar to *Cytherelloidea* cf. *C. westaustraliensis* Bate, 1972, but the two differ on the following points (comparing RVs) : *spirocostata* is a smaller species (500 x 330 µ vs 640 x 400 µ); on the lateral surface the lower portion of the inner loop lies at ~mid-valve height in *spirocostata*, while it is lower in cf. *C. westaustraliensis* (25% valve height); the trajectory of the outer loop in the antero-dorsal areas differs - in cf. *C. westaustraliensis* it remains inboard and almost joins the dorsal loop, while in *spirocostata* it rises and cuts the DM just behind the highest point of the valve.

Suborder PODOCOPINA Sars, 1886
Superfamily BAIRDIOIDEA Sars, 1888
Family BAIRDIIDAE Sars, 1988

Remarks.- Bairdiids are common in the late Cretaceous-Tertiary of Australia, New Zealand and southern South America. To my knowledge they have been found fossil in Antarctica only in the late Cretaceous of the Antarctic Peninsula, where *Bairdoppilata* is extant (Hartmann, 1997), but there are yet no records of it from the Tertiary.

Genus *Bairdoppilata* Coryell, Sample & Jennings, 1935

Bairdoppilata cf. *B. austracretacea* (Bate, 1972)
(Pl. 1, Fig. 10)

1972 *Bairdia austracretacea* Bate, 16, pl. 4, figs 1, 2, 5, 8, 11, 12; pl. 5 fig. 6, text-figs 6, 7A-I, 8.

Material.- 30 valves, 3 carapaces.

Illustrated specimen.- OS16614, RVD#5053. C, sample #68, Pukehou.

Other comparative material.- OS16615, RVD#5054. C, sample #35, Waipara.

Occurrence.- This is one of the few species that occurs in the Maastrichtian at both Waipara (#35, 12%; #33, 2%) and Pukehou (#68 and 71, <1%).

Remarks.- Bate (1972) characterised this species as "high domed", with an acuminate PM outline. Adults that he illustrated had a low length/height ratio (mean 1.64). Specimens from New Zealand have these attributes, with a mean l/h ratio of 1.54. Neale (1975) also recorded a single, juvenile valve of this species in his Gingin material, but his illustration suggests that it is not conspecific. Fauth *et al.* (2003) found several specimens of *Bairdoppilata* (*B.* sp.) in the Campanian of James Ross Island, which they mentioned (p. 97) "resemble *Bairdia austracretacea*", but from their descriptions and illustrations, it has a strongly posteriorly sloping, straight DM, and clearly is not conspecific.

Bairdoppilata sp. 5052
(Pl. 1, Fig. 11)

Material.- Five valves, two carapace

Illustrated specimen.- OS16617, RVD#5052. LV, sample 68, Pukehou.

Occurrence.- Occurs in small numbers in samples 68 and 71 (<1%) at Pukehou, while there is possibly one valve in sample #35 at Waipara and a further valve in the Maastrichtian at Rewa Stream (sample #48).

Remarks.- This species is quite distinct from the more abundant *B*. cf. *austracretacea* Bate. It is more elongate (length/height ratio 1.93), and has a relatively long, straight DM and an extended, spoon-shaped PM outline.

Bairdoppilata? sp. 5092
(Pl. 1, Fig. 12)

Material.- 2 carapaces.

Illustrated material.- OS16619, RVD#5092. C, DJ631.1, Snow Hill Island, Campania.

Occurrence.- Restricted to sample DJ631.1 from the base of the Cross Island Traverse on Snow Hill Island (upper part of the Haslam Crag Member of the Snow Hill Formation).

Remarks.- Fauth *et al.* (2003) recovered bairdiids (referred to *Bairdia* sp.) from several samples on James Ross Island, but our material is too poorly preserved to make any meaningful comparison with theirs.

Family BYTHOCYPRIDIDAE Maddocks, 1969

Genus *Bythocypris* Brady, 1880

Bythocypris cf. *B. sudaustralis* McKenzie, Reyment & Reyment, 1991
(Pl. 1, Fig. 13)

1991 *Bythocypris sudaustralis* McKenzie, Reyment & Reyment, 142, pl. II, figs 2-3.
1995 *Bythocypris sudaustralis* McKenzie, Reyment & Reyment; Ayress, fig. 4.3-4.

Material.- One valve and three carapaces.

Illustrated specimen.- OS16620, RVD#4981. C, sample 71, Pukehou, Maastrichtian.

Other comparative material.- OS16621, RVD#4980. C, sample 68, Pukehou, Maastrichtian.

Occurrence.- Found at Pukehou, where it is rare (#71, 2%, #68, <1%), and a single valve at Woodside Creek (#3), both Maastrichtian.

Remarks.- Previously recorded from the Late Eocene and Late Oligocene of South Australia (holotype) and Victoria, respectively (McKenzie *et al.,* 1991; Majoran, 1996a), and the Late Eocene of south Canterbury (New Zealand) by Ayress (1995). Both these examples are somewhat slimmer (l/h ratios of 2.0 and 2.3, respectively) than my Maastrichtian species from New Zealand (l/h = 1.84), but otherwise very close in overall morphology. Bate (1975) recovered two species of the genus from the Santonian-Campanian of Western Australia (?*B* sp. Type A and ?*B* sp. Type B), but both of these have an arched DM, as does *B. chapmani* Neale (which Neale synonymised with ?*B* sp. Type A Bate). *Bythocypris howchiniana* Chapman, 1917 also from the Gingin Chalk (as illustrated by Neale 1975) is closer in overall outline to *Bythocypris* cf. *B. sudaustralis,* but is a much smaller species (690-523 μ vs 1010 μ).

Bythocypris cf. *B. chapmani* Neale, 1975
Pl. 1.14

1917 *Bairdia arquata* Münster; Chapman, 52, pl. XIII, fig. 3.
1972 ?*Bythocypris* sp. Type A Bate; 18, text-fig. 9.
1975 *Bythocypris chapmani* Neale, 8, pl. 1, fig. 10, pl. 5, figs 3, 5-7.
non 1830 *Cythere arquata* Münster, 63.

Material.- Six valves.

Illustrated specimen.- OS16624, RVD#5043. RV, sample 35, Waipara, Maastrichtian.

Occurrence.- Rare at Waipara (#33 & 35, 1%), and a single valve in the Maastrichtian at Pukehou (#68, <1%).

Remarks.- Poorly preserved material, but the best specimen shows the characteristic gently convex median and concave antero-dorsal sections of the DM, and weakly concave VM. The New Zealand species is slightly larger than Neale's Santonian type material from the Gingin Chalk (1000 µ vs 800 µ).

Family PONTOCYPRIDIDAE Müller, 1894

Genus *Argilloecia* Sars, 1866

Argilloecia? sp. 2 Fauth & Seeling, 2003
(Pl. 1, Fig. 15)

2003 *Argilloecia*? sp. 2 Fauth & Seeling in Fauth *et al.*, 100, pl. 1, figs 17-18.

Material.- One valve, four carapaces.

Illustrated specimen.- OS16626, RVD#5061. C, sample DJ633.29, 52m, Snow Hill Island.

Other comparative material.- OS16627, RVD#5062. C, sample DJ633.1, 40m, Snow Hill Island

Occurrence.- Found in samples DJ633.5, 633.10, and 633.29 in the Second Ice Gulley from the late Campanian Snow Hill Island Formation, Snow Hill Island.

Remarks.- Fauth & Seeling's (2003) specimens were not well-preserved, in contrast to the new material, which is in surprisingly good condition. The overall shape leads me to believe the two are conspecific, although my specimens are slightly larger (850x390 µ, vs 705x278 µ). Unfortunately, good internal views are still unavailable, so the species' generic status remains uncertain. On James Ross Island, Fauth *et al.* (2003) found it over almost the whole of the Hamilton Point Member (the upper Santa Marta Formation) section, and my material extends its range upwards into the lower part of the overlying Snow Hill Formation.

Family PARACYPRIDIDAE Sars, 1923

Genus *Paracypris* Sars, 1866

Paracypris sp. 5040
(Pl. 1, Fig. 16)

Material.- One valve, two carapaces.

Illustrated specimen.- OS16631, RVD#5040. RV, sample 71, Pukehou, Maastrichtian.

Occurrence.- Found only in sample #71, Pukehou.

Remarks.- Bate (1972) and Neale (1975) recorded trace numbers of *Paracypris* sp. in their Santonian-Campanian material from Western Australia, but both these species are less slender [l/h ratios: 2.19 (Neale), 2.23 (Bate), 2.44 (herein)], and have less pointed posterior outlines. In overall shape, the Pukehou species is closest to Ayress's (1995, fig. 4.6) illustration of *P. eocuneata* (Hornibrook) from the late Eocene of south Canterbury, but the specimens illustrated herein has been taphonomically distorted anterodorsally.

Paracypris? sp. 5080
(Pl. 1, Fig. 17)

Material.- One carapace.

Illustrated specimen.- OS16633, RVD#5080. C, sample 66, Mangatarata Road.

Occurrence.- Found only in the Maastrichtian at Mangatarata Road.

Remarks.- Generic placement is uncertain. This species differs from *P*. sp. 5040 at Pukehou by its distinctly less acuminate PM outline, and its weakly convex VM.

Paracypris sp. Bertels, 1973
Pl. 1.18

1973 *Paracypris* sp. Bertels, 314, pl. 1, figs 7a-b.
?2003 *Paracypris* sp. Fauth & Seeling in Fauth *et* al., 98, pl. 1, figs 13-14.

Material.- One valve, 16 carapaces.

Illustrated specimen.- OS16634, RVD#5038. C, sample DJ633.29, Snow Hill Island, Campanian.

Other comparative material.- OS16635, RVD#5039. C, sample DJ633.29.

Occurrence.- In samples DJ633.29 (52m), .12 (81m) and .22 (95m) in the Second Ice Gulley from the late Campanian Snow Hill Island Formation, Snow Hill Island. Samples 29 and 12 were from argillite interbeds within *Thyasira townsendi* - rich limestones, while sample 22 near the top of the sequence was from sulphurous grey muddy sands (Dingle, 1995, p. 7-8). The argillites from which sample 29 was recovered have been tectonically incorporated into the base of the limestone build-up, which is probably an allochthonous feature (see Fig. 2.3).

Remarks.- Fauth & Seeling (2003) recorded *Paracypris* sp. from the lower part of the Santa Marta Formation. This species is probably conspecific with my material from the Second Ice Gulley on Snow Hill Island, which is well preserved, although no good internal views are available. Bertels's (1973, pl. 3.8a) species is very similar in outline to the Snow Hill Island species, differing only in possessing a slightly more pointed postero-ventral outline. Her material came from the lower Danian of central Patagonia.

Family PONTOCYPRIDIDAE Müller, 1894

Genus *Maddocksella* McKenzie, 1981

Maddocksella sp. 5047

(Pl. 2, Fig. 1)

Material.- One crushed carapace.

Illustrated specimen.- OS16639, RVD#5047. Sample 33, Waipara, Maastrichtian.

Remarks.- Although crushing has distorted the antero-dorsal outline, this species seems similar in outline to the illustration of *Maddocksella argilloeciaformis* (Whatley & Downing) in McKenzie *et al*. (1991, pl. III fig. 8) from the Late Oligocene of South Australia.

The late Eocene species described from Seymour Island by Szczechura (2001) (?*M*. sp.) has a gently arched DM, whereas *Maddocksella* sp. 5047 has a straight DM.

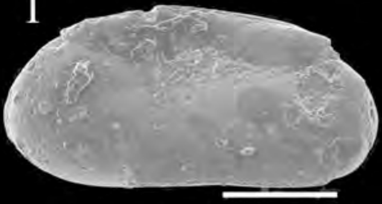
Superfamily CYTHEROIDEA Baird, 1850
Family PROGONOCYTHERIDAE Sylvester-Bradley, 1948
Subfamily PROGONOCYTHERINAE Sylvester-Bradley, 1948

Genus *Majungaella* Grekoff, 1963

Remarks.- This genus is relatively common in the mid- and late Cretaceous of Australia (Bate, 1972; Neale 1975; Krömmelbein, 1975) and throughout the lower to late Cretaceous in Patagonia and late Cretaceous in the Antarctic Peninsula (see e.g. Ballent *et al.,* 1998 and Fauth *et al.,* 2003).

Plate 2. ***1**, Maddocksella* sp. 5047, RV, Waipara #33, Maastrichtian, OS16639, RVD5047. ***2**, Majungaella wilsoni* sp. nov. Holotype, LV, Waipara #35, Maastrichtian, OS16640, RVD4963. ***3**, Majungaella wilsoni* sp. nov. Paratype, RV, Waipara #35, Maastrichtian, OS16641, RVD4964. ***4**, Majungaella wilsoni* sp. nov. Paratype, RV interior, Waipara #35, Maastrichtian, OS16644, RVD4968. ***5**, Majungaella wilsoni* sp. nov. Paratype, C dorsal view, Waipara #35, Maastrichtian, OS16643, RVD4967. ***6**, Majungaella waiparaensis* sp. nov. Paratype, C dorsal view, Waipara #33, Maastrichtian, OS16650, RVD4960. ***7**, Majungaella waiparaensis* sp. nov. Holotype, LV, Waipara #35, Maastrichtian, OS16646, RVD4956. **8**, *Majungaella waiparaensis* sp. nov. Paratype, RV, Waipara #35, Maastrichtian, OS16647, RVD4957. ***9**, Majungaella waiparaensis* sp. nov. Paratype, RV, Waipara #33, Maastrichtian, OS16653, RVD4962. ***10**, Majungaella australis?* Rossi de Garcia & Proserpio 1980, RV, Snow Hill Island DJ628.32, Campanian, OS16655, RVD4979. ***11**, Majungaella* sp. 4978, LV, Pukehou #71, Maastrichtian, OS16656, RVD4978. ***12**, Parahystricocythere ericea* sp. nov. Holotype, LV, Waipara #33, Maastrichtian, OS16657, RVD4969. ***13**, Parahystricocythere ericea* sp. nov. Paratype, RV, Waipara #33, Maastrichtian, OS16658, RVD4970. ***14**, Parahystricocythere ericea* sp. nov. Paratype, LV interior, Waipara #33, Maastrichtian, OS16660, RVD4972. ***15**, Parahystricocythere ericea* sp. nov. Paratype, RV interior, Waipara #33, Maastrichtian, OS16662, RVD4974. ***16**, Parahystricocythere ericea* sp. nov. Paratype, C dorsal view, Waipara #33, Maastrichtian, OS16664, RVD4976. ***17**, Parahystricocythere* sp. 5070, RV, Te Wainohu Point #75, Santonian, OS16667, RVD5070. ***18**, Apateloschizocythere*? *colleni* sp. nov. Holotype, LV, Coverham #9, Cenomanian, OS16668, RVD5096. ***19**. Apateloschizocythere*? *colleni* sp. nov. Paratype, RV, Coverham #9, Cenomanian, OS16672, RVD5099. Scales, µ: 300- 2, 3, 14; 250- 1; 200- 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 15, 16, 17, 18, 19.

Plate 2

1


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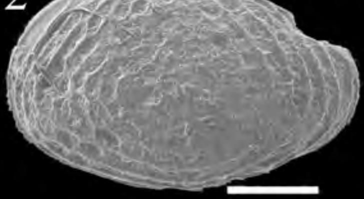
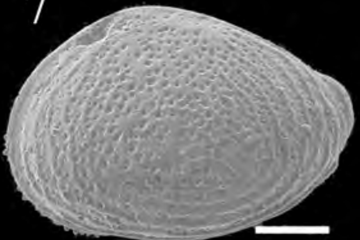


3


4


5


6


7


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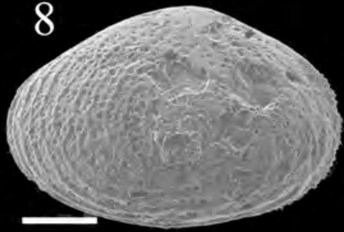

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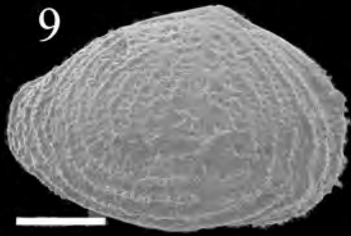

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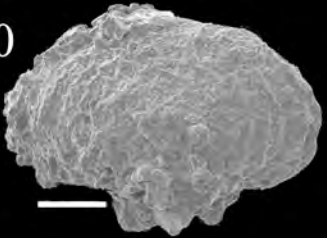

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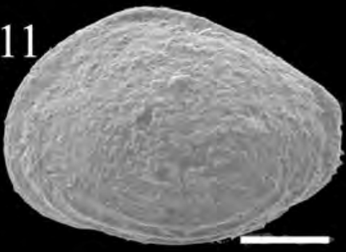

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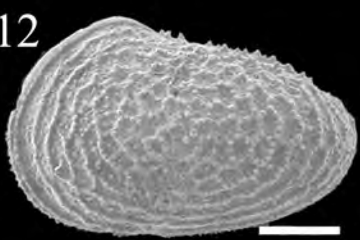

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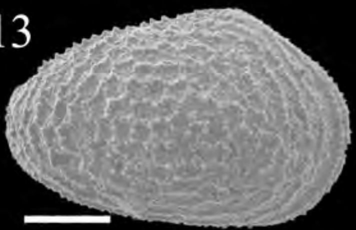
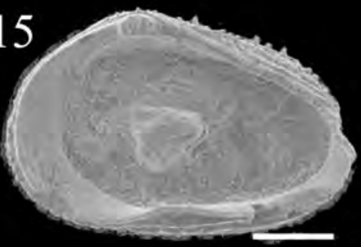


14


15


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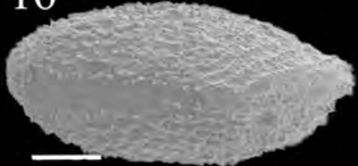

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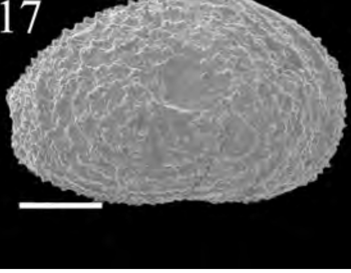

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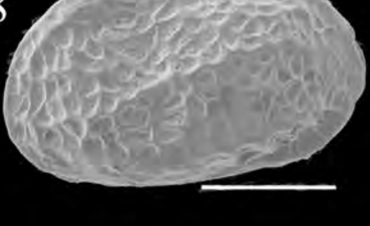

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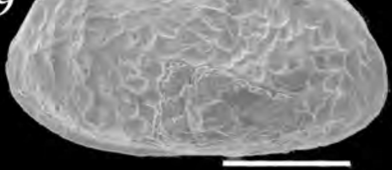


Majungaella wilsoni sp. nov.

(Pl. 2, Figs. 2-5)

Derivation of name.- Named for the late Dr Derek D. Wilson, previously of the Geological Survey of New Zealand, who guided the author through the late Cretaceous Mid-Waipara Gorge sequence in May 1981.

Material.- 32 valves, 3 carapaces.

Holotype.- OS16640, RVD#4963. LV, Waipara #35, Maastrichtian.

Paratypes.- OS16641, RVD#4964. RV, Waipara #35, Maastrichtian; OS16642, RVD#4966. RV, Waipara #35, Maastrichtian; OS16643, RVD#4967. C, Waipara #35, Maastrichtian; OS16644, RVD#4968. RV, Waipara #35, Maastrichtian.

Diagnosis.- Pseudo-amygdaloidal in lateral outline, ornamented with coarse reticulation and ribs sub-parallel to valve margins.

Description.- Moderately large species with almond-shaped lateral outline. AM broadly rounded, weakly spinose ventrally, with an AM rim, which is broadest in the dorsal half. VM broadly convex with slight ventral overhang. Broadly rounded anterior cardinal angle, DM almost straight, PM narrow, bluntly rounded. Carapace almost elliptical in dorsal view. Ornamented with seven relatively strong ribs, the four distal-most of which run sub-parallel to the valve margins. Inter-rib areas strongly reticulate. Internal features poorly displayed. Hinge appears to be entomodont, AMA moderately wide with a vestibule and numerous RPC (up to ?28).

Dimensions.-

	length	height	width
OS16640, Holotype, LV	880	520	
OS11641, Paratype, RV	850	520	
OS16642, Paratype, RV	855	?	
OS16643, Paratype, C	730		510
OS16644, Paratype, RV	>810	520	

Occurrence.- Confined to Waipara Gorge, New Zealand. Abundant in sample 35 (16%) and rare (2%) in sample 33.

Remarks.- The preservation of all specimens of this species is surprisingly poor - valves are invariably corroded and broken. Other ostracod species in the same samples can be well-preserved, so I conclude that the shell chemistry or crystalline structure of *wilsoni* was particularly susceptible to the prevailing taphonomic processes.

A suggestion by one of the reviewers of this paper (Prof. A. R. Lord) is that specimens of *M. wilsoni* sp. nov. could be reworked. Militating partially against such a likelihood are: the ratios of adults/instars (19/8), and valves/carapace (23/2), which point to a degree of original population structure having been preserved; and the question of why reworking should preferentially have affected (apparently) only one species? The possibility of reworking remains however, and only additional collecting will resolve it.

The amygdaloidal outline and coarse reticulation easily distinguish *M. wilsoni* from *M waiparaensis* sp. nov. and *M*. sp. 4978 from our other New Zealand faunas. Its ornamentation is most similar to *M. ticka* (Krömmelbein, 1975) from the middle Cretaceous of central Queensland, but these two species differ in valve outline (the latter is somewhat less elongate - l/h ratio of 1.585 vs ~1.65 for *wilsoni*), and the larger size of *ticka* (~1000 μ vs 850-800 μ). In dorsal views the AM area of *ticka* is distinctly more compressed that *wilsoni*.

Majungaella waiparaensis sp. nov.

(Pl. 2, Figs. 6-9)

Derivation of name.- Waipara Gorge, New Zealand, locality of type.

Material.- 41 valves and 5 carapaces.

Holotype.- OS16646, RVD#4956. LV, Waipara #35, Maastrichtian.

Paratypes.- OS16647, RVD#4957. RV, Waipara #35, Maastrichtian; OS16648, RVD#4958. LV, Waipara #35, Maastrichtian; OS16640, RVD#4959. RV, Waipara #35, Maastrichtian; OS16650, RVD#4960. C, Waipara #35, Maastrichtian; OS16651, RVD#4965. LV, Waipara #35, Maastrichtian; OS16652, RVD#4961. RV, Waipara #33, Maastrichtian; OS16653, RVD#4962. RV, Waipara #33, Maastrichtian.

Diagnosis.- Large species, ovate-sub-triangular in lateral view, delicately ornamented with fine reticulation and five weak primary ribs sub-parallel to valve margins.

Description.- Broadly rounded AM with small stubby spines ventrally, PM short, truncated, slightly upturned dorsally. DM almost straight in RV, slightly convex in LV. VM gently convex, sweeping upwards posteriorly. Greatest valve height at ~45% length. Carapace is elliptical in dorsal view, and anterior and posterior marginal areas are not compressed. Ornamented overall with fine reticulation and five subdued primary ribs sub-parallel to the valve margins. The primary ribs bifurcate in the posterior part of the valve to produce a further three, secondary, ribs. Central valve area has no clearly defined reticulation/rib pattern with several small smooth areas. Internal features are not well-seen. Incomplete views show an entomodont hinge; AMA has a narrow vestibule with numerous (>25) fine RPC.

Dimensions.-

	length	height	width	l/h ratio
OS16646, Holotype, LV	960	670		1.43
OS16647, Paratype, RV	950	640		1.48
OS16648, Paratype, LV	920	680		1.35
OS16649, Paratype, RV	940	640		1.47
OS16650, Paratype, C	960		600	
OS16652, Paratype, RV	850	540	1.57	
OS16653, Paratype, RV	800	525		1.52

Occurrence.- Confined to Waipara Gorge, New Zealand: abundant in sample 35 (22%), rare in sample 33 (2%).

Remarks.- Three similar species of *Majungaella* were recognised by Whatley & Ballent (1996) from the Cretaceous of Australia: *M. annula* Bate, 1972, *M. ticka* (Krömmelbein, 1975) and *M. scheibnerovae* (Krömmelbein, 1975). Of these, the most similar in shape and ornamentation to *M. waiparaensis* sp. nov. is *M. scheibnerovae* (Albian-Cenomanian of Queensland), but Krömmelbein's species is larger, has coarser reticulation and a stronger rib pattern that converges in the antero-dorsal region. The subdued and delicate surface ornamentation of *waiparaensis* also distinguishes it from two late Cretaceous species in Patagonia and the Antarctic Peninsula, which have distinctly coarser features (*M. australis* Rossi de García & Proserpio, 1980, and *M.* sp. Ballent *et al.,* 1998). The species most similar to *M. waiparaensis* sp. nov. are three Cenozoic taxa from Antarctica: *M. antarctica* Szczechura, 2001 (Eocene, Seymour Island), *M.* sp. 4471 Dingle & Majoran 2001 (Oligocene, Victoria Land Basin, Ross Sea) and *M.* sp. nov. (as ?*Loxocythere* sp. Szczechura & Błaszyk, 1996, Pliocene, Cockburn Island). All three are characterised by large size and subdued lateral surface ornamentation. In *antarctica* and *M.* sp. nov., the reticulation has been reduced to punctation and there are typically antero-dorsal areas of celation which extend in patches to the central valve area. In comparison to *M.* sp. 4471, *M. waiparaensis* sp. nov. has a very similar overall shape and ornamentation, but can be distinguished by its slightly more extended posterior outline, which also has a more prominent "lip" on its dorsal side.

Majungaella australis? Rossi de García & Proserpio, 1980
(Pl. 2, Fig. 10)

1980 *Majungaella australis* Rossi de García & Proserpio, 27, pl. 3, figs 3, 4, 7.
1998 *Majungaella australis* Rossi de García & Proserpio; Ballent, Ronchi & Whatley, 50, pl.1, fig. 13.
2003 *Majungaella australis* Rossi de García & Proserpio; Fauth & Seeling, 100, pl. 2, figs 1-3.
non 1975 *Tumidoleberis australis* Bertels, 1975, 120, pl. 6, figs 4-5, 6a-b.

Material.- One valve.

Illustrated specimen.- OS16655, RVD#4979. RV, sample DJ628.32, Late Campanian.

Occurrence.- Found only in sample DJ628.32 from Haslam Crag Formation, 102m above base of section on Haslam Crag, Snow Hill Island.

Remarks.- Partly crushed specimen. Identification is uncertain, but the relatively strong ornamentation suggests that it is conspecific with *M. australis* rather than *M.* sp. Fauth & Seeling, which is weakly ornamented. Fauth *et al.* (2003) recorded *australis* over most of the section through the upper part of the Santa Marta Formation at Hamilton Point on James Ross Island, and the present record possibly extends the upper limit of its range into the Haslam Crag Member of the overlying Snow Hill Formation (see Pirrie *et al.,* 1997a).

Majungaella sp. 4978
(Pl. 2, Fig. 11)

Material.- One carapace.

Illustrated specimen.- OS16656, RVD#4978. LV, sample 71, Pukehou, Maastrichtian.

Occurrence.- Found only at Pukehou.

Dimensions.- Length 780μ, height 540μ.

Remarks.- A new species of *Majungaella* with a distinctive, truncated, weakly spinose PM. This is the only representative of the genus found in the outcrops on North Island, New Zealand.

Genus *Parahystricocythere* gen. nov.

Type species.- *Parahystricocythere ericea* sp. nov.

Diagnosis.- Large, ovate to subpyriform, blind, reticulate, spinose progonocytherid. Hinge is entomodont with a relatively long, narrow, posterior section to the ME, above which lies an accommodation groove in the LV. Wide AMA with a narrow vestibule and ~27 hair-like RPC.

Remarks.- The definition of this genus as a separate taxon rests in large measure on the structure of its hinge, and here I have followed the terminology used in the Treatise (Moore, 1961).

As its name implies, this taxon has many similarities to Bate's (1972) genus *Hystricocythere*, and were it not for the fact that their respective type species have different hinges, (*H. imitata* has a hemimerodont hinge), and if Bate's diagnosis were also amended to include large species, the development of a narrow vestibule and an increase in the number of anterior RPC (from ~14), the new species *P. ericea* could be accommodated satisfactorily therein. However, I feel that making Bate's diagnosis elastic enough to incorporate a different hinge type would be too confusing phylogentically.

As it is, the new genus fits comfortably within the subfamily Progonocytherinae as re-defined by Whatley & Ballent (1996), (although the MS of *Parahystricocythere* gen. nov. remain unknown), but not specifically within any of the existing genera. Whatley & Ballent (1996) considered only five genera to be valid members of the subfamily: *Progonocythere* Sylvester-Bradley, *Glyptocythere* Brand & Malz, *Majungaella* Grekoff, *Fastigatocythere* Wienholz and *Dromacythere* Ware & Whatley, and *P. ericea* sp. nov. does not conform to the amended diagnoses of any of these. An additional factor, although not of generic significance, is that none of the current progonocytherid genera have species with spinose ornamentation.

Of the current progonocytherid genera, *Majungaella* seems to be the closest to *Parahystricocythere* gen. nov., and given the known stratigraphic distribution of the progonocytherids in this part of Australasia in the late Cretaceous, it seems the most obvious progenitor for the new genus.

Apart from a different hinge, *Parahystricocythere* is a parahomeomorph of *Hystricocythere* Bate, and there remains the remote prospect that *Parahystricocythere ericea* belongs in *Hystricocythere* if the specimens on which Bate (1972) erected *H. imitata* were immature (they were very small). If adults were to be found they might possess an entomodont hinge (the hinges of Bate's types are particularly weak). This would allow *Hystricocythere* to be placed in the Progonocytherinae and *Parahystricocythere* would become a junior homonym.

Both Bate (1972) and Neale (1975) considered this possibility, but on the balance of evidence concluded that they did have adults with hemimerodont hinges, although Bate (1972 p. 76) himself recognised the uncertain taxonomic status of his new genus by not allocating it to any family. To further test this, both Professor Alan Lord (Senckenberg Museum) and myself have looked at additional, rich assemblages from the region, and could find only small hemimerodont adults. We had to conclude that Bate's original premise was correct. As a consequence, *H. imitata* and *P. ericea* sp. nov. must be placed in separate genera.

A further possibility exists that gene reactivation within an evolutionary sequence of *Hystricocythere* resurrected an entomodont hinge after it had been "lost" from earlier progonocytherid ancestors (see Dingle 2003 for the principle, which was originally based on optical structures). At the present time I feel that a conventional approach would be more generally acceptable.

There is no currently-available evidence to suggest that *Parahystricocythere* gen. nov. survived beyond latest Cretaceous time.

Parahystricocythere ericea sp. nov.

(Pl. 2, Figs. 12-16)

Derivation of name.- Latin, *ericius* = hedgehog, a fanciful allusion to the small, prominent, hedgehog-shaped elevation on the postero-dorsal margin.

Material.- 58 valves, 7 carapaces.

Holotype.- OS16657, RVD#4969. LV, Waipara #33, Maastrichtian.

Paratypes.- OS16658, RVD#4970. RV, Waipara #33, Maastrichtian; OS16659, RVD #4971. RV, Waipara #33, Maastrichtian; OS16660, RVD#4972. LV, Waipara #33, Maastrichtian; OS16661, RVD#4973. RV, Waipara #33, Maastrichtian; OS16662, RVD#4974. RV, Waipara #33, Maastrichtian; OS16663, RVD#4975. C, Waipara #33, Maastrichtian; OS16664, RVD#4976. C, Waipara #33, Maastrichtian; OS16665, RVD#4977. LV, Waipara, #33, Maastrichtian.

Diagnosis.- Large, blind, finely spinose species with a distinctly upturned postero-ventral outline and a prominent anterior cardinal extension in LV. Characterised by a small, spinose postero-dorsal (hedge-hog-like) elevation.

Description.- Ovate (RV) to sub-pyriform (LV) outlines. Broadly rounded AM with small antero-ventral spines; PM narrowly rounded, upswept postero-ventrally in LV, with a small, but distinct postero-dorsal notch in both valves. VM broadly convex, DM gently concave behind prominent anterior cardinal angle in LV, almost straight in RV. In both valves there is a low but prominent elevation at the posterior end of the DM which is surmounted with small spines (the "hedge-hog"). Overall valve surfaces are reticulate with densely spinose muri. Reticulation is more prominent in the central part of the valve and this area is surrounded by six narrow, finely spinose ribs that run subparallel to the valve margins. In dorsal view the carapace is elongate-ovate with a wide relatively spine-free AM border, and a prominent line of small spines along the crest of the postero-dorsal "hedge-hog"-like elevation. There is no eye tubercle. Internal features are imperfectly known. Hinge is entomodont with strong terminal elements. In RV, ATE is a large, arched quadrate bar with five strong teeth, while the PTE is a narrow, ovate bar with 5-6 teeth. In LV, ME is a narrow, straight, relatively long and finely denticulate bar that expands at the anterior end, with four relatively large, rounded teeth. A prominent, straight accommodation groove runs adjacent to the LV hinge. Marginal areas have not been well-seen, but AMA is relatively wide with up to 27 straight, hair-like RPC. The is a narrow anterior vestibule. MS not seen.

Dimensions.-

	length	height	width	l/h ratio
OS16657, Holotype, LV	900	550		1.64
OS16658, Paratype, RV	830	530		1.57
OS16659, Paratype, RV	870	540		1.61
OS16660, Paratype, LV	930	560		1.66
OS16661, Paratype, RV	900	550		1.64
OS16662, Paratype, RV	860	550		1.56
OS16663, Paratype, C	880	550		1.60
OS16664, Paratype, C	900		500	
OS16665, Paratype, LV	830	520		1.60

Occurrence.- Known only from uppermost Maastrichtian sediments at Waipara Gorge, New Zealand. It is most common in sample 33 (at 37%, it is the dominant species in the fauna), and rare in sample 35 (1.4%).

Remarks.- *Parahystricocythere ericea* sp. nov. is a parahomeomorph of *Hystricocythere imitata* Bate. The most significant difference is the hinge (entomodont vs hemimerodont), but there are others. *P. ericea* sp. nov. is >70% longer, and has a more rounded PM outline and a distinctly more convex VM in both RV and LV. There is also the postero-dorsal notch in lateral outline that *H. imitata* lacks, while *P. ericea* sp. nov has almost double the 14 anterior RPC of Bate's species.

Parahystricocythere sp. 5070
(Pl. 2, Fig.17)

Material.- One valve.

Illustrated specimen.- OS16667, RVD#5070. RV, sample 75, Te Wainohu Point.

Occurrence.- Occurs only in sample 75 from Teratan Stage (Santonian) argillites south of Te Wainohu Point.

Remarks.- This specimen is very similar to *Parahystricocythere ericea* sp. nov. from the uppermost Maastrichtian at Waipara, but it differs on several subtle points: the AM outline is more extended, and the highest point of the valve, which lies over the ATE, is in a relatively more posterior location. Also the PM outline is more truncated. Overall, the valve has a lower length/height ratio than typical female RVs from Waipara. The hinge is somewhat more robust than in *P. ericea* sp. nov., although structurally identical.

Family SCHIZOCYTHERIDAE Mandelstam, 1960
Subfamily SCHIZOCYTHERINAE Mandelstam, 1960

Genus *Apateloschizocythere* Bate, 1972

Remarks.- Bate (1972 p. 30) erected this genus on two criteria: the lack of "an eye node, and the possession of an antimerodont hinge". The former criterion is one I have discussed as being controversial and flawed in supporting generic determinations (e.g. Dingle, 2003), but the absence of internal views in my material leaves discrimination within the Schizocytherinae, between, for example, *Apateloschizocythere* and some species of *Amphicytherura*, something of a lottery.

Apateloschizocythere? *colleni* sp. nov.
(Pl. 2, Figs.18-19; Pl. 3, Figs. 1-2, Text-Fig. 4.1-2)

Derivation of name.- Named for Dr John Collen, Victoria University, who guided the author through the Coverham sections in 1981.

Material.- Nine carapaces (one lost).

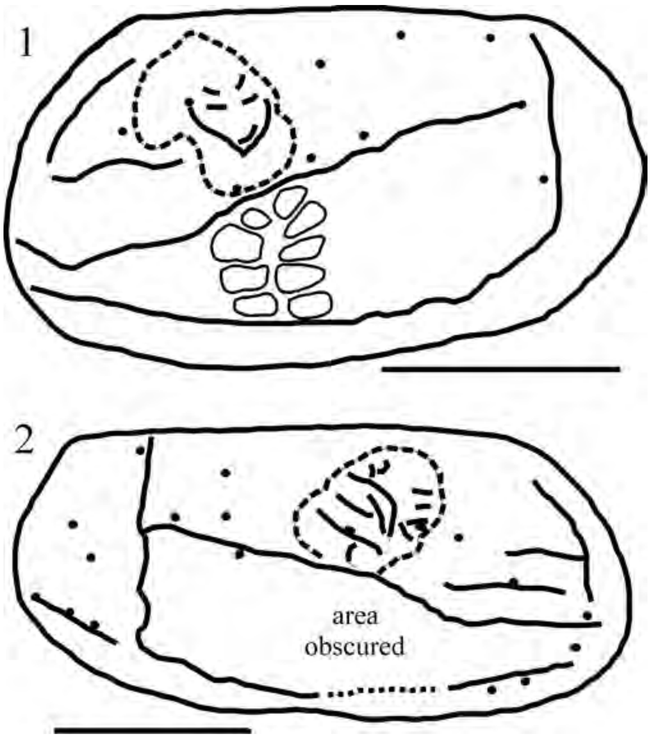


Figure 4. *Apateloschizocythere*? *colleni* sp. nov., sample 9, Coverham, Cenomanian. Main and secondary rib disposition. Normal pore openings are shown by dots. The surface depression lying dorsal to the median diagonal rib is delimited by dashed lines, while the petal-like arrangement of depressed reticulae ventral to the rib are shown for the RV. 1. Holotype NHM PM OS16668, RVD5096, LV. 2. Paratype NHM PM OS16672, RVD5099, RV. Scale bars = 200μ.

Holotype.- OS16668, RVD#5096. C, sample 9, Coverham, Cenomanian.

Paratypes.- OS16669, RVD#5095; OS16670, RVD#5097; OS16671, RVD# 5098; OS16672, RVD#5099. All carapaces from sample 9, Coverham, Cenomanian.

Other comparative material.- NHM PM OS16673.

Diagnosis.- Reticulate species with two distinctive, reticulate depressions either side of an inflected diagonal median-lateral ridge. Rounded PM.

Description.- Quadrate, relatively large (for the genus) species with broadly, asymmetrically rounded AM, somewhat acuminate PM, but not caudate. DM and VM almost straight, parallel. VM sweeps upward posteriorly. Both valves have a wide, distinctive flange-like surface adjacent to the postero-ventral margin. Lateral surfaces carry three prominent lineaments: a vertical elevation that follows a irregular course from the postero-dorsal area towards the VM, where it swings anteriorly and becomes a well-defined but low rib that proceeds roughly parallel to the VM, almost to the AM. The main lateral surface rib runs diagonally from the postero-dorsal region, where it may or may not join the vertical rib, to a ventral position at or very close to the AM. There is a distinctive inflection just in front of valve mid-length. There is a further short rib parallel to the AM in the dorsal quarter, as well as two or three short riblets just above and parallel to the anterior part of the main diagonal rib. Valve surface is coarsely reticulate overall, but muri are rounded, not sharp. Both the shape and distribution of the primary reticulae appear random. Where the valve surface is well-enough preserved many, if not all, of the reticulae are seen to be occupied by delicate secondary reticulation and carry sieve pores. There are also prominent open, normal pores on small nodes at various locations, especially where muri intersect. These have been observed particularly in areas dorsal to the diagonal rib, posterior of the vertical rib and antero-ventrally.

A distinctive feature of the lateral surface is the presence of two shallow surface depressions adjacent to the diagonal rib, immediately anterior of valve mid-length. The depression below the diagonal rib occupies the whole surface between this rib and the ventro-lateral rib and has a very distinctive petal-like arrangement of nine reticulae in two quasi-vertical rows - four anteriorly. The depression above the diagonal ridge is more irregular in shape, deeper, with a vertical cleft-like central feature, several riblets, and extends almost to the DM. No ocular structures are present.

In dorsal view, outline is amygdaloidal, with a wide smooth inward sloping DM surface located behind the anterior cardinal area. Perimeter of this surface is formed by a sharp edge along the DMs of the two valves. The dorsal flange of the RV overlaps the edge of the LV. AM in dorsal view is bluntly rounded, whereas PM outline is pointedly constricted.

No single valves were available, so no internal features have been observed.

Dimensions.-

	length	height	width
OS16668, Holotype, C	550	300	
OS16669, Paratype, C	600	300	
OS16670, Paratype, C	550		250
OS16671, Paratype, C	550		260
OS16672, Paratype, C	601	290	

Occurrence.- Found only in sample #9 from the Saw Pit Mudstone (Ngaterian = Cenomanian) in Nidd Stream at Coverham.

Remarks.- There are many similarities between *Apateloschizocythere*? *colleni* sp. nov. and Bates' genotype (*A. geniculata* Bate), in particular overall shape, structure of sieve pores, lateral rib disposition, absence of eyes, and the aspect of the DM in dorsal view. The two species differ with *A.*? *colleni* sp. nov. lacking a PM caudal process and sharp reticulate muri. The new species is also considerably larger that *A. geniculata*: mean length 570: vs 470:). However, until internal views of the New Zealand species are available its placement in *Apateloschizocythere* rather than *Amphicytherura* or *Schizocythere* is uncertain. Currently I favour the former on the species' possession of well-structured reticulation, its lateral rib (rather than ridge) disposition and the presence of sieve pores.

The closest morphotype to *Apateloschizocythere*? *colleni* sp. nov. is *A. mclachlani* Dingle, 1981 from the Campanian of South Africa, but the latter has a more pronounced caudal process, sharper, more blade-like muri, and a distinct, wing-like process at the posterior end of its ventral rib. *A. laminata* (Dingle, 1971) from the Maastrichtian of South Africa also has many similar features, but has a prominent anterior cardinal elevation in the LV and a convex VM. *A. fimbriata* from the Maastrichtian of Egypt has a caudal process, and a ventral ride with a postero-ventral "fringe" (Bassiouni & Luger, 1990). *Apateloschizocythere* sp. A from the Palaeocene-Eocene of the Maud Rise differs in possessing a distinctive vertical rib that runs from the anterior-cardinal angle to the oblique median lateral rib, and a PM caudal process (Majoran & Dingle, 2002).

Apateloschizocythere? *colleni* sp. nov. is the oldest reported representative of the genus, suggesting that it may have originated in Australasia.

Family KRITHIDAE Mandelstam, 1958

Genus *Krithe* Brady, Crosskey & Robertson, 1874

Remarks.- Bate (1972) found only three valves of *Krithe* in his study of West Australian late Cretaceous ostracods, while Neale (1975) did not report the genus in the Gingin Chalk. Likewise, there are no previous reports of it from the Maastrichtian of Patagonia (Bertels 1975) or the late Cretaceous of the Antarctic Peninsula (Fauth & Seeling 2003). In contrast, in New Zealand *Krithe* occurs in modest numbers in the Maastrichtian at Waipara and Pukehou (mean, 1.8-4.6%, respectively), and is the most abundant taxon (in a sparse fauna) in the Maastrichtian at Mangatarata Road.

In all three regions, *Krithe* is widely reported and abundant from overlying Palaeogene strata.

Krithe sp. 5055
(Pl. 3, Fig. 3)

Material.- Three valves.

Illustrated specimen.- OS16674, RVD#5055. LV, sample 68, Pukehou.

Occurrence.- Occurs in samples #68 from Pukehou, and #35 from Waipara Gorge, where it occurs in trace numbers.

Remarks.- This species is similar to *Krithe* sp. Bate 1972 from the Campanian of north Western Australia, but is even more elongate (l/h ratio 2.44 vs 2.08), and has more a pronounced VM concavity.

Krithe sp. 5056
(Pl. 3, Fig. 4)

Material.- 28 valves, 26 carapaces.

Illustrated specimen.- OS16677, RVD#5056. LV, sample 68, Pukehou.

Other comparative material.- OS16678, RVD#5057. LV, sample #35, Waipara Gorge.

Occurrence.- Occurs in small numbers in all samples at Waipara (1-2%), and Pukehou (2-4%).

Remarks.- A relatively squat species (l/h ~1.89) with broadly rounded AM and PM, with a small, distinct postero-ventral acumination in well-preserved specimens. *Krithe* sp. 5056 is reminiscent of one specimen of the larger variety of *Krithe* sp. illustrated by Ayress (1995, pl. 6, fig. 5) from the Late Eocene of south Canterbury (l/h ratio 1.89 vs 1.84), but the latter has a somewhat higher postero-dorsal shoulder. In Ayress's fauna, *Krithe* sp. is the third most abundant taxon, suggesting to him that deposition was in a quiet, outer shelf environment <500 m water depth.

Krithe sp. 5079
(Pl. 3, Fig. 5)

Material.- 14 valves.

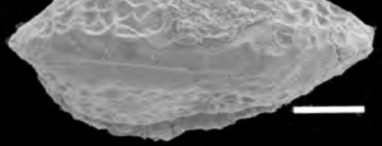
Illustrated specimen.- OS16680, RVD#5079. LV, sample 66, Mangatarata Road.

Occurrence.- Occurs only in the Maastrichtian of Mangatarata Road.

Plate 3. ***1**, Apateloschizocythere*? *colleni* sp. nov. Paratype, C dorsal view, anterior to right, Coverham #9, Cenomanian, OS16670, RVD5097. **2**, *Apateloschizocythere*? *colleni* sp. nov. Paratype, C ventral view, anterior to left, Coverham #9, Cenomanian, OS16671, RVD5098. ***3**, Krithe* sp. 5055, LV, Pukehou #68, Maastrichtian, OS16674, RVD5055. ***4**, Krithe* sp. 5056, LV, Pukehou #68, Maastrichtian, OS16677, RVD5056. ***5**, Krithe* sp. 5079, LV, Mangatarata Road #66, Maastrichtian, OS16680, RVD5079. ***6**, Cythereis* cf. *C. brevicosta* Bate 1972, RV, Pukehou #68, Maastrichtian, OS16683, RVD5018. ***7**, Scepticocythereis* cf. *S. ornata* Bate 1972, RV, Pukehou #71, Maastrichtian, OS16684, RVD5028. **8**, *Scepticocythereis* cf. *S. ornata* Bate 1972, LV, Pukehou #68, Maastrichtian, OS16686, RVD5024. ***9**, Scepticocythereis* cf. *S. ornata* Bate 1972, LV, Waipara #33, Maastrichtian, OS16685, RVD5030. **10**, *Scepticocythereis* cf. *S. ornata* Bate 1972, RV, Woodside Creek #3, Maastrichtian, OS16687, RVD5088. ***11**, Scepticocythereis*? sp. 5044, LV, Waipara #35, Maastrichtian, OS16698, RVD5044. ***12**, Limburgina postaurora* sp. nov. Holotype, LV, Waipara #35, Maastrichtian, OS16701, RVD5012. ***13**, Limburgina postaurora* sp. nov. Paratype, RV, Waipara #35, Maastrichtian, OS16703, RVD5011. ***14**, Limburgina postaurora* sp. nov. Paratype, LV, Waipara #35, Maastrichtian, OS16702, RVD5010. **15**, *Trachyleberis hornibrooki* sp. nov. Holotype, LV, Waipara #33, Maastrichtian, OS16705, RVD5008. ***16**, Trachyleberis hornibrooki* sp. nov. Paratype, RV, Waipara #33, Maastrichtian, OS16708, RVD5007. **17**, *Trachyleberis hornibrooki* sp. nov. Paratype, C dorsal view, Waipara #33, Maastrichtian, OS16712, RVD5075. ***18**, Trachyleberis hornibrooki* sp. nov. Paratype, RV interior, Waipara #33, Maastrichtian, OS16710, RVD5073. Scales, µ: 300- 3, 5, 6, 7, 8, 10, 12, 13, 14, 17, 18; 250- 4, 9, 11, 15, 16,

Plate 3

1



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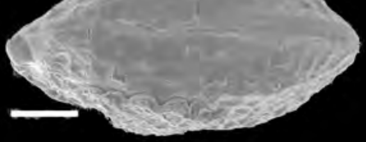

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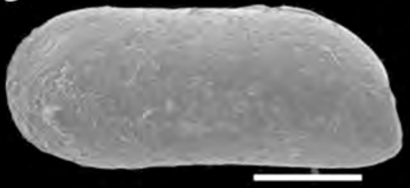

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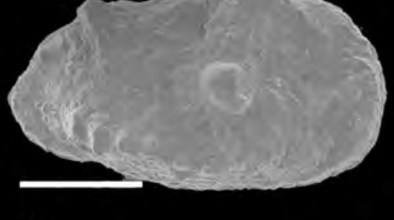

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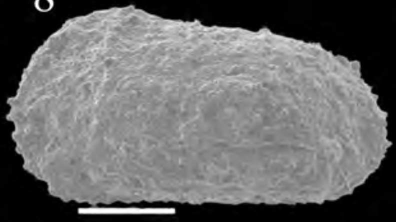

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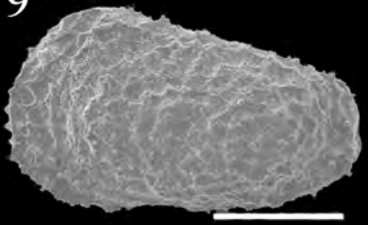

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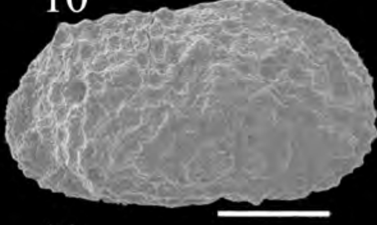

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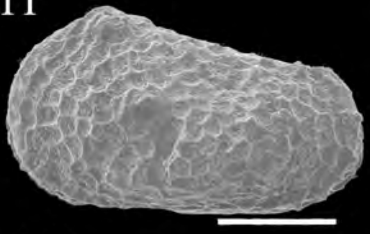

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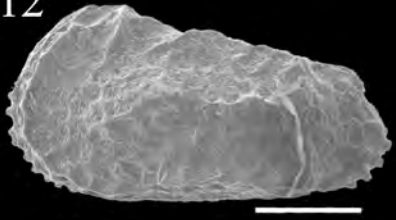

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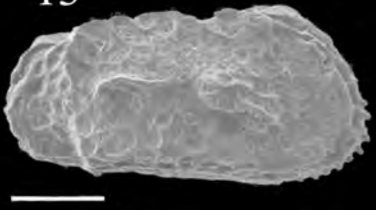

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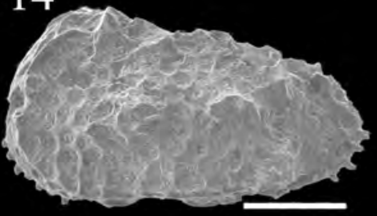

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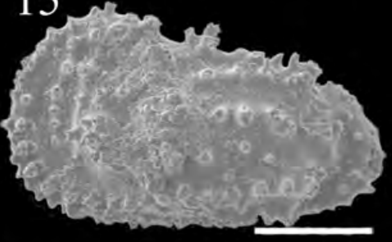

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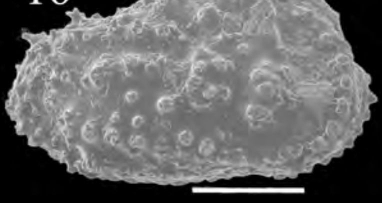

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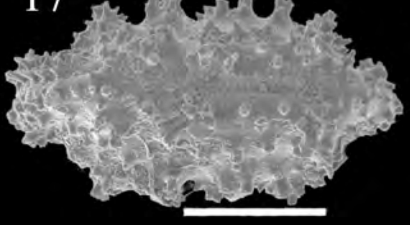

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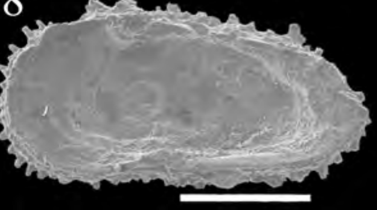


Remarks.- AM more narrowly rounded than in *K.* sp. 5056, and overall, the carapace is slimmer (l/h = 2.00 vs 1.89). In contrast, *K.* sp 5079 is distinctly less elongate than *K.* sp. 5055 (l/h = 2.44).

Krithe sp. 631.1
(not illustrated)

Material.- One crushed carapace. OS16682.

Occurrence.- Found only in sample DJ631.1 from the base of the Cross Island Traverse on Snow Hill Island (upper part of the Campanian Haslam Crag Member of the Snow Hill Formation).

Remarks.- Although the single specimen is crushed, I am confident it belongs in *Krithe* (the posterior depression is clearly visible), and it compares favourably in general dimensions and outline to *Krithe* sp. 5056 from the Maastrichtian of Pukehou, New Zealand (this paper).

This is the first record of *Krithe* from either the Mesozoic or Palaeogene of the Antarctic Peninsula.

Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948
Subfamily TRACHYLEBERIDINAE Sylvester-Bradley, 1948

Genus *Cythereis* Jones, 1849

Cythereis cf. *C. brevicosta* Bate, 1972
(Pl. 3, Fig. 6)

1917 *Cythereis ornatissima* Reuss sp. var. *nuda* Jones & Hinde; Chapman, 55, pl. XIII, fig. 5, pl. XIV, fig. 11.
1972 *Cythereis brevicosta* Bate, 57, pl. 20, figs 9-10, text-figs 31A-D.
1975 *Cythereis brevicosta* Bate subsp. *obtusa* Neale, 52, pl. 2, figs 5-6, pl. 7, figs 4-7, pl. 8, figs 1-4.

Material.- Two valves.

Illustrated specimen.- OS16683, RVD#5018. RV, sample 68, Pukehou, Maastrichtian.

Occurrence.- Very rare, restricted to single valves in the Maastrichtian of Woodside Creek (sample #3) and Pukehou (sample #68).

Remarks.- Preservation is poor, but the overall shell morphology is close to the types illustrated by Bate (1972) from the Santonian of Western Australia. The only significant difference is the less symmetric PM outline in New Zealand specimens, but the lack of internal views does not allow a more rigorous assessment of this species' generic status.

Genus *Scepticocythereis* Bate, 1972

Scepticocythereis cf. *S. ornata* Bate, 1972
(Pl. 3, Figs. 7-10)

1972 *Scepticocythereis ornata* Bate, 68, pl. 26, figs 1-8; pl. 27, figs 11-12; text-figs 37A-F.
1975 *Scepticocythereis ornata* Bate, Neale, 61, pl. 21, fig. 4; text-figs 12d, f, h.
non 1917 *Cythereis ornatissima* Reuss var. *reticulata* Jones & Hinde, Chapman, 55, pl. 14, fig. 12.
non 1975 *Scepticocythereis ornata* Bate, Neale, pl. 2, fig. 10.

Material.- 120 valves, 20 carapaces.

Figured material.-

	length	height	width	l/h ratio
OS16684, RVD#5028, RV, #71 Pukehou	1140	600		1.9
OS16686, RVD#5024, LV, #68 Pukehou	1220	650		1.87
OS16685, RVD#5030, LV, #33 Waipara	780	400		1.95
OS16687, RVD#5088, LV, #3 Woodside	1000	570		1.75

Other material.-

	length	height	width	l/h ratio
OS16688, RVD#5027, LV, #71 Pukehou	1100	650		1.69
OS16692, RVD#5026, C, #71 Pukehou	1180		580	
OS16689, RVD#5023, RV, #68 Pukehou	1170	620		1.89

OS16690, RVD#5025, C, #68 Pukehou	1200		580	
OS16691, RVD#5029, RV, #33 Waipara	800	430		1.86

Other comparative material.- NHM PM OS slides 16693, 16694, 16695, 16696 & 16697.

Occurrence.- Occurs in the late Maastrichtian of New Zealand at Pukehou (where it is an important component of the fauna - 12% in both samples), at Waipara Gorge (#33 ~3%, #35 <1%), and at Woodside Creek (sample #3).

Remarks.- Neale (1975 p. 61) had difficulty in accepting Bate's genus as anything other than a sub-genus of *Limburgina*, although he retained the distinction in his monograph. This I suspect is because Bate himself made the mistake of including Chapman's specimen (1917, pl. 14, fig. 12.) within his new genus in the synonymy for *ornata*, whereas Neale's own illustrations [1975 pl. 2 fig. 10 (Chapman's specimen), and pl. 21 fig. 4 (*S. ornata)*] clearly show their non-conspecificy. Neale (1975, p. 55) selected one of Chapman's specimens (CPC 7140) as the holotype for his new species *Limburgina aurora* Neale, and this is a female of the same species as the Chapman specimen (CPC 7142) that Bate had synonymised with *S. ornata*. A misunderstanding was inevitable.

Majoran (1996b) described *Scepticocythereis sanctivincentis* sp. nov. from the Late Eocene of South Australia. He differentiated his species from *S. ornata* Bate on a somewhat different frontal muscle scar, and the distinctly inflated ventral portion of the AM. It also differs in its sharply alate aspect in both dorsal and ventral views.

There are two New Zealand populations. The Pukehou specimens are larger and relatively squatter than those from Waipara (means >1100 μ and 1.84 l/h vs 790 μ and 1.91, respectively). In comparison, Bate's material is intermediate in length, but has the same l/h ratio as the Pukehou populations (890 μ and 1.84). The specimens from Woodside Creek are intermediate in dimensions from these two localities.

The Maastrichtian New Zealand representatives of the species differ principally from the Santonian Australian types in having a slightly less acuminate PM outline, and a somewhat more robust paramphidont hinge (which has a dentate ME). While no details of MS could be seen in the New Zealand samples (because of relatively poor preservation many of the valves are cracked and all are plugged with coarse silt), the overall spinose/reticulate ornamentation, and lack of prominent SCT and longitudinal ridges conform well to Bate's generic diagnosis.

Scepticocythereis? sp. 5044
(Pl. 3, Fig. 11)

Material.- Three valves, two carapaces.

Illustrated specimen.- OS16698, RVD#5044. C, sample 35, Waipara.

Other comparative material.- OS16700 contains RVD#5045, LV, and RVD#5046, C. Both are from sample 35, Waipara.

Occurrence.- Known only from the Maastrichtian: sample #35, Waipara Gorge, and two probably conspecific valves from sample #48, Rewa Stream.

Remarks.- Reticulate species with a more quadrate outline than *Scepticocythereis* cf. *S. ornata* Bate, particularly in the postero-dorsal area. Also it is non-spinose and smaller.

Genus *Limburgina* Deroo, 1966

Limburgina postaurora sp. nov.
(Pl. 3, Figs. 12-14)

Derivation of name.- Reference to morphological closeness to *L. aurora* Neale, but also to its younger stratigraphical level.

Material.- 77 valves, 4 carapaces.

Holotype.- OS16701, RVD#5012. LV, Waipara, sample 35, Maastrichtian.

Paratypes.- OS16703, RVD#5011, C, Waipara #35, Maastrichtian; OS16702, RVD#5010, LV, Waipara #35, Maastrichtian.

Other comparative material.- NHM PM OS16704.

Diagnosis.- Large, coarsely reticulate, elongate species with three short, sharp, longitudinal ridges, a prominent vertical ocular ridge, and in the posterior quarter a continuous or broken ridge linking the DM and VM.

Description.- Large, elongate, posteriorly tapering species of typical "*Cythereis*" outline, with three longitudinal lateral ridges. There is a considerable degree of intra-specific variability in the prominence of various features of ornamentation. Highest point of the valve lies in the anterior third above an eye tubercle which is crossed by a short, narrow vertical ridge (most prominent in LVs). AM broadly round, coarsely spinose below mid-height. PM acuminate, less so in RV, bearing four stout spines ventrally. VM almost straight, DM tapering posteriorly, but the outline is obscured by sharp DM ridge that ends anteriorly in a downward deflection above the modest-sized SCT. A sharp VM ridge is continuous with a strong AM ridge and is linked by a prominent ridge at about three-quarter valve length to the DM ridge. Typically this ridge is continuous, but it varies in prominence from a sharp feature to a saddle between two conical swellings at the posterior ends of the marginal ridges. The AM ridge lies close to the margin, but at its dorsal end veers inboard and in some specimens abuts the ocular ridge. The median longitudinal ridge is short, prominent, and dorsally-convex. In some specimens it extends to the SCT, but is not connected to the ridge linking the dorsal and ventral margins. The eye tubercle varies from a prominent hemisphere to a swelling mostly obscured by the ocular ridge. Overall, the surface is coarsely reticulate, with smooth muri. Internal features are poorly preserved and incompletely known. The AMA are narrow, non-vestibulate and appear to carry few (?8) RPC. Hinge holamphidont, with asymmetric ATE and plug-like PTE in RV. The ME is smooth, but there is a suggestion in some LVs that the ME anterior tooth is subdivided.

Dimensions.-

	length	height	ratio
OS16701, Holotype, LV	1120	590	1.90
OS16703, Paratype, RV	1140	550	2.07
OS16702, Paratype, LV	1100	620	1.77
mean			1.91

Occurrence.- Restricted to samples 35 and 33 from the Maastrichtian of the Laidmore Formation at Waipara Gorge, New Zealand.

Remarks.- Both Bate (1972) and Neale (1975) described species of *Limburgina* from Western Australia: *formosa* (Campanian) and *aurora* (Santonian), respectively, but the two species do not appear to have co-existed. They differ in length/height ratio (*aurora* being more elongate, means 1.89 vs 1.73), valve length (mean *aurora* 873 µ vs 1127 µ) and steepness of the postero-dorsal margin (*formosa* being steeper). *L. postaurora* is intermediate in many of its features to these two species: it is relatively elongate (mean l/h ratio >1.90), is large (~1100µ), and has a steep postero-dorsal margin. If differs from both the Australian species in lacking spinose muri in its reticulation and in possessing sharper longitudinal ridges and a prominent ocular ridge. The SCT in *L. postaurora* is less prominent than in *L. aurora*, while in the latter, the median longitudinal elevation (in contrast to a ridge) is spinose.

At Waipara *L. postaurora* is overall the most abundant trachyleberid (16-26%), while Neale (1975, p. 59) remarked that *L. aurora* is occasionally common (up to 10%) in the Santonian of Western Australia. In contrast, Bate (1972) found only 11 specimens of *L. formosa* in his three samples.

Genus *Trachyleberis* Brady, 1898

Trachyleberis hornibrooki sp. nov.

(Pl. 3, Figs. 15-18; Pl. 4, Fig. 1)

Derivation of name.- For Dr N. De B. Hornibrook who first recognised *Trachyleberis* in New Zealand.

Material.- 33 valves, 15 carapaces.

Holotype.- OS16705, RVD#5008. LV, Waipara #33, Maastrichtian.

Paratypes.- OS16709, RVD#5009, LV, Waipara #33, Maastrichtian; OS16708, RVD #5007, C, Waipara #33, Maastrichtian; OS16706, RVD#5005, C, Waipara #35, Maastrichtian; OS16707, RVD #5006, LV, Waipara #35, Maastrichtian; OS16710, RVD#5073, RV (broken valve), Waipara #33, Maastrichtian; OS16711, RVD#5074, LV, (broken valve), Waipara #33, Maastrichtian; OS16712, RVD#5075, C, Waipara #33, Maastrichtian.

Other comparative material.- NHM PM OS16713.

Diagnosis.- Compact species with numerous stout, turreted or bladed spines arranged in seven distinct lineaments. SCT crowned by spinous elevation, while there is a further prominent "castle" of spines in an antero-ventral location relative to the SCT. The DM has three elaborately turreted elevations.

Description.- Medium-sized species (mean of types ~850µ), rather squat, sub-quadrate in lateral outline. LVs taper posteriorly more than RV. AM broadly and symmetrically rounded with stout spines particularly in ventral part; PM bluntly rounded, not drawn out, with 3-4 stubby spines in ventral corner; VM almost straight; DM weakly concave and strongly spinose. Highest point of valve lies at <30% valve length. Surface smooth except for numerous short, stout spines which are typically turreted or blade-like. There are seven distinct spine lineaments: immediately adjacent to AM (1); this is continuous with a line adjacent to the whole VM (2); a pre-ocular line of 3-6 spines sub-parallel to the AM (3); an ocular line with 4-5 spines (4), which extends from the anterior cardinal angle to a point immediately adjacent to a complex antero-ventral "castle"-like elevation with five spines; an oblique line of 4 spines that links the "castle" with the DM (5); an oblique line of 4 spines running from the SCT to the postero-dorsal cardinal angle (6); and 4-5 spines on a sinuous longitudinal median elevation (7), that does not continue to the SCT. The SCT is a complex cluster of 4-5 spines. There are also three elaborate spinose elevations on the DM: at ~mid-length, at the postero-dorsal corner, and immediately posterior to the latter. Internal views limited because of poor preservation. AMA wide, probably avestibulate, with at least 20 RPC. Hinge holamphidont: in RV ATE is possibly subdivided, peg-like, while PTE is smooth and low. Anterior end of ME in LV is a prominent smooth tooth.

Dimensions.-

	length	height	l/h
OS16705, Holotype, LV	810	450	1.8
OS16709, Paratype, LV	990	600	1.65
OS16708, Paratype, C	820	450	1.82
OS16706, Paratype, C	760	450	1.69
OS16707, Paratype, LV	900	500	1.8
OS16712, Paratype, C	840		

Occurrence.- Restricted to samples 35 and 33 from the Maastrichtian of the Laidmore Formation at Waipara Gorge, New Zealand.

Remarks.- Numerous species of *Trachyleberis* have been described from the late Cretaceous and early Tertiary of Australia and New Zealand, and *T. hornibrooki* sp. nov. can be distinguished from all by a combination of three main criteria: its relatively small size (mean length ~850:), compact outline (l/h ratio ~1.75 is lower than any of these previously recorded species), and the linear arrangement of its lateral surface spines.

Of the three Santonian-Campanian species from Western Australia (Bate, 1972; Neale 1975), *anteplana* Bate is larger (~1000 µ, although compact, l/h = 1.79) and is spine free post-adjacent to the AM; *penneyi* Neale is smaller, but more elongate (l/h = 1.83); while *raynerae* Neale is larger and particularly elongate (l/h ~1.87). None have the distinctive spine pattern of *hornibrooki* sp. nov.

The closest morphotype to *T. hornibrooki* sp. nov. is *T. thomsoni* Hornibrook, 1952 from the middle Eocene to early Oligocene of South Island, New Zealand, (= *Actinocythereis* aff. *thomsoni*, Ayress 1993a & 1995). This species has a pattern of spine lineaments very similar to *hornibrooki* sp. nov, including a pre-ocular line, but it differs in possessing a posterior extension of the median longitudinal line that curves down to link with the VM lineament. It is also much more elongate (l/h ~1.92), with a distinctly acuminate PM outline.

Hornibrook's (1952) type species *T. thomsoni* was collected from 29 fathoms on the *New Golden Hind Expedition* in the southern fjords in 1946, but he also allocated material of Palaeocene age to this species (not illustrated). Ayress's Eocene specimens (1993a and 1995) are probably not conspecific with either Hornibrook's (1952) types (l/h = 2.14, and no pre-ocular spines) or what Swanson (1969) and Ayress (1993b) considered to be *T. thomsoni* from the Oligocene-Miocene of South Island.

Hornibrook (1952, 1953) recorded a further eight species of the genus from Tertiary to Recent sediments of New Zealand: *scabrocuneata*, (Brady, 1880), *tridens* sp. nov., *brevicosta* sp. nov., *probesioides* sp. nov., *rugibrevis* sp. nov., *retizea* sp. nov., *zeacristata* sp. nov., and *proterva* sp. nov., but all these differ from *T. hornibrooki* sp. nov. on the points from which they were originally differentiated from *T. thomsoni,* as this remains the closest Neogene New Zealand species to it.

McKenzie *et al*. (1991 and 1993) recorded four distinct taxa of *Trachyleberis* from the Eocene-early Oligocene of SE Australia (*brevicosta major*, *brevicosta australis*, *careyi* sp. nov. and *paucispinosa* sp. nov.), and all differ from *T. hornibrooki* sp. nov on various aspects of the three criteria mentioned above. In particular *paucispinosa* has relatively few and elongate spines, *careyi* is a particularly large species (1110-1260 μ), lacks a pre-ocular lineament, and has an acuminate PM outline, while the two subspecies of *brevicosta* have large numbers of un-oriented spines.

A further species has been described from the Eocene of South Australia by Majoran (1996a): *T. maslinensis*. It can be distinguished from *T. hornibrooki* sp. nov. by being generally smaller, and exhibiting a greater range in size and density of surface spines, which also do not form well-defined lineaments. The SCT of *T. maslinensis* is moreover not well-developed, in contrast to *T. hornibrooki* sp. nov. Majoran (1996a) also recorded *T. thomsoni* from these faunas, but did not illustrate specimens, and merely stated that his new species was smaller and more spinose.

I do not consider the species *Trachyleberis*? *thomsoni ayressi* and *T.*? sp. Milhau (1993) from the lower Miocene of North Island, New Zealand to be congeneric with *Trachyleberis*.

Genus *Rayneria* Neale, 1975

Rayneria? *punctata* sp. nov.

(Pl. 4, Fig. 2-7)

Derivation of name.- Reference to punctate ornamentation.

Material.- 18 valves.

Holotype.- OS16714, RVD#5015. LV, Waipara #35, Maastrichtian.

Paratypes.- OS16716, RVD#5014, LV, Waipara #35, Maastrichtian; OS1616718, RVD#5017, LV, Waipara #35, Maastrichtian, (broken valve); OS16715, RVD#5013, RV, Waipara #35, Maastrichtian; OS16717, RVD#5016, LV, Waipara #35, Maastrichtian; OS1616719, RVD#5019, LV, Pukehou #68, Maastrichtian; OS16720, RVD#5076, RV (broken), Waipara #33, Maastrichtian; OS16721, RVD#5077, LV (broken), Waipara #33, Maastrichtian; OS16722, RVD#5090, LV, Pukehou #68, Maastrichtian.

Diagnosis.- Relatively large species with a prominent, flared AM rib which diverges from the margin above mid-height and crosses the eye tubercle. The ventro-lateral rib is upturned sharply anterior to the modest SCT. Intercostal areas weakly reticulate. Overall the valve surface is densely covered in small punctae.

Description.- Valves have robust appearance, with a posteriorly tapering, quadrate outline in lateral view. AM very broadly rounded, non-spinose. PM bluntly rounded, feebly spinose in ventral corner; in RV, PM is somewhat ventrally deflected. DM and VM almost straight, converging posteriorly. There are three relatively short longitudinal costae: that on the DM is irregular, nodose and extends from an angular postero-dorsal process to about mid-length, anterior to which it descends to terminate above the low, round SCT. The latter has a low, irregular anterior extension. A median ridge extends from the SCT along the line of maximum length to a position below the angular postero-dorsal process. The third costa traces a gentle convex trajectory just inboard of the VM and extends anteriorly from a small prominent postero-ventral process and terminates in front of the SCT extension around which it loops abruptly to about mid-valve height. The anterior part of the valve is dominated by a wide, flared AM rib that diverges from the margin about mid-height and runs obliquely towards the DM across the eye tubercle. The AM rib is continuous with a bladed rib that extends along the VM. Inter-costal areas are very weakly and coarsely reticulate, while the whole valve surface is densely covered in small rounded punctae. These punctae occur on the costae, and are absent only from their crests. Unfortunately poor preservation has denied access to internal features of this species.

Dimensions.-

	length	height	width
OS16714, Holotype, LV	770	450	
OS16716, Paratype, LV	850	510	
OS16718, Paratype, LV	>720	500	
OS16715, Paratype, RV	800	450	
OS16717, Paratype, LV	810		220
OS16719, Paratype, LV	770	450	
OS16722, Paratype, LV	910	570	

Occurrence.- Occurs only as a minor component in Maastrichtian samples from Waipara Gorge (1-5%), and is rare (<1%) in sample 68 from Pukehou.

Remarks.- Lack of internal views precludes a more definite generic assignment for *R.*? *punctata* sp. nov., but the surface features accord well with the essential elements cited by Neale (1975). The new species is somewhat larger than *Rayneria ginginensis* Neale (mean 800 μ vs ~670 μ), and further differs in being essentially non-spinose. Only one other example of Neale's genus has been reported in the literature: *R. nealei* Dingle from the Santonian-Campanian of south eastern Africa (Dingle 1980). This species is small (~540 μ), and is ornamented intercostally with few, relatively large punctae. Neale's genus appears to have been confined to the latest Cretaceous of southern Africa and Australasia.

Family CYTHERIDEIDAE Sars, 1925

Genus *Rostrocytheridea* Dingle, 1969

Remarks.- The stratigraphical and geographical distribution of this genus was recently reviewed by Ballent & Whatley (2007), who concluded that it was confined to Gondwanaland, and that it ranged in age from late Jurassic to ?mid-Campanian. This can now be extended to the latest Maastrichtian (in New Zealand).

They listed thirteen species, nine of which have been formally described. Although in only four of these has the number of anterior RPC been seen, there appears to have been a sharp reduction in the number from 25-30 in the Hauterivian species of South Africa/Argentina to 9 in the Albian-Santonian of Australia, and 12 in the Maastrichtian of New Zealand.

Rostrocytheridea pukehouensis sp. nov.

(Pl. 4, Figs. 8-13)

Derivation of name.- Pukehou, North Island, New Zealand, locality of types.

Material.- 704 valves, 145 carapaces.

Holotype.- OS16724, RVD#4982. RV, female, Pukehou #68, Maastrichtian.

Paratypes.- OS16725, RVD#4983, LV, female, Pukehou #68, Maastrichtian; OS16726, RVD#4984, RV, male, Pukehou #68, Maastrichtian; OS16727, RVD#4985, LV, male, Pukehou #68, Maastrichtian; OS16728, RVD#4986, LV, female, Pukehou #68, Maastrichtian; OS16729, RVD#4988, RV, male, Pukehou #68, Maastrichtian; OS16733, RVD#4989, C, male, Pukehou #68, Maastrichtian; OS16731, RVD#4990, C, female, Pukehou #68, Maastrichtian; OS16732, RVD#4991, RV, female, Pukehou #71, Maastrichtian; OS16734, RVD#5072, LV, female, Pukehou #68, Maastrichtian.

Diagnosis.- Large, smooth, strongly sexually dimorphic species with paddle-shaped, non-spinose, ventrally-directed PM, and broadly rounded AM with a narrow, stepped periphery.

Description.- Large species (~1000 μ). Sexual dimorphism is strong, with presumed females plumper and less elongate than males (l/h ratio of types 1.69 vs 2.10, respectively). AM asymmetrically rounded with a prominent, two-stepped periphery that produces an outer flange, most noticeably below mid-height. PM narrow, paddle-shaped and typically strongly ventrally-directed. DM weakly convex in female RV, otherwise almost straight. VM of females broadly convex, and in males almost straight (LV) or weakly concave at about mid-length (RV). Overall, surface entirely smooth except for large normal pore apertures - typically there are ~25.

Despite the large assemblages, internal features are poorly known. The hinge is strongly antimerodont. The RV ATE is a robust, elongate-oval tooth with four subdivisions, while the PTE is narrower, more elongate, with six subdivisions. The ME is a straight crenulate groove. LV dentition is complementary, with the addition of a dorsal accommodation groove. AMA moderately wide with a narrow vestibule and ~12 straight RPC. There are ~9 short RPC in the PMA. MS not seen.

Dimensions.-

	length	height	width
OS16724, Holotype, RV	1040	600	
OS16725, Paratype, LV	1020	600	
OS16726, Paratype, RV	1040	500	
OS16727, Paratype, LV	1120	590	
OS16728, Paratype, LV	1010	600	
OS16729, Paratype, RV	1180	510	
OS16733, Paratype, C	1150		530
OS16731, Paratype, C	970	580	
OS16732, Paratype, RV	1010	600	
OS16734, Paratype, LV	1040	550	

Occurrence.- Restricted to the Maastrichtian at Pukehou, New Zealand, where it dominates samples 68 and 71 (80% and 57%, respectively).

Remarks.- Two species of this genus occur in the Santonian of Western Australia (*westaustraliensis* (Chapman) and *canaliculata* Bate), but neither can be confused with *R. pukehouensis* sp. nov.: Chapman's species has coarse reticulation and a stout postero-ventral spine, while Bate's species has a strongly depressed AM rim and a distinctly dentate PM.

The new species is most similar in general outline and surface features to the type species from the Hauterivian of South Africa (*R. chapmani* Dingle), but the females of the New Zealand species are more tear-shaped, while the paddle-shaped PM outline is distinct from the rounded point of *chapmani*. Fauth & Seeling's (2003) Campanian species from Antarctica (*R. hamiltonensis*) is similar in shape to *R. pukehouensis* sp. nov., but has a broad marginal rim that extends continuously along almost the entire anterior and ventral margins, while its PM "beak" carries small marginal spines.

This New Zealand record is the youngest known occurrence of the genus.

Rostrocytheridea aff. *R. allaruensis*? Krömmelbein, 1975
(Pl. 4, Fig. 14)

1975 *Rostrocytheridea? allaruensis* Krömmelbein, 457, pl. 4, figs 14-15.

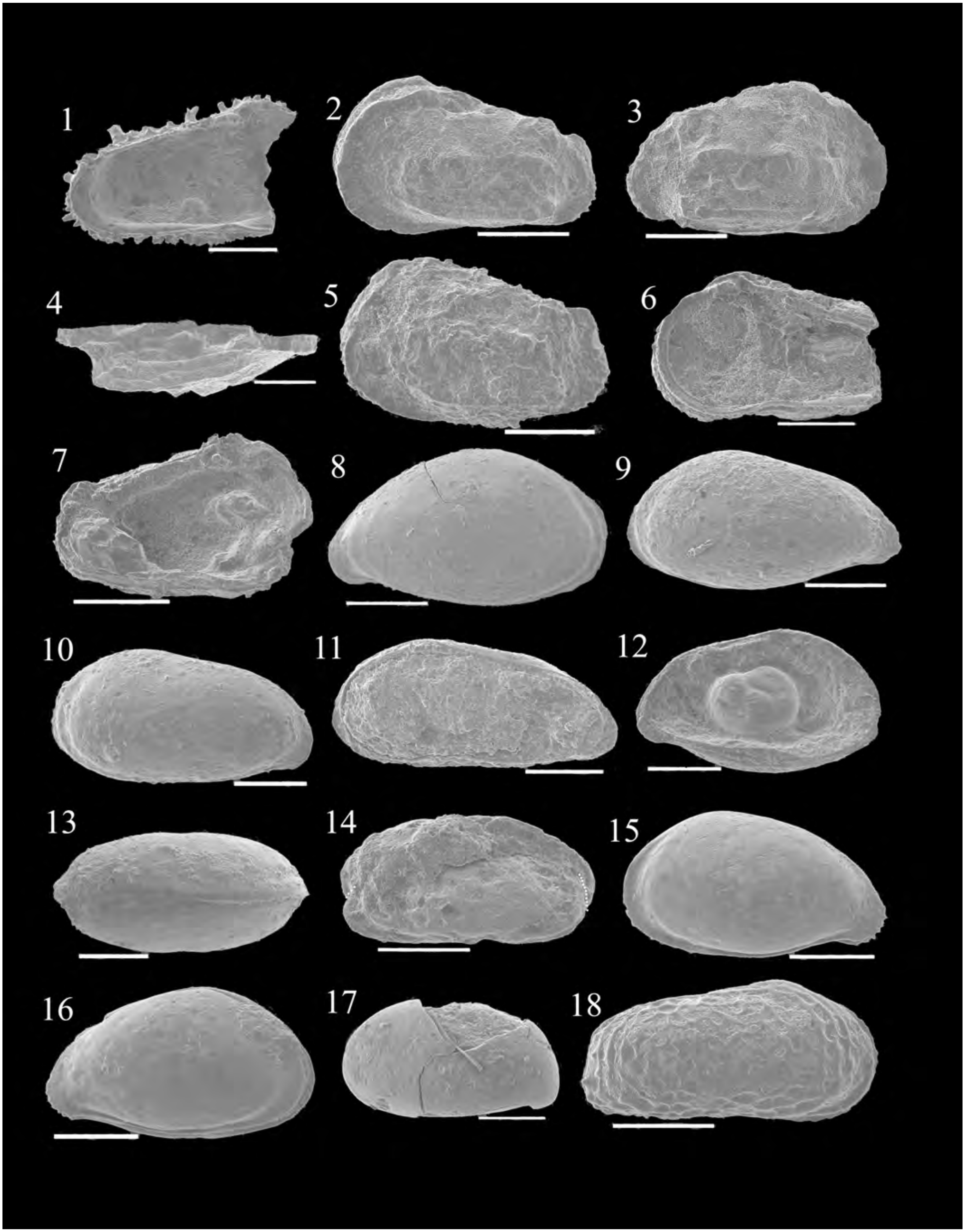
Illustrated material.- OS16738, RVD#5069. Partly disarticulated carapace.

Occurrence.- Found only in sample #50, from the Springhill Formation on the upper Rewa Stream. This is an uppermost Ngaterian Stage (Cenomanian) mudstone.

Remarks.- Identification of this small species (length = 650 µ) is uncertain, but the overall outline, particularly the elongate, weakly "beaked" PM outline, along with a smooth exterior surface with numerous large NPC openings, suggest placement within *Rostrocytheridea*. Krömmelbein's species from the Albian-Cenomanian of Queensland is the closest described species, but the New Zealand taxon differs in possessing no fine AM and PM spines.

Plate 4. ***1****, Trachyleberis hornibrooki* sp. nov. Paratype, LV interior, Waipara #33, Maastrichtian, OS16711, RVD5074. ***2****, Rayneria? punctata* sp. nov. Holotype, LV, Waipara #35, Maastrichtian, OS16714, RVD5015. ***3***, *Rayneria? punctata* sp. nov. Paratype, RV, Waipara #35, Maastrichtian, OS16715, RVD5013. ***4****, Rayneria*? *punctata* sp. nov. Paratype, LV, ventral view, Waipara #35, Maastrichtian, OS16717, RVD5016. ***5****, Rayneria? punctata* sp. nov. Paratype, LV, Pukehou #68, Maastrichtian, OS16722, RVD5090. ***6****, Rayneria? punctata* sp. nov. Paratype, RV, internal view, Waipara #33, Maastrichtian, OS16721, RVD5077. ***7****, Rayneria*? *punctata* sp. nov. Paratype, LV, internal view, Waipara #33, Maastrichtian, OS16720, RVD5076. ***8****, Rostrocytheridea pukehouensis* sp. nov. Holotype, RV&, Pukehou #68, Maastrichtian, OS16724, RVD4982. ***9****, Rostrocytheridea pukehouensis* sp. nov. Paratype, LV♀, Pukehou #68, Maastrichtian, OS16725, RVD4983. ***10****, Rostrocytheridea pukehouensis* sp. nov. Paratype, LV ♂, Pukehou #68, Maastrichtian, OS16727, RVD4985. ***11****, Rostrocytheridea pukehouensis* sp. nov. Paratype, RV ♂, Pukehou #68, Maastrichtian, OS16729, RVD4988. ***12****, Rostrocytheridea pukehouensis* sp. nov. Paratype, LV, internal view ♀, Pukehou #68, Maastrichtian, OS16734, RVD5072. ***13****, Rostrocytheridea pukehouensis* sp. nov. Paratype, C, dorsal view ♂, Pukehou #68, Maastrichtian, OS16733, RVD4989. ***14***, *Rostrocytheridea* aff. *R. allaruensis*? Krömmelbein 1975, C, RV (the two valves have slipped laterally - RV has moved ventrally in relation to LV), Rewa Stream #50, Cenomanian, OS16738, RVD5069. ***15****, Rostrocytheridea hamiltonensis* Fauth & Seeling 2003, LV, Snow Hill Island DJ633.5, Campanian, OS16739, RVD4998. ***16****, Rostrocytheridea hamiltonensis* Fauth & Seeling 2003, RV, Snow Hill Island DJ633.5, Campanian, OS16740, RVD4999. ***17****, Rostrocytheridea?* sp. 4992, LV, LV, Waipara #35, OS16749, RVD4992. ***18****, Ameghinocythere eagari* sp. nov. Holotype, RV, Pukehou #71, Maastrichtian, OS16750, RVD4993. Scales, µ: 300- 1, 5, 7, 8, 9, 10, 11, 12, 13, 15, 16, 18; 250- 2, 3, 6, 14, 17; 200- 4.

Plate 4



This record suggests that *Rostrocytheridea* had a similarly long history in New Zealand (Cenomanian to Maastrichtian) as it had in Australia (Albian-Cenomanian to Santonian).

Rostrocytheridea hamiltonensis Fauth & Seeling, 2003
(Pl. 4, Figs. 15-16)

2003 *Rostrocytheridea hamiltonensis* Fauth & Seeling in Fauth *et al.*, 102, pl. 2, figs 8-12.

Material.- Three valves, eleven carapaces.

Illustrated specimens.- OS16739, RVD#4998, C, female, sample DJ633.5, (15m), Snow Hill Island Formation, Campanian; OS16740, RVD#4999, C, female, sample DJ633.5, (15m), Snow Hill Island Formation, Campanian.

Other comparative material.- OS16742, RVD#5000, C, male?, DJ677.3, clay within Hobbs Glacier Formation, Campanian; OS16746, RVD#5001, C, male?, DJ677.3, clay within Hobbs Glacier Formation, Campanian.

Occurrence.- All specimens of this species so far recorded are from the Campanian of the northern Antarctic Peninsula. In the present study I recorded it at five horizons in the Snow Hill Island Formation (Snow Hill Island: Second Ice Gulley and Haslam Crag), and in Pirrie's (1995) sample 677.3 of clay within the Hobbs Glacier Formation (James Ross Island). Fauth *et al.* (2003) also recorded it at sixteen horizons in the upper Santa Marta Formation (James Ross Island). The latter lie stratigraphically lower within the Campanian sequence than those on Snow Hill Island (see Pirrie *et al.*, 1997a).

Remarks.- This species has very prominent and widely-spaced NPC, and it is these canals, when impregnated with calcite cement that produce small upstanding pillars whenever parts of the outer layer or the whole shell are eroded or corroded away. This phenomenon gives rise to the appearance in some specimens of their being "strongly ornamented with nodes" that was mistakenly described by Fauth *et al.* (2003, p. 102) as celation.

Rostrocytheridea? sp. 4992
(Pl. 4, Fig. 17)

Material.- One broken and slightly crushed valve. OS16749, RVD#4992.

Occurrence.- Found only in Maastrichtian sample 35, Waipara Gorge.

Remarks.- The generic status of this species in uncertain. Its tapering, rounded PM outline distinguishes it from *R. pukehouensis* sp. nov. and is more akin to *R. opisthorhynchus* Ballent & Whatley (2007) from the late Jurassic-early Cretaceous of Argentina.

This is the only record of a possible *Rostrocytheridea* species from the Laidmore Formation.

Family PECTOCYTHERIDAE Hanai, 1957

Genus *Ameghinocythere* Whatley, Moguilevsky, Toy, Chadwick & Ramos, 1997

Ameghinocythere eagari sp. nov.
(Pl. 4, Fig. 18; Pl. 5, Figs. 1-3)

Derivation of name.- Named for Dr Stephen Eagar, fellow ostracod worker at Victoria University, Wellington, who guided the author to outcrops in the southern part of North Island, New Zealand in May 1981.

Material.- 12 valves and 21 carapaces.

Holotype.- OS16750, RVD#4993. RV, Pukehou# 71, Maastrichtian.

Paratypes.- OS16751, RVD#4994, LV, Pukehou #71, Maastrichtian; OS16752, RVD#4995, RV, Pukehou #71, Maastrichtian; OS16753, RVD#4996, C, Pukehou #71, Maastrichtian; OS16754, RVD #4997, C, Pukehou #71, Maastrichtian.

Other comparative material.- NHM PM OS16755.

Diagnosis.- A relatively large species (~850 μ) with coarse reticulation and strong ribbing, particularly sub-parallel to AM and PM. There is a cluster of 5-7 stout, blunt tubercles in the postero-ventral corner of the lateral surface.

Description.- Elongate, sub-rectangular outline, with extended, rounded AM and truncated PM outlines. In RV, the PM slopes noticeably posteriorly. DM and VM almost straight, converging slightly posteriorly. VM weakly convex just anterior to mid-length. In dorsal view, valve flanks are almost parallel, and there is a pronounced constriction along the AM. Maximum width lies at about 60% valve length. Valves are coarsely reticulate overall, with polygonal fossae and strong ribbing that is most prominent in three lines sub-parallel to the AM and PM. In the postero-ventral part of the valve there are between five and seven stout, blunt tubercles, the two most-prominent of which are perforate and lie adjacent to the postero-ventral corner. Internal features not well-seen. AMA is relatively broad with 11 well-spaced RPC. What little could be seen of the hingement does not conflict with illustrations of the type species.

Dimensions.-

	length	height	width	l/h ratio
OS16750, Holotype, RV	880	420		2.10
OS16751, Paratype, LV	850	400		2.13
OS16752, Paratype, RV	850	390		2.18
OS16753, Paratype, C	830		380	
OS16754, Paratype, C	860		390	

Occurrence.- Confined to the Pukehou section, New Zealand, where it is one of the two dominant species in sample 71 (20%), but is rare in sample 68 (0.4%).

Remarks.- The outline of *A. eagari* sp. nov. is very similar to the type species (*A. reticulata* Whatley *et al*.), except that the former is more elongate (mean l/h ratio 2.14 vs 1.98) and considerably larger (~850 µ vs ~620 µ). In dorsal outline the new species has parallel flanks, compared to the more elliptical outline of the genotype.

This is the first record of the genus in Australasia, but pectocytherids are relatively common and diverse in the Santonian-Campanian of Western Australia (five species of *Munseyella*, *Paramunseyella* and *Premunseyella*, making up to 15% of the ostracod fauna) (Chapman, 1917; Bate, 1972; Neale, 1975). However, there is no record of *Ameghinocythere* having extended its distribution into Australia during Tertiary times, and it seems to have become extinct in pre-Eocene strata in New Zealand.

The species of *Ameghinocythere* recorded as ?*A.* cf. *Cytheromorpha? flexuosa* Bertels (1975) by Szczechura (2001) from Eocene strata on Seymour Island, Antarctic Peninsula is very similar in outline and ornamentation to *A. eagari* sp. nov. However, the new species is considerably larger (Szczechura's species has a mean length of 630 µ), has a coarser reticulate ornamentation, and possesses a less broad PM outline.

I am satisfied that Szczechura's species belongs in *Ameghinocythere*, although the original record of *Cytheromorpha*? *flexuosa* sp. nov. by Bertels (1975) (from the middle Maastrichtian of Patagonia), with which she compared it, was only tentatively allocated to their new genus by Whatley *et al*. (1997). Illustrations of the holotype (Bertels, 1975, pl. 6 fig. 13) are of a species with a distinctly compressed AM area, which is not the case for Szczechura's (2001) material. Hence the conspecificy of the two taxa seems doubtful, and further, I am not convinced that Bertel's species belongs in *Ameghinocythere*.

Ameghinocythere lutheri sp. nov.

(Pl. 5, Figs. 4-7)

Derivation of name.- Named for Dr Axel Luther, previously of Heidelberg University, who discovered the first Cretaceous ostracods from James Ross Island.

Material.- Two carapaces.

Holotype.- OS16756, RVD#5032. C, sample DJ633.5, Snow Hill Island, Late Campanian.

Paratype.- OS16757, RVD#5033, C, sample DJ633.12, Snow Hill Island, Late Campanian.

Diagnosis.- Species with weakly concave DM and VM giving a waisted outline in lateral view. Reticulate ornamentation overall, with a low but prominent inclined ridge sub-parallel to AM that continues close to the DM before flaring inboard in the posterior part of the valve.

Description.- Sub-quadrate outline in lateral view. AM rounded, asymmetric; PM asymmetrically rounded and ventrally extended. DM and VM weakly concave producing a waisted outline at about mid-length. Relatively squat in dorsal view, valve sides almost parallel, AM has a prominent chord. Surface with subdued, but coarse, reticulation overall. There is a prominent rib that runs from an antero-ventral location, sub-parallel and inclined to the AM and which marks a low step in the lateral surface. This rib attaches itself to a ridge running parallel to the DM that diverges from the DM at about 2/3 valve length and runs sub-parallel to the PM to a position just above mid-height. This continuous ribbing is a characteristic feature in dorsal view, where it creates a flared feature at the posterior end of the DM. No eye spot seen.

No internal views were seen.

Dimensions.-

	length	height	width	l/h ratio
OS16756, Holotype, C	780	375		2.09
Os16757, Paratype, C	630		320	

Occurrence.- Known only from two samples in the Snow Hill Island Formation of the Second Ice Gulley on Snow Hill Island (15m and 81m above the base of the sequence). Sample DJ633.5 (15m) was a soft, grey muddy sand, while DJ633.12 (81m) was from a grey argillite interbed within a *Thyasira townsendi* (White 1890) - rich limestone that itself lies within weakly-sulphurous muddy sands at the top (70-100m) of the Second Ice Gulley sequence (see Dingle, 1995, p.7-8).

Remarks.- *Ameghinocythere lutheri* sp. nov. is similar in shape, ornamentation and size to *?A.* cf. *Cytheromorpha? flexuosa* Bertels (1975) as illustrated by Szczechura (2001) from the Eocene of Seymour Island, but it differs in having a more acuminate PM outline and in details of surface ornamentation; in particular, *A. lutheri* sp. nov. possesses a prominent ridge posterior and subparallel to the AM. There are ridges sub-parallel to the AM in Szczechura's species, but none is dominant and the low step seen in the anterior area of *A. lutheri* sp. nov. is lacking.

Ameghinocythere lutheri sp. nov. has many features in common with *A. eagari* sp. nov. from New Zealand, but the main differences are *lutheri*'s more evenly rounded AM outline, its less prominent anterior cardinal angle, and its more inflated outline in dorsal view (length/width ration of 1.97 vs 2.21, respectively). Also, *A. lutheri* sp. nov. is significantly smaller than *A. eagari* sp. nov. (mean lengths: 705 µ vs 854 µ, respectively). This is currently the oldest record (Late Campanian) of a genus which became such a characteristic, if minor, element of the Cenozoic faunas of Patagonia, the Antarctic Peninsula, and the Ross Sea area (e.g. Dingle & Majoran, 2001), and which is widespread on the modern continental shelf off Patagonia (e.g. Whatley *et al.,* 1997).

Ameghinocythere? sp. 5078

(Pl. 5, Fig. 8)

Material.- One carapace.

Illustrated specimen.- OS16758, RVD#5078, C, Maastrichtian.

Occurrence.- Found only in sample #66, Mangatarata Road.

Remarks.- Overall carapace outline and size (length = 800 µ) is very similar to that of *A. eagari* sp. nov., but *A*? sp. 5078 is less elongate (l/h = 1.09 vs 2.09), and lacks reticulate ornamentation.

Family CYTHERURIDAE Müller, 1894

Subfamily CYTHEROPTERINAE Hanai, 1957

Genus *Cytheropteron* Sars, 1888

Cytheropteron sp. 5034

(Pl. 5, Figs. 9-10)

Material.- Two carapaces.

Illustrated specimens.- OS16760, RVD#5036, C, sample DJ631.1; OS16759, RVD#5034, C, sample DJ631.1. Both Campanian, Snow Hill Island.

Occurrence.- Found only in sample DJ631.1 from the base of the Cross Island Traverse in the Snow Hill Island Formation (upper part of the Haslam Crag Member).

Remarks.- This is certainly a new species, but with only two slightly damaged carapaces there is insufficient material on which to base a diagnosis. Both Fauth *et al.* (2003) and Bertels (1975) recorded similar small species from the Campanian and Maastrichtian of James Ross Island and Patagonia, respectively. These differ from *Cytheropteron* sp. 5034 in both having more strongly alate profiles in dorsal view, and being smooth (*C.* sp. Bertels), and finely reticulate (*C.* sp. Fauth & Seeling), respectively. The new species is coarsely reticulate overall, has blunt alae and a downturned PM acumination. It is delicately arrow-shaped in dorsal view with a strong DM chordate ridge. There is no record of the genus *Cytheropteron* from the Eocene of Seymour Island (Szczechura 2001), and the two species reported from other Antarctic Peninsula sites at King George Island (Oligocene) and Cockburn Island (Pliocene) by Błaszyk (1987) and Szczechura & Błaszyk (1996), respectively, are non-alate taxa.

Genus *Pelecocythere* Athersuch, 1979

Pelecocythere? sp. 5042
(Pl. 5, Fig. 11)

Material.- Two broken valves.

Illustrated specimen.- OS16761, RVD#5042, RV, sample 33, Waipara, Maastrichtian.

Other comparative material.- OS16762, RVD#5041, LV, sample 71, Pukehou, Maastrichtian.

Occurrence.- A rare species found only at Waipara (#33) and Pukehou (#71).

Remarks.- Both the specimens are incomplete. I believe that this species, along with *Cytheropteron carinoalatum* Bate, 1972 and *Cytheropteron collisarboris* Neale, 1975, belongs in *Pelecocythere*. The genus was originally created by Athersuch (1979) for a Recent deep-water species from the NE Atlantic (*P. sylvesterbradleyi* sp. nov., ~3600 m), to which was added *P. purii* Neale, also from the Recent of the deep NE Atlantic (4000-5000 m, Neale, 1988a). Whatley & Coles (1987) subsequently reported *P. sylvesterbradleyi* (along with a new species *P. foramena*) from sediments as old as Late Miocene in the deep North Atlantic.

The three late Cretaceous species from Australasia that I am suggesting also belong here are continental shelf species, but they show all the general features cited by Athersuch (1979), in particular the long alar rim pierced by pore canals, although the latter feature is not clearly indicated in the New Zealand species because of poor preservation. This implies that *Pelecocythere* originated in shallow water in the late Cretaceous of NE Gondwanaland before subsequently moving into abyssal habitats, where it occurs widely today. This transformation had begun by Middle Palaeocene times, at the latest, because Majoran & Dingle (2001) reported a species (*P.* sp.) from the Maud Rise (currently lying at 2080 m) which they commented bore a strong resemblance to *Cytheropteron carinoalatum* Bate. Currently, the shallowest modern species of *Pelecocythere* of which I am aware, is *P. galleta* from 1408m in the Scotia Sea (Whatley *et al.,* 1988).

Family LOXOCONCHIDAE Sars, 1925
Subfamily LOXOCONCHINAE Sars, 1925

Genus *Mandelstamia* Lubimova, 1955

Mandelstamia antarctica Fauth & Seeling, 2003
(Pl. 5, Fig. 12)

2003 *Mandelstamia antarctica* Fauth & Seeling in Fauth *et al.*, 101, pl. 2, fig 4-7.

Material.- Two valves, seven carapaces.

Illustrated specimen.- OS16763, RVD#5059, C, sample DJ677.3 "Hobbs Glacier Formation", James Ross Island, Campanian clast in glacial till.

Other comparative material.- OS16764, RVD#5058, C, sample DJ633.31 Snow Hill Island Formation section, Second Ice Gulley, Snow Hill Island, Campanian.

Occurrence.- Found at four sites: DJ633.31 at the base of the Snow Hill Island Formation section in the Second Ice Gulley, Snow Hill Island; DJ628.41, 135m above the base of the Haslum Crag Member, immediately below the lower ash band near the top of Haslum Crag on Snow Hill Island; DJ629.2 in the Santa Marta Formation at Ula Point on James Ross Island; and most abundantly at DJ677.3 from clay intercalations in the Hobbs Glacier Formation at Hamilton Point, James Ross Island.

Remarks.- This was the most abundant species in the Campanian samples described by Fauth *et al.* (2003) from

James Ross Island. Despite this, they were unable to obtain any internal views of their species, and a similar situation ensued with my material. Surface reticulation is slightly coarser in the specimens available to me, and the best-preserved specimen illustrated here is smaller than the holotype, although the valve proportions are identical (l/h ratio 1.66).

Indeterminate species

Remarks.- These are relatively poorly-preserved material from Pukehou, Mangatarata Road and Woodside Creek (Maastrichtian, New Zealand), and Snow Hill Island, and James Ross Island (Campanian, Antarctic Peninsula).

Indet. sp. 5060
(not illustrated)

Material.- One internal carapace cast: OS16770, RVD#5060.

Occurrence.- Sample DJ633.5, 15m above the base of the Snow Hill Island Formation section in the Second Ice Gulley, Snow Hill Island, Campanian.

Remarks.- A corroded and broken internal cast of a carapace. Outline similar to *Argilloecia* sp. 2 of Fauth & Seeling (2003), particularly the marked concavity of the VM outline.

Indet. sp. 5081
(Pl. 5, Fig. 13)

Material.- Two carapaces.

Illustrated specimen.- OS16771, RVD#5081, C, sample 66, Mangatarata Road, Maastrichtian.

Occurrence.- Found only at Mangatarata Road.

Remarks.- Elongate, apparently smooth, tapering posteriorly, PM with marked caudal process.

Indet. sp. 5082
(Pl. 5, Fig. 14)

Material.- One carapace.

Illustrated specimen.- OS16772, RVD#5082, sample 66, Mangatarata Road, Maastrichtian.

Occurrence.- Found only at Mangatarata Road.

Remarks.- Elongate, ovate outline, smooth surface, AM evenly rounded, extended with rim. DM and VM almost parallel.

Indet. sp. 5083
(Pl. 5, Fig. 15)

Material.- One carapace.

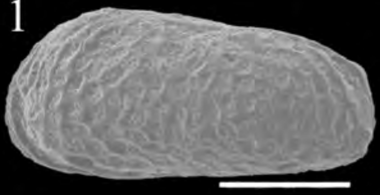
Illustrated specimen.- OS16773, RVD#5083, sample 66, Mangatarata Road, Maastrichtian.

Occurrence.- Found only at Mangatarata Road.

Remarks.- Outline reminiscent of *Cytherois*.

Plate 5. ***1**, Ameghinocythere eagari* sp. nov. Paratype, LV, Pukehou #71, Maastrichtian, OS16751, RVD4994. ***2**, Ameghinocythere eagari* sp. nov. Paratype, C, dorsal view (anterior is to right), Pukehou #71, Maastrichtian, OS16750, RVD4996. ***3**, Ameghinocythere eagari* sp. nov. Paratype, C, ventral view (anterior is to left), Pukehou #71, Maastrichtian, OS16754, RVD4997. ***4**, Ameghinocythere lutheri* sp. nov. Holotype, RV, Snow Hill Island DJ633.5, Campanian, OS16756, RVD5032. ***5**, Ameghinocythere lutheri* sp. nov. Holotype, LV, Snow Hill Island DJ633.5, Campanian, OS16756, RVD5093. ***6**, Ameghinocythere lutheri* sp. nov. Paratype, C, dorsal view (anterior is to right), Snow Hill Island DJ633.12, Campanian, OS16757, RVD5033. ***7**, Ameghinocythere lutheri* sp. nov. Paratype, C, ventral view (anterior is to left), Snow Hill Island DJ633.12, Campanian, OS16757, RVD5094. ***8**, Ameghinocythere*? sp. 5078, C right view, Mangatarata Road #66, Maastrichtian, OS16758, RVD5078. ***9**, Cytheropteron* sp. 5034, RV, Snow Hill Island DJ631.1, Campanian, OS16759, RVD5034. ***10**, Cytheropteron* sp. 5034, C, dorsal view (anterior is to right), Snow Hill Island DJ631.1, Campanian, OS16760, RVD5036. ***11**, Pelecocythere*? sp. 5042, RV, Waipara #33, Maastrichtian, OS16761, RVD5042. ***12**, Mandelstamia antarctica* Fauth & Seeling 2003, LV, James Ross Island DJ667.3, Campanian, OS16763, RVD5059. ***13**,* Indeterminate sp. 5081. C left view, Mangatarata Road #66, Maastrichtian, OS16771, RVD5081. ***14**,* Indeterminate sp. 5082, C right view, Mangatarata Road #66, Maastrichtian, OS16772, RVD5082. ***15**,* Indeterminate sp. 5083, C right view, Mangatarata Road #66, Maastrichtian, OS16773, RVD5083. ***16**,* Indeterminate sp. 5085, RV, Woodside Creek #3, Maastrichtian, OS16775, RVD5085. ***17**,* Indeterminate sp. 5089, C left view, Pukehou #68, Maastrichtian, OS16777, RVD5089. ***18**,* Indeterminate sp. 5091, C left view, James Ross Island DJ677.3, Campanian, OS16778, RVD5091. Scale, μ: 300- 1, 2, 3, 8, 11, 14, 15, 17; 250- 4, 5, 7, 13, 16 ; 200- 6, 18; 150- 12; 100- 9, 10.

Plate 5

1


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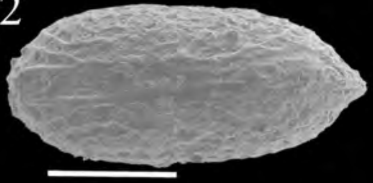

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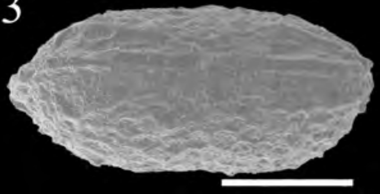

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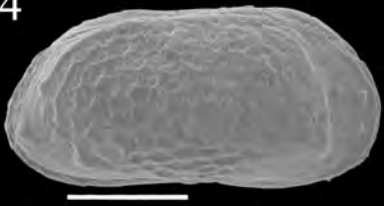

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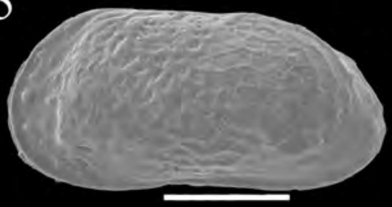

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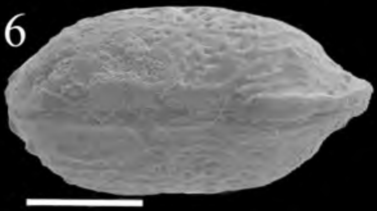

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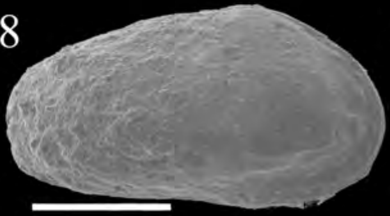

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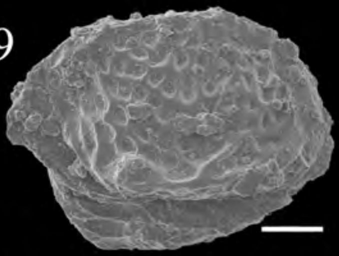

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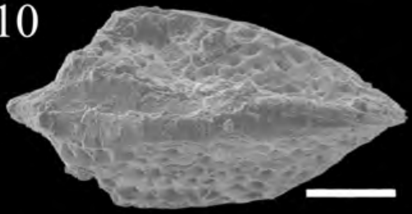

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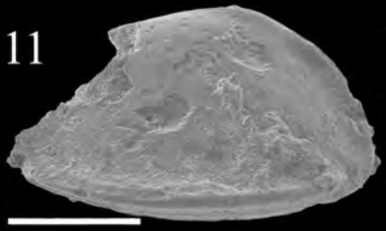

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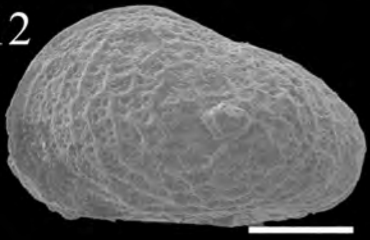

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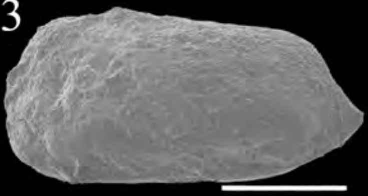

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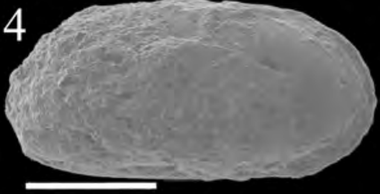

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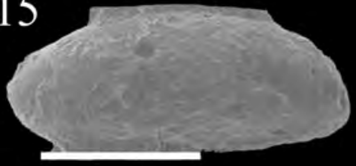

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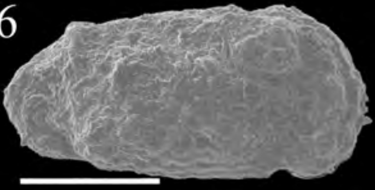

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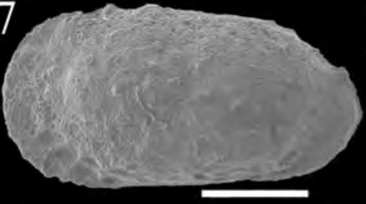

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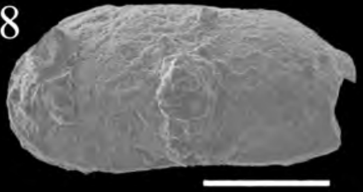

Indet. sp. 5084
(not illustrated)

Material.- One valve: OS16774, RVD#5084.

Occurrence.- Found only at Woodside Creek (#3, Maastrichtian).

Remarks.- "*Cythereis*"-like outline, but matrix on outer surface obscures features.

Indet. sp. 5085
(Pl. 5, Fig. 16)

Material.- One valve.

Illustrated specimen.- OS16775, RVD#5085, RV, sample 3, Woodside Creek., Maastrichtian.

Occurrence.- Found only at Woodside Creek.

Remarks.- Trachyleberid-like outline, but matrix on outer surface obscures features.

Indet. sp. 5087
(not illustrated)

Material.- One valve: OS16776, RV#5087.

Occurrence.- Found only at Woodside Creek (#3, Maastrichtian).

Remarks.- Broken valve. Smooth surface, elongate, box-shaped posterior outline. VM has a keel-like appearance.

Indet. sp. 5089
(Pl. 5, Fig. 17)

Material.- Three carapaces, one valve.

Illustrated specimen.- OS16777, RVD#5089, C sample 68, Pukehou, Maastrichtian.

Occurrence.- Confined to sample #68 from Pukehou.

Remarks.- Four specimens of similar appearance, but none well-enough preserved to allow allocation to a particular taxon. Assuming they are of one species, the best-preserved is relatively large (length = 1030 µ), subquadrate, relatively smooth with sparse, small pustules and a weak SCT. Neither Bate (1972) nor Neale (1975) described a species similar to it.

Indet. sp. 5091
(Pl. 5, Fig. 18)

Material.- One carapace.

Illustrated specimen.- OS16778, RVD#5091, C, sample DJ677.3, James Ross Island.

Occurrence.- Found only at Hamilton Point, in the Hobbs Glacier Formation, Campanian.

Remarks.- Ovate, smooth carapace. DM straight, VM weakly concave.

Indet. sp. 5092
(not illustrated)

Material.- One carapace: OS16779, RVD#5092.

Occurrence.- Sample DJ631.1 from base of Snow Hill Island Formation on the Cross Island Traverse, Snow Hill Island.

Remarks.- Poorly preserved specimen of partially separated carapace with a shape reminiscent of *Argilloecia*.

Indet. sp. 633.29
(not illustrated)

Material.- One carapace: OS16780.

Occurrence.- Sample DJ633.29, 52m above the base of the Snow Hill Island Formation section in the Second Ice Gulley, Snow Hill Island.

Remarks.- An internal cast, with only the ventral surface intact. I suspect this specimen belongs to *Majungaella*.

Indet. sp. 633.15/22
(not illustrated)

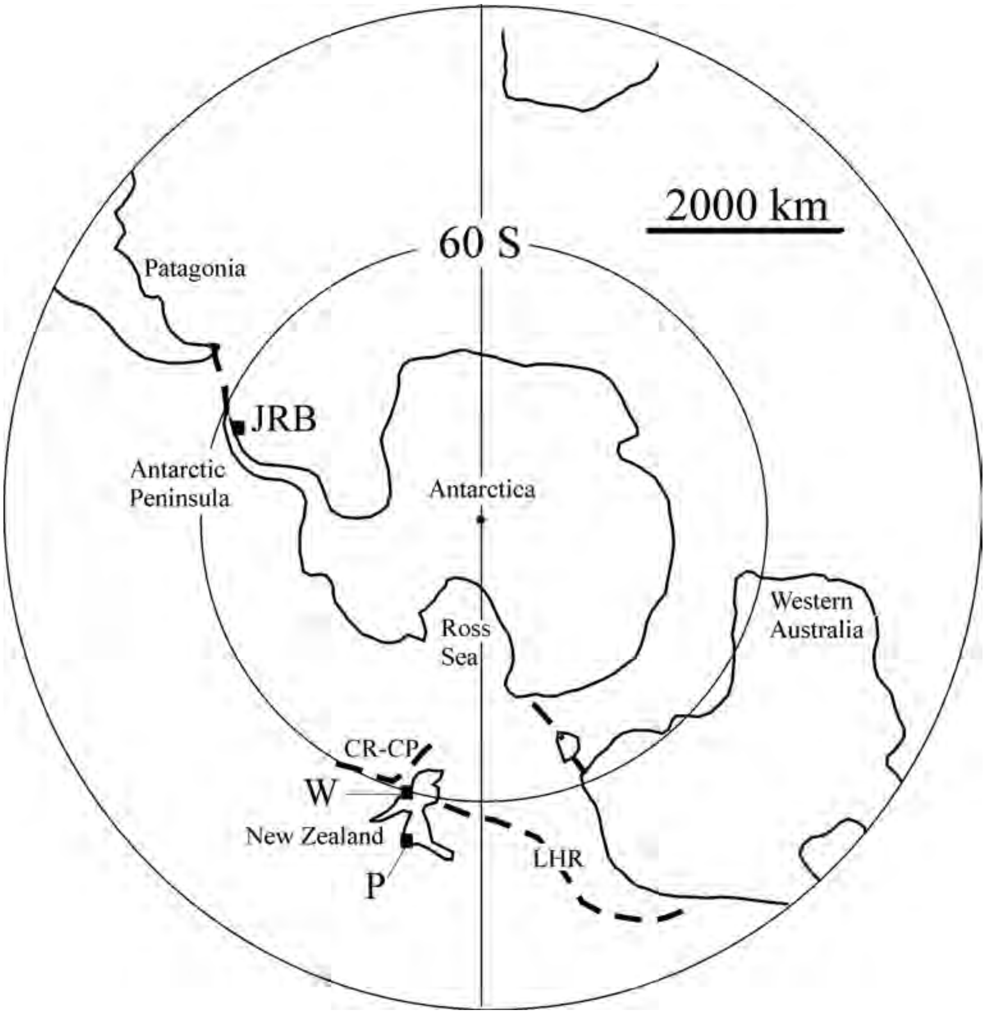

Figure 5. Palaeogeographical reconstruction of high-latitude Gondwanaland at ~70 My (early Maastrichtian). Based primarily on Lawver *et al.* (1992), with details of New Zealand from Hollis (2003), and Sutherland *et al.* (2001). Abbreviations: CR-CP, Chatham Rise/Campbell Plateau; JRB, James Ross Basin (James Ross, Snow Hill and Seymour islands); LHR, Lord Howe Rise; P, Pukehou; W, Waipara. Heavy dashed lines are shallow-marine elevations. Latitudes are 30° apart. Location of Fig. 1 is shown as a black square - James Ross Basin.

Material.- One valve (OS16780) and one carapace (OS16781).

Occurrence.- Found in the Snow Hill Island Formation sequence in the Second Ice Gulley, Snow Hill Island (DJ633) at 55m (.15) and 95m (.22) above the base thereof.

Remarks.- Two damaged internal casts that are reminiscent of the shape of *Paracypris*.

Indet. sp. 628.32
(not illustrated)

Material.- One valve: OS16783.

Occurrence.- Sample DJ628.32 from Haslam Crag Formation, 102m above base of section on Haslam Crag, Snow Hill Island.

Remarks.- Poorly preserved and broken, reticulate specimen of RV of unknown affinity

4. DISCUSSION AND CONCLUSIONS

A total of sixty species was recognised from the Upper Cretaceous of Antarctica (19) and New Zealand (41). Several of the genera had not been identified previously in New Zealand (e.g. *Apateloschizocythere, Rostrocytheridea*, *Majungaella*, *Ameghinocythere, Parahystricocythere* and various trachleberids), allowing comparisons and new correlations to be made between the Upper Cretaceous faunas of Australasia, Antarctica and Patagonia.

I shall review the data area by area, before drawing some general, Gondwana-wide conclusions.

4.1. New Zealand

Cenomanian and Santonian: Two Cenomanian sites contained ostracods (#9, Coverham; #50, Rewa Stream). The faunas are sparse (presumably reflecting selective preservation) but their stratigraphical significance is out of proportion to their size.

At Coverham we see the probable earliest representative of the Gondwanide genus *Apateloschizocythere* Bate. Previous records from South Africa, Australia, Egypt and the Maud Rise off Antarctica range Coniacian to Palaeocene, but are most abundant in Santonian to Maastrichtian strata (Bate, 1972; Dingle, 1981; Bassiouni & Luger, 1990; Majoran & Dingle, 2002). During mid-Cretaceous times there would have been no impediment to communication between New Zealand (Cenomanian) and southern-most South Africa (Coniacian: Dingle, 1985) via, for example, the Antarctic Peninsula and the shallow-water Falkland Plateau (see Lawver *et al.,* 1992, fig. 7).

A further significant Cenomanian find is the single carapace of *Rostrocytheridea*? cf. *R.*? *allaruensis* from sample #50 in Rewa Stream. This record is pene-contemporaneous with that of Krömmelbein (1975) from the Great Artesian Basin in western Queensland (Albian-Cenomanian), making these the oldest records from Australasia of a genus that was already widely distributed in East/South Africa and Patagonia by late Jurassic/Neocomian time and western Indian by Albian times.

The sole Santonian ostracod-bearing sample was #75 from Te Wainohu Point. Although only one valve was obtained, this was of the new genus *Parahystricocythere*, and probably a species separate from *P. ericea* sp. nov. from the Maastrichtian at Waipara. In late Cretaceous time, as at present, Waipara and Te Wainohu lay ~450 km apart (Hollis 2003). Significantly, *P. ericea* lived in warm, shallow conditions, and was absent from the Maastrichtian at Pukehou, which lies only ~50 km west of Te Wainohu Point. The suggestion is that in Santonian time, the facies at Te Wainohu was probably shallow and warm.

Late Maastrichtian: Maastrichtian faunas were recovered from six localities (Woodside Creek, Waipara, Rewa Stream, Mangatarata Road, Pukehou and Te Wainohu Point), but from only two (Waipara and Pukehou) were these abundant and diverse (Table 3).

The faunas at Waipara and Pukehou were recovered from just below the Maastrichtian/Danian boundary (Waipara - 0.5-2 m and Pukehou - ~10 m), and they show some strong contrasts, as well as similarities.

The two Waipara assemblages (samples #33 and #35) are both trachyleberid-rich (*Trachyleberis hornibrooki* sp. nov. and *Limburgina postaurora* sp. nov.), but can be distinguished by having either common *Parahystricocythere ericea* (#33) or *Majungaella* spp. plus *Bairdoppilata* spp (#35). Both Pukehou assemblages (#68 and 71), on the other hand, are dominated by *Rostrocytheridea pukehouensis* sp. nov. plus *Scepticocythereis* cf. *S. ornata,* but they can be distinguished from each other by having either abundant *Ameghinocythere eagari* sp. nov. (#71) or only trace numbers of non-*Scepticocythereis* trachyleberids and *Cytherella* sp. 5051 (#68). A further difference between faunas from the two areas is that while *Cytherelloidea* cf. *C. westaustraliensis* occurs in both samples at Waipara, the species is absent from Pukehou.

This distribution suggests that in New Zealand, the presences of *Rostrocytheridea* and *Majungaella* are almost mutually exclusive: only one uncertain valve of *Rostrocytheridea*? was found at Waipara (#35), and two valves of *Majungaella* are known from Pukehou (#71). In contrast, some species are common to both localities: *S.* cf. *S. ornata*, *Krithe* sp. 5056, *Bairdoppilata* cf. *B. austracretacea* and *Rayneria*? *punctata* sp. nov. Overall, there is a greater species diversity at Waipara (17 spp in 401 valves, 1/14) compared to Pukehou (16 spp in 1283 valves, 1/80).

Contrasts between the faunas at Waipara and Pukehou probably reflect different depositional environments (Fig. 5). Both were clay rich, indicating muddy sea-floors, but the lithofacies at Waipara is sandier and glauconitic, and in his K/T palaeogeographical reconstructions Hollis (2003, figs 2 & 5) postulated it lying in a sheltered, south-facing embayment at the junction of the Chatham Rise Peninsula and the mainland (i.e. in a proximal position within the Canterbury Basin). In contrast, Pukehou (~400 km NW) lay off a more exposed, north-facing coast swept by cold surface currents and in an outer shelf "bathyal slope" environment relative to the East Coast Basin (Hollis, 2003). This evidence suggests that the dominant taxa during latest Maastrichtian times at these two sites (*Majungaella* spp and *Rostrocytheridea pukehouensis*) preferred shallow and warm (Waipara), and deep and cool habitats (Pukehou), respectively. It also indicates a cool outer shelf habitat for the genus *Ameghinocythere* at Pukehou.

How do these postulated preferences compare with those of other, better-known ostracods? In modern seas, *Krithe* is wide-spread both on continental shelves and in deep-ocean basins, but is particularly diverse and relatively abundant in the latter (e.g. Coles *et al.,* 1994). Dingle *et al.* (1990) undertook a case study across the continental margin off southwestern Africa and found that *Krithe* occurs over two depth-zones: 238 - ~1500 m, and 1500->4000 m, in which its relative abundance in relation to the total ostracod populations peaks at ~ 500-700 m, and >1700 m. These two *Krithe* assemblages are constrained by two major water-masses with contrasting properties: the shallower assemblage lies under the Antarctic Intermediate Water[3] (AAIW), while the deeper assemblage lies under the North Atlantic Deep (NADW) and Antarctic Bottom (AABW) waters[4]. Each assemblage has its own species-profile and no species straddles the boundary, which is the shear zone between the AAIW (5 spp) and the NADW (7 spp). Significantly, the deeper assemblage is by far the most important relative to overall ostracod abundances: >50% vs <20% (mean values across the whole margin for samples in which the genus occurs). In summary, *Krithe* is most diverse and abundant under the NADW and AABW masses (the upper limit of which is ~1500 m, hereabouts) (Dingle *et al.,* 1990).

Majoran *et al.* (1997) suggested that there were also large ranges in the tolerance of *Krithe* species during late Cretaceous times, at least over the southern oceans, but that it eschewed high latitude deep-water locations. It is instructive to consider its distribution in time, and spatially, off southern Africa. The genus first appears in the upper Campanian, and rises sharply in abundance in the middle Maastrichtian, which event (on other evidence) was thought to coincide with an increase in continental shelf water depth (Dingle, 1980). It also occurs in the subtropical Lower Miocene inner-mid shelf assemblages off south-western Africa, before the initiation of cool-water Benguela upwelling (although it is relatively rare - <5%) (Dingle *et al.,* 2001).

This evidence suggests that while the presence of *Krithe*, in both late Cretaceous and modern seas, cannot be taken as an indicator of cool water, its occurrence in continental margin facies in relatively large numbers, signifies(d) at least outer-shelf environments. The occurrence of *Krithe* at Pukehou (2-6% of the fauna) is commensurate with an outer shelf setting, while the low water temperature postulated by Hollis (2003) might be evidence of the development of a retrothermal trait.

Cytherelloidea is generally considered a thermophilic taxon in modern shallow seas (minimum of 10ºC, e.g Sohn 1962, Zhao & Wang 1988), and in shallow-water Cretaceous facies this relationship probably also obtained (e.g. Neale 1984, 1988). However, caution is needed in applying this template away from the continental shelves, because Boomer & Whatley (1995) have shown that certain demes of *Cytherelloidea* living on north-central Pacific guyots adapted during Palaeocene times to progressive sinking of the guyots to abyssal depths by adopting retrothermal tendencies (e.g. their *Cytherelloidea* sp. 1). A similar explanation was offered by Majoran *et al.* (1997) and Majoran & Widmark (1998) for the occurrence of *C. megaspirocostata* in late Maastrichtian sediments from the Maud Rise, a subsided continental fragment off Antarctica, where descendants persisted until Eocene

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[3] mean values: temperature = 6ºC, salinity = 34.51‰, dissolved oxygen = 3.7 ml/l

[4] mean values: temperature = <3ºC, salinity = 34.8‰, dissolved oxygen = >4 ml/l

times (Majoran & Dingle, 2002, as *Cytherelloidea* sp.). However, such cases appear to have been isolated and geographically specific, as well as relatively short-lived events, as there is no evidence that *Cytherelloidea* generally adopted a retrothermal tendency. This suggests that all shallow water occurrences of the genus indicate thermophilic habits, and in this regard the presence of *Cytherelloidea* is compatible with its restriction to the Waipara area (where it is relatively common, 2-6%).

Despite their relative abundances close to the K/T boundary, it is probable that both *Rostrocytheridea* and *Majungaella* locally became extinct in Australasia over the Mesozoic/Cenozoic transition (neither species has been recorded from the Eocene of New Zealand or Australia). While the former also became extinct worldwide across the K/T boundary (see Ballent & Whatley 2007), this evidence suggests that the Tertiary Antarctic *Majungaella* lineages derived from indigenous stock. The warm-water taxon *Parahystricocythere* also appears to have become extinct both locally and regionally across the K/T transition (suggesting a range of Santonian - Maastrichtian). In contrast, the cool water population of *Ameghinocythere eagari* at Pukehou probably did survive into the lowermost Tertiary and went on to re-colonise Antarctica and Patagonia, despite seeming to have left no descendants in the local (i.e. Australasian) Palaeogene.

Of the other Maastrichtian faunas from New Zealand, only those from Woodside Creek and Mangatarata Road contained more than 20 valves (23 and 24, respectively). Woodside Creek lies ~150 km northeast of Waipara and the depositional environment of the Mead Hill Formation has been judged by Strong (1977, p. 694), on the basis of the planktonic and benthic foraminifera, to have been warm-water, upper slope, and subject to coastal upwelling (Hollis, 2003, p. 313). The facies differences between Waipara and Woodside Creek probably account for the contrast between their respective ostracod faunas: *Cytherella* is relatively abundant at Woodside Creek (and rare at Waipara), while neither of the two shallow-water, thermophilic taxa (*Majungaella* and *Parahystricocythere*) were found at Woodside Creek.

The similarity between the Pukehou and Mangatarata Road faunas that is worthy of emphasis is the mutual relatively high abundance of *Krithe*, suggesting deposition at the latter site in relatively deep (and possibly cool) water. This is not surprising as the two localities lie only ~20 km apart and approximately along strike.

4.2. Late Cretaceous of Australasia

Despite the Maastrichtian localities in New Zealand being separated by ~5500 km and ~20 my from the Santonian-Campanian localities in Western Australia, there were some strong affinities between their respective faunas. Specifically, both regions contained *Majungaella* and *Rostrocytheridea*, as well as several closely-related trachyleberid species (*Scepticocythereis* cf. *S. ornata*, *Cythereis* cf. *C. brevicosta*, *Rayneria*, *Trachyleberis* and *Limburgina*). In addition, there is the homeomorphic commonality of *Hystricocythere* and *Parahystricocythere*. This suggests that there were relatively shallow water connections between the two areas in late Cretaceous time (Fig. 5), presumably via the Lord Howe Rise (for example, see the reconstructions in Sutherland *et al.,* 2001).

Comparing the faunas of the two regions in detail, however, highlights some important differences (although this exercise is not straightforward, as neither Bate (1972) nor Neale (1975) provided comprehensive statistical data on abundances). The Santonian fauna of Western Australia was species-rich (49 spp) and dominated by an association of *Cytherella*, *Cytherelloidea* and *Paramunseyella* (47% of the total), with species of *Rostrocytheridea*, *Majungaella*, *Limburgina* and *Trachyleberis* constituting a further 18%. Although this fauna has similarities to that found at Waipara, it differs principally in possessing *Rostrocytheridea*, and in the fact that the New Zealand fauna was relatively species poor (only 17 spp).

In contrast, the Campanian in Western Australia, while also species-rich (40 spp), contains certain taxa that are found in New Zealand, but not in the underlying Santonian (*Krithe*, *Bairdoppilata*), and is similarly devoid of *Rostrocytheridea* (Bate, 1972). This suggests that the Australian Campanian fauna may be a closer analogue to the Maastrichtian fauna at Waipara than the local (west Australian) Santonian, which Neale (1975) concluded was deposited in a relatively warm (minimum 10ºC), clear, shallow sea (~100 m)).

The deeper, cooler-water New Zealand Pukehou *Rostrocytheridea*-rich, *Cytherelloidea*-free fauna, on the other hand, appears to have no analogue in Australia, implying that the two specimens of *Majungaella* sp. 4978 found therein (sample #71) are the only known retrothermal representative of the genus known from Australasia.

This evidence suggests that the quasi-mutually-exclusive relationship between *Majungaella* and *Rostrocytheridea* in the Maastrichtian of New Zealand, may have been presaged by the Australian Campanian assemblages described by Bate (1972), and implies that the last time the two genera co-existed as significant faunal elements in Australasia was during Santonian time. Neither taxa are known to have survived into the Palaeogene in Australia or New Zealand.

A further important difference between the two regions is that although there are at least six species of pectocytherids in the Santonian-Campanian of Western Australia (Bate, 1972; Neale, 1975), the genus *Ameghinocythere* in Australasia seems to have been restricted to the Pukehou/Mangatarata Road area of New Zealand.

4.3. Late Cretaceous of Patagonia and West Antarctica

Our knowledge of this region comes from work on the late Campanian-Middle Maastrichtian of Patagonia by Bertels (1975, 1977), Rossi de García & Proserpio (1980), Ballent *et al.* (1998) and Ballent & Whatley (2007), and by Fauth *et al.* (2003) on the Late Campanian Santa Marta Formation from James Ross Island in the Antarctic Peninsula. The present paper focuses on the slightly younger Campanian strata on adjacent Snow Hill Island in the James Ross Basin archipelago.

The Campanian fauna of James Ross Island is moderately species-rich (15 spp, in 955 valves, 1/64), and is dominated by *Mandelstamia antarctica* (49%), with abundant *Rostrocytheridea* (22%) and *Majungaella* (14%) and common *Cytherelloidea* (3.5%) (Fauth *et al.,* 2003). In the Snow Hill Island strata, both *Rostrocytheridea* and *Mandelstamia* continue to be relatively abundant, but *Cytherelloidea* is missing and there is only a single, tentatively identified specimen of *Majungaella*. One significant presence is the previously unknown taxon *Ameghinocythere*.

By comparison, the late Campanian of Patagonia contains both *Majungaella* and rare *Rostrocytheridea* (Ballent *et al.,* 1998; Ballent & Whatley, 2007), while in the overlying middle Maastrichtian, which is characterised by several species that have affinities with west Africa (for example *Togoina*, *Veenia* (*Nigeria*), Bertels 1975), small numbers of *Majungaella "australis"* (Bertels)[5] have been recorded, but *Rostrocytheridea* is absent (Ballent & Whatley, 2007).

Can we relate these regional faunal fluctuations to environmental changes? Evidence for late Cretaceous water temperatures in this region is equivocal, but the presence of *Cytherelloidea* in the late Campanian Santa Marta Formation of the James Ross Basin (Fauth *et al.,* 2003) suggests deposition in relatively warm shelf waters, while its absence in the overlying Snow Hill Island Formation may indicate that latest Campanian times coincided with somewhat more distal environments. Also, the sedimentological palaeotemperature proxies for this part of the sequence suggest high frequency fluctuations on an overall warm (but declining) signal (see Dingle & Lavelle, 2000, fig. 2). If it is the case, then the Snow Hill Island sections may also record a temperate/cool episode during which the *Rostrocytheridea hamiltonensis* populations adapted to waters cooler than the slightly earlier populations had experienced during deposition of the James Ross Island sequences. There is currently no record of ostracods from Maastrichtian strata in the James Ross Basin.

Ecological evidence is also sparse from Patagonia (~2000 km father north, Fig. 5). Ballent & Whatley's (2007, p. 123) assumption that the presence of *Rostrocytheridea* signified "warm... normal salinity, shallow-water environments" is no longer valid (given the cool, deeper water occurrences at Pukehou), while the shelfal warm-water indicator *Cytherelloidea* has not been reported from the late Cretaceous of Patagonia. This means that we have no

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[5] Originally described as *Tumidoleberis australis* sp. nov. by Bertels (1975), creating a subjective homonym of *Majungaella australis* sp. nov. Rossi de García & Proserpio (1980) (see Dingle & Majoran, 2001) which Whatley *et al.* (2005) have referred to *M. pseudonymos*.

unequivocal evidence for the thermal preference of the Campanian species *Rostrocytheridea*? sp. Ballent & Whatley (2007) from southern Patagonia, although for the middle Maastrichtian of northern Patagonia (which does not contain *Rostrocytheridea*), Bertels (1975) was able to infer (from the presence of "scarce" carinate planktonic foraminifera) that her species *Majungaella "australis"* (= *pseudonymos*) lived in relatively warm (minimum of 17ºC) outer shelf (minimum of 150m) conditions.

The fate of the various taxa across the K/T boundary in the Patagonia-northern Antarctic Peninsula area is unknown in detail, primarily because no Maastrichtian-Palaeocene ostracods have been recovered from the James Ross Basin. In Patagonia, Danian faunas have been described by Bertels (1973), but neither *Rostrocytheridea* nor *Majungaella* occur, and appear to have become extinct in South America. In contrast, the spiral-patterned *Cytherelloidea spirocostata* Bertels (or a very close relative) occurs both in the Campanian Santa Marta Formation (recorded as *C. megaspirocostata* by Fauth *el al*., 2003), and in Danian of northern Patagonia (Bertels, 1973).

The situation above the K/T boundary was different farther south. From the James Ross Basin (Fig. 5), Szczechura (2001) recorded both *Majungaella* and *Ameghinocythere* in the upper Eocene of Seymour Island (30 m below the horizon dated at ~34.2 My, Dingle *et al.,* 1998), but *Rostrocytheridea* is absent. This suggests that *Majungaella* locally survived the K/T extinctions, but whether or not this was the case with *Ameghinocythere* is more difficult to judge. This is because the Tertiary species of the genus from Seymour Island are more similar to *A. eagari* from the Maastrichtian of Pukehou than to the local *A. lutheri* from the Campanian of Snow Hill Island. This evidence, at face value, suggests that the latter colonised New Zealand in the ~8 My period before the end of the Maastrichtian, only for a species very similar to *A. eagari* to have reversely colonised the Antarctica Peninsula sometime during the following ~30 My.

Considering palaeoenvironments, the Eocene on Seymour Island is a pre-glacial sequence, but sedimentological and geochemical indicators suggest that the terrestrial climate was relatively cold, and marine conditions cool (Dingle *et al.,* 1998). This implies that by late Eocene time in the northern Antarctic Peninsula, *Majungaella* had adapted to significantly cooler conditions than had prevailed during deposition of the Late Campanian Santa Marta Formation on James Ross Island and the latest Maastrichtian Upper Laidmore Formation at Waipara (see relative positions in Fig. 5).

4.4. Summary of conclusions on ostracod distributions in southern Gondwanaland

Several palaeozoogeographical conclusions can be drawn from the present study, some of which are summarised in Figure 6.

1. The first appearance of the genus *Apateloschizocythere* Bate can probably be extended to New Zealand, while its later evolution took place in at least five Gondwanide locations. After its appearance in the Cenomanian of New Zealand (*A.*? *colleni*, sp. nov., this paper) it appeared and persisted until Santonian-Campanian time in Western Australia (*A. geniculata* Bate). It also occurs in the Coniacian of southern Africa (*A.* cf. *A. mclachlani* Dingle) and persisted until late Maastrichtian time (*A. laminata* Dingle). It also spread to deep-water on the edge of Antarctica (Maud Rise) (*A.* sp. Majoran & Widmark) where it persisted in Campanian to Palaeocene sediments (Majoran & Dingle, 2002). The genus is also known from mid-Maastrichtian strata in southern Egypt (Bassiouni & Luger 1990).

2. A genus para-homeomorphic to Bate's (1975) *Hystricocythere* appeared in New Zealand in Santonian times: *Parahystricocythere* evolved a modified hinge to produce an otherwise almost identical taxonomic group. *Hystricocythere* is first known from the Albian-Cenomanian of western Queensland (Krömmelbein 1975) and it ranged into the Campanian of Western Australia (Bate 1975). While communication between these regions of eastern Gondwanaland in early Upper Cretaceous time is not problematical, the issue of provenance for the two homeomorphs is not straightforward.

Ballent (1998, p.372) has recorded a species (*Hystricocythere*? sp.) that probably belongs to one of these two genera, from Albian sediments in the Austral Basin of Patagonia. Unfortunately all five of her specimens were carapaces and no new records have been made (Ballent, pers. comm., 2008), so we remain in doubt as to whether

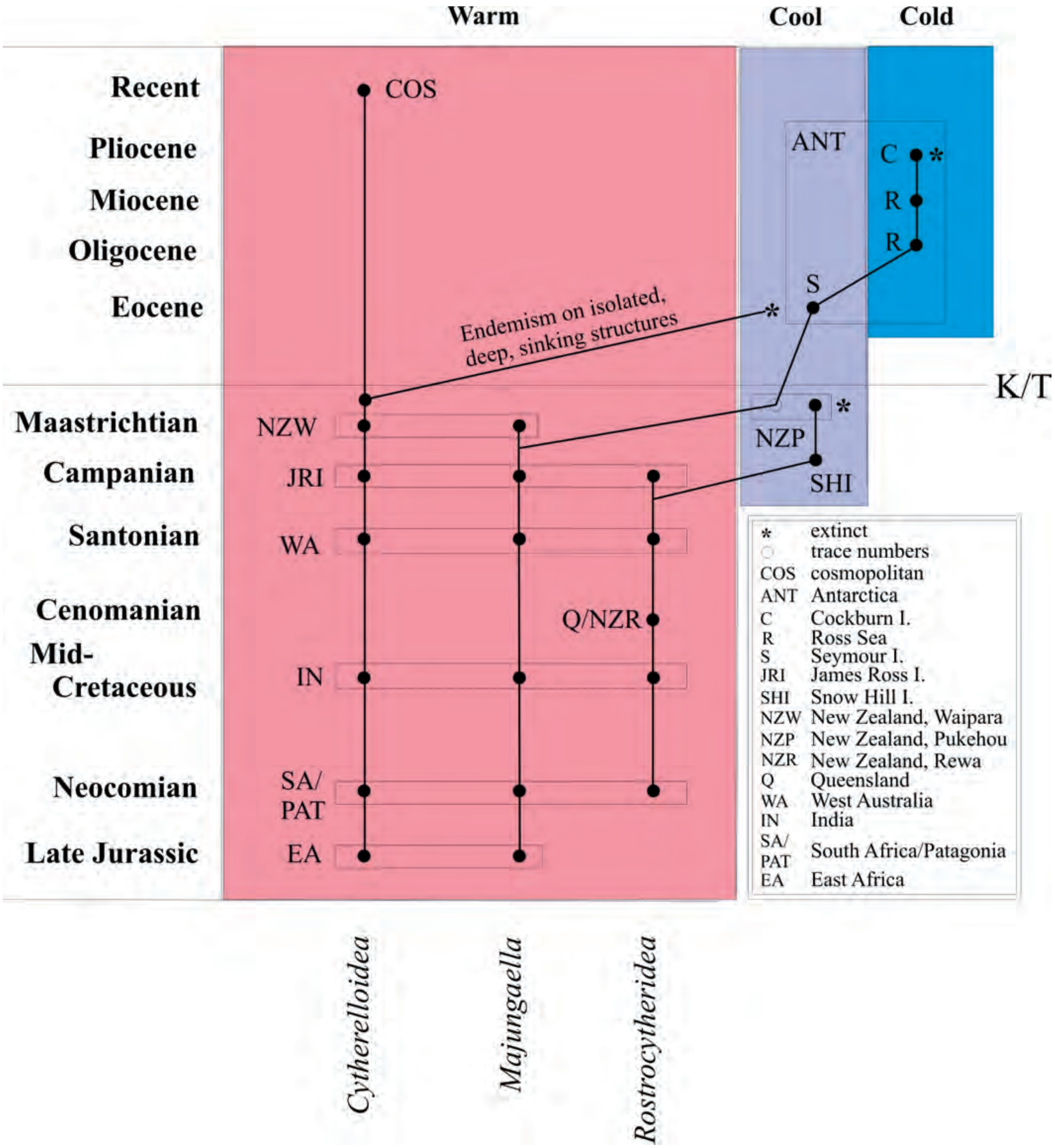

Figure 6. Temporal and spatial distribution of species of *Cytherelloidea*, *Majungaella* and *Rostrocytheridea* in Gondwanaland. Thermal preferences are indicated by shading, showing the date and locality of the acquisition of retrothermal tendencies, and extinctions, for *Majungaella* and *Rostrocytheridea*. The development of retrothermalism on sinking isolated oceanic features refers to central Pacific guyots (Boomer & Whatley, 1995) and the Maud Rise (Majoran & Widmark, 1998). Other data are based on numerous sources cited in the text, as well as the present study.

this species could be the nominal ancestor of the morphoplexus that originated the entomodont (*Parahystricocythere*) or hemimerodont (*Hystricocythere*) hinge.

3. *Rostrocytheridea*. Prior to the present study, the three records of this genus in Australasia were from Australian localities. *R. allaruensis* Krömmelbein (1975) occurs in the Albian-Cenomanian Allaru Mudstone [which was deposited in a wide, warm, shallow epi-continental, interior sea in western Queensland e.g. Ludbrook (1978, fig. 8, p. 237)], while *R. canaliculata* Bate (1972) and *R. westaustraliensis* (Chapman) occur in the Santonian of Western Australia [the latter lived in relatively warm, shallow water: Neale (1975, p. 76)]. These occurrences conformed to the previous perception of *Rostrocytheridea* as a warm-water taxon (e.g. Ballent & Whatley, 2007).

The abundance of *R. pukehouensis* from the Maastrichtian at Pukehou shows that by the end of Cretaceous times the genus had developed a retrothermal disposition, prior to its probable local extinction. The fact that the genus is represented by only a dubious single valve in the warm Maastrichtian habitat at Waipara suggests that this was not merely a response to the outer-shelf/upper slope setting at Pukehou.

It is intriguing to speculate on the date that a retrothermal habitat was acquired in New Zealand, and although the evidence is tenuous, I suggest that it post-dated Cenomanian time. This is because the solitary record of *R.* cf. *R. allaruensis*? in Cenomanian sample #50 at Rewa Stream is at a locality that, 30 My later, was still probably under warm water (Maastrichtian sample #48 contains *Scepticocythereis*? sp. 5044, which occurs elsewhere only in warm water facies at site #35). Johnston (1980, p.17) deduced that the Springhill Formation at Rewa Stream was deposited on the continental shelf, from which he identified at least six species of Ngataran Stage *Inoceramus*. The New Zealand Maastrichtian Pukehou occurrences are the youngest record of *Rostrocytheridea*.

Elsewhere, while *Rostrocytheridea* became extinct in Patagonia before Maastrichtian time (see Ballent & Whatley, 2007), it persisted in the James Ross Basin archipelago at least until deposition of the Late Campanian Snow Hill Island Formation (on Snow Hill Island - this paper).

4. *Majungaella* colonised much (if not all) of the Antarctic coastline during the Tertiary (e.g. Dingle & Majoran, 2001; Whatley *et al.,* 2005). It had adapted to the cool (pre-glacial) environments in the James Ross Basin by the end of Eocene time (Szczechura, 2001), and full-blown glacial waters by Oligocene time (Ross Sea: Dingle & Majoran, 2001). The earliest evidence of such retrothermal tendencies in the genus is *M*. sp. 4978 which occurs sparsely in the cool, late Maastrichtian outer shelf environment at Pukehou (this paper).

5. The presence of *Krithe* at Pukehou, which Hollis (1993) concluded was a relatively cool water locality, may be evidence of further retrothermalism (leading to deep-water habitation), in this case for an extant taxon that has had a long history of habitation on relatively warm continental shelves.

6. New data allow me to comment on one of the characteristic Cretaceous ostracod associations of Gondwanaland - the *Majungaella/Rostrocytheridea/Cytherelloidea* trio. Figure 6 summarises the history of this relationship over a period of ~70 My.

As pointed out above, shelfal species of *Cytherelloidea* predicate warm, shallow, marine waters, which suggests that both *Majungaella* and *Rostrocytheridea* favoured similar conditions when associated with it. *Majungaella* and *Cytherelloidea* are first recorded together in the late Jurassic subtropical proto-Indian Ocean gulf off East Africa (e.g. Bate 1975) and are joined by *Rostrocytheridea* in latest Jurassic-early Cretaceous time in southern Africa (e.g. Dingle, 1969) and the Neuquén Basin of Argentina (e.g. Musacchio, 1979). In southern Africa, the trio did not persist much beyond the Hauterivian, with *Rostrocytheridea* dying out by the mid-Cretaceous and *Majungaella* prior to the Campanian. Evidence for the trio's co-existence in similar habitats after Neocomian time in Argentina is equivocal, although all three taxa survived (separately) in the region until at least the Campanian (Ballent *et al.,* 1998; Ballent & Whatley, 2007).

Elsewhere in Gondwanaland, evidence for the tripartite relationship is more widespread: *Majungaella/Rostrocytheridea/Cytherelloidea* occur together in Albian to Cenomanian beds in the Kutch area of India (Andreu *et al.,* 2007), the Santonian of Western Australia (Bate, 1972;

Neale, 1975) and in the late Campanian Santa Marta Formation of James Ross Island (Fauth *el al.,* 2003). The latter was probably the last occasion on which they shared the same habitat, because *Cytherelloidea* is missing from the younger Campanian Snow Hill Island Formation on Snow Hill Island, while *Rostrocytheridea* is missing from the Campanian in Western Australia. In the former example, I suspect that the water temperatures may have dropped and only *Rostrocytheridea* could adapt, while in Australia this taxon became extinct.

Within the uppermost part of the Mesozoic succession at Waipara (within ~50 cm of the K/T) there are abundant *Cytherelloidea* and *Majungaella*, but I found only one uncertain coexisting representative of *Rostrocytheridea*. Four hundred kilometres away, in the deeper cool waters at Pukehou, *Cytherelloidea* was absent, and dominant *Rostrocytheridea* coexisted with the earliest known, but very rare, retrothermal species of *Majungaella* (*M.* sp. 4978).

In summary. There is no evidence to suggest that *Cytherelloidea* acquired a general retrothermal tendency (in contrast to relatively short-lived retrothermal endemism induced by isolated, sinking of oceanic structures - Fig. 6 - see discussion above), while latest Campanian demes of *Rostrocytheridea hamiltonensis* may have occupied cool habitats in the Antarctic Peninsula (Snow Hill Island Formation) and certainly *R. pukehouensis* inhabited such upper Maastrichtian niches in New Zealand. While species of *Majungaella* (sp. 4978) had developed a retrothermal disposition at least by the latest Maastrichtian time (at Pukehou), the tendency may have developed by mid-Upper Cretaceous times in *M*. sp. K9A3 which Dingle (1996) recorded (but unfortunately did not illustrate) in Albian-Santonian continental slope (and presumably cool water) sediments from off southern Namibia. (See McMillan 1990 for a discussion of the K9A3 environment). By Eocene time, only retrothermal Antarctic species of *Majungaella* were extant (Fig. 6).

6. The earliest known species of *Ameghinocythere* (*A. lutheri* sp. nov.) is from the late Campanian Snow Hill Island Formation, but this is less similar to Palaeogene-Recent South American species of the genus than *A. eagari* sp. nov. from the latest Maastrichtian, cool waters of Pukehou. The latter is very close to ?*A.* cf. *Cytheromorpha*? *flexuosa* Bertels (Szczechura, 2001) which lived in the cool late Eocene sea of Seymour Island in the James Ross Basin. There are similar species in the late Oligocene and early Miocene glacio-marine sediments of the Ross Sea area (Dingle, 2000; Dingle & Majoran, 2001), and contemporaneously in Patagonia (see Echevarria, 1991, who recorded it as *Cytheromorpha*? sp.).

4.5. Age of the Hobb's Glacier Formation, James Ross Island

The type outcrop of this formation at Rabot Point (Pirrie *et al.*, 1997b) has been dated using strontium isotopes as Miocene (9.9 Ma; Dingle & Lavelle, 1998b). The ostracod fauna described herein from an outcrop (DJ677.3) of the supposed formation at Hamilton Point (Pirrie, 1995) is clearly of late Cretaceous age. Hence, either the two sequences are not coeval, or the latter is from a clast of Cretaceous clay incorporated within the Miocene glacial horizon.

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6. REFERENCES

Andreu, B., Colin, J. P. & Singh, J. 2007. Cretaceous (Albian to Coniacian) ostracodes from the subsurface of the Jaisalmer Basin, Rajasthan, India. *Micropaleontology*, 53(5), 345-370.

Athersuch, J. 1979. On *Pelecocythere sylvesterbradleyi* Athersuch gen. et sp. nov. *Stereo-Atlas of Ostracod Shells*, 6, 13-20.

Ayress, M.A. 1993a. Middle Eocene Ostracoda (Crustacea) from the coastal section, Bortonian Stage, at Hampden, South Island, New Zealand. *New Zealand Natural Sciences*, 20, 15-21.

Ayress, M.A. 1993b. Ostracod biostratigraphy and palaeoecology of the Kokoamu Greensand and Otekaike Limestone (Late Oligocene to Early Miocene), North Otago and South Canterbury, New Zealand. *Alcheringa*, 17, 125-151.

Ayress, M.A. 1995. Late Eocene Ostracoda (Crustacea) from the Waihao District, South Canterbury, New Zealand. *Journal of Paleontology*, 69 (5), 897-921.

Ballent, S.C. 1998. Ostrácodos del Albiano de la Cuenca Austral, Argentina. *Ameghiniana*, 35 (4), 355-377.

Ballent, S.C., Ronchi, D.I. & Whatley, R.C. 1998. The ostracod genus *Majungaella* Grekoff in Argentina. *Revista Geologica de Chile*, 25 (1), 45-55.

Ballent, S.C. & Whatley, R.C. 2007. The distribution of the gondwanide ostracod *Rostrocytheridea* Dingle: palaeozoological implications, *Geological Journal*, 42, 113-125.

Bassiouni, M.A.A. & Luger, P. 1990. Maastrichtian to Early Eocene Ostracoda from southern Egypt. Palaeontology, palaeoecology, palaeobiogeography and biostratigraphy. *Berliner Geowissenschaftliche Abhandlungen (A)*, 120 (2), 755-928.

Bate, R.H. 1972. Upper Cretaceous Ostracoda from the Carnarvon Basin, Western Australia. *Special Papers in Palaeontology*, 10, 1-85.

Bate, R.H. 1975. Ostracods from Callovian to Tithonian sediments of Tanzania, East Africa. *Bulletin of the British Museum (Natural History), Geology*, 26 (5), 163-223.

Bertels, A. 1973. Ostracodes of the type locality of the Lower Tertiary (lower Danian) Rocanian Stage and Roca Formation of Argentina. *Micropaleontology*, 19 (3), 308-340.

Bertels, A. 1975. Upper Cretaceous (middle Maastrichtian) ostracodes of Argentina. *Micropaleontology*, 21 (1), 97-130.

Bertels, A. 1977. Cretaceous Ostracoda - South Atlantic. In: Swain, F. M. (Ed.), *Stratigraphic Micropaleontology of Atlantic Basin and Borderlands*. Elsevier, Amsterdam, 271-304.

Błaszyk, J. 1987. Ostracods from the Oligocene Polonez Cove Formation of King George Island, West Antarctica. *Palaeontologia Polonica*, 49, 63-81.

Boomer, I. & Whatley, R.C. 1995. Cenozoic Ostracoda from guyots in the western Pacific: Holes 865B and 866B (Leg 143). In. Winterer, E.L., Sager, W.W., Firth, J.V. & Sinton, J.M. (eds). *Proceedings of the Ocean Drilling Program, Scientific Results*, 143, 75-86. College Station, Texas.

Chapman, F. 1917. Monograph of the Foraminifera and Ostracoda of the Gingin Chalk. *Bulletin of the Geological Survey of Western Australia*, 72, 1-87.

Coles, G.P., Whatley, R.C. & Moguilevsky, A. 1994. The ostracod genus *Krithe* from the Tertiary and Quaternary of the North Atlantic. *Palaeontology*, 37 (1), 71-120.

Dingle, R.V. 1969. Marine Neocomian Ostracoda from South Africa. *Transactions of the Royal Society of South Africa*, 38, 139-164.

Dingle, R.V. 1971. Some Cretaceous ostracodal assemblages from the Agulhas Bank (South African continental margin). *Transactions of the Royal Society of South Africa*, 39, 393-418.

Dingle, R. V. 1980. Marine Santonian and Campanian Ostracods from a borehole at Richards Bay, Zululand. *Annals of the South African Museum*, 82 (1), 1-70.

Dingle, R.V. 1981. The Campanian-Maastrichtian Ostracoda of South-East Africa. *South African Museum Annals*, 85, 1-181.

Dingle, R.V. 1985. Turonian, Coniacian and Santonian Ostracoda from south-east Africa. *South African Museum Annals*, 96 (5), 123-239.

Dingle, R.V. 1994. Quaternary ostracods from the continental margin off south-western Africa. Part III. Oceanographical and sedimentary environments. *Annals of the South African Museum*, 103 (7), 383-441.

Dingle, R.V. 1995. Report of field work undertaken in the Snow Hill-James Ross Islands area and around Low Head, King George Island: December 1994-February 1995. *British Antarctic Survey, Report Gen\1994\GL1* (unpublished), 17 pp.

Dingle, R V. 1996. Cretaceous Ostracoda of the SE Atlantic & SW Indian oceans: a stratigraphical review and atlas. In: Jardine, S., Klasz, I, de & Debenay, J.P. (Eds) *Geologie de l'Afrique et de l'Atlantique Sud. Actes Colloques Angers 1994. Bulletin des Centres Recherches Exploration-Production Elf-Aquitaine, Memoire*, 16, 1-17.

Dingle, R.V. 2000. Ostracoda from CRP-1 and CRP-2/2A,Victoria Land Basin, Antarctica. *Terra Antartica*, 7(4), 479-492.

Dingle, R.V. 2003. Some palaeontological implications of putative, long-term, gene reactivation. *Journal of the Geological Society, London*, 160, 815-818.

Dingle, R.V. & Lavelle, M. 1998a. Late Cretaceous - Cenozoic climatic variations of the northern Antarctic Peninsula: new geochemical evidence and review. *Palaeogeography Palaeoclimatology Palaeoecology*, 141, 215-232.

Dingle, R.V. & Lavelle, M. 1998b. Antarctic Peninsular cryosphere: Early Oligocene (c. 30Ma) initiation and a revised glacial chronology. *Journal of the Geological Society, London*, 155, 433-437.

Dingle, R.V. & Lavelle, M. 2000. Antarctic Peninsula Late Cretaceous-Early Cenozoic palaeoenvironments and Gondwana palaeogeographies. *Journal of African Earth Sciences*, 31 (1), 91-105.

Dingle, R.V., Lord, A.R. & Boomer, I.D. 1990. Deep-water Quaternary Ostracoda from the continental margin off south-western Africa. (SE Atlantic Ocean). *South African Museum Annals*, 99 (9), 245-366.

Dingle, R.V., Marenssi, S.A. & Lavelle, M. 1998. High latitude Eocene climate deterioration: evidence from the northern Antarctic Peninsula. *Journal of South American Earth Sciences*, 11 (6), 571-579.

Dingle, R.V. & Majoran, S. 2001. Palaeo-climatic and -biogeographical implications of Oligocene Ostracoda from CRP-2/2A and CRP-3 drillholes, Victoria Land Basin, Antarctica. *Terra Antartica*, 8 (4), 369-382.

Dingle, R.V., McMillan, I.K., Majoran, S. & Bisset, L. 2001. Palaeo-oceanographical implications of Early-Middle Miocene subtropical ostracod faunas from the continental shelf of the SE Atlantic Ocean. *Palaeogeography Palaeoclimatology Palaeoecology*, 173, 43-60.

Echevarria, A.E. 1991. Ostrácodos del Oligoceno del sudeste del Lago Cardiel, Santa Cruz, Argentina. *Ameghiniana*, 28, 267-285.

Fauth, G., Seeling, J. & Luther, A. 2003. Campanian (Upper Cretaceous) ostracods from southern James Ross Island, Antarctica. *Micropaleontology*, 49 (1), 95-107.

Hall, W.D.M. 1963. The Clarence Series at Coverham, Clarence Valley. *New Zealand Journal of Geology and Geophysics*, 6 (1), 28-37.

Hall, W.D.M. 1964. *The Geology of Coverham and the upper Waima Valley, Marlborough*. Unpublished MSc thesis, Victoria University, Wellington, 82 pp.

Hartmann, G. 1997. Antarktische und Subantarktische Podocopa (Ostracoda). *Synopses of the Antarctic Benthos*, Edit. Wägele, J.W. & Sieg, J. Volume 7. Koenigstein, Koeltz Scientific Books, 355 pp.

Henderson, R.A. 1973. Clarence and Raukumara Series (Albian-?Santonian) Ammonoidea from New Zealand. *Journal of the Royal Society of New Zealand*, 3 (1), 71-123.

Hollis, C.J. 2003. The Cretaceous/Tertiary boundary event in New Zealand: profiling mass extinction. *New Zealand Journal of Geology and Geophysics*, 46, 307-321.

Hollis, C.J. & Strong, C.P. 2003. Biostratigraphic review of the Cretaceous/Tertiary boundary transition, mid-Waipara River section, North Canterbury, New Zealand. *New Zealand Journal of Geology and Geophysics*, 46, 243-253.

Hornibrook, N. de B. 1952. Tertiary and Recent marine Ostracoda of New Zealand: their origin, affinities, and distribution. *New Zealand Geological Survey Palaeontological Bulletin*, 18, 82 pp.

Hornibrook, N. de B. 1953. Some New Zealand Tertiary Marine Ostracoda useful in stratigraphy. *Transactions of the Royal Society of New Zealand*, 82 (2), 303-311.

Johnston, M.R. 1980. Geology of the Tinui-Awatoitoi District. *New Zealand Geological Survey Bulletin,* 94, 62 pp.

Kingma, J.T. 1971. Geology of the Te Aute Subdivision. *New Zealand Geological Survey Bulletin n. s.,* 70, 173 pp.

Krömmelbein, K. 1975. Ostracoden aus der Kreide des Great Artesian Basin, Queensland, Australien. *Senckenbergiana Lethaea*, 55, 455-483.

Lawver, L.A., Gahagan, L.M. & Coffin, M.F. 1992. The development of paleoseaways around Antarctica. The Antarctic paleoenvironment: a perspective on global change. *American Geophysical Union, Antarctic Research Series*, 56, 7-30.

Ludbrook, N.H. 1978. Australia. In: *The Phanerozoic Geology of the World II. The Mesozoic, A.* Moullade, M. & Nairn, A. E. M. (Eds), Elsevier Scientific Publishing, Amsterdam, 209-249.

Majoran, S. 1996a. Late Eocene Ostracoda of the Blanche Point Formation, South Australia. *Revista Española de Paleontología,* 11 (1), 18-34.

Majoran, S. 1196b. On *Scepticocythereis sanctivincentis* Majoran sp. nov. *Stereo-Atlas of Ostracod Shells*, 23 (5), 17-20.

Majoran, S. & Dingle, R.V. 2001. Palaeoceanographical changes recorded by Cenozoic deep-sea ostracod assemblages from the South Atlantic and the Southern Ocean (ODP Site 1087 and 1088). *Lethaia*, 34, 63-83.

Majoran, S. & Dingle, R.V. 2002. Cenozoic deep-sea ostracods from Maud Rise, Weddell Sea, Antarctica (ODP Site 689): a palaeoceanographical perspective. *Geobios*, 35, 137-152.

Majoran, S. & Widmark, J. G. V. 1998. Response of deep-sea ostracod assemblages to Late Cretaceous palaeoceanographical changes: ODP Site 689 in the Southern Ocean. *Cretaceous Research*, 19, 843-872.

Majoran, S., Widmark, J.G.V. & Kucera, M. 1997. Palaeoecological preferences and geographical distribution of Late Maastrichtian deep-sea ostracods in the South Atlantic. *Lethaia,* 30, 53-64.

McKenzie, K.G., Reyment, R.A. & Reyment, E.R. 1991. Eocene-Oligocene Ostracoda from South Australia and Victoria, Australia. *Revista Española de Paleontología,* 6 (2), 135-175.

McKenzie, K.G., Reyment, R.A. & Reyment, E.R. 1993. Eocene Ostracoda from the Browns Creek Clays at Browns Creek and Castle Cove, Victoria, Australia. *Revista Española de Paleontología*, 8 (1), 75-116.

McMillan, I. K. 1990. Foraminiferal biostratigraphy of the Barremian to Miocene rocks of the Kudu 9A-1, 9A-2 and 9A-3 boreholes. *Communications of the Geological Survey of Namibia*, 6, 23-29.

Milhau, B. 1993. Nouveaux ostracodes du Miocène inférieur de Nouvelle-Zélande. *Geobios*, 26 (2), 161-200.

Moore, R.C. 1961. *Treatise on Invertebrate Paleontology. Part Q, Arthropoda 3, Crustacea, Ostracoda*. University of Kansas Press, 442 pp.

Musacchio, E.A. 1979. Ostrácodos del Cretácico Inferior en el Grupo Mendoza, Cuenca del Neuquén, Argentina. *VII Congreso Geológico Argentino, Neuquén, Actas,* II, 459-473.

Neale, J. W. 1975. The ostracod fauna from the Santonian chalk (Upper Cretaceous) of Gingin, Western Australia. *Special Papers in Palaeontology*, 16, 1-81.

Neale, J.W. 1984. The Ostracoda and Uniformitarianism. II The earlier record: Cretaceous to Cambrian). *Proceedings of the Yorkshire Geological Society*, 44 (4), 442-478.

Neale, J.W. 1988a. The anatomy of the ostracod *Pelecocythere purii* sp. nov. and some features connected with the abyssal mode of life in this and some other deep water forms. In: Hanai, T., Ikeya, N. & Ishizaki, K. (eds), *Evolutionary Biology of Ostracoda*. Kodansha-Elsevier, Tokyo, 709-720.

Neale, J.W. 1988b.Ostracoda - a historical perspective. In: Hanai, T., Ikeya, N. & Ishizaki, K. (eds), *Evolutionary Biology of Ostracoda*. Kodansha-Elsevier, Tokyo, 3-15.

Pirrie, D. 1995. The Sedimentology and Stratigraphy of South East James Ross Island, Antarctica. Field Report 1994/1995 Antarctic Field Season. Unpublished *British Antarctic Survey Report*, 35 pp.

Pirrie, D., Crame, J.A., Lomas, S.A. & Riding, J.B. 1997a. Late Cretaceous stratigraphy of the Admiralty Sound region, James Ross Basin, Antarctica. *Cretaceous Research*, 18, 109-137.

Pirrie, D. Crame, J.A., Riding, J.B., Butcher, A.R. & Taylor, P.D. 1997b. Miocene glaciomarine sedimentation in the northern Antarctic Peninsula region: the Hobbs Glacier Formation, James Ross Island. *Geological Magazine*, 136, 745-762.

Rossi de García, E. & Proserpio, C. 1980. Ostrácodos del Cretácico superior de la Patagonia, República Argentina (Hoja 44e, Valle General Racedo). Chabut. In: *Congreso Argentino de Paleontología y Bioestratigrafía, No. 2, Actas y Congreso Latinoamericano de Paleontología, No.1, Actas,* Vol. 2, 15-34.

Sohn, I.G. 1962. The ostracode genus *Cytherelloidea*, a possible indicator of paleotemperature. *United States Geological Survey Professional Paper*, 450-D, D144-D147 (Article 162.

Strong, C.P. 1977. Cretaceous-Tertiary boundary at Woodside Creek, north-eastern Marlborough. *New Zealand Journal of Geology and Geophysics*, 20 (4), 687-696.

Strong, C.P. 1984. Cretaceous-Tertiary boundary, Mid-Waipara River section, North Canterbury, New Zealand. *New Zealand Journal of Geology and Geophysics*, 27, 231-234.

Szczechura, J. 2001. Ostracods from the Eocene of Seymour Island, Antarctic Peninsula. *Palaeontologia Polonica*, 60, 157-181.

Szczechura, J. & Błaszyk, J. 1996. Ostracods from the *Pecten* Conglomerate (Pliocene) of Cockburn Island, Antarctic Peninsula. *Palaeontologia Polonica*, 55, 175-186.

Sutherland, R., King, P. & Wood, R. 2001. Tectonic evolution of Cretaceous rift basins in south-eastern Australia and New Zealand. *Petroleum Exploration Society of Australia, Eastern Australian Basins Symposium, Melbourne*, 3-13.

Swanson, K.M. 1969. Some Lower Miocene Ostracoda from the Middle Waipara District, New Zealand. *Transactions of the Royal Society of New Zealand*, 7 (3), 33-48.

van Morkhoven, F.P.C.M. 1963. *Post-Palaeozoic Ostracoda. Volume II, Generic Descriptions*. Elsevier, Amsterdam, 478 pp.

Webb, P. N. 1971. New Zealand Late Cretaceous (Haumurian) foraminifera and stratigraphy. *New Zealand Journal of Geology and Geophysics*, 14 (4), 795-828.

Whatley, R.C. & Ballent, S.C. 1996. A review of the Mesozoic ostracod genus *Progonocythere* and its close allies. *Palaeontology*, 39 (4), 919-939.

Whatley, R.C. & Coles, G. 1987. The Late Miocene to Quaternary Ostracoda of Leg 94, Deep Sea Drilling Project. *Revista Española de Micropaleontología*, 19 (1), 33-97.

Whatley, R.C., Ballent, S.C. & Szczechura, J. 2005. Antarctic Tertiary Progonocytheridae: The last refuge of *Majungaella*, the survivor of a long lineage, a geographical and physiological migration from low to high latitudes. *Palaeogeography Palaeoclimatology Palaeoecology*, 225, 302-316.

Whatley, R.C., Chadwick, J., Coxill, D. & Toy, N. 1988. The ostracod family Cytheruridae from the Antarctic and south-west Atlantic. *Revista Española de Micropaleontología*, 20 (2), 171-203.

Whatley, R.C., Moguilevsky, A., Toy, N., Chadwick, J. & Ramos, M.I.F. 1997. Ostracoda from the south west Atlantic. Part III. The littoral fauna from between Tierra del Fuego and the Rio de la Plata. *Revista Española de Micropaleontología*, 29, 5-83.

Wilson, D.D. 1963. Geology of Waipara Subdivision (Amberley and Motunau Sheets S68 and S69). *New Zealand Geological Survey Bulletin, n. s.* 64, 122 pp.

Zhao, Q. & Wang, P. 1988. Distribution of modern Ostracoda in the shelf seas off China. In: Hanai, T., Ikeya, N. & Ishizaki, K. (Eds), *Evolutionary Biology of Ostracoda*. Kodansha-Elsevier, Tokyo, 805-821.

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Transported foraminifera in Palaeozoic deep red nodular limestones exemplified by latest Permian *Neoendothyra* in the Zal section (Julfa area, NW Iran)

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Resumen

Se describen e ilustran los foraminíferos y algas del Pérmico Superior (Changhsingense) de la sección de Zal en el noroeste de Irán. La asociación se encuentra compuesta por las algas *Permocalculus* y *Gymnocodium*, asociadas a pequeños foraminíferos Fusulinata Biseriamminoidea, Palaeotextularioidea, Miliolata Cornuspiroidea y Nodosariata, y proceden de calizas rojas nodulares de tipo Ammonitico-Rosso. Los Fusulinida *Nankinella, Reichelina* y *Codonofusiella* se encuentran en la base, mientras que los últimos niveles del Pérmico contienen abundantes *Neoendothyra reicheli*, cuyo tipo de depósito es discutido en el presente trabajo, así como la presencia de las calizas rojas nodulares en el Paleozoico.

Palabras clave: Foraminíferos, Pérmico Superior, Triasico Inferior, Bioestratigrafía, Tafonomía, Irán.

Abstract

The foraminifera and algae of the Zal section in NW Iran and from the Changhsingian Ali Bashi Formation (Late Permian) are listed and illustrated. They are composed by *Permocalculus* and *Gymnocodium* algae, *Codonofusiella*, *Reichelina* and *Nankinella,* Fusulinida and Cornuspiroidea, Nodosariata, Biseriamminodea and Palaeotextularioidea. They are included in red nodular limestones of Ammonitico Rosso type. The highest Permian beds contain an assemblage of *Neoendothyra reicheli*, whose type of deposit is discussed as an example of the problematic presence of foraminifera in red nodular limestones during the Palaeozoic. These populations may have been transpoted by buoyancy (as *Neoendothyra*) but appear also in place in the Devonian-Tournaisian examples of griotte nodular limestones in southern France including the taxa *Eotournayella*, *Eoeptotournayella* or *Globivavulina*?

Keywords: Foraminifera, Late Permian, Early Triassic, Biostratigraphy, Taphonomy, Iran.

1. INTRODUCTION

Important P/T boundary sections are located in Iran, for example in NW, NE and Central Iran and in the Alborz region (all belonging to the Iranian Plate), and in the Zagros fold belt (belonging to the Arabian Plate).

There are almost continuous sedimentary marine sequences across the Permian-Triassic boundary in Iran. These sections are among the best sections in the world, which extend over a distance of more than 1400 km from the Julfa area in the northwest to the Hambast Range in Central Iran. The Iranian sections provide good examples for studying the P/T-Extinction event because they are probably the only pelagic sections in the world without an anoxia event at the P/T boundary. Late Permian foraminiferal assemblages from the Hambast region of

Central Iran and their extinction have recently been described by Mohtat-Aghai and Vachard (2005). Isotope studies across the P/T-boundary at Shahreza, Central Iran, and Zal and Julfa, northwest Iran, are presented by Korte *et al.* (2004a) and Kozur (2004), in Shareza by Korte *et al.* (2004b), and in Julfa by Korte *et al.* (2004c) and Korte and Kozur (2005). Kozur (2007) discussed the biostratigraphy and event stratigraphy in Iran around the Permian-Triassic Boundary.

In this paper, the marine limestones of latest middle Permian to late Permian age and of the Permian-Triassic boundary of Northwest Iran (Julfa/Zal range) were studied with respect to microfacies, palaeogeography and biostratigraphy. More than 100 samples were collected for thin section preparation from the Zal section, and 45 samples from the Julfa area.

Foraminifera are one of the most important index microfossils due to their worldwide distribution and accurate stratigraphic ranges. They are in particular, an excellent tool for testing biological crises. Foraminifera have been utilized for the K/T crisis, but can also be of interest for the P/T crisis. This remarkable event is the largest of the five major extinctions, and referred to by Erwin (1993) as "the mother of mass extinctions". According to Sepkoski (1989, 1990, 1992) perhaps as many as 90% of all the species from the late Permian disappeared during the P/T crisis. Post-extinction recovery of plant and marine ecosystems was slow, occurring over 4-5 million years (e.g. Looy *et al.*, 1999; Erwin, 2001). Paradoxically, in the Zal section, the environment, although unfavourable for foraminifera (deep-sea nodular limestones) shows a rapid increase of the genus *Neoendothyra* just below the PTB. The aim of this paper is to emphasize this phenomenon, to try to find some explanations for this increase, and provide some conclusions about the relation between the deep nodular limestone and the foraminifera during the Late Palaeozoic.

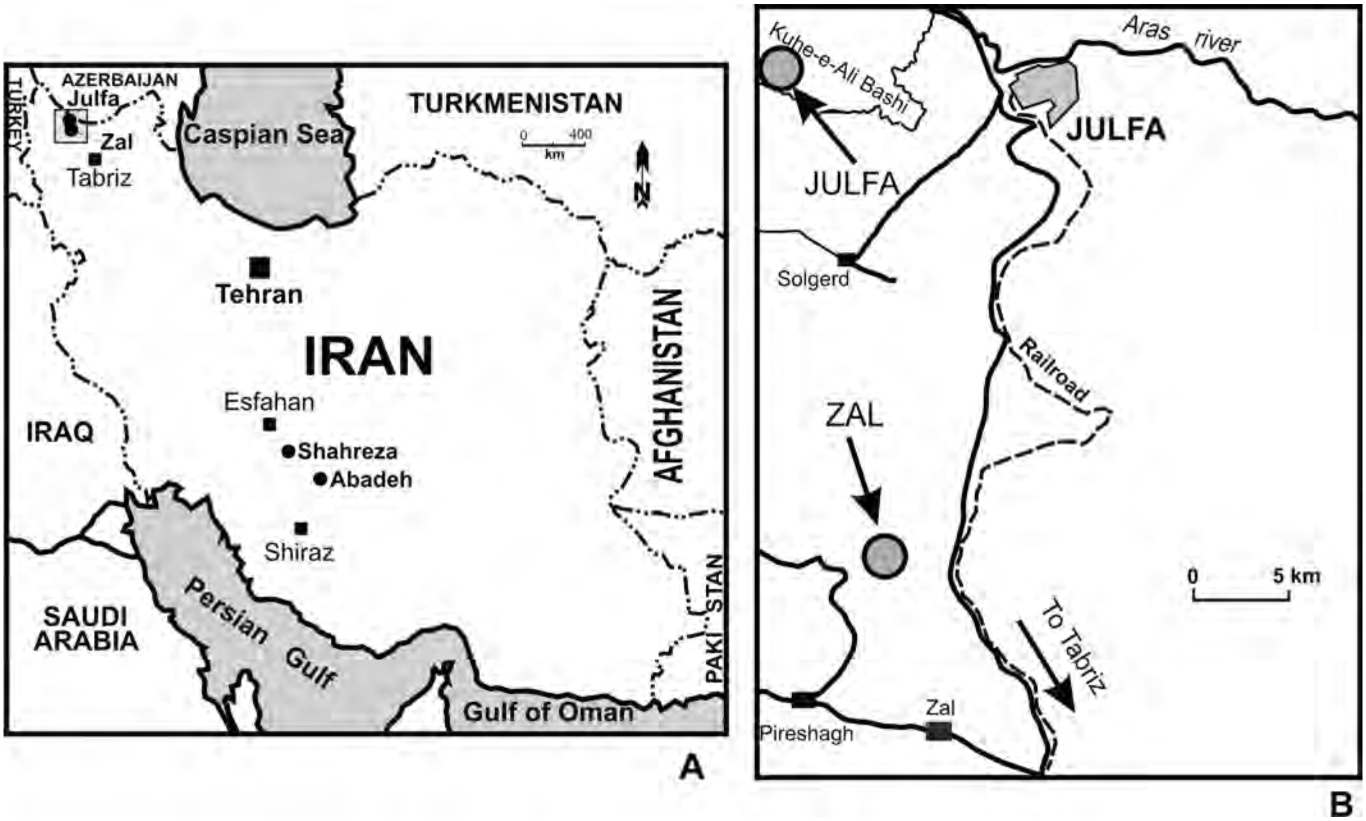

Figure 1. Maps showing locations of important P/T boundary sections in Iran (A) and the studied sections Julfa (Ali Bashi) and Zal in the Julfa area, NW Iran (B).

2. GEOLOGICAL SETTING

Iran essentially comprises eight different geological provinces. Most important for the Permian palaeobiogeography and biostratigraphy is the Sanandaj-Sirjan thrust belt located in the northwestern part of Iran, where the Julfa and Zal sections are located. Permian/Triassic Boundary sections are known from Julfa (NW Iran) and Abadeh/Shahreza (Central Iran) (e.g. Partoazar, 1995). The Permian-Triassic boundary beds are well known from the Julfa area (NW Iran) and have been described by several authors (Ruzhentsev and Sarytcheva, 1965; Stepanov *et al.*, 1969; Teichert *et al.*, 1973; Altiner *et al.*, 1979; Partoazar, 1995, 2002). Whereas the Ali Bashi section is particularly well studied the Zal section is less well studied (Korte *et al.*, 2004a, Kozur, 2007).

The Julfa and Zal sections belong to the Sanandaj-Sirjan belt, a geological province which extends from the Persian Gulf to Northwest Iran. This belt is interpreted as part of the Tethyan microcontinent (terrane), which was obducted from the African-Arabian plate during the Permian. This belt was formed by the coalescence of several blocks or microplates and was located near to the Equator during Late Permian and Early Triassic time (e.g. Scotese and Langford, 1995).

According to the most classical geodynamic hypothesis, the architecture of the Sanandaj Sirjan basin during the Late Permian was controlled by the opening of the Neotethys from Australia to the east Mediterranean area (e.g. Sharland *et al.,* 2001). This opening corresponds to the drifting of the Cimmerian superterrane and the final closing of Palaeotethys northward in the Middle Triassic time.

We studied samples from the Julfa and Zal sections which are located in a NW-SE trending range about 160 km North of Tabriz, in the province of East Azerbaijan (Fig. 1, 2). The very fossiliferous Julfa section Kuh-e-Ali Bashi is located about 10 km west of the town of Julfa in northwest Iran. The Zal section is located 22 km SSW of the town of Julfa and 4 km NE of the village Pireshagh (38°44´S and 45° 35´ E) (Fig. 1). Partoazar (1995) distinguished four lithologic units (units A-D) and 10 subunits in the Permian and four units (units E-H) in the early Triassic. In this paper only the subunits 8-10 in the Permian and the lower part of unit (E) in the Early Triassic are studied (Fig. 2). The Upper Permian - Lower Triassic successions of Julfa and Zal are very similar and consist of the (1) Julfa Formation (units A-B of Partoazar, 1995) composed of grey limestones of late Midian/Dzhulfian (i.e. Capitanian/Wuchapingian) age, (2) Ali Bashi Formation (units C-D of Partoazar, 1995) composed of reddish nodular ammonoid-bearing (*Paratirolites*) limestones of Dorashamian/Changhsingian age and (3) Elika Formation (unit E of Partoazar, 1995) characterized by grey, thin bedded limestones of Early Triassic age. These Formations are subdivided into lithostratigraphical units with different micro- and macrofossil assemblages comprising foraminifera, conodonts, fish plates, calcareous algae, ostracods, brachiopods, crinoids, gastropods, rugose corals, nautiloids and ammonoids.

3. LITHOLOGY

3.1. Julfa Formation (Unit B, Subunit 8)

In the Zal section the upper 36 m of the Julfa Formation are composed of thin bedded dark grey to black micritic fossiliferous limestone containing ammonoids, brachiopods, bryozoans, corals, crinoids and mollusk shells. These limestones are even bedded in the lower part and form limestone horizons up to 2 m thick. In the upper part thin (mostly 10-20 cm) wavy to nodular micritic limestone beds are intercalated in dark grey to grey and brown marly shales and marls. The marly shale and marl intercalations are up to 2 m thick. Limestones are composed of bioclastic mudstones and wackestones. Three fossils assemblage zones have been distinguished by Partoazar (1995), the lower two coinciding with the lower Julfa Beds and the third with the upper Julfa Beds:

a) *Araxilevis-Orthotetina* Zone (corresponding to the *Araxilevis* beds of the type-Dzhulfian),

b) *Pseudogastrioceras* - *Permophricodothyris* Zone (corresponding to the *Araxoceras-Oldhamina* beds of the type-Dzhulfian), and

c) *Haydenella-Pseudowellerella* Zone (corresponding to the *Vedioceras Haydenella* beds of the type-Dzhulfian).

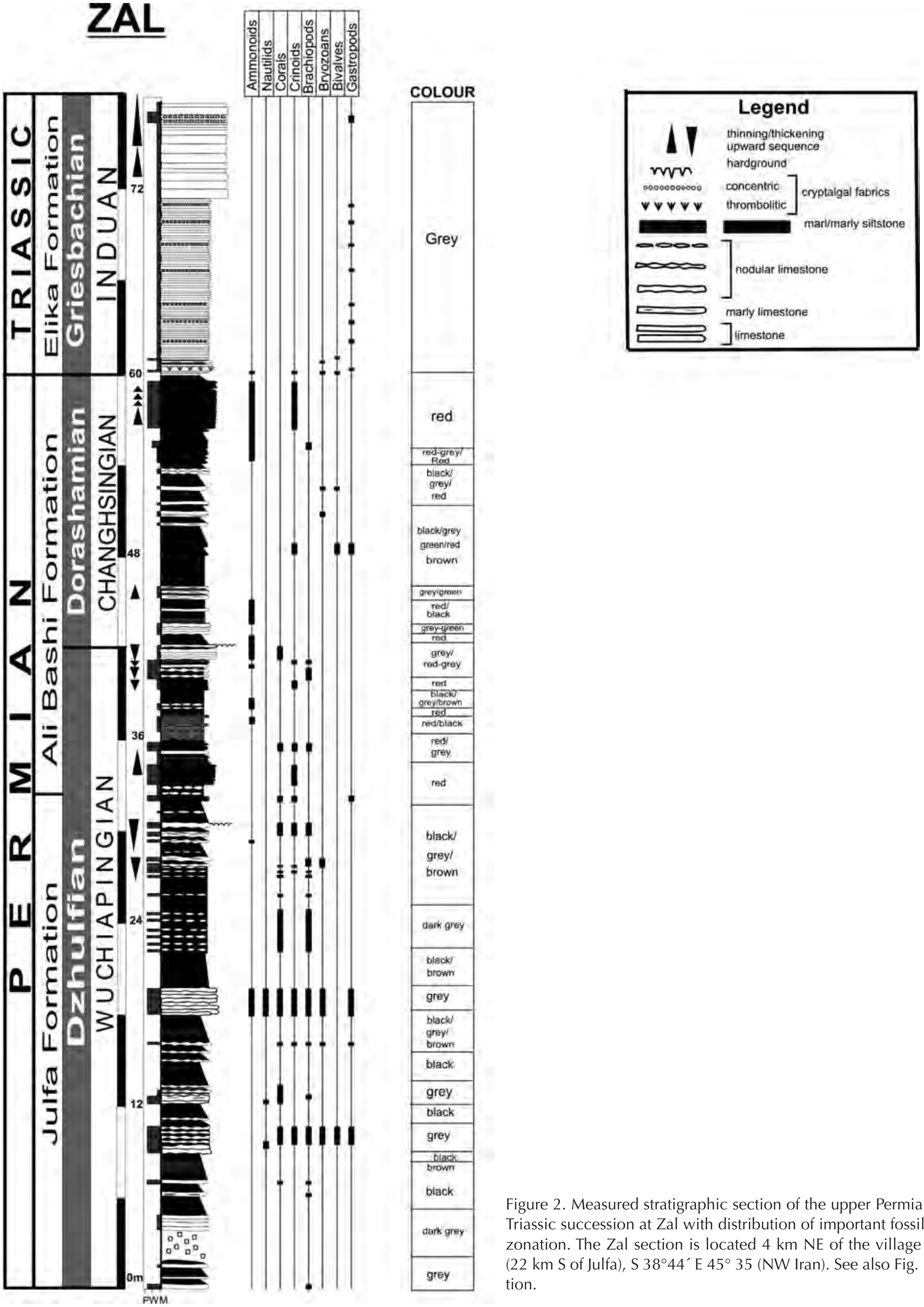

Figure 2. Measured stratigraphic section of the upper Permian to lower Triassic succession at Zal with distribution of important fossils and biozonation. The Zal section is located 4 km NE of the village Pireshagh (22 km S of Julfa), S 38°44´ E 45° 35 (NW Iran). See also Fig. 1 for location.

The upper 10 m the Julfa Formation (unit 3) consist of grey and reddish-grey marls, shales and micritic limestones (mud- and wackestone) which can be correlated with the late Dzhulfian *Vedioceras* Beds. The limestones are strongly bioturbated and nodular. The fossil assemblage includes abundant brachiopods, crinoids, bryozoans, colonial rugose corals, gastropods, ammonoids and nautiloids. The microfauna is represented by foraminifera, ostracods and conodonts. The fauna indicates a late Dzhulfian (Wuchiapingian) age. The uppermost part of the Julfa Formation is marked by a 4 m thick cliff-forming succession of reddish-grey marls und nodular marly limestones grading upwards into reddish-grey nodular micritic limestones with transported corals.

The depositional environment of the Julfa Formation is interpreted as shallow to middle shelf with maximum water depths of less than 100 m.

3.2. Ali Bashi Formation (Units C-D, Subunits 9-10)

We draw the boundary between the Julfa and Ali Bashi Formation at the base of the first red coloured marl and marly shale as this boundary is easy to recognize in the field. The Ali Bashi Formation at Zal measures 26 m. The lower few meters consists of ledge-forming, red and grey marly limestone with thin marl intercalations. The limestones contain fossils including crinoids, corals and brachiopods. Above follows a succession of red, black, grey, green and brown coloured marly shale and marl with intercalated thin, nodular marly limestone and micritic limestone beds. The uppermost part is composed of approximately 2 m of dominantly red, subordinately grey, nodular, thin bedded micritic limestone and thin marl intercalations overlain by 3 m of wavy bedded red micritic limestones containing crinoids and ammonoids ("*Paratirolites* limestone") forming a prominent ledge. The limestones of the Ali Bashi Formation contain mainly conodonts, ostracods, fish remains and ammonoids and are poor in foraminifera. The fauna indicates a Dorashamian (Changhsingian) age. The Ali Bashi Formation is assumed to represent deposits of a deeper shelf environment. The depositional environment of the Ali Bashi Formation was a deeper well oxygenated shelf, probably below the storm wave base. In the upper part *(Paratirolites* Beds) the sedimentation rate was much lower than in the Julfa Formation probably because of a greater distance to the shoreline and reduced input of siliciclastic sediment.

3.3. Elika Formation (Unit E)

The red nodular *Paratirolites* limestone of the uppermost Ali Bashi Formation is overlain by approximately 0,5 m of reddish-brown shales ("boundary clay") representing the Permian/Triassic boundary. The boundary clay is overlain by a 1,4 m thick unit of reddish-grey, thin- to very thin-bedded micritic limestones with mass accumulations of *Claraia*, microgastropods and ostracods followed by a 9,5 m thick unit of almost unfossiliferous planar bedded micritic limestones with horizons containing intraclasts and oncoid-like grains.

According to the litho- and biofacies characteristics such as intraformational erosion and reworking, filamentous algal fabrics and mass accumulations of bivalves on bedding planes, the lower Elika Formation accumulated in an open marine environment above the storm wave base and within the photic zone. The uppermost part of the Boundary Clay probably accumulated at relatively shallow water depths of a few tens of meters.

The occurrence of true stromatolites at Shahreza and Abadeh indicates deposition in a shallow shelf environment.

4. ZAL MICROPALAEONTOLOGY

The series in Zal displays: *Permocalculus* spp. (*P*. cf. *solidus* (Pia, 1937); *P.* cf. *fragilis* (Pia, 1937); *P.* cf. *digitatus* Elliott, 1955) (Pl. 1, figs. 1-3); *Gymnocodium bellerophontis* (Rothpletz, 1894) Pia, 1937 (Pl. 1, fig. 4); coprolites (Pl. 1, figs. 5-6); *Nankinella* sp. (Pl. 1, fig. 7); *Codonofusiella kwangsiana* Sheng, 1963 (Pl. 1 figs. 8-10); *Reichelina pulchra* K.V. Miklukho-Maklay, 1954 (Pl. 1, fig. 11); *Pseudovermiporella* ex gr. *nipponica* (Endo in Endo and Kanuma, 1954) (Pl. 1, fig. 12); *Glomomidiella* sp. (Pl. 1, fig. 16); *Crassiglomella* sp. (Pl. 1, figs. 13-15, Pl. 2, fig. 1); *Hoyenella* sp. (Pl. 2, fig. 2); *Brunsispirella* aff. *linae*

(Vachard and Gaillot in Vachard *et al.,* 2005) (Pl. 2, fig. 3); *Louisettita elegantissima* Altiner and Brönnimann, 1980 (Pl. 2, fig. 10); *Climacammina* sp. (Pl. 2, figs. 14-15); *Pseudolangella* sp. (Pl. 2, fig. 16); *Protonodosaria* sp. (Pl. 2, fig. 20); *Nodosinelloides* sp. (Pl. 2, fig. 22); *Pachyphloia schwageri* Sellier de Civrieux and Dessauvagie, 1965 (Pl. 2, fig. 17); *Geinitzina* sp. (Pl. 2, fig. 21, 23); *Neogeinitzina* sp. (Pl. 2, fig. 18); *Polarisella* ex gr. *elabugae* (Cherdyntsev, 1914) (Pl. 2, fig. 19); *Langella* ? sp. (Pl. 2, fig. 24); *Frondina permica* Sellier de Civrieux and Dessauvagie, 1965 (Pl. 2, figs. 25-26); *Frondina* ? sp. (Pl. 2, fig. 27); *Robuloides* sp. (Pl. 2, fig. 28). The last Permian limestone bed is particularly interesting because it contains relatively numerous *Neoendothyra reicheli* Reitlinger, 1965 (Pl. 2, figs 4-13). This microfauna is biostratigraphically poorly significant and indicates only the Late Permian (Wuchiapingian and Changhsingian) (Gaillot and Vachard, 2007). The main markers are the genera *Crassiglomella* Gaillot and Vachard, 2007; *Brunsispirella* Gaillot and Vachard, 2007 and *Louisettita* Altiner and Brönnimann, 1980. As these latter taxa were largely described in Gaillot and Vachard (2007), here we describe only the taxon *Neoendothyra*.

5. SYSTEMATIC PALEONTOLOGY

Superfamily ENDOTHYROIDEA Brady, 1884
nomen translat. Glaessner, 1945 (ex family)
Family ENDOTHYRIDAE Brady, 1884
nomen correct. Rhumbler, 1895 (pro family Endothyrina)
Subfamily NEOENDOTHYRINAE Reitlinger in Rauzer-Chernousova *et al.*, 1996

Neoendothyra Reitlinger, 1965

Type species.- *Neoendothyra reicheli* Reitlinger, 1965.

Synonyms.- *Robuloides* sensu Loeblich and Tappan (1987) (pars); *Multidiscus* sensu Gu *et al.*, 2002 (pars: only pl. 1, fig. 17).

Diagnosis.- Test lenticular, endothyroid, with carinate periphery. Lateral and basal supplementary deposits well developed. Wall calcareous microgranular. Aperture terminal, basal, simple.

Description.- Endothyroid coiling, i.e. with constant deviation of axis from approximately 30 to 60°. Carinate periphery (main difference with *Endothyra*). Chambers semi-hemispherical. 3-4 whorls of volution. 8-10 chambers at the last whorls. Secondary deposits are crusts on the floor of chamber and lateral deposits are present. Rare spines in the last chambers. Wall brownish, microgranular.

Discussion.- The wall is not really black as in *Endothyra*, so Rauzer-Chernousova *et al.*, 1996 classified this genus in the Endothyranopsinae and not in the Endothyrinae. Groups of species were defined by Vachard and Ferrière (1991). Evolute species are part of *Linendothyra* Mamet and Pinard, 1992 and uncoiled ones of *Neoendothyranella* Nestell and Nestell, 2006. The synonymy with *Robuloides*, proposed by Loeblich and Tappan (1987) is erroneous (Gaillot, 2006; Gaillot and Vachard, 2007). The Triassic species of *Neoendothyra* belong generally to *Endoteba* ex gr. *badouxi* (see Vachard *et al*., 1994).

Occurrence.- The Late Carboniferous-Early Permian specimens of Canadian Artic (Pinard and Mamet, 1998) are transitional forms with endothyrids, also observed in the Early Permian of China and the Carnic Alps (Lin, 1985; Vachard and Krainer, 2001). The FAD (first appearance datum) of the typical forms is late Chihsian (= Kubergandian/Roadian) in age, in South China (Lin *et al*., 1990). The acme is late Midian in Sumatra, Transcaucasia, Montenegro, Turkey, central Alborz (Iran), Oman, Afghanistan, Cambodia, Thailand, Malaya, south China, Texas, Mexico, Guatemala, and perhaps Bolivia. LAD in the Late Permian in South China (Lin *et al*., 1990), Thailand, Malaysia, Primorye and Japan. Up to the PTB (Permian/Triassic Boundary) in Iran.

Neoendothyra reicheli Reitlinger, 1965
(Pl. 2, Figs. 4-13)

1965 *Neoendothyra reicheli* n. sp. Reitlinger, p. 61-62, pl. 1, figs. 6-9.

Plate 1

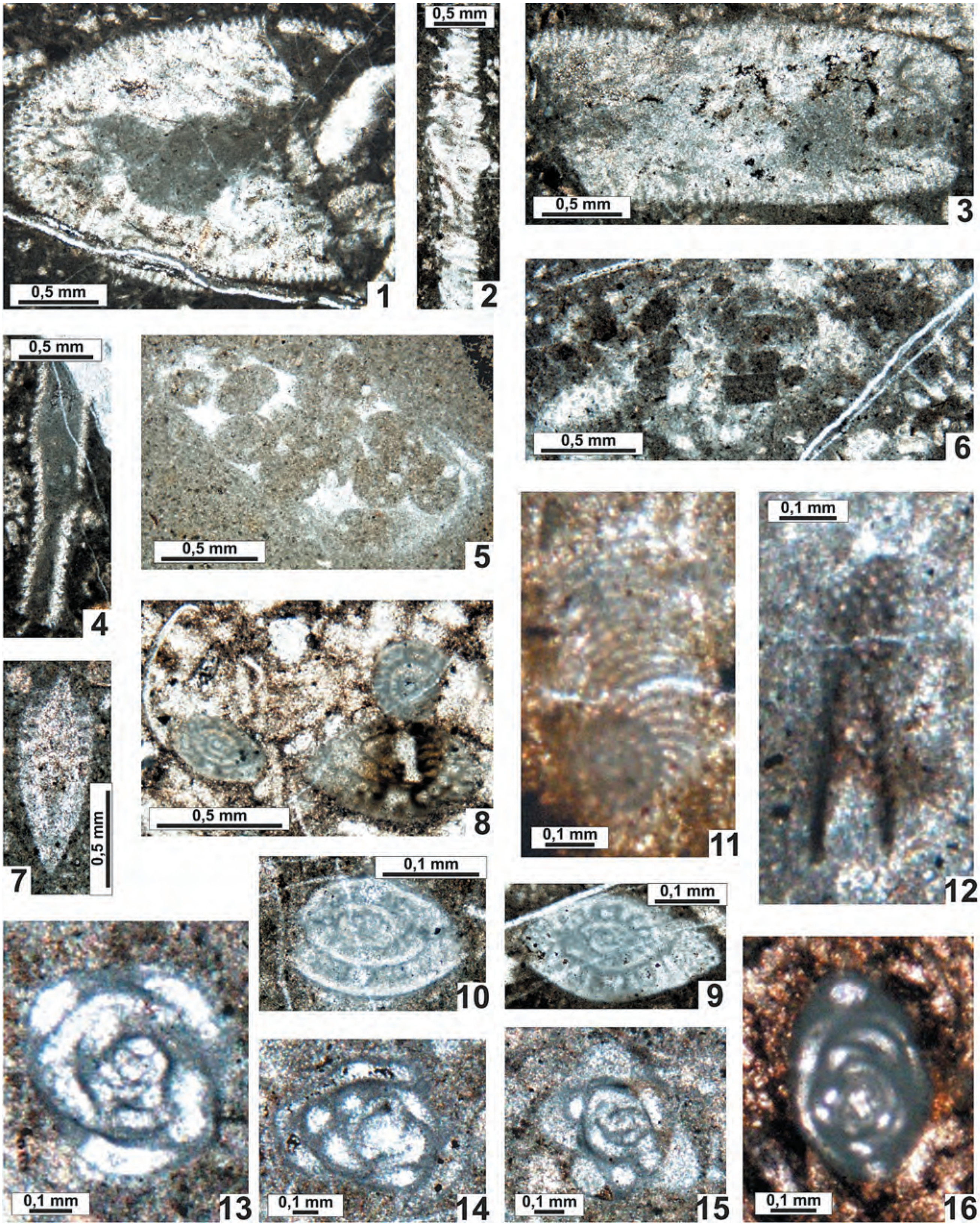

Plate 1. ***1-3***, *Permocalculus* spp. (*P.* cf. *solidus* (Pia, 1937), x 30; *P.* cf. *fragilis* (Pia, 1937), x 20; *P.* cf. *digitatus* Elliott, 1955, x 30). ***4***, *Gymnocodium bellerophontis* (Rothpletz, 1894) Pia, 1937, x 28. ***5-6***, coprolites, both, x 36. ***7***, *Nankinella* sp., subaxial section, x 37. ***8-10***, *Codonofusiella kwangsiana* Sheng, 1963; *8*, x 5; *9*, x 12; *10*, x 18. ***11***, *Reichelina pulchra* K.V. Miklukho-Maklay, 1954, x 20. ***12***, *Pseudovermiporella* ex gr. *nipponica* (Endo in Endo and Kanuma, 1954), x 22. ***13-15***, *Crassiglomella* sp. *13*, x 75; *14-15*, x 50. ***16***, *Glomomidiella* sp. x 90.

1973 *Neoendothyra reicheli* Reitlinger - Bozorgnia, p. 93-94, pl. 38, figs. 2, 4-9, pl. 39, figs. 3-4.
1979 *Neoendothyra reicheli* Reitlinger - Nguyen Duc Tien, p. 108-109, pl. 8, figs. 15-17 (with 4 references in synonymy).
1983 *Neoendothyra reicheli* Reitlinger - Jenny-Deshusses, p. 136, pl. 1, figs. 8-9 (with 6 references in synonymy).
non 1983 *Neoendothyra reicheli* Reitlinger - Salaj *et al*., p. 90, pl. 39, fig. 3 (= *Endoteba* ex gr. *badouxi*).
1984 *Neoendothyra reicheli* Reitlinger - Altiner, p. 262-264, pl. 2, figs. 21-22.
1986 *Neoendothyra reicheli* Reitlinger - Kobayashi, p. 140, pl. 3, figs. 4-5, 10.
1986 *Neoendothyra* aff. *compressa* Sosnina - Vuks and Chediya, pl. 9, fig. 4.
1986 *Neoendothyra reicheli* Reitlinger - Nguyen Duc Tien, pl. 4, fig. 3.
p. 1987 *Neoendothyra reicheli* Reitlinger - Loeblich and Tappan, pl. 437, figs. 1-4 (non synonymy with *Robuloides*, non fig. 5 = *Endoteba* ex gr. *badouxi*).
1988 *Neoendothyra reicheli* Reitlinger - Kobayashi, pl. 1, fig. 16.
v. p. 1991 *Neoendothyra* ex gr. *reicheli* Reitlinger - Vachard and Ferrière, p. 210, pl. 2, figs. 1, 3 (non pl. 1, figs. 7-8, two other species) (with 18 references in synonymy).
1992 *Neoendothyra reicheli* Reitlinger - Ueno, fig. 9. 23.
1995 *Neoendothyra reicheli* Reitlinger - Partoazar, pl. (1)5, fig. 1, pl. (2)4, fig. 3?, pl. (3)2, fig. 6.
1996 *Neoendothyra reicheli* Reitlinger - Leven and Okay, pl. 9, figs. 32-34.
1996 *Neoendothyra reicheli* Reitlinger - Rauzer-Chernousova *et al*., p. 46, pl. 12, figs. 1-2.
non 1998 *Neoendothyra reicheli* Reitlinger - Pinard and Mamet, p. 108-109, pl. 35, fig. 13 (with 11 references in synonymy) (either a species of the group *N. parva*, or another genus).
v. ? 2002 *Neoendothyra reicheli* Reitlinger - Vachard *et al*., pl. 1, figs. 3-6 (the wall seems to become agglutinating).
v. 2002 *Neoendothyra reicheli* Reitlinger - Fontaine *et al*., pl. 11, figs. A-D.
v 2005 *Neoendothyra reicheli* Reitlinger - Mohtat Aghai and Vachard, pl. 1, figs. 9-12.
v 2006 *Neoendothyra reicheli* Reitlinger - Gaillot, p. 40-41, pl. I.36, fig. 3?, pl. I.43, figs. 5?, 6?, pl. III.13, fig. 8

Dimensions.- Diameter = 0.300-0.450 mm, width = 0.145-190 mm, ratio w/D = 0.40-0.53, number of whorls: 3, wall thickness = 0.015-0.020 mm .

Occurrence.- Late Midian of Transcaucasia, Alborz, Cambodia, Afghanistan, Turkey and Zagros (Iran). Wuchiapingian-Changhsingian of Iran.

6. THE DEEP-WATER RED NODULAR LIMESTONES

Red nodular limestones (griottes, Ammonitico Rosso) are relatively abundant from the Cambrian to the Jurassic. According to Cecca *et al*. (1992), the Ammonitico Rosso facies seems to disappear in the earliest Cretaceous (late Berriasian). Nevertheless, recent examples were mentioned from the Red Sea (Egypt), the Ionan Sea (Greece), and the Bahamas and Florida Straits (e.g. Cecca *et al*., 1992). These limestones are interpreted as red pelagic condensed nodular limestones which clearly indicate a dramatic fall in the rate of $CaCO_3$ sedimentation as emphasized by the presence of hard grounds encrusted by ferromanganese nodules as well as stromatolithic overgrowths. (Cecca *et al*., 1992; Flügel, 2004). During the Palaeozoic, they are rich in goniatites, orthoceratids, trilobites, bacterial stromatolites, radiolaria, pelagic ostracods, problematical algae *Globochaetete*, etc. Some foraminifera are present in these limestones. The problem

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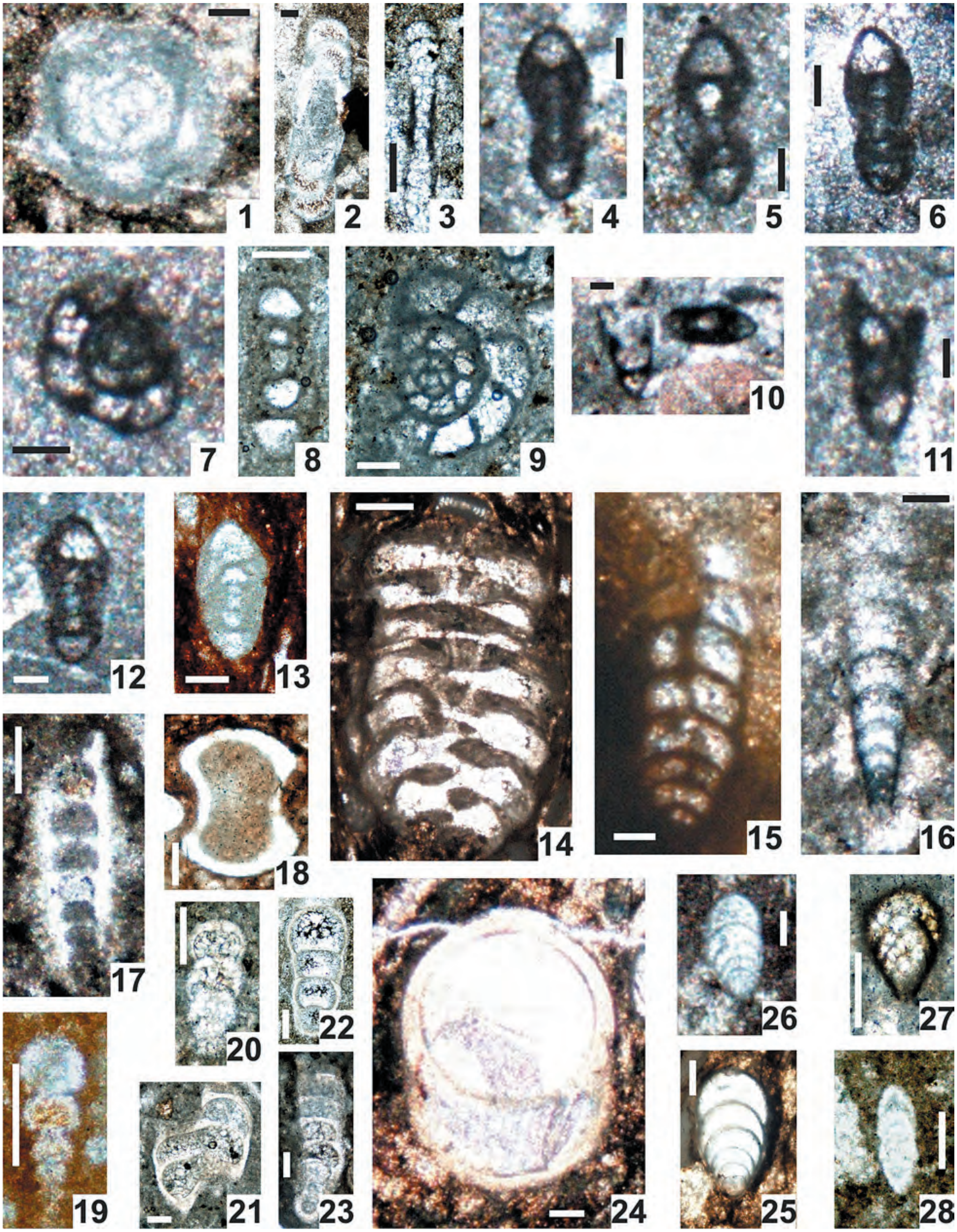
Plate 2. ***1***, *Crassiglomella* sp., x 70. ***2***, *Hoyenella* sp., x 40. **3,** *Brunsispirella* aff. *linae* (Vachard and Gaillot in Vachard *et al*., 2005), x 90. **4-13**. *Neoendothyra reicheli* Reitlinger, 1965; *4-6*, x 80; *7-8*, x 120; 9, x 90; *10*, x 50; *11*, x 80; *12*, x 75; *13*, x 90; *10*, *Louisettita elegantissima* Altiner and Brönnimann, 1980, x 50. ***14-15***, *Climacammina* sp. *14*, x 115; *15*, x 90. ***16***, *Pseudolangella* sp., x 95. ***17***, *Pachyphloia schwageri* Sellier de Civrieux and Dessauvagie, 1965, x 140. ***18***, *Neogeinitzina* sp., x 90. ***19***, *Polarisella* ex gr. *elabugae* (Cherdyntsev, 1914) x 210. ***20***, *Protonodosaria* sp., x 120. ***21, 23***, *Geinitzina* sp., both x 50. **22**, *Nodosinelloides* sp. x 60. ***24***, *Langella*? sp. x 70. ***25-26***, *Frondina permica* Sellier de Civrieux & Dessauvagie, 1965, both x 70. ***27***, *Frondina*? sp., x 150. ***28***, *Robuloides* sp., x 120.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to discuss is to know if these foraminifera are adapted to a strong palaeobathymetry or transported by buoyancy and deposited in deep-water sedimentary environments. The Cambrian examples are developed in the Barrios de Luna Fm. in northern Spain and fausses-griottes of southern France (e.g., Alvaro, 2002). The Devonian and Viséan series of Montagne Noire and French Pyrenees (southern France) and Cantabrian Mountains and Spanish Pyrenees are accurately studied (e.g. Vachard, 1973, 1974; Perret *et al.*, 1994; Nemirovska, 2005; Randon, 2006). The Ammonitico Rosso facies developed essentially during the rifting of the continental margins preceding the opening of oceans, especially in the Mesozoic Tethys (Cecca *et al.*, 1992). This facies seems to be related with: (a) a relative paucity in planktonic carbonate microfossils; (b) periods preceding the development of flysch facies; (c) a relatively poor oceanic circulation; (d) the presence of bottom currents; (e) their development seems to be exactly situated between the period of platform drowning and an oceanic opening.

7. PALAEOBATHYMETRY OF RED NODULAR LIMESTONES

The term Ammonitico Rosso can be used for the Permian deposits, as indicated by Cecca *et al.* (1992, with references). An attempt of palaeobathymetric subdivision was proposed by some authors (Perret *et al.*, 1994; Randon, 2006). The basement of the Jurassic Ammonitico consists of oceanic or continental crust (Cecca *et al.*, 1992, p. 57). Nodular carbonates are currently forming at 300-800 m (Mullins *et al.*, 1980; Heydari *et al.*, 2003). Nevertheless, the Jurassic Ammonitico Rosso contains pennular corals whose modern equivalents are not deeper than 230-240 m (Gill *et al.*, 2004). Mamet and Boulvain (1990), Préat *et al.* (1999, 2000, 2005) and Mamet and Préat (2005, 2006a-b) related the red colouration to the formation of bacterial activity in poorly oxygenated environments. We agree with Heydari *et al.* (2003) in considering that the bottom waters were well oxygenated during their deposition. Poorly oxygenated waters seem to be more favourable to the deposit of black shales or blank chert, such as the Tournaisian lydites, for example. We consider here that the red nodular limestones covered the continental slopes in straits or narrow ocean palaeogeography. The upper slope deposit (more than 100 m deep, perhaps to *circa* 250 m) with crinoids, brachiopods, trilobites, bivalves, bryozoans, gastropods, numerous ostracods and conodonts; the middle slope is characterized by the appearance of the problematical algae *Globochaete* and the ammonoids, and the acme of conodonts; the lower slope is characterized by a rarity and/or diappearance of all groups. In the basinal facies only radiolaria are present in the uppermost limestones grading into to cherts or turbiditic sequences.

8. PALAEOBATHYMETRY OF DEEP-WATER FORAMINIFERA

Benthic foraminfers are widely used as proxies for palaeodepth,. However, the exact types of constraints are poorly understood (van der Zwann *et al.*, 1999). Nevertheless, it is evident that, during the Palaeozoic, foraminifera, many algae and pseudo-algae are restricted to the inner platform. On the palaeoslope some zonations are known up to the aphotic zone (Madi *et al.*, 1996; Pille *et al.*, 2006; Pille, 2008). The deepest foraminifera in this case are opportunistic small forms, such as *Earlandia, Endothyra, Howchinia*. Nevertheless, some rare foraminifera are observed in the Viséan griottes of Spain (Randon, 2006, p. 167): *Eotuberitina, Vicinesphaera, Parathurammina, Earlandia minor* and *Endothyra prisca*. The foraminifera are generally present in the middle ramp (Randon, 2006). This is also the case in the latest Permian limestone of Zal, because of the observed assemblages. The question is if these forms are autochthonous or transported. In fact, some are undoubtely in place, for example: the *Tolypammina* attached on ferrobacterian endostromatolithes and the apparently free foraminifera which share the same recrystallization (microfauna of hard ground sensu Vachard, 1974); e. g. *Eotournayella* (Vachard, 1973, 1974; Boulin *et al.*, 1987). Similarly, some *Eoseptatournayella* might be in place because recrystallized in silica, in supragriottes of Montagne Noire (southern France) and Carnic Alps (Ebner, 1973; Vachard, 1974).

In the Palaeozoic, many morphologies attributed to agglutinating foraminifera (class Textulariata) are in fact only typical of calcareous tests (class Fusulinata) without any homeomorph among the Textulariata; the best examples are the false *Ammobaculites* of Gutschick and Treckman, 1959 and Gutschick *et al.*, 1961 which are true *Rectoseptatournayella* Brazhnikova and Rostovceva in Anonymous, 1963 (compare Eickhoff, 1974, fig. 19 and Gutschick *et al.*, 1961, pl. 3, figs. 22-24 or Gutschick and Treckman, 1959, pl. 37, figs. 14-17). Furthermore, other types of preservation are unquestionably recrystallisations: for example the pyritized molds described by Vachard and Mouravieff (1994). Many homeomorphs between Textulariata and Fusulinata can be listed during the Palaeozoic (and Triassic): e.g. (a) the genera *Hyperammina* Brady, 1878 and *Earlandia* Plummer, 1930, (b) *Textularia* Defrance in de Blainville, 1824 and *Palaeotextularia* Schubert, 1921, (c) *Ammobaculites* Cushman, 1910 with many different genera among the Fusulinida, especially *Insolentitheca* Vachard in Bensaid *et al.*, 1979 emend. Vachard and Cózar, 2004; (d) *Spiroplectammina* Cushman, 1927 confused with *Palaeospiroplectammina* Lipina, 1965 and *Spireitlina* Vachard in Vachard and Beckary, 1991; (e) *Ammodiscus* Reuss, 1862 with *Pseudoammodiscus* Conil and Lys in Conil and Pirlet, 1970; (f) *Glomospira* Rzehak, 1885 with *Pseudoglomospira* Bykova in Bykova and Polenova, 1955; (g) *Tolypammina* Rhumbler, 1895 with diverse genera of Fusulida, especially *Scalebrina* Conil and Longerstaey in Conil *et al.*, 1980 or with the Miliolida *Calcivertella* Cushman and Waters, 1928 (see for example, "*Tolypammina*" encrusting Late Pennsylvanian *Triticites* Girty, 1904 illustrated by Hageman *et al.* (2004)).

Inversely some transported microfauna and microflora exist, because their walls are not altered, for example in the Devonian griottes (Vachard, unpublished data) and in the Viséan-Serpukhovian griottes (Randon, 2006). In the latest Permian, in our studied sections this is the case for *Neoendothyra*.

9. DISCUSSION: DEPTH VERSUS BUOYANCY

Some foraminifera of the Ammonitico Rosso limestones are autochthonous: the *Tolypammina* encrusting the conodonts and the bacterial stromatolites, as well as the microfauna of hard-grounds. Other ones are transported post-mortem by flottability: *Endothyra prisca*, etc. of the Viséan; *Neoendothyra* of the Late Permian.

The problem is the discovery of a method which permits to discriminate the living forms on the bottom from the form which come by buoyancy. Optical method seem constitute by (a) a the type of filling of the chambers, (b) the mineralogical transformations of the test, (c) the taphonomic alterations of the tests (see Cózar, 2003a-b). In the case of the *Eotournayella* the wall appears recrystallized because, in the case of *Endothyra* and *Neoendothyra* they are not affected.

Some foraminifera seem to live in this environment. They have generally a double microhabitat: (1) at the interface water sediment, (2) infaunal but probably in the top 10 cm of the sediment column as such as 75% of the modern benthic foraminifera (van der Zwann *et al.*, 1999) in this part the oxygenation was good, whereas the organic flux is probably poor or relatively poor (red colour of the sediment, but some bacterian bioconstructions). This double microhabitats generate morphological adaptations (especially uncoiling which occasionally becomes generic differences); e.g. (a) *Pseudoammodiscus* and *Eotournayella* Lipina and Pronina, 1964; (b) *Eoseptatournayella* Lipina in Anonymous, 1963; *Septatournayella* Lipina, 1955 and *Rectoseptatournayella* Brazhnikova and Rostovceva in Anonymous, 1963; (c) *Forschia* Mikhailov, 1935-*Forschiella* Mikhailov, 1935; (d) *Endothyra* [Phillips, 1846] Brady, 1876 emend. China, 1965, and *Mikhailovella* Ganelina, 1956; (e) *Neoendothyra* Reitlinger, 1965-*Neoendothyranella* Nestell and Nestell, 2006. Examples (a) and (b) may exist also in the carbonate ramps but were always observed in pelagic nodular limestone by our team. Inversely, (c), (d) and (e) are only known in shallow carbonate ramp. In Zal we have no *Neoendothyranella* but true *Neoendothyra*. Consequently, we conclude that many Palaeozoic foraminifera shared two microhabitats at the interface of the sediment or infaunal at different depths. *Eotournayella* and *Eoseptatournayella* lived in deep environments, the other one in shallow environments. If present in nodular limestones, *Eotournayella* and *Eoseptatournayella* were fossilized in situ; the other one, especially *Endothyra* and *Neoendothyra* were transported. Nevertheless, we have observed (material Vachard, 1974, 1977) some specimens contained in late Tournaisian nodular red limestones ("secondes griottes"), a foraminifer with a morphology of *Globivalvulina* Schubert, 1921, but entirely silicified, with an agglutinate or exceptionally large quartz crystallites. For this taxon, it is impossible to conclude if it is autochthonous or transported. As no breaks nor truncature facets are observed in the tests, no clinostratifications, no grains or structures related to a high hydrodynamism, no gradded bedding, no tempestite sequences etc. they were not transported by current on the bottom, but the buoyoancy is most probably responsible of their transport. Another type of foraminifera is really in situ in deep sediment; they are part of the *Tolypammina* of the literature. *Tolypammina* Rhumbler, 1895 is mentioned from the Silurian to the Recent. In the Devonian they are generally present in the griottes, especially interstratified in the endostromatolites bacterian or eventually attached on conodont (Tücker, 1973; Vachard, 1973, 1974; Schneider, 1970). Apparently, these *Tolypammina* do not exhibit really an agglutinate but the same recrystallization: ferromanganese and silica than as *Eotournayella, Tikhinella*, etc. of the same environment. As the *Tolypammina* are necessarily *in situ* because of their attachment on the deep bacterial endostromatolite, this form can be also a recrystallized Fusulinata: *Tscherdyncevella* or an undescribed genus. No equivalent of this form is present in our Permian samples, but a model can be provided by the recent genus *Ammodiscellites* attached on the phosphoritic hardgrounds of Peru (Resig and Glenn, 1997).

For the Zal section it is difficult to say where was the platform and where lived *Neoendothyra* before transport. A Bahamian model is possible due to the work of Mullins *et al*., 1980 and the location within the Neotethys ocean. This Bahamian platform may be migrated from Southeast to Northeast, because the Ammoniitico is Wordian in Eastern Oman (Hauser *et al*., 2000), Late Wuchiapingian in Abadeh (e.g. Mohtat Aghai and Vachard, 2005) and Changhsingian in Zal, Ali Bashi (Iran) and Dorasham (Armienia-Transcaucasia pro parte) (e.g. Kotlyar *et al*., 1984).

10. CONCLUSIONS

1. The Zal section contains algae Gymnocodiaceae; coprolites; rare Biseriamminoidea and Palaeotextularioidea, fusulinids *Nankinella* sp.; *Codonofusiella kwangsiana*; *Reichelina pulchra*; Miliolata and Nodosoriata.
2. The last Permian beds contain the Endothyroidea *Neoendothyra reicheli* in a deep red nodular limestone.
3. The occurrences of foraminifera in the griottes-Ammonitico Rosso in the Palaeozoic have two causes: *in situ* or coming by buoyancy.
4. In Zal, the *Neoenthyra* are transported by buoyancy and deposited by setting.
5. The environment of deposit can be in a middle slope (250-500 m deep).
6. The origin of the *Neoendothyra* can be situated on islands similar to Bahamas, within the Neotethys.
7. There is a migration of the nodular facies from the Wordian in Eastern Oman to the latest Permian in Zal. This may constitute an important regional palaeogeographic character.

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12. REFERENCES

Altiner, D. 1984. Upper Permian foraminiferal biostratigraphy in some localities of the Taurus Belt. *International Symposium of the Geology of the Taurus Belt 1983*, Reprint M.T.A., 255-268.

Altiner, D. and Brönnimann, P. 1980. *Louisettita elegantissima*, n.gen. n.sp., un nouveau foraminifère du Permien supérieur du Taurus oriental (Turquie). *Notes du Laboratoire de Paléontologie de l'Université de Genève*, 6 (3), 39-43.

Altiner, D., Baud, A., Guex, J. and Stampfli, G. 1979. La limite Permien-Trias dans quelques localités du Moyen-Orient: recherches stratigraphiques et micropaléontologiques. *Rivista Italiana di Paleontologia*, 85 (3-4), 683-714.

Álvaro, J. 2002. *The Lower-Middle Cambrian transition in the Western Mediterranean region: biodiversity and palaeogeographical pattern*. Thèse d'Habilitation de l'Université de Lille. (Unpublished).

Anonymous 1963. Resheniya Vtrorogo kollokviuma po sistematike endothyroidnykh foraminifer, organizovallogo coordinatsionnoi komissei po mikropaleontologii v Moskve v aprele 1962. Voprosy Mikropaleontologii, 7, 36-46 (in Russian; French translation, Pietresson de Saint-Aubin, R., Bureau de Recherches Géologiques et Minières, 4488, attributed to Brazhnikova *et al.*).

Bensaid, M., Termier, H., Termier, G. and Vachard, D. 1979. Le Carbonifère (Viséen supérieur-Bachkirien) entre Bou Chber et Ich ou Mellal (Maroc Central). *Annales de la Société géologique du Nord*, 98, 189-204 (dated 1978).

Blainville, H.M. de, 1824. *Dictionnaire des Sciences Naturelles*, 32, 1-567.

Boulin, J., Bouyx, E., Collomb, P. and Vachard, D. 1987. Présence de Dévonien supérieur dans des calcaires cristallins de la série volcano-sédimentaire d'Awpar (Hindou Kouch occidental, Afghanistan). Implications paléogéographiques et structurales. *Comptes Rendus de l'Académie des Sciences de Paris*, 304, série II, 16, 1009-1012.

Bozorgnia, F. 1973. Paleozoic foraminiferal biostratigraphy of central and east Alborz Mountains, Iran. *National Iranian Oil Company, Geological Laboratories*, Publication 4, 1-185.

Brady, H.B. 1876. A monograph of Carboniferous and Permian foraminifera (the genus *Fusulina* excepted). *Palaeontographical Society of London*, 30, 1-166.

Brady, H.B. 1878. On the Reticularian and Radiolarian Rhizopoda (Foraminifera and Polycystina) on the North Polar Expedition of 1875-76. *Annals and Magazine of Natural History*, series 5 1, 425-440.

Brady, H.B. 1884. Report of the foraminifera dredged by H.M.S. Challenger during the years 1873-1876. *Reports on the Scientific Results of the Exploratory Voyage of the H.M.S. Challenger, Zoology*, 9, 1-814.

Bykova, E.V. and Polenova, E.N. 1955. Foraminifery, radiolarii i ostrakody Devona Volgo-Uralskoi oblasti (Foraminifera and radiolaria from the Volga-Ural area and the central Devonian Field and their stratigraphical importance). *Trudy VNIGRI*, 87, 1-141 (in Russian, French translation, C.E.D.P. n° 1603, BRGM, 154 p.).

Cecca, F., Fourcade, E. and Azéma, J. 1992. The disappearance of the "Ammonitico Rosso". *Palaeogeography, Palaeoclimatology, Palaeoecology*, 99, 55-70.

Cherdyntsev, W. 1914. K faune foraminifer permskikh otlozhenii vostochnoi polosy Evropeiskoi Rossii (The fauna of foraminifera of the Permian deposits of the eastern belt of European Russia). *Trudy Obshchestva Estestvoispytateley pri Imperatorskomy Kazanskomy Universitety*, 46 (5), 3-88 (in Russian).

China, W.E. 1965. Opinion 724. *Endothyra bowmani* Phillips (1846) (Foraminifera): valided under the plenary powers. *Bulletin of Zoological Nomenclature*, 22 (1), 37-39.

Conil, R. and Pirlet, H. 1970. Le calcaire carbonifère du synclinorium de Dinant et le sommet du Famennien. Colloque sur la stratigraphie du Carbonifère. *Congrès et Colloques de l'Université de Liège*, 55, 47-63.

Conil, R., Longestaey P.J. and Ramsbottom, W.H.C. 1980. Matériaux pour l'étude micropaléontologique du Dinantien de Grande-Bretagne. *Mémoires de l'Institut Géologique de l'Université de Louvain*, 30 (imprinted 1979), 1-115.

Cózar, P. 2003a. Foraminiferal Taphofacies in the Mississippian Rocks of the Guadiato Area, SW Spain. *Facies*, 49, 1-18.

Cózar, P. 2003b. Taphonomical analysis of the infilling and early mineralization in endothyrids (Foraminiferida Mississippian). *Palaeogeography, Palaeoclimatology, Palaeoecology,* 193, 561-574.

Cushman, J.A. 1910. *A monograph of the Foraminifera of the North Pacific Ocean, part 1.*

Astrorhizidae and Lituolidae. United States National Museum, Proceedings, Bulletin 71, 1-134.

Cushman, J.A. 1927. *An outline of a re-classification of the Foraminifera*. Cushman Laboratory Foraminiferal Research, Contributions*, 3 (1), 1-105.*

Cushman, J.A. and Waters J.A. 1928. Some Foraminifera from the Pennsylvanian and Permian of Texas. *Contributions from the Cushman Laboratory for Foraminiferal Research*, 4 (2), 31-55.

Ebner, F. 1973. Foraminiferen aus dem Paläozoikum der karnischen Alpen. *Mitteilungen der Abteilung für Geologie, Paläontologie und Bergbau am Landemuseum Joanneum Graz*, 34, 389-441.

Eickhoff, G. 1974. Stratigraphic significance of silicified foraminifera in the upper Devonian of Central Europe. In: Bouckaert, J. and Streel, M. (Eds.), *International Symposium on Namur*, 1974; Belgian micropaleontological limits from Emsian to Viséan, Publication 11, 1-14.

Elliott, G.F. 1955. The Permian calcareous alga *Gymnocodium*. *Micropaleontology*, 1 (1), 83-90.

Endo, R. and Kanuma, M. 1954. Stratigraphical and paleontological studies of the Later Paleozoic calcareous algae in Japan, VII. Geology of the Mino Mountain Land and southern part of Hida Plateau, with description of the algal remains found in those districts. *The Science Reports of the Saitama University*, B, 1 (3), 177-205.

Erwin, D.H. 1993. *The Great Paleozoic Crisis: Life and Death in the Permian*. Columbia University Press, New York, 327 pp.

Erwin, D.H. 1994. The Permo-Triassic extinction. *Nature*, 367, 231-236.

Erwin, D.H. 2001. Lessons from the past: biotic recoveries from mass extionctions. *Proceedings of the National Academy of Sciences*, 98, 5399-5403.

Flügel, E. 2004. *Microfacies of carbonate rocks, analysis, interpretation and application.* Springer Publisher, New York, Berlin, Heidelberg, 1-976.

Fontaine, H., Salyapongse, S., Nguyen Duc Tien and Vachard, D. 2002. The Permian of Khao Tham Yai area in Northeast Thailand. *The Symposium on Geology of Thailand*, 26-31 August 2002, 58-76.

Gaillot, J., 2006. *The Late Permian-Early Triassic Khuff Formation in the Middle-East, sequence biostratigraphy and palaeoenvironments by means of calcareous algae and foraminifera*. 687 pp., Ph. D., University of Lille, 3 vol. (unpublished).

Gaillot, J. and Vachard, D. 2007. The Khuff Formation (Middle East) and time-equivalents in Turkey and South China: biostratigraphy from Capitanian to Changhsingian times (Permian), new foraminiferal taxa, and palaeogeographical implications. *Coloquios de Paleontología*, 57, 37-223.

Ganelina, R.A. 1956. Foraminifery vizeiskikh otlozhenii severo-zapadnykh raionov Podmoskovnoi Kotloviny (Viséan foraminifera from the northwestern areas of the Moscow Depression). *Trudy VNIGRI*, 98, *Mikrofauna SSSR*, 8, 61-159 (in Russian; French translation: BRGM, 1626: 1-81).

Gill, G.A., Santantonio, M. and Lathuillère, B. 2004. The depth of pelagic deposits in the Tethyan Jurassic and the use of corals: an example from the Apennines. *Sedimentary Geology*, 166 (3-4), 311-334.

Girty, G.H. 1904. *Triticites*, a new genus of Carboniferous foraminifera. *American Journal of Science*, 4th ser., 17, 234-240.

Glaessner, M.F. 1945. Principles of micropaleontology. *Melbourne University Press*, 1-269.

Gu, Song-zhu, Pei, Jing-cheng, Yang, Feng-qing and Gao, Yong-qun 2002. Smaller Foraminifera fauna from the Changxingian of the Sidazhai section, Ziyun County, southern Guizhou Province. *Acta Micropaleontologica Sinica*, 19 (2), 163-169.

Gutschick, R.C. and Treckman, J.F. 1959. Arenaceous foraminifera from the Rockford Limestone of northern Indiana. *Journal of Paleontology*, 23 (2), 229-250.

Gutschick, R.C., Weiner, J.L. and Young, L. 1961. Lower Mississippian arenaceous foraminifera from Oklahoma, Texas and Montana. *Journal of Paleontology*, 35 (6), 1193-1221.

Hageman, S.A., Kaesler, R.L. and Broadhead, T.W. 2004. Fusulinid taphonomy: encrustation, corrasion, compaction and dissolution. *Palaios*, 19, 610-617.

Hauser, M., Vachard, D., Martini, R., Matter, A., Peters, T. and Zaninetti, L. 2000. The Permian sequence reconstructed from reworked carbonate clasts in the Batain Plain (Northeastern Oman). *Comptes Rendus de l'Académie des Sciences*, 320, 273-279.

Heydari, E., Hassanzadeh, J., Wade, W.J. and Ghazi, A.M. 2003. Permian-Triassic boundary interval in the Abadeh section of Iran with implication for mass extinction: Part 1. Sedimentology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 193, 405-423.

Jenny-Deshusses, C. 1983. *Le Permien de l'Elbourz Central et Oriental (Iran): stratigraphie et micropaléontologie (foraminifères et algues*). Thèse Université de Genève, no. 2103, 1-214 (unpublished).

Kobayashi, F. 1986. Middle Permian foraminifera of the Gozenyama Formation, southern Kwanto Mountains, Japan. *Bulletin of the National Science Museum, series C (Geology and Paleontology)*, 12 (4), 131-163.

Kobayashi, F. 1988. Middle Permian foraminifera of the Omi Limestone, central Japan. *Bulletin of the National Science Museum, series C (Geology and Paleontology),* 14 (1), 1-35.

Korte C. and Kozur, H.W. 2005. Carbon isotope stratigraphy across the Permian/Triassic boundary at Julfa (NW Iran), Peitlerkofel (Sass de Pütia, Sass de Putia), Pufels (Bula, Bulla), Tesero (all three Southern Alps, Italy) and Gerennavár (Bükk Mts., Hungary). *J. Alpine Geol.*, 47, 119-135.

Korte, C., Kozur, H.W. and Mohtat-Aghai, P. 2004b. Dzhulfian to lowermost Triassic ?^{13}C record at the Permian/Triassic boundary section at Shahreza, Central Iran. *Hallesches Jahrbuch Geowissenschaften*, Reihe B, Beiheft 18, 73-78.

Korte, C., Kozur, H.W. and Partoazar, H. 2004a. Negative carbon isotope excursion at the Permian/Triassic boundary section at Zal, NW Iran. *Hallesches Jahrbuch Geowissenschaften*, Reihe B, Beiheft 18, 69-71.

Korte C., Kozur, H.W., Joachimski, M.M., Strauss, H., Veizer J. and Schwark, L. 2004c. Carbon, sulfur, oxygen and strontium isotope records, organic geochemistry and biostratigraphy across the Permian/Triassic boundary in Abadeh, Iran. *Int. J. Earth Sci.* (*Geol. Rundschau*), 93, 565-581.

Kotlyar, G.V., Zakharov, Yu.D., Kochirkevich, B.V., Kropacheva, G.S., Rostovtsev, K.O., Chediya, I.O., Vuks G.P. and Guseva, E.A. 1984. *Pozdnepermskii etap evolyutsii organicheskogo mira, Dzhulfinskii i Dorashamskii yarusy SSSR* (Evolution of the latest Permian biota, Dzhulfian and Dorashamian stages of the USSR). Akademiya Nauk SSSR, Dalnevostochnyi Nauchnyi Tsentr, Biologo-Pochvennyi Institut, Leningrad, 200 pp. (in Russian).

Kotlyar, G.V., Zakharov, Yu.D., Kropacheva, G.S., Pronina, G.P., Chediya, I.O. and Burago,

V.I. 1989. Pozdnepermskii etap evolyutsii organicheskogo mira, Midinskii yarus SSSR (Evolution of the latest Permian biota, Midian regional stage of the USSR). *Leningrad "Nauka", Leningradskoe Otdelennie*, 1-177 (in Russian).

Kozur, H. W. 2004. Pelagic uppermost Permian and the Permian-Triassic boundary conodonts of Iran. – Part 1: Taxonomy. *Hallesches Jahrbuch Geowissenschaften*, Reihe B, Beiheft 18, 39-68.

Kozur, H.W. 2007. Biostratigraphy and event stratigraphy in Iran around the Permian-Triassic Boundary (PTB): Implications for the causes of the PTB biotic crisis. *Global and Planetary Change*, 55 (1-3), 155-176.

Leven, E.Ya. and Okay, A.I. 1996. Foraminifera from the exotic Permo-Carboniferous limestone blocks in the Karakaya complex, north western Turkey. *Rivista Italiana di Paleontologia e Stratigrafia,* 102 (2), 139-174.

Lin, J.X. 1985. Foraminifera from the Lower Permian Oixia Formation of Jiahe, Guangdong. *Comment. Geolog., Beijing*, 31 (4), 289-295.

Lin, J.X., Li, L.X. and Sun, Q.Y. 1990. *Late Paleozoic foraminifera in South China*. Science Publication House Beijing, 1-269 (in Chinese).

Lipina, O.A. 1955. Foraminifery Turneiskogo yarusa i verkhnei chasti Devona Volgo-uralskoi oblasti i zapadnogo sklona Srednego Urala (Foraminifera of the Tournaisian stage and of the upper part of the Devonian from the Volga-Ural area and from the western slope of central Urals). *Akademiya Nauk SSSR, Trudy Instituta Geologii*, 163, geologichevskaya seriya 70, 1-96 (in Russian; French translation: BRGM n° 1640).

Lipina, O.A. 1965. Sistematika Turneiellid (Systematics of tournayellids). Akademiya Nauk SSSR, Geologicheskii Institut, 130, 1-115 (in Russian).

Lipina, O.A. and Pronina, T.V., 1964. Novyi poddrod turneiell iz verkhnefrasnskikh otlozhenii Urala. (New tournayellid subgenus in the late Frasnian of Urals). *Paleontologicheskii Zhurnal*, 1964 (6), 125-126.

Loeblich, A.R. and Tappan, H. 1987. *Foraminiferal genera and their classification*. Van Nostrand Reinhold Company Publisher 2 volumes: 1 vol. text: X + 970 p., 1 vol. plates: VIII + 212 p. + 847 pl.

Looy, C. V., Brugman, W. A., Dilcher, D. L. and Visscher, H. 1999. The delayed resurgence of equatorial forests after the Permian-Triassic ecologic crisis. *Proceedings National Academy of Sciences USA*, 96, 13857-13862.

Madi, A., Bourque, P.A. and Mamet, B. 1996. Depth-related ecological zonation of a Carboniferous carbonate ramp: upper Viséan of Béchar Basin, western Algeria. *Facies*, 35, 59-80.

Mamet, B. and Boulvain, F. 1990. Constructions hématitiques de griottes carbonifères (Asturies, Espagne). *Bulletin de la Société belge de Géologie*, 99 (2), 229-239.

Mamet, B. and Pinard, S. 1992. Note sur la taxonomie des petits foraminifères du Paléozoïque supérieur. *Bulletin de la Société belge de Géologie*, 99 (dated 1990), 373-398.

Mamet, B. and Préat, A. 2005. Why is "red marble" red? *Revista Española de Micropaleontología*, 37 (1), 13-21.

Mamet, B. and Préat, A. 2006a. Iron-bacterial mediation in Phanerozoic red limestones: State of the art. *Sedimentary Geology*, 185, 147-157.

Mamet, B. and Préat, A. 2006b. Jurassic microfacies, Rosso Ammonitico limestone, Subbetic Cordillera, Spain. *Revista Española de Micropaleontología*, 38 (2-3), 219-228.

Mikhailov, A. 1935. K voprosu filogenii kamennougolnykh foraminifer (To the question of the phylogeny of the Carboniferous foraminifera). *Izvestiya Leningradskogo Geologo-Gidro-Geodezicheskogo Tresta*, 2-3 (7-8), 38-42 (in Russian).

Miklukho-Maklay, K.V. 1954. Foraminifery verkhnepermskikh otlozhenii severnogo Kavkaza (Foraminifera from the Late Permian deposits of the northern Caucasus). *Trudy VSEGEI, Gosgeoltekhizdat*, 1, 1-163 (in Russian; French translation BRGM n° 2683, 1-216).

Mohtat-Aghai, P. and Vachard, D. 2005. Late Permian foraminiferal assemblages from the Hambast region (Central Iran) and their extinctions. *Revista Española de Micropaleontología*, 37 (2), 205-227.

Mullins, H. T., Neumann, A.C., Wilber, A.J. and Boardman, M.R. 1980. Nodular carbonate sediment on Bahamian slopes: possible precursors to nodular limestones. *Journal of Sedimentary Petrology,* 50 (1), 117-131.

Nestell, M.K. and Nestell, G.P. 2006. Middle Permian (late Guadalupian) foraminifera from Dark Canyon, Guadalupe Mountains, New Mexico. *Micropaleontology*, 52 (1), 1-50.

Nemyrovska, T.I. 2005. Late Viséan/early Serpukhovian conodont succession from the Triollo section, Palencia (Cantabrian Mountains, Spain). *Scripta Geologica*, 129, 13-89.

Nguyen Duc Tien 1979. *Etude micropaléontologique (foraminifères) de matériaux du Permien du Cambodge*. Thèse 3e Cycle, Université Paris Sud, Orsay, 1-166. (Unpublished).

Nguyen Duc Tien 1986. Foraminifera and algae from the Permian of Kampuchea. In: *The Permian of Southeast Asia*, Appendix 2, Fontaine H. *et al.* (Eds), *CCOP Technical Bulletin*, 18, 116-137.

Partoazar, H. 1995. Permian deposits in Iran. In: *Treatise on the Geology of Iran*. A. Hushmandzadeh (ed.), 22, 1-7 +1-340. (In Iranese with English abstract).

Partoazar, H. 2002. Permian-Triassic boundary conodonts from Julfa-Abadeh Belt along Northwest and Central Iran. *Permophiles*, 41, 34-40.

Perret, M. F., Vachard, D., Aguirre, P. and Crasquin-Soleau, S. 1994. Micropaléontologie des calcaires épibathyaux à *Globochaete* (algue problématique) du Carbonifère des Pyrénées. *Geobios*, 27 (6), 659-675.

Phillips, J. 1846. On the remains of microscopic animals in the rocks of Yorkshire. *Proceedings of the Geological and Polytechnic Society of the West Riding of Yorkshire* (1844-1845), 2, 274-285.

Pia, J. von 1937. Die wichtigsten Kalkalgen des Jungpaläozoikums und ihre geologische Bedeutung. *Compte Rendu du 2e Congrès Avancement Etudes de Stratigraphie du Carbonifère, Heerlen*, 1935, 2, 765-856.

Pille, L. 2008. *Foraminifères et algues calcaires du Mississippien supérieur (Viséen supérieur-Serpoukhovien) : rôles biostratigraphique, paléoécologique et paléogéographique aux échelles locale, régionale et mondiale.* Ph.D. Université de Lille, 3 vol., 1-226 + 1-255 + 72 pl. (Unpublished).

Pille, L., Vachard, D. and Aretz, M. 2006. Paleobathymetric zonation of the Viséan coral-thrombolite reef-mounds of the Montagne Noire (southern France). *Kölner Forum für Geologie und Paläontologie*, 15, 102-103.

Pinard, S. and Mamet, B. 1998. Taxonomie des petits foraminifères du Carbonifère supérieur-Permien inférieur du bassin de Sverdrup, Arctique canadien. *Paleontographica Canadiana*, 15, 1-253.

Plummer, H.J. 1930. Calcareous foraminifera in the Brownwood shale near Bridgeport, Texas. *Bulletin University of Texas*, 3019, 5-21.

Préat, A., Mamet, B., Bernard, A. and Gillan, D. 1999. Rôle des organismes microbiens dans la formation des matrices rougeâtres paléozoïques: exemple du Dévonien, Montagne Noire. *Revue de Micropaléontologie*, 42 (2), 161-182.

Préat, A., Mamet, B., De Ridder Ch., Boulvain, F. and Gillan, D. 2000. Iron bacterial and fungal mats, Bajocian stratotype (Mid-Jurassic, northern Normandy, France). *Sedimentary Geology*, 137, 107-126.

Préat, A., Morano, S., Loreau, J.P., Durlet, C. and Mamet, B. 2005. Petrography and biosedimentology of the Rosso Ammonitico Veronese (middle-upper Jurassic, north-eastern Italy). *Facies*, 52, 265-278.

Randon, C. 2006. *Conodontes du Dévonien supérieur-Carbonifère inférieur (Thaïlande, Europe), paléontologie et implications géologiques*. Thèse de Doctorat de l'Université de Lille, 1-457. (Unpublished).

Rauzer-Chernousova, D.M., Bensh, F.R., Vdovenko, M.V., Gibshman, N.B., Leven, E.Ya., Lipina, O.A., Reitlinger, E.A., Solovieva, M.N. and Chediya, I.O. 1996. Spravochnik po sistematike foraminifer Paleozoya; Endothyroidy, Fuzulinoidy (Reference-book on the systematics of Paleozoic foraminifera; Endothyroida and Fusulinoida). *Rossiiskaya Akademiya Nauk, Geologicheskii Institut, Moskva "Nauka"*, 1-207 (in Russian).

Reitlinger, E.A. 1950. Foraminifery srednekamennougolnykh otlozhenii tsentralnoi chasti Russkoi platformy (isklyuchaya semeistvo Fusulinidae) [Foraminifera from Middle Carboniferous of the central part of the Russian Platform (excepting the family Fusulinidae)]. *Akademiya*

Nauk SSSR., Trudy Geologicheskogo Instituta, 126, geologichevskaya seriya 47, 1-127 (in Russian, French translation BRGM n° 1456).

Reitlinger, E.A. 1965. Razvitie foraminifer v pozdnepermskogo i ranne-triasovyuf epokhi na territorii Zakavkazya (Development of the foraminifera in the Late Permian and Early Triassic times in Transcaucasia). *Voprosy Mikropaleontologii*, 9, 45-70 (in Russian).

Resig, J.M. and Glenn, C.R. 1997. Foraminifera encrusting phosphoritic hardgrounds of the Peruvian upwelling zone: taxonomy, geochemistry, and distribution. *Journal of Foraminiferal Research*, 27 (2), 133-150.

Reuss, A.E. 1862. Entwurf einer systematischen Zusammenstellung der Foraminiferen. *Sitzungberichte der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Classe* (1861) 44 (1), 355-396.

Rhumbler, L. 1895. Entwurf eines natürlichen Systems der Thalamophoren. *Nachr. Königl. Gesell. Wiss. Göttingen, Math.-Phys. Kl.,* Jahr. 1895, 51-98.

Rothpletz, A. 1894. *Ein geologischer Querschnitt durch die Ost-Alpen nebst Anhang über die sog. Glarner Doppelfalte*. E. Schweizerbart'sche Verlag, 1-268, Stuttgart.

Ruzhentsev, V. E. and Sarycheva T.G. 1965. *Razvitie i smena morskikh organizmov na rubezhe paleozoya i mezozoya* (Development and succession of marine organisms at the Palaeozoic-Mesozoic boundary). Akademiya Nauk SSSR, Trudy Paleontologicheskikh Institut, 108, 1-431 (in Russian).

Rzehak, A. 1885. Bemerkungen über einige Foraminiferen der Oligocän Formation. *Verhandlungen des Naturforschenden Vereins in Brünn*, 23, 123-129.

Salaj, J., Borza, K. and Samuel, O. 1983. Triassic Foraminifera of the West Carpathians. *Geologicky Ustav Dionyza Stura*, 1-213.

Schneider, J. 1970. Foraminiferen als Epibionten auf Conodonten aus dem Ober-Devon des Kellerwaldes (Rheinisches Schiefergebirge) und des Harzes, Göttingen Arbeiten. *Geologie und Paläontologie,* 5, H. Martin-Festschrift, 89-98.

Schubert, R.J. 1921. Paläontologische Daten zur Stammesgeschichte der Protozoen. *Paläontologische Zeitschrift*, 3 (2) (1920), 129-188.

Scotese, C.R. and Langford, R.P. 1995. Pangea and the Paleogeography of the Permian. In:

Scholle, P.A., Peryt, T.M. and Ulmer-Scholle, D.S. (Eds.), *The Permian of Northern Pangea*, 1: Paleogeography, Paleoclimates, Stratigraphy, Springer-Verlag, 3-19.

Sellier de Civrieux, J.M. and Dessauvagie, T.F.J. 1965. Reclassification de quelques Nodosariidae, particulièrement du Permien au Lias. *Maden Tetkik ve Arama Enstitüsü Yayinlarindan (M.T.A.),* 124, 1-178.

Sepkoski, J.J. 1989. Periodicity in extinction and the problem of catastrophism in the history of life. *Journal Geological Society London*, 146, 7-19.

Sepkoski, J.J. 1990. The taxonomic structure of periodic extinction. In: Sharpton, V.L. and Ward, P.D. (Eds.), *Global Catastrophes in Earth History*. Geological Society America, Special Paper, 247, 33-44.

Sepkoski, J.J. 1992. *A Compendium of Fossil Marine Animal Families*. 2nd Edition, Milwaukee Public Museum**,** Contributions Biology Geology, 83, 1-156.

Sharland, P.R., Archer, R., Casey, D.M., Davies, R.B., Hall, S.H., Heward, A.P., Horbury, A.D. and Simmons, M.D. 2001. Arabian Plate Sequence Stratigraphy. *GeoArabia*, Special Publication, 2, 1-371.

Sheng, J.C. 1963. Permian fusulinids of Kwangsi, Kueichow and Szechuan. *Palaeontologica Sinica* n.s., B, 10, 1-247 (in Chinese and English).

Stepanov, D. L., Golshani, F. and Stöcklin, J. 1969. Upper Permian and Permian-Triassic boundary in north-Iran. *Reports Geological Survey Iran*, 12, 1-72.

Teichert, C., Kummel, B. and Sweet, W. 1973. Permian-Triassic Strata, Kuh-e-Ali Bashi, northwestern Iran. *Bulletin Museum Comparative Zoology Harvard University*, 145 (8), 359-472.

Tucker, M.E. 1973. Ferromanganese nodules from the Devonian of the Montagne Noire (S. Fance) and West Germany. *Geologische Rundschau,* 62 (1), 137-153.

Ueno, K. 1992. Permian foraminifera from the Takakurayama Group of the southern Abukuma Mountains, Northeast Japan. *Transactions and Proceedings Paleontological Society Japan*, n.s., 168, 1265-1295.

Vachard, D. 1973. Remarques sur les Foraminifères des calcaires griottes *sensu lato* (Frasnien inférieur-Tournaisien inférieur) du versant méridional de la Montagne Noire (Aude - Hérault). *Compte Rendu Sommaire Société géologique de France,* 1 (4), 116-118.

Vachard, D. 1974. *Contribution à l'étude stratigraphique et micropaléontologique (algues et foraminifères) du Dévonien-Carbonifère inférieur de la partie orientale du versant méridional de la Montagne Noire (Hérault, France)*. Thèse de 3e Cycle, 408 pp. (Unpublished).

Vachard, D. and Beckary, S. 1991. Algues et foraminifères bachkiriens des coal balls de la Mine Rosario (Truebano, Léon, Espagne). *Revue de Paléobiologie*, 10 (2), 315-357.

Vachard, D. and Cózar, P., 2004. *Insolentitheca* emend., *Protoinsolentitheca* n. gen. and Caligellidae emend., permanent cysts of Paleozoic foraminifera? *Rivista Italiana di Paleontologia e Stratigrafia*, 110 (3), 591-603.

Vachard, D. and Ferrière, J. 1991. Une association à *Yabeina* (foraminifère fusulinoïde) dans le Midien (Permien supérieur) de la région de Whangaroa (Baie d'Orua, Nouvelle-Zélande). *Revue de Micropaléontologie*, 34 (3), 201-230.

Vachard, D. and Krainer, K. 2001. Smaller foraminifera, characteristic algae and pseudo-algae of the latest Carboniferous/early Permian Rattendorf Group, Carnic Alps (Austria/Italy). *Rivista Italiana de Paleontologia e Stratigrafia*, 107 (2), 169-195.

Vachard, D. and Mouravieff, N. 1994. Nouvelles faunes des Semitextulariinae (Foraminifères) dans le Frasnien franco-belge. Livre jubilaire Conil. *Mémoires Institut Géologie Université de Louvain*, 35, 213-219.

Vachard, D., Martini, R., Rettori, R. and Zaninetti, L. 1994. Nouvelle classification des Foraminifères endothyroïdes du Trias. *Geobios*, 27 (5), 543-557.

Vachard, D., Hauser, M., Martini, R., Zaninetti, L., Matter, A. and Peters, T. 2002. Middle Permian (Midian) foraminiferal assemblages from the

Batain Plain (Eastern Oman): their significance to Neotethyan paleogeography. *Journal of Foraminiferal Research*, 32 (2), 155-172.

Vachard, D., Gaillot, J., Vaslet, D. and Le Nindre, Y.M. 2005. Foraminifera and algae from the Khuff Formation (late Middle Permian-Early Triassic) of central Saudi Arabia. *GeoArabia*, 10 (4), 137-186.

Van der Zwann G.J., Duijnstee, I.A.P., den Dulk, M., Ernst, S.R., Jannink, N.T. and Kouwenhoven, T.J. 1999. Benthic foraminifera: proxies or problems? A review of palaeoecological concepts. *Earth-Science Reviews*, 46, 213-236.

Vuks, G.P., and Chediya, I.O. 1986. Foraminifery lyudyanzinskoi svity bukhty neizvestnaya (Yuznnoe Primorye) (Foraminifera from the Lyudyansk Suite (southern Primoye). In: *Korrelyatsiya Permo-Triasovykh otlozhenii Vostoka SSSR* (Correlations of Permian-Triassic deposits of Eastern USSR). Academy of Sciences USSR, Far-Eastern Scientific Centre, Institute of Biology and Pedology, Project IGCP no. 203, 82-88 (in Russian).

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The Upper Cretaceous planktic foraminiferal genus *Hendersonia* was erected by Georgescu and Abramovich (2008, p.100). Since its publication we found out that this name is preoccupied by *Hendersonia* Dall, 1905 (Gastropoda, Neritopsina, Helicinidae); its type species is *Hendersonia occulta* (Say, 1831).

A new name is proposed for the Upper Cretaceous planktic foraminifer genus, namely *Hendersonites*, in order to avoid homonymy. The original etymology of the name is maintained. The new name is formed by adding a different Latin suffix, "-ites".

REFERENCE

Georgescu, M.D, and Abramovich, S. 2008. Taxonomic revision and phylogenetic classification of the Late Cretaceous (Upper Santonian-Maastrichtian) serial planktonic foraminifera (Family Heterohelicidae Cushman, 1927) with peripheral test wall flexure. *Revista Española de Micropaleontología*, 40, 97-114.

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Müller, A. H. 1979. Fossilization (Taphonomy). In: *Treatise on Invertebrate Paleontology* (Eds. R. A. Robison and C. Teichert). The University of Kansas Press & The Geological Society of America, Boulder, 2-78.

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Genus *Thomasinella* Schlumberger, 1893
Thomasinella punica Schlumberger, 1893

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