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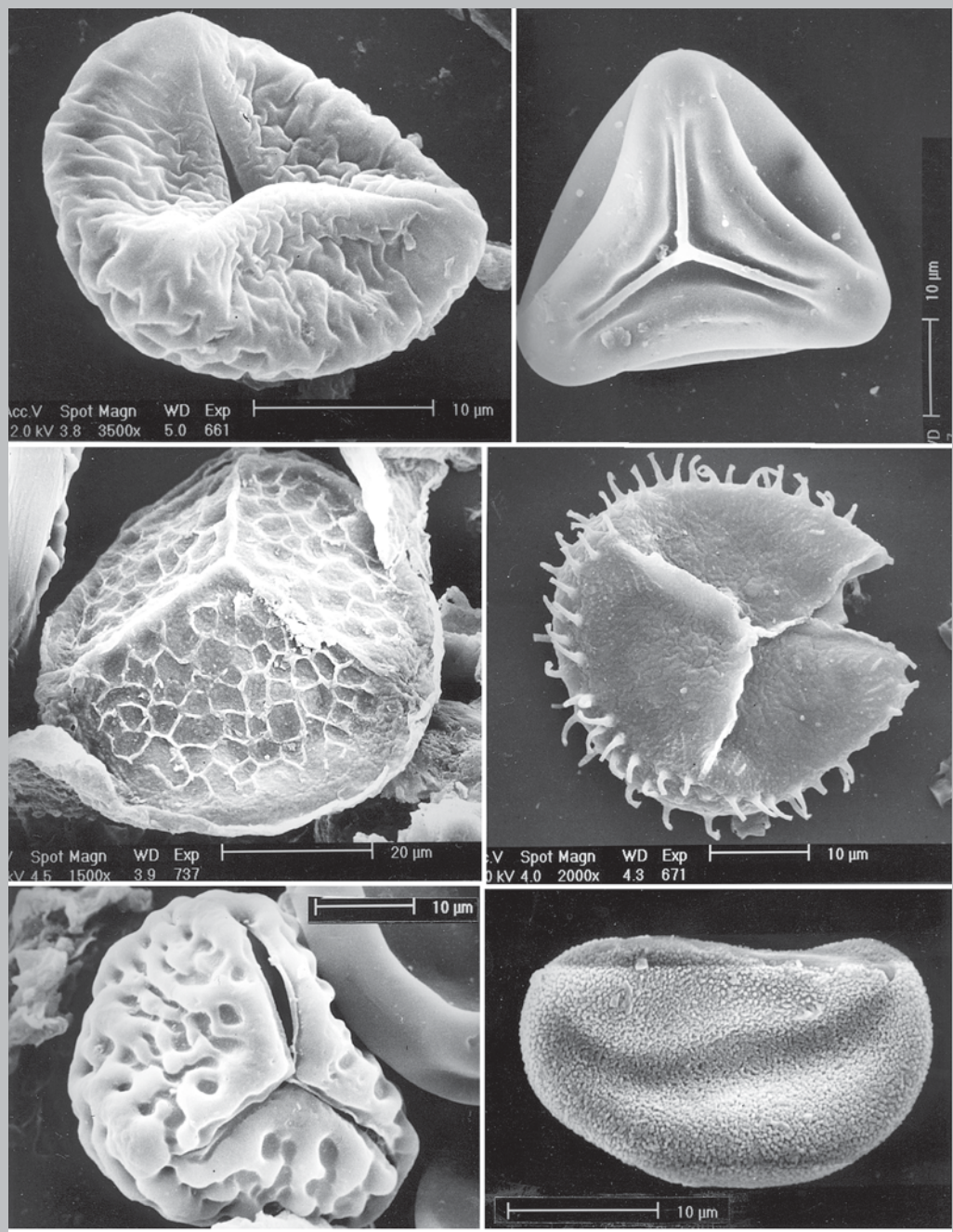

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Portada: Palinomorfos del Daniense (Paleoceno) de la provincia de Chubut (Patagonia, Argentina). Microfotografías de W. Volkheimer, L. Scafati y D.L. Melendi.

Cover: Danian (Paleocene) palinomorphs from Chubut province (Patagonia, Argentina). Microphotographs by W. Volkheimer, L. Scafati and D.L. Melendi.

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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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Keep *tables* few and simple. Plan them so that take up the entire width of the printed page (180 mm) or the width of one column (85 mm). Captions are to be typed separately.
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Análisis morfoestadístico del género *Palaeoglobigerina* (Foraminifera, Globigerinida) del Paleoceno basal, y descripción de una nueva especie

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Resumen

Se han analizado los datos biométricos medidos sobre ejemplares del género *Palaeoglobigerina* Arenillas, Arz y Náñez, para tratar de delimitar estadísticamente las especies que incluye. *Palaeoglobigerina* es un género planctónico del Daniense basal que agrupa a especies de concha trocoespiralada muy pequeña, con 3 a 4 cámaras en la última vuelta de espira y pared calcítica hialina, lisa y microperforada con poros cilíndricos o poros en túmulo incipientes. El análisis morfoestadístico ha permitido delimitar cuatro especies: *Pg. alticonusa* (Li, McGowran y Boersma), *Pg. minutula* (Luterbacher y Premoli Silva), *Pg. fodina* (Blow) y una cuarta que no había sido formalmente definida: *Pg. luterbacheri* n. sp. Esta nueva especie se caracteriza por 4 cámaras en la última vuelta de espira, lado espiral generalmente plano, contorno ecuatorial subcuadrado y abertura interiomarginal umbilical-extraumbilical.

Palabras clave: Foraminíferos planctónicos, Taxonomía, holotipo, Daniense, Túnez

Abstract

[*Morphostatistical analysis of the genus* Palaeoglobigerina *(Foraminifera, Globigerinida) from the basal Paleocene, and description of a new species*] Biometric data measured on specimens of *Palaeoglobigerina* Arenillas, Arz y Náñez have been statistically analyzed in order to delimit the species that included in this genus. *Palaeoglobigerina* is a basal Danian planktic genus which includes species with minute trochospiral test, 3 to 4 chambers in the last whorl of the spire, and wall calcareous hyaline, smooth and microperforate with pore-murals or incipient pore-mounds. The morphostatistical analysis has allowed to delimit four species: *Pg. alticonusa* (Li, McGowran and Boersma), *Pg. minutula* (Luterbacher and Premoli Silva), *Pg. fodina* (Blow), and one fourth that had not been formally defined: *Pg. luterbacheri* n. sp. This new species is characterized by 4 globular chambers in the last whorl of spire, spiral side usually flat, equatorial outline subsquadrate, and aperture interiomarginal umbilical-extraumbilical.

Keywords: Planktic foraminifera, Taxonomy, holotype, Danian, Tunisia

1. INTRODUCCIÓN

Las asociaciones de foraminíferos planctónicos del Daniense basal se caracterizan por su poca diversidad, con especies esencialmente cosmopolitas, conchas morfológicamente simples y muy pequeñas si las comparamos con las del Maastrichtiense Superior. Estas asociaciones oligotáxicas aparecen después del evento de extinción en masa del límite Cretácico/Paleógeno (K/Pg), en el que se extinguieron más del 90% de las especies de foraminíferos planctónicos presentes en el Maastrichtiense terminal (Smit, 1982; D'Hondt, 1991; Molina *et al*., 1998). Las escasas especies que sobrevivieron al evento K/Pg sufrieron un fenómeno de disminución en tamaño

(Arenillas *et al*., 2000), similar al acontecido en otros eventos de extinción y que ha sido denominado efecto Lilliput por Urbanek (1993). Algunas de ellas, como *Guembelitria cretacea, Guembelitria* cf. *trifolia*, *Hedbergella holmdelensis* y *Hedbergella monmouthensis*, se han propuesto como los grupos basales de las primeras líneas evolutivas de foraminíferos planctónicos del Daniense (Olsson *et al*., 1992, 1999; Arenillas y Arz, 1996, 2000; Apellániz *et al*., 2002).

Las primeras especies que aparecieron en el Daniense lo hicieron siguiendo un modelo de radiación evolutiva (D'Hondt, 1991; Arenillas *et al*., 2000). Dichas especies pertenecen a los géneros *Woodringina* Loeblich y Tappan, *Chiloguembelina* Loeblich y Tappan, *Palaeoglobigerina* Arenillas, Arz y Náñez, y *Parvularugoglobigerina* Hofker, y pueden ser agrupadas en dos grandes grupos monofiléticos: las formas biseriadas (*Woodringina* y esencialmente *Chiloguembelina*) y las formas trocoespiraladas (*Palaeoglobigerina* y *Parvularugoglobigerina*). Son especies progenitoras pioneras que se extinguieron tempranamente al ser sustituidas por una nueva generación de especies progenitoras más evolucionadas y de mayor tamaño pertenecientes a los géneros *Eoglobigerina* Morozova, *Parasubbotina* Olsson, Hemleben, Berggren y Liu, *Globanomalina* Haque, *Praemurica* Olsson, Hemleben, Berggren y Liu, y *Globoconusa* Khalilov (Arenillas y Arz, 1996, 2000; Molina, 2006).

Las primeras especies de concha trocoespiralada del Daniense están caracterizadas por su pequeño tamaño, pared calcárea hialina microperforada y escasamente ornamentada, y han sido generalmente agrupadas en el género *Parvularugoglobigerina* (Olsson *et al*., 1992, 1999; Li *et al*., 1995; Berggren y Norris, 1997). La especie-tipo de este género, *Parvularugoglobigerina eugubina* (Luterbacher y Premoli Silva), presenta 5 a 6,5 cámaras en la última vuelta de espira y abertura principal en posición umbilical-extraumbilical. Otros autores han preferido excluir de este género a especies caracterizadas por un menor número de cámaras en la última vuelta de espira (4 o menos cámaras) y, en general, con la abertura en posición intraumbilical. Estas especies han sido frecuentemente asignadas a los géneros *Globoconusa* o *Eoglobigerina* (Keller, 1988; Brinkhuis y Zachariasse, 1988; Canudo *et al*., 1991; Keller, 1993; Keller *et al*., 1995; Arenillas y Arz, 1996; Olsson *et al*., 1999; Apellániz *et al*., 2002). Sin embargo, estos dos últimos géneros incluyen especies más modernas y con unas características morfológicas y microestructurales diferentes (Arenillas y Arz, 2000). Por esta razón, se ha definido recientemente un nuevo género, *Palaeoglobigerina*, para agrupar dichas especies (Arenillas *et al*., 2007).

Debido a su morfología simple, algunos especialistas en foraminíferos planctónicos del Daniense basal han sido cautos a la hora de definir o identificar especies en *Parvularugoglobigerina* y *Palaeoglobigerina* (Stainforth *et al*., 1975; Toumarkine y Luterbacher, 1985; Liu y Olsson, 1992; Olsson *et al*., 1992, 1999; Berggren y Norris, 1997). Otros autores han intentado reconocer y delimitar más especies (Luterbacher y Premoli Silva, 1964; Orue-Etxebarría, 1985; Salaj, 1986; Li *et al*., 1995; Arenillas y Arz, 1996, 2000; Apellániz *et al*., 2002), debido a que la variabilidad morfológica reconocible en estos primeros géneros del Daniense es, en algunos casos, tan amplia como en otros géneros más antiguos o más modernos en los que se han reconocido un mayor número de especies (Arenillas *et al*., 2007). El objetivo de este trabajo es analizar estadísticamente la variabilidad morfológica del género *Palaeoglobigerina*, a partir de datos biométricos obtenidos en ejemplares procedentes del corte de El Kef (Túnez), para delimitar morfológicamente las especies que incluye. La utilización de análisis morfoestadísticos para la delimitación de especies no es frecuente entre los taxónomos de foraminíferos planctónicos. Sin embargo, es una herramienta útil para resolver el debate en torno a cuántas especies reales hay en el Daniense basal. Este análisis ha permitido delimitar y definir una nueva especie, denominada *Palaeoglobigerina luterbacheri* en honor al Prof. Dr. HansPeter Luterbacher, que fue uno de los primeros en reconocerla en Ceselli y Gubbio, Italia, aunque sin proporcionar una definición formal.

2. MATERIAL Y MÉTODOS

El holotipo y paratipos de la nueva especie propuesta proceden de material recogido en el Daniense basal de la Formación El Haria de la sección de El Kef, centro-noroeste de Túnez (Fig. 1). El corte de El Kef fue elegido como el estratotipo del límite K/Pg en 1989, debido a su excelente exposición y continuidad estratigráfica (ver

revisión reciente en Molina *et al*., 2006). La Formación El Haria consiste en margas y calizas micríticas de edad Maastrichtiense superior y Paleoceno, emplazada entre la Formación Abiod, de edad Campaniense-Maastrichtiense, y la Formación Jebel Madhkour del Eoceno Inferior (Burollet, 1967; Said, 1978). Aunque las especies de *Palaeoglobigerina* se han reconocido en muchos cortes del Tetis, Golfo de México y Caribe (Arz *et al*., 1999; Arenillas *et al*., 2004, 2006), se ha elegido la sección estratotípica de El Kef para definir la nueva especie y para realizar el estudio biométrico y morfoestadístico debido a que la conservación de los foraminíferos planctónicos es muy buena, y a que son abundantes en todos los niveles estratigráficos muestreados.

El Daniense basal de El Kef fue muestreado en intervalos centimétricos o decimétricos (Arenillas *et al*., 2000). Las muestras fueron disgregadas en agua con la ayuda de H_2O_2, levigadas con un tamiz de 63 micras, tratadas con ultrasonidos y secadas con una estufa a menos de 50ºC. Se obtuvo una fracción representativa de más de 300 ejemplares por cada muestra, y los ejemplares se montaron en celdillas múltiples para su conservación y posterior revisión. El estudio morfoestadístico se basó en medidas biométricas tomadas por Arenillas *et al*. (2007) sobre más de 90 ejemplares de *Palaeoglobigerina* extraídos de dos de estas celdillas, que corresponden a muestras de dos niveles estratigráficos situados a 1,75 y 2 m sobre el límite K/Pg de El Kef (muestras KF13,75 y KF14). Los ejempla-

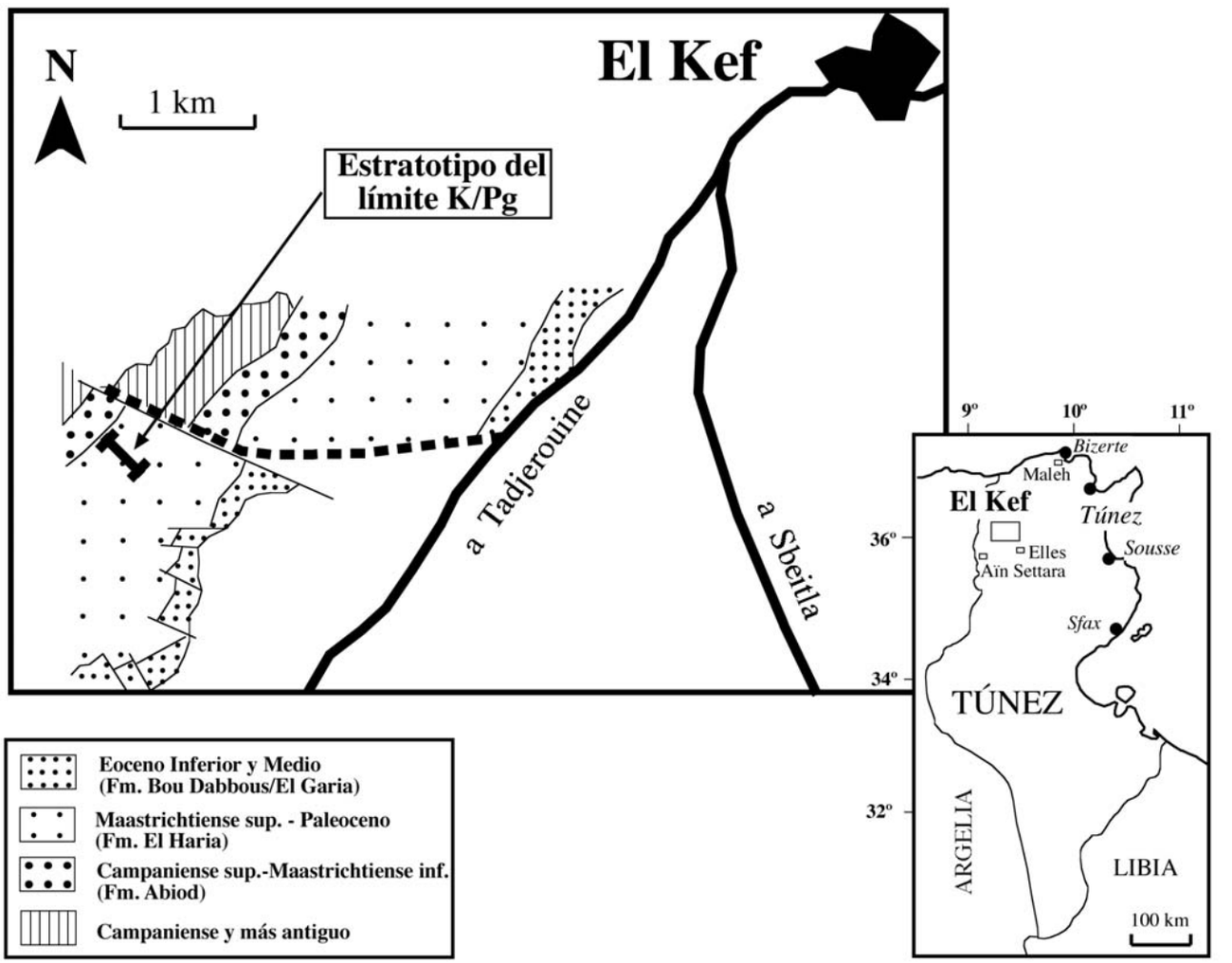


Figura 1. Localización geográfica y contexto geológico del corte de El Kef (Túnez), el cual es el estratotipo del límite K/Pg y la localidad-tipo de *Palaeoglobigerina luterbacheri* n. sp.

Figure 1. Geographical location and geological setting of the El Kef section (Tunisia), which is the K/Pg boundary stratotype and the type-locality of Palaeoglobigerina luterbacheri *n. sp.*

res-tipo de *Palaeoglobigerina luterbacheri* n. sp. fueron obtenidos de la muestra KF15,00 (3 m por encima del límite K/Pg). El holotipo y paratipos de la nueva especie fueron fotografiados en el Servicio de Microscopía de la Universidad de Zaragoza (España), utilizando un Microscopio Electrónico de Barrido (MEB) JEOL JSM 6400, y depositados en el Museo Paleontológico de la Universidad de Zaragoza - Gobierno de Aragón.

La Figura 2 muestra la distribución estratigráfica de las especies de foraminíferos planctónicos identificadas en el Daniense inferior de El Kef (Arenillas *et al.*, 2000). La zonación seguida en este trabajo se basa en la de Arenillas *et al.* (2004), quienes reconocieron tres biozonas divididas en dos subbiozonas cada una: Subzonas de *Hedbergella holmdelensis* y de *Parvularugoglobigerina longiapertura* (para la Zona de *Guembelitria cretacea*), Subzonas de *Parvularugoglobigerina sabina* y de *Eoglobigerina simplicissima* (para la Zona de *Parvularugoglobigerina eugubina*), y Subzonas de *Eoglobigerina trivialis* y de *Subbotina triloculinoides* (para la Zona de *Parasubbotina pseudobulloides*). Esta biozonación se compara con la de Berggren y Pearson (1995) en la Figura 2. Las distribuciones estratigráficas de las especies de foraminíferos planctónicos en El Kef es semejante a las encontradas en cortes procedentes de diversas paleolatitudes, situados fundamentalmente en Túnez, España, Italia, México, Cuba y Argentina (Molina *et al.*, 1998; Arz *et al.*, 1999; Arenillas *et al.*, 2000, 2004, 2006; Náñez *et al.*, 2002).

Los parámetros biométricos utilizados para la delimitación de las especies se muestran en la Figura 3, y las medidas biométricas y valores de índices biométricos en las Tablas 1-4. Para la delimitación de especies de *Palaeoglobigerina* se ha utilizado como parámetros biométricos la longitud (L), la anchura (W) y la altura (H) de la concha, y la longitud (CL), la anchura (CW) y la altura (CH)

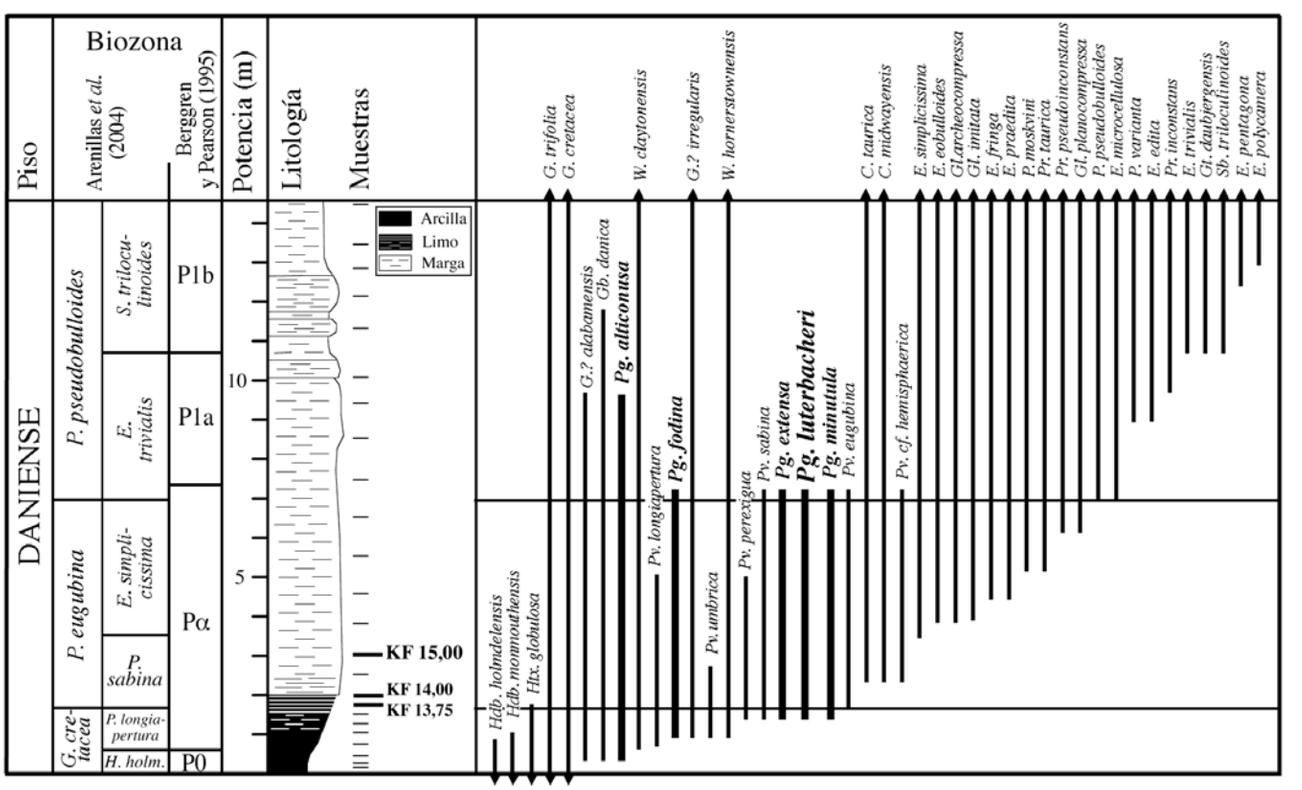


Figura 2. Rangos estratigráficos de especies y géneros de foraminíferos planctónicos de la parte basal del Daniense en el corte de El Kef, destacando las especies de *Palaeoglobigerina* (líneas gruesas). Posición estratigráfica de las muestras utilizadas para el análisis morfoestadístico y del nivel-tipo (muestra KF15.00) de *Palaeoglobigerina luterbacheri* n. sp.

Figure 2. Stratigraphical ranges of planktic foraminiferal species and genera of the basal part of the Danian at the El Kef section, emphasizing the species of Palaeoglobigerina *(thick lines). Stratigraphical position of the samples used for the morphostatistical analysis and of the type-level (sample KF15.00) of* Palaeoglobigerina luterbacheri *n. sp.*

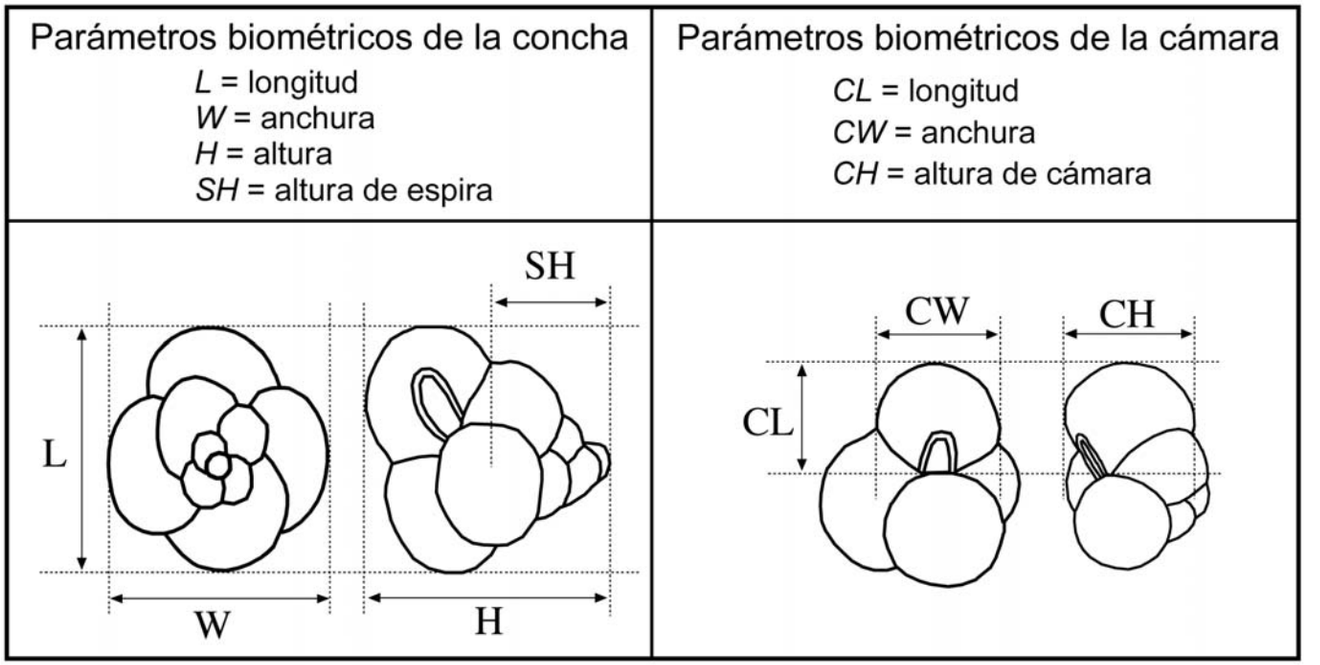


Figura 3. Parámetros biométricos, abreviaturas y convenciones descriptivas utilizadas en el análisis biométrico y morfológico del género *Palaeoglobigerina*.

Figure 3. Biometric parameters, abbreviations and descriptive terms used for the biometric and morphologic analyses of the genus Palaeoglobigerina.

de la última cámara (Fig. 3). Con la utilización de la altura de espira (SH) en lugar de la altura de la concha (H) se obtienen resultados similares. Como variables en los análisis estadísticos se han utilizado 5 índices biométricos: W/L, H/L, CW/W, CL/L y CH/H (expresados en tanto por ciento).

El estudio morfoestadístico incluye análisis univariantes, bivariantes y multivariantes. Los análisis univariantes, figurados mediante histogramas (distribución de frecuencias), se basan en los valores del índice biométrico más adecuado para discriminar las especies, analizándolas una a una; se han aplicado diversas pruebas estadísticas (*t*-Student, Kolmogorov-Smirnov, Mann-Whitney y ANOVA) para refutar o aceptar las hipótesis nulas (= dos poblaciones pertenecen a la misma especie), estimando la probabilidad (*p*) de que las poblaciones de ejemplares pertenezcan a la misma especie (Figs. 4, 5 y 6). Los análisis bivariantes, figurados mediante diagramas de dispersión (gráficos XY), se basan como los anteriores en valores de los índices biométricos más adecuados para la delimitación de las especies, analizándolas una a una y añadiendo envolventes convexas y elipses de 95% de confianza. También se ha aplicado análisis de varianza multivariante (MANOVA) de dos en dos poblaciones de datos, utilizando datos bivariantes (= dos índices biométricos) para las pruebas estadísticas (lambda de Wilk y traza de Pillai), e incluyendo un diagrama de dispersión obtenido con análisis de variaciones canónicas (CVA) (Fig. 7).

Los análisis multivariantes utilizados son: análisis de agrupamientos, análisis de componentes principales y análisis discriminante. El análisis de agrupamientos o *cluster* se ha basado en las medidas de distancia Euclídea entre todos los ejemplares (modo-R) a partir de los valores de índices biométricos (variables), con el fin de obtener grupos dentro de los ejemplares analizados y tratar así de delimitar especies (Fig. 8). El análisis de componentes principales (PCA) se ha aplicado a los valores de índices biométricos (variables) para identificar, a partir de una matriz de varianza-covarianzas, los dos autovectores o *eigenvectors* (componentes principales) que agrupen la mayor parte de la varianza del conjunto multidimensional de datos biométricos. La posición de los datos originales en un gráfico XY, dónde X e Y son el sistema de coordenadas dado por

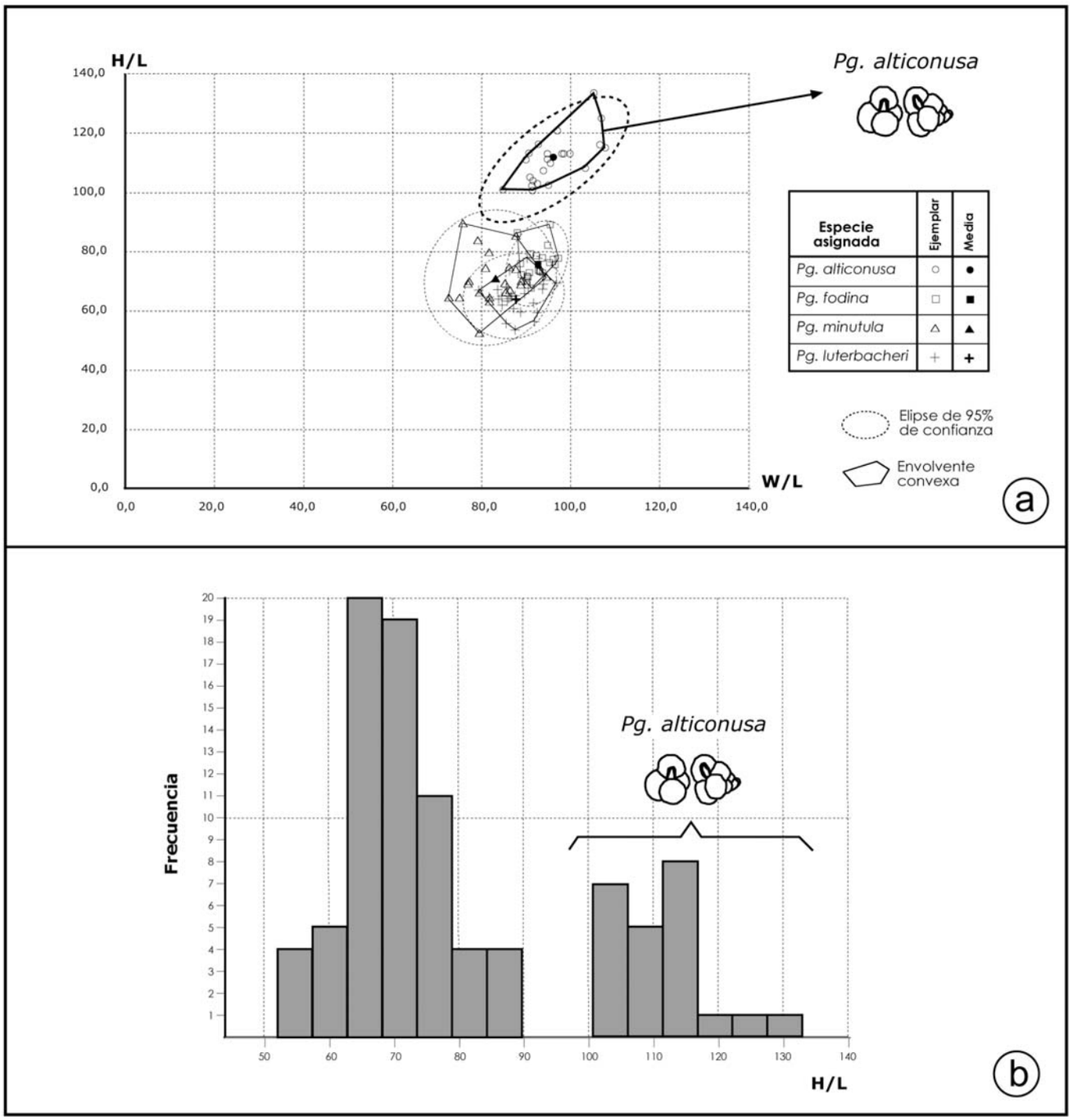


Figura 4. Análisis bivariante H/L x W/L (a) y univariante W/L (b) para delimitar la especie *Palaeoglobigerina alticonusa* del resto de especies de *Palaeoglobigerina* (*Pg. fodina, Pg. minutula, Pg. luterbacheri*).

Figure 4. H/L x W/L bivariate (a) and W/L univariate (b) analyses to delimit the species Palaeoglobigerina alticonusa *of the remainder of species of* Palaeoglobigerina *(*Pg. fodina, Pg. minutula, Pg. luterbacheri*).*

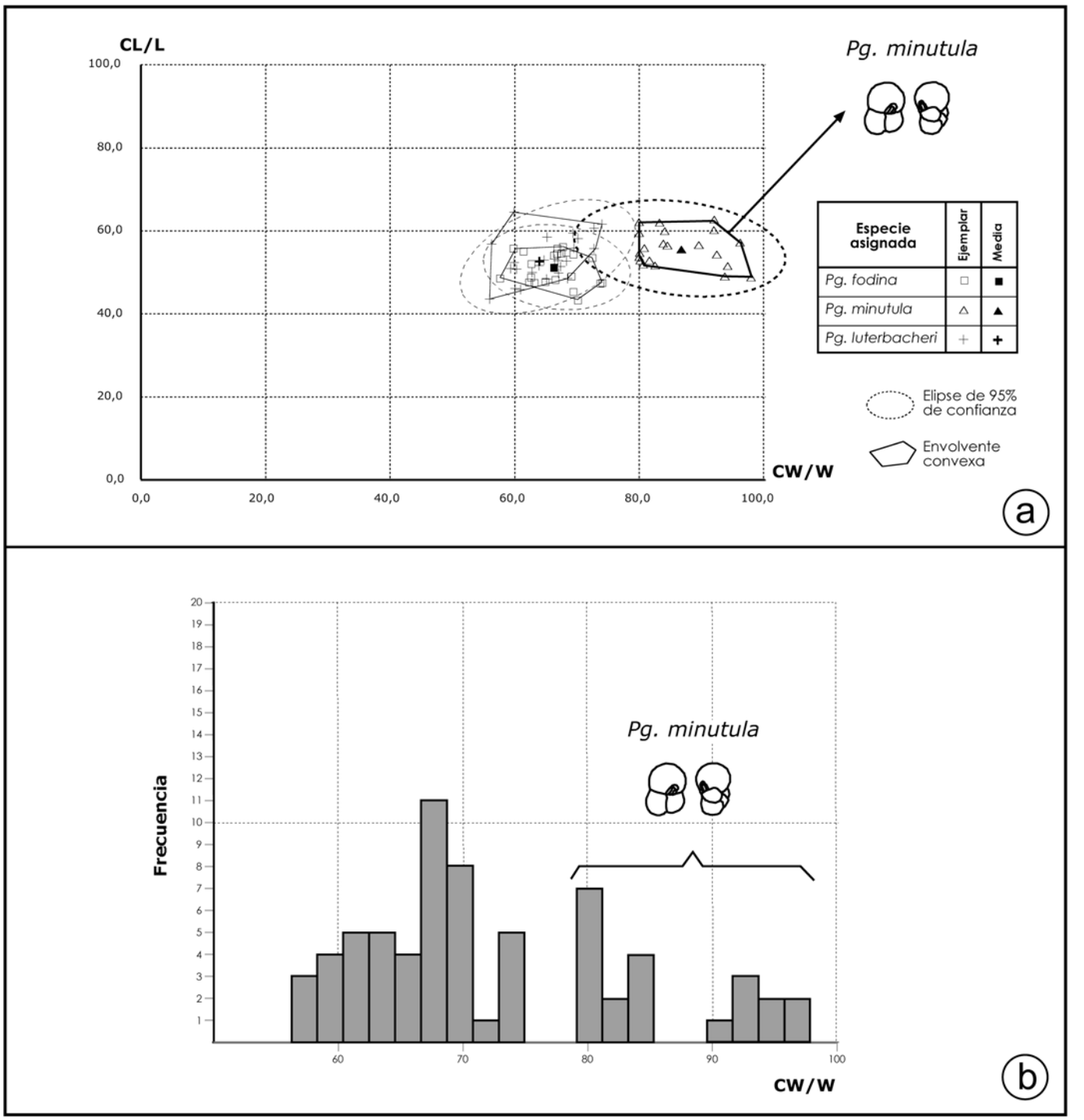


Figura 5. Análisis bivariante CW/W x CL/L (a) y univariante CW/W (b) para delimitar la especie *Palaeoglobigerina minutula* de *Palaeoglobigerina fodina* y *Palaeoglobigerina luterbacheri*. Se aprecian dos grupos dentro de *Pg. minutula*, que podrían representar especies diferentes.

Figure 5. CW/W x CL/L bivariate (a) and CW/W univariate (b) analyses to delimit the species Palaeoglobigerina minutula *of* Palaeoglobigerina fodina *and* Palaeoglobigerina luterbacheri. *Two groups inside* Pg. minutula *are appreciated, that could represent different species.*

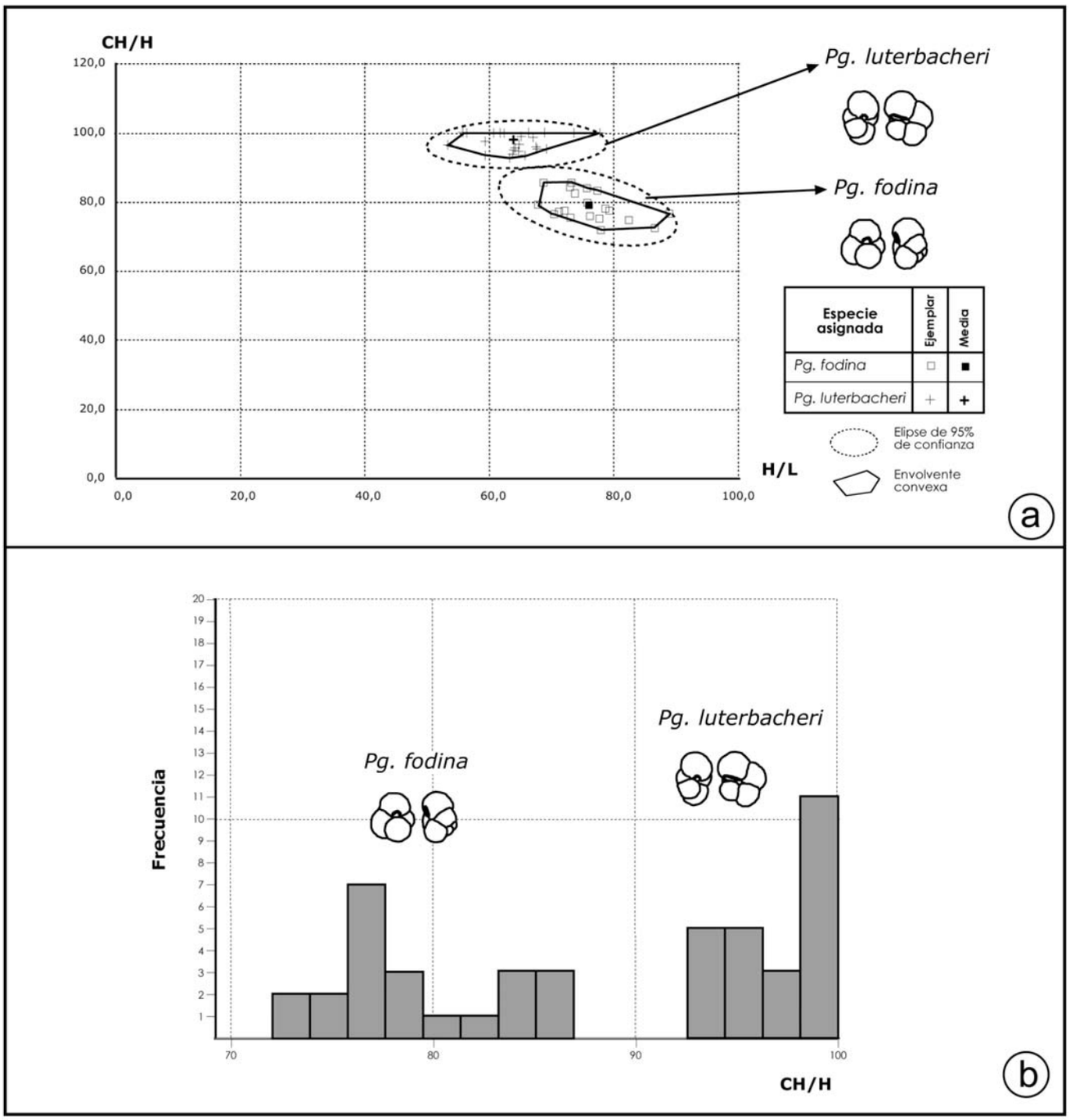


Figura 6. Análisis bivariante CH/H x H/L (a) y univariante CH/H (b) para delimitar las especies *Palaeoglobigerina fodina* y *Palaeoglobigerina luterbacheri*.

Figure 6. CH/H x H/L bivariate (a) and CH/H univariate (b) analyses to delimit the species Palaeoglobigerina fodina *and* Palaeoglobigerina luterbacheri.

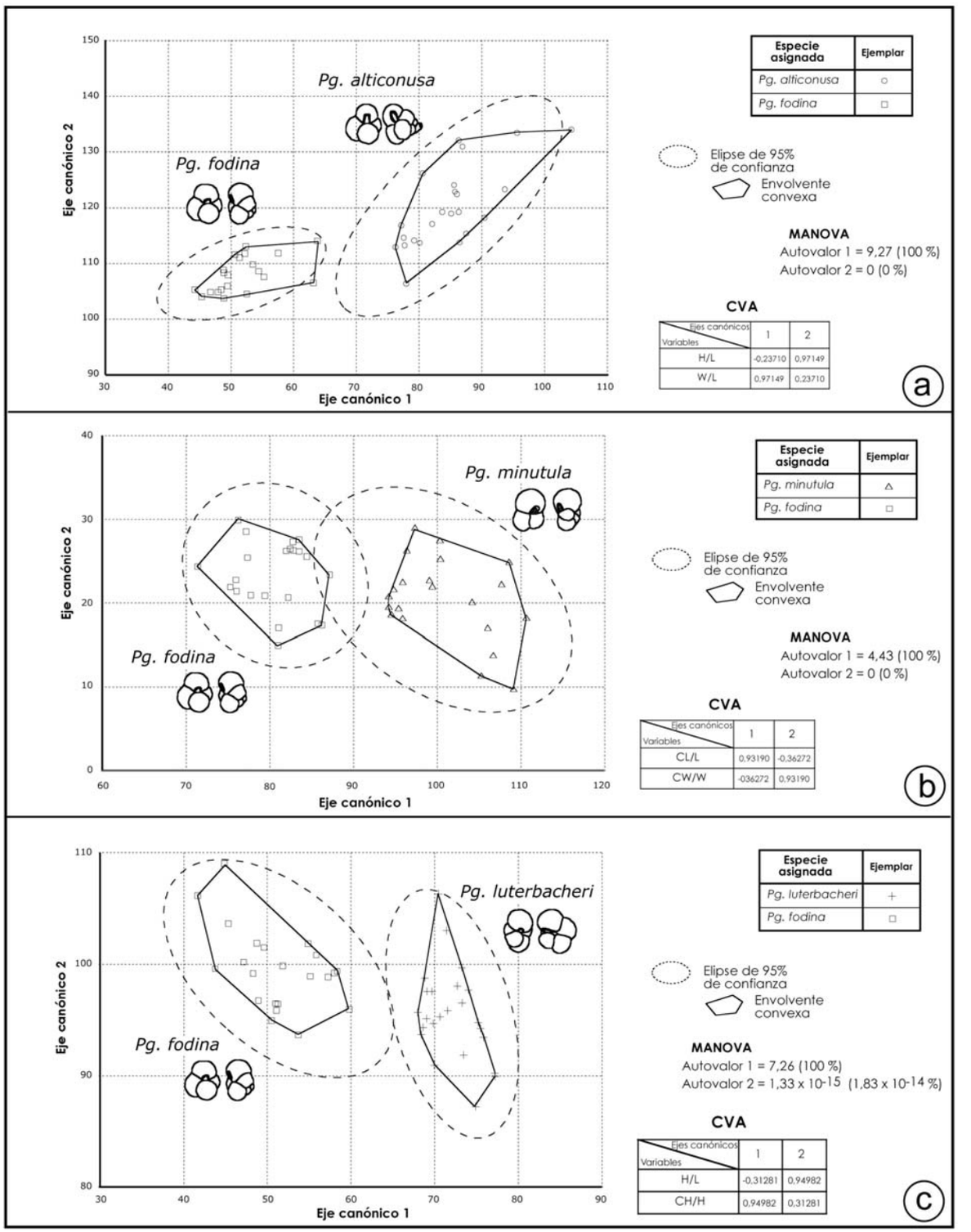


Figura 7. Análisis de varianza multivariante (MANOVA) y análisis de variaciones canónicas (CVA) aplicado a poblaciones de datos bivariantes de *Pg. alticonusa* y *Pg. fodina* (a), *Pg. minutula* y *Pg. fodina* (b), y *Pg. luterbacheri* y *Pg. fodina* (c).

Figure 7. Multivariate analysis of variance (MANOVA) and canonical variates analysis (CVA) applied to population of bivariate data of Pg. alticonusa *and* Pg. fodina *(a), Pg. minutula and* Pg. fodina *(b), and* Pg. luterbacheri *and* Pg. fodina *(c).*

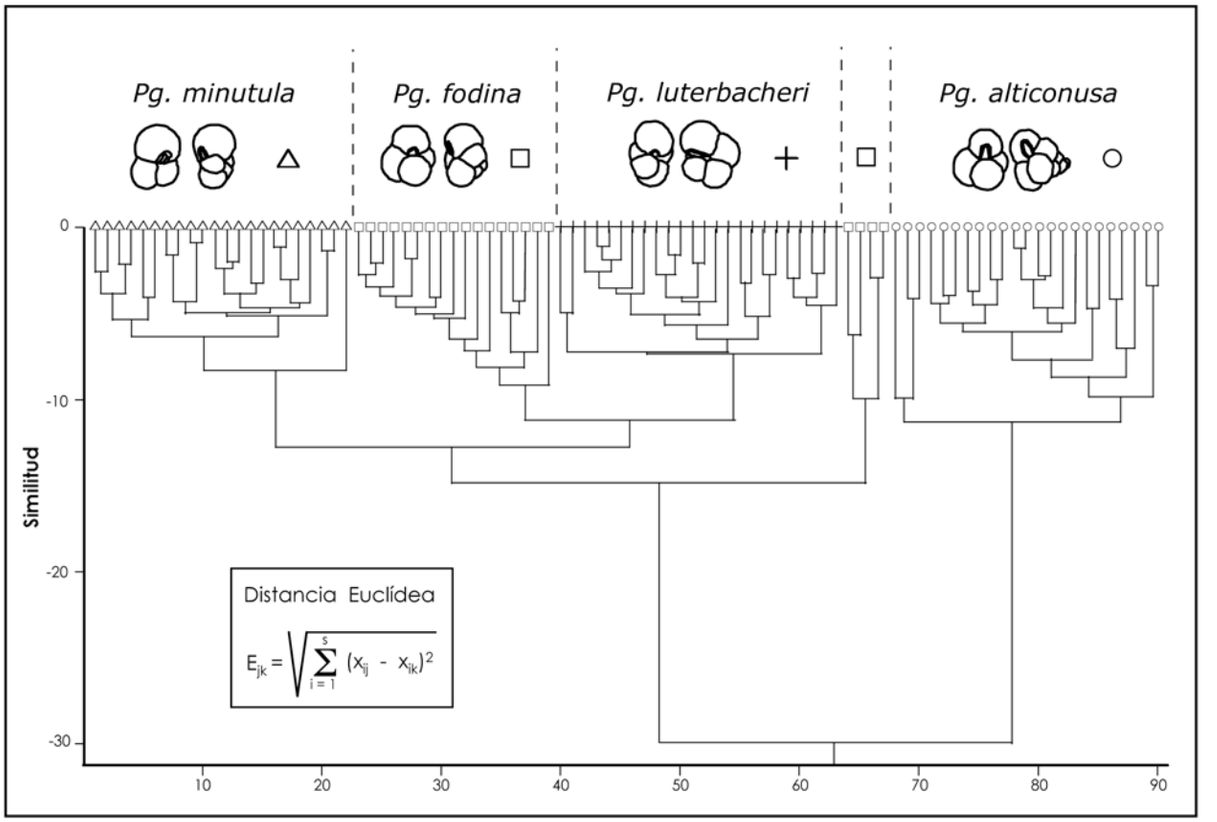


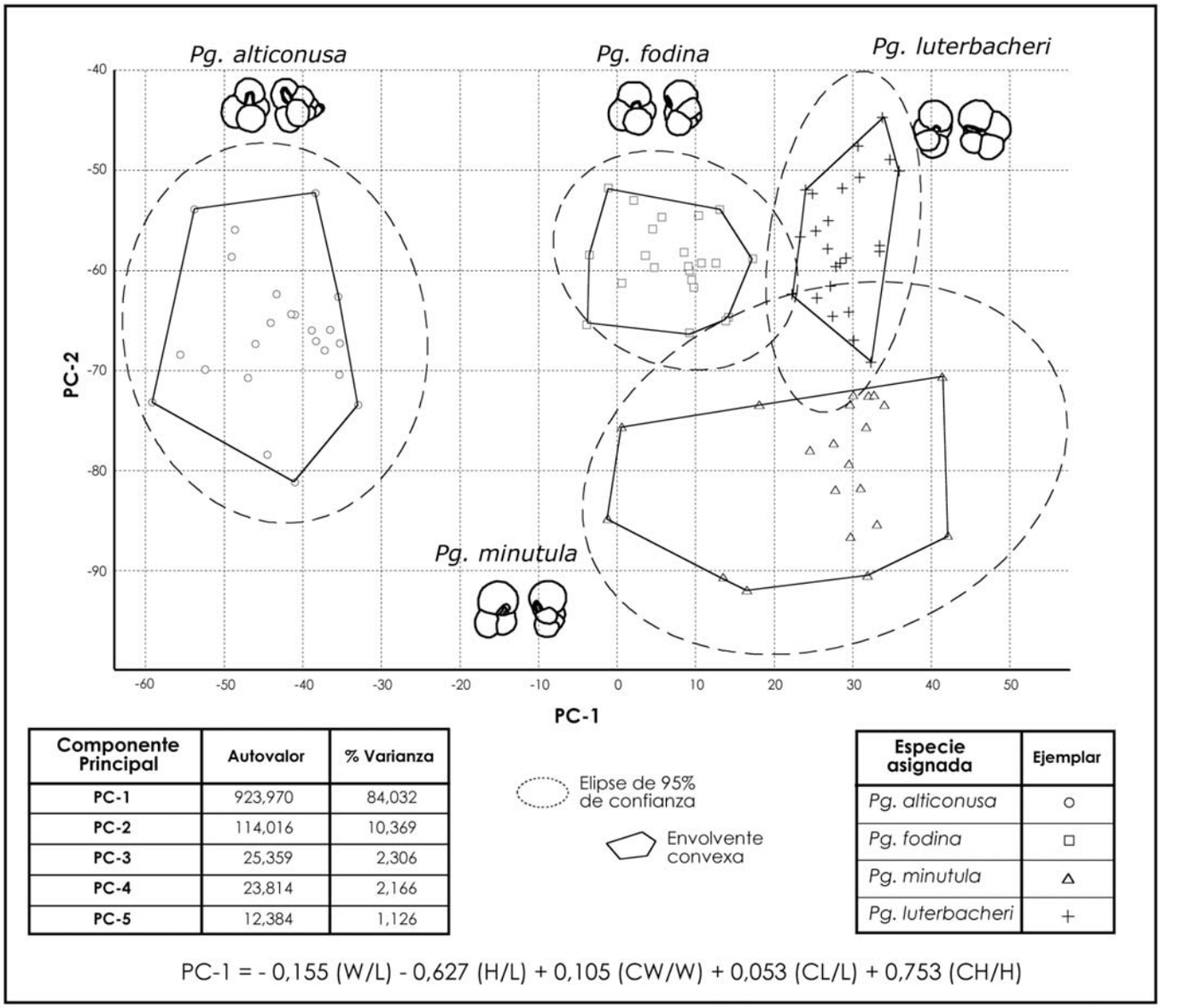
Figura 8. Análisis de agrupamientos o *cluster* basado en medidas de distancia Euclídea y aplicadas a los valores de índices biométricos de todos los ejemplares de *Palaeoglobigerina* (modo-R). E_{jk} = distancia euclídea entre ejemplar *j* y ejemplar *k*; X_{ij} = valor de la variable *i* (índice biométrico *i*) del ejemplar *j*; X_{ik} = valor de la variable *i* (índice biométrico *i*) del ejemplar *k*.

Figure 8. Cluster analysis based on Euclidean distance measures and applied to the values of biometric indices of all of specimens of Palaeoglobigerina *(R-mode). E_{jk} = euclidean distance between specimen j and specimen k; X_{ij} = value of the variable i (biometric index i) of the specimen j; X_{ik} = value of the variable i (biometric index i) of the specimen k.*

los dos primeros componentes principales, permite visualizar grupos que delimitan las especies, añadiendo envolventes convexas y elipses de 95% de confianza (Fig. 9). El análisis discriminante se ha aplicado a grupos (poblaciones) de datos multivariantes (valores de índices biométricos), de dos en dos poblaciones, para averiguar si las especies son diferentes o no. Este análisis proporciona un histograma que representa la distribución de frecuencias según el eje proporcionado por la función discriminante calculada (Fig. 10) y permite aplicar la prueba estadística *Hotelling's* T^2 o traza de Hotelling (equivalente multivariante del *t*-Student) para refutar o aceptar las hipótesis nulas (= las dos poblaciones pertenecen a la misma especie) y estimar la probabilidad de que las poblaciones pertenezcan a la misma especie. Complementariamente, se ha aplicado un análisis de varianza multivariante (MANOVA) de dos en dos poblaciones de datos, esta vez utilizando datos multivariantes (Fig. 11). Este tipo de análisis se aplica normalmente a todo el conjunto de poblaciones, pero los resultados gráficos obtenidos son semejantes a los del PCA y no se muestran en este trabajo. El software utilizado para el estudio morfoestadístico es el programa PAST, versión 1.44, de Øyvind Hammer, D. A. T. Harper y P. D. Ryan (Junio, 2006, http://folk.uio.no/ohammer/past). Para más detalles, ver Hammer *et al.* (2001).

3. CLASIFICACIONES PREVIAS

La clasificación de foraminíferos planctónicos danienses adoptada en este trabajo para las especies de *Palaeoglobigerina* está basada en la de Arenillas *et al.* (2007), la cual es a su vez una pequeña modificación de las de Are-



Componente Principal	Autovalor	% Varianza
PC-1	923,970	84,032
PC-2	114,016	10,369
PC-3	25,359	2,306
PC-4	23,814	2,166
PC-5	12,384	1,126

Especie asignada	Ejemplar
Pg. alticonusa	○
Pg. fodina	□
Pg. minutula	△
Pg. luterbacheri	+

Figura 9. Análisis de componentes principales (PCA), aplicado a los valores de índices biométricos de todos los ejemplares de *Palaeoglobigerina*.

Figure 9. Principal components analysis (PCA), applied to the values of biometric indices of all of specimens of Palaeoglobigerina.

nillas y Arz (1996, 2000). Estos autores realizaron una revisión taxonómica de clasificaciones previas, tales como las de Luterbacher y Premoli Silva (1964), Hofker (1978), Blow (1979), Toumarkine y Luterbacher (1985), Loeblich y Tappan (1987), D'Hondt (1991), MacLeod (1993), Li *et al*. (1995), Berggren y Norris (1997), Olsson *et al*. (1999) y Apellániz *et al*. (2002), y aportaron una nueva clasificación que difiere de las anteriores tanto en el número de especies consideradas como en la asignación taxonómica y la posición sistemática de algunas de ellas.

Las especies de *Palaeoglobigerina* se caracterizan por tener una concha trocoespiralada muy pequeña, globosa o subcónica, cámaras subesféricas o globulares, con 3 a 4 cámaras en la última vuelta y una abertura interiomarginal, normalmente intraumbilical y rodeada por un fino labio imperforado. Su pared es calcítica hialina, lisa y microperforada, con poros cilíndricos o, en ocasiones, poros en túmulo incipientes. Este tipo de pared es semejante a la que presentan las especies de *Parvularugoglobigerina*, razón por la cual las especies de *Palaeoglobigerina* han sido frecuentemente agrupadas en este género (D'Hondt

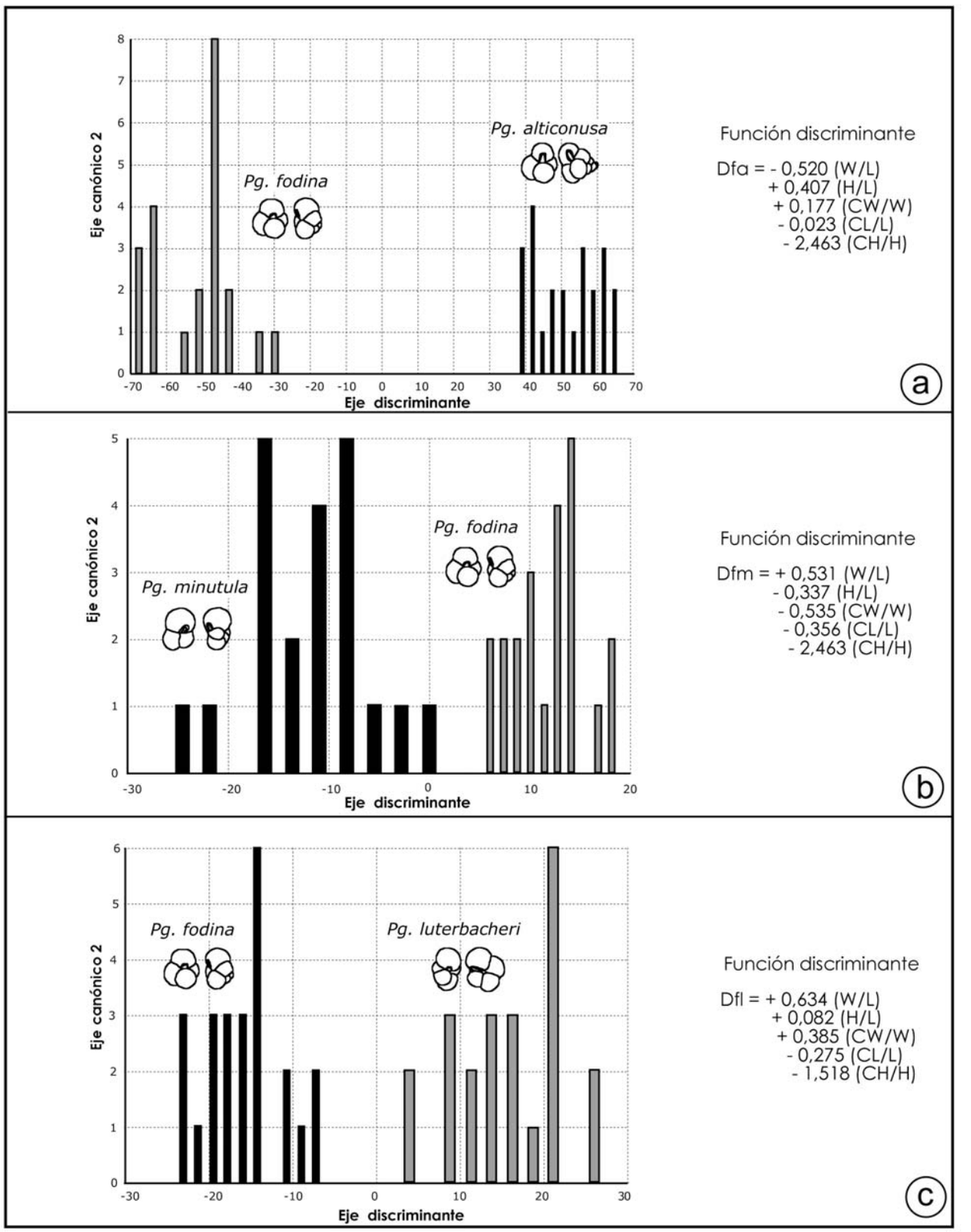
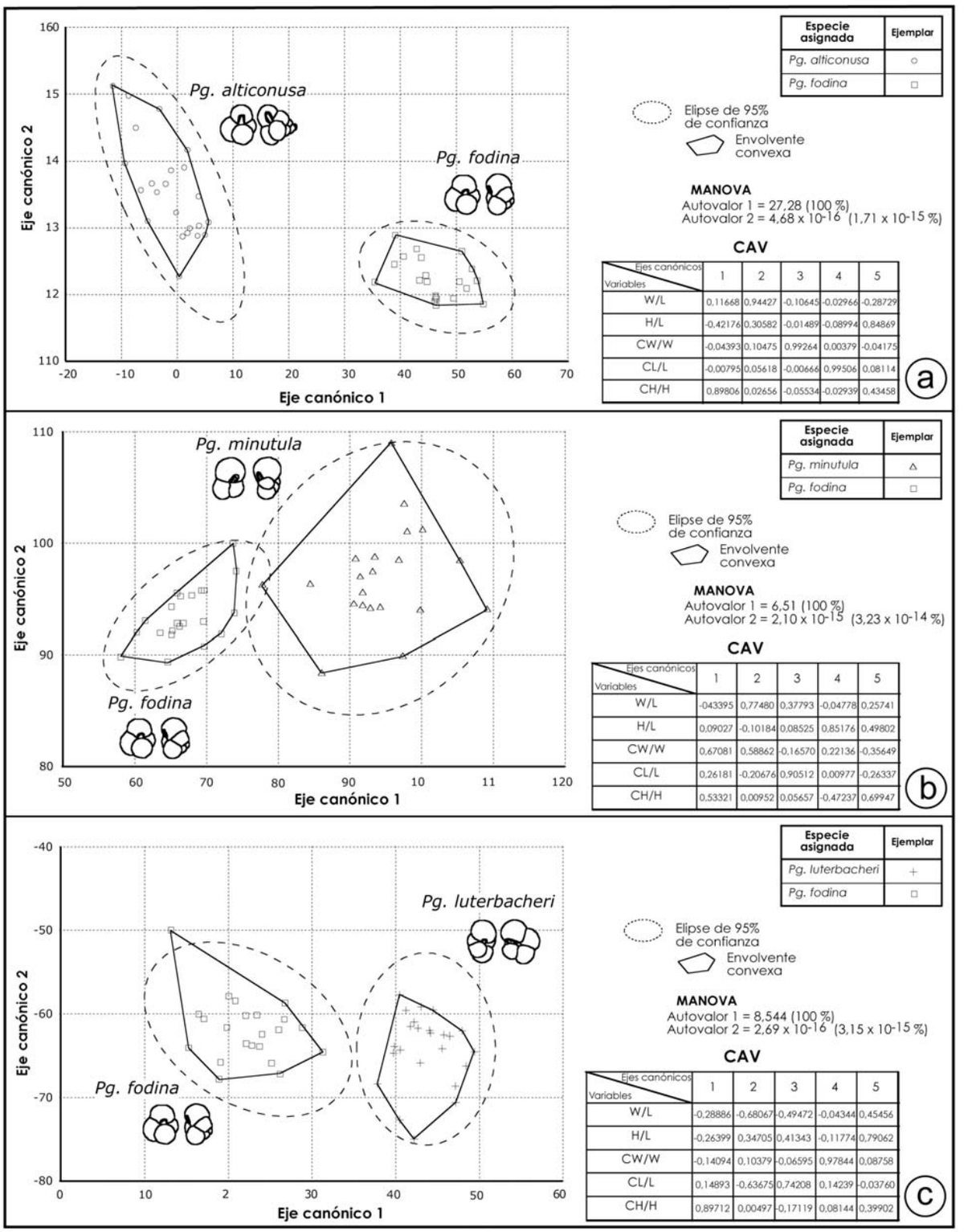


Figura10. Análisis discriminante aplicado a las poblaciones de datos multivariantes (valores de índices biométricos) de *Pg. alticonusa* y *Pg. fodina* (a), *Pg. minutula* y *Pg. fodina* (b), y *Pg. luterbacheri* y *Pg. fodina* (c).

Figure 10. Discriminant analysis applied to the multivariate data (values of biometric indices) of Pg. alticonusa *and* Pg. fodina *(a),* Pg. minutula *and* Pg. fodina *(b), and* Pg. luterbacheri *and* Pg. fodina *(c).*



Variables \ Ejes canónicos	1	2	3	4	5
W/L	0,11668	0,94427	-0,10645	-0,02966	-0,28729
H/L	-0,42176	0,30582	-0,01489	-0,08994	0,84869
CW/W	-0,04393	0,10475	0,99264	0,00379	-0,04175
CL/L	-0,00795	0,05618	-0,00666	0,99506	0,08114
CH/H	0,89806	0,02656	-0,05534	-0,02939	0,43458

Variables \ Ejes canónicos	1	2	3	4	5
W/L	-043395	0,77480	0,37793	-0,04778	0,25741
H/L	0,09027	-0,10184	0,08525	0,85176	0,49802
CW/W	0,67081	0,58862	-0,16570	0,22136	-0,35649
CL/L	0,26181	-0,20676	0,90512	0,00977	-0,26337
CH/H	0,53321	0,00952	0,05657	-0,47237	0,69947

Variables \ Ejes canónicos	1	2	3	4	5
W/L	-0,28886	-0,68067	-0,49472	-0,04344	0,45456
H/L	-0,26399	0,34705	0,41343	-0,11774	0,79062
CW/W	-0,14094	0,10379	-0,06595	0,97844	0,08758
CL/L	0,14893	-0,63675	0,74208	0,14239	-0,03760
CH/H	0,89712	0,00497	-0,17119	0,08144	0,39902

Figura 11. Análisis de varianza multivariante (MANOVA) y análisis de variaciones canónicas (CVA) aplicado a poblaciones de datos multivariantes de *Pg. alticonusa* y *Pg. fodina* (a), *Pg. minutula* y *Pg. fodina* (b), y *Pg. luterbacheri* y *Pg. fodina* (c).

Figure 11. Multivariate analysis of variance (MANOVA) and canonical variates analysis (CVA) applied to population of multivariate data of Pg. alticonusa *and* Pg. fodina *(a),* Pg. minutula *and Pg. fodina (b), and* Pg. luterbacheri *and* Pg. fodina *(c).*

y Keller, 1991; Liu y Olsson, 1992, 1994; Berggren y Norris, 1997; Olsson *et al.*, 1999). Sin embargo, otros autores (Arenillas y Arz, 1996, 2000) aconsejaron diferenciar taxonómicamente dos géneros, correspondientes a *Palaeoglobigerina* y *Parvularugoglobigerina*, ya que las especies del primero difieren de las del segundo por su menor número de cámaras tanto en el estadio neánico (3,5 a 4 frente a 4 a 4,5 cámaras) como en el adulto (3-4 frente a 4-9 cámaras).

De acuerdo a Arenillas *et al*. (2007), el género *Palaeoglobigerina* incluye al primer grupo de especies: *Pg. alticonusa* (Li, McGowran y Boersma), *Pg. fodina* (Blow), *Pg. extensa* (Blow), *Pg. minutula* (Luterbacher y Premoli Silva) y *Pg.* cf. *fringa* (sensu Luterbacher y Premoli Silva, 1964), siendo *Pg. fodina* la especie-tipo del género y *Pg.* cf. *fringa* la nueva especie definida en este trabajo: *Pg. luterbacheri*. Por otro lado, el género *Parvularugoglobigerina* incluye al segundo grupo de especies: *Pv. longiapertura* (Blow), *Pv. perexigua* Li, McGowran y Boersma, *Pv. umbrica* (Luterbacher y Premoli Silva), *Pv. eugubina* (Luterbacher y Premoli Silva), *Pv. sabina* (Luterbacher y Premoli Silva), y *Pv.* cf. *hemisphaerica* (sensu Blow, 1979), siendo *Pv. eugubina* la especie-tipo del género.

Las especies de *Palaeoglobigerina* han sido también asignadas frecuentemente al género *Globoconusa* (Keller, 1988; Brinkhuis y Zachariasse, 1988; Canudo *et al.*, 1991; Li y Radford, 1991; Arenillas y Arz, 1996; Arenillas *et al.*, 2000). Sin embargo, *Globoconusa* tiene mayor tamaño, papilas grandes y gruesas, e incluye formas más modernas tales como *Globoconusa daubjergensis* (Brönnimann) y *Globoconusa conusa* Khalilov. En este sentido, Salaj (1986) describió un nuevo género, *Postrugoglobigerina*, que incluía especies como *Postrugoglobigerina hariana* Salaj y *Postrugoglobigerina praedaubjergensis* Salaj. El género *Palaeoglobigerina* podría caer en sinonimia con *Postrugoglobigerina*. Sin embargo, la especie-tipo utilizada para definir *Postrugoglobigerina*, *P. hariana*, fue descrita con 5 cámaras en la última vuelta (Salaj, 1986) y podría ser un sinónimo junior de *Pv. sabina* (Arenillas *et al.*, 2000, 2007). En ese caso, *Postrugoglobigerina* se trataría de un sinónimo junior de *Parvularugoglobigerina*, tal como es normalmente considerado (Olsson *et al.*, 1999), y no un sinónimo senior de *Palaeoglobigerina*.

Atendiendo a las figuraciones y a las distribuciones bioestratigráficas mostradas por otros autores, algunas especies de *Palaeoglobigerina* han sido probablemente incluidas en numerosas ocasiones en diversas especies del género *Eoglobigerina* (Salaj, 1986; Keller, 1988; Canudo *et al.*, 1991; Berggren y Norris, 1997; Olsson *et al.*, 1999; Apellániz *et al.*, 2002). Sin embargo, esta asignación es un error ya que *Eoglobigerina* es un género más moderno y se caracteriza por presentar pared macroperforada (poros en copa), con espinas y frecuentemente reticulada (Blow, 1979; Loeblich y Tappan, 1987; Olsson *et al.*, 1992, 1999).

4. ANÁLISIS MORFOLÓGICO ESTADÍSTICO

Arenillas *et al*. (2007) delimitaron las especies de *Palaeoglobigerina* en función de la altura de la concha o de la espira, de la anchura de la cámara, del número de cámaras, de la tasa de crecimiento en tamaño de las cámaras, y de la forma y posición de la abertura. Las medidas que se tomaron permitieron calcular índices biométricos (W/L, H/L, CW/W, CL/L y CH/H) y, a partir de diagramas de dispersión (bivariantes), mostrar gráficamente agrupamientos que correspondían a poblaciones de las diferentes especies consideradas. A partir de estos datos biométricos (Tablas 1-4), hemos realizado un tratamiento estadístico con el objetivo de delimitar las especies de *Palaeoglobigerina* más objetivamente y definir formalmente la nueva especie *Pg. luterbacheri*. El análisis morfoestadístico se ha realizado sobre ejemplares de cuatro de las cinco especies de *Palaeoglobigerina* consideradas en la clasificación de Arenillas *et al*. (2007), es decir, *Pg. alticonusa*, *Pg. minutula, Pg. fodina* y *Pg.* cf. *fringa* (= *Pg. luterbacheri*). No se ha podido delimitar biométricamente la quinta especie considerada, *Palaeoglobigerina extensa* (Blow) (ver Fig. 2), debido al escaso material disponible de la misma.

4.1. Análisis univariantes y bivariantes

Los índices biométricos H/L y W/L permitieron a Arenillas *et al*. (2007) discriminar *Pg. alticonusa* de las otras tres especies analizadas, *Pg. minutula, Pg. fodina* y *Pg. luterbacheri*, debido a que presenta una mayor altura de

concha (H) y de espira (SH). Los resultados fueron representados mediante un diagrama de dispersión, a los que se ha añadido envolventes convexas y elipses de 95% de confianza en el presente trabajo (Fig. 4a). El índice biométrico que permite delimitar *Pg. alticonusa* del resto de especies de *Palaeoglobigerina* es fundamentalmente H/L. La distribución de frecuencias del valor de H/L de todos los ejemplares analizados, y figurados en histogramas de 15 intervalos (Fig. 4b), permite distinguir claramente los ejemplares de *Pg. alticonusa* de los de las otras tres especies. La especie que presenta mayores afinidades con *Pg. alticonusa* es *Pg. fodina*, pues comparte un mayor número de caracteres. Varias pruebas estadísticas a partir de los valores de H/L sugieren que ambas representan diferentes especies, dado que la probabilidad obtenida de que ambas especies sean la misma es muy baja ($p < 0,05$). Las pruebas *t*-Student y Kolmogorov-Smirnov dan probabilidades de tan sólo $p_t = 3,76 \times 10^{-21}$ y $p_{KS} = 4,20 \times 10^{-11}$ respectivamente. La comparación de medias (Mann-Whitney) y el análisis de varianza (ANOVA) dan probabilidades de $p_{MW} = 9,85 \times 10^{-9}$ y $p_A = 3,76 \times 10^{-21}$ respectivamente. Se ha aplicado un análisis MANOVA con datos bivariantes (H/L y W/L) para *Pg. alticonusa* y *Pg. fodina*, obteniendo también probabilidades muy bajas de que ambas sean la misma especie con las pruebas lambda de Wilk y traza de Pillai: $p_{Wl} = p_{Pt} = 6,24 \times 10^{-22}$. Este análisis permite diferenciar ambas especies en el diagrama de dispersión obtenido con CVA (Fig. 7a).

Eliminando los datos biométricos de *Pg. alticonusa*, los índices CL/L y CW/W permitieron a Arenillas *et al.* (2007) delimitar *Pg. minutula* de las otras dos especies analizadas restantes, *Pg. fodina* y *Pg. luterbacheri*, debido a que *Pg. minutula* presenta una mayor anchura de cámara (CW). Los resultados fueron también representados mediante un diagrama de dispersión, a los que se ha añadido en este trabajo envolventes convexas y elipses de 95% de confianza (Fig. 5a). El índice biométrico que permite delimitar *Pg. minutula* de las otras dos especies mencionadas es CW/W. La distribución de frecuencias del valor de CW/W de los ejemplares analizados de las tres especies, y figurados en histogramas de 20 intervalos (Fig. 5b), permite distinguir los ejemplares de *Pg. minutula* de los de las otras dos especies. El histograma obtenido permite visualizar dos grupos o variantes de la especie, uno en torno al valor CW/W = 82% y otro en torno al valor CW/W = 94%, aunque no se ha podido encontrar otros criterios que permitan sugerir dos especies diferentes (crípticas) de *Pg. minutula*. La especie que presenta mayores afinidades con *Pg. minutula* es *Pg. fodina*. Las diversas pruebas estadísticas (*t*-Student, Kolmogorov-Smirnov, Mann-Whitney y ANOVA) a partir de los valores de CW/W sugieren que ambas representan diferentes especies, ya que dan probabilidades muy bajas de que sean la misma: $p_t = 3,17 \times 10^{-15}$, $p_{KS} = 1,18 \times 10^{-10}$, $p_{MW} = 2,14 \times 10^{-8}$ y $p_A = 3,17 \times 10^{-15}$. El análisis MANOVA con datos bivariantes (CL/L y CW/W) para *Pg. minutula* y *Pg. fodina* encontró también probabilidades muy bajas con las pruebas lambda de Wilk y traza de Pillai: $p_{Wl} = p_{Pt} = 2,00 \times 10^{-22}$, lo que permite diferenciarla en un diagrama de dispersión obtenido con el análisis CVA (Fig. 7b).

Finalmente, los índices biométricos CH/H y H/L permitieron a Arenillas *et al.* (2007) delimitar *Pg. fodina* y *Pg. luterbacheri*, ya que *Pg. fodina* presenta una altura de concha (H) mayor que *Pg. luterbacheri,* si se compara con los otros dos parámetros (L ó CH). Como en los dos casos anteriores, los resultados fueron presentados en un diagrama de dispersión, a los que se ha añadido envolventes convexas y elipses de 95% de confianza (Fig. 6a). El índice biométrico que permite delimitar ambas especies entre sí es CH/H. La distribución de frecuencias del valor de CH/H de los ejemplares analizados de las dos especies, y figurados en histogramas de 15 intervalos (Fig. 6b), permite distinguir las poblaciones de ambas especies. Las diversas pruebas estadísticas (*t*-Student, Kolmogorov-Smirnov, Mann-Whitney y ANOVA) a partir de los valores de CH/H sugieren que ambas representan diferentes especies, ya que dan probabilidades muy bajas de que ambas sean la misma: $p_t = 1,67 \times 10^{-18}$, $p_{KS} = 4,20 \times 10^{-11}$, $p_{MW} = 9,85 \times 10^{-9}$ y $p_A = 6,36 \times 10^{-21}$. El análisis MANOVA con datos CH/H y H/L para *Pg. luterbacheri* y *Pg. fodina* encontró probabilidades muy bajas de que sean la misma especie: $p_{Wl} = p_{Pt} = 1,90 \times 10^{-22}$, y permite diferenciarlas en el diagrama de dispersión obtenido con el análisis CVA (Fig. 7c).

4.2. Análisis multivariantes

El análisis de agrupamientos basados en la distancia Euclídea de todos los ejemplares analizados a partir de los valores de índices biométricos (variables) ha producido un dendrograma que muestra 2 grupos (*clusters*) bien

diferenciados: grupo *Pg. alticonusa* y grupo *Pg. minutula-Pg. fodina-Pg. luterbacheri*. Dentro de este último, se pueden reconocer otros 3 grupos o subgrupos principales (Fig. 8). Los 4 grupos corresponden muy bien a las 4 poblaciones de ejemplares previamente clasificados en las 4 especies de *Palaeoglobigerina* analizadas *(Pg. minutula, Pg. fodina, Pg. luterbacheri* y *Pg. alticonusa*). Aparece un quinto grupo de 4 ejemplares identificados previamente como *Pg. fodina*, con una mayor similaridad a *Pg. alticonusa*. Este resultado sugiere que *Pg. fodina* presenta unas características intermedias entre *Pg. alticonusa* y las otras dos especies analizadas, *Pg. minutula* y *Pg. luterbacheri*. Esta es la razón por la cual otros análisis multivariantes de comparación de parejas de especies se haya utilizado *Pg. fodina* como especie de referencia en la discriminación.

El análisis de componentes principales aplicado a los datos multivariantes de índices biométricos (variables) también permite agrupar los ejemplares de las 4 especies en conjuntos (envolventes convexas) destacables en el gráfico XY, donde X e Y son los dos componentes principales PC-1 y PC-2 (Fig. 9). La PC-1 abarca más del 84% de la varianza y la PC-2 más del 10% de la varianza, sugiriendo que el análisis ha permitido delimitar las 4 especies con bastante nivel de confianza. Las elipses de 95% de confianza figuradas en el gráfico sugieren una clara delimitación de *Pg. alticonusa*, y cierto solapamiento en las otras tres especies (*Pg. minutula, Pg. fodina* y *Pg. luterbacheri*), debido a su mayor similitud.

El análisis discriminante se ha aplicado de dos en dos poblaciones, tomando como referencia a la población de ejemplares clasificados previamente como *Pg. fodina*. El análisis discriminante entre *Pg. alticonusa* y *Pg. fodina* sugiere que ambas especies son diferentes con una alta probabilidad, dado que los histogramas permiten diferenciar claramente ambas poblaciones y la traza de Hotelling estima una probabilidad muy baja (p_{T2} = 3,35 x 10^{-27}) de que sean la misma (Fig. 10a). El análisis discriminante entre *Pg. minutula* y *Pg. fodina* sugiere que ambas especies son diferentes aunque sus histogramas no están tan separados como en el caso anterior, sugiriendo una mayor similitud; no obstante, la traza de Hotelling estima una probabilidad muy baja (p_{T2} = 3,40 x 10^{-15}) de que ambas especies sean la misma (Fig. 10b). El análisis discriminante entre *Pg. luterbacheri* y *Pg. fodina* también sugiere que ambas especies son diferentes, ya que la traza de Hotelling estima una probabilidad muy baja (p_{T2} = 1,60 x 10^{-18}) (Fig. 10c).

Finalmente se ha aplicado un análisis MANOVA con datos multivariantes, es decir con todos los índices biométricos, para diferenciar *Pg. minutula, Pg. luterbacheri* y *Pg. alticonusa* con respecto a *Pg. fodina*. El análisis MANOVA entre *Pg. alticonusa* y *Pg. fodina* sugiere nuevamente que ambas especies son diferentes con una alta probabilidad (Fig. 11a), tal como se muestra en el diagrama obtenido con el análisis CVA; pruebas lambda de Wilk (p_{Wl} = 4,68 x 10^{-16}) y traza de Pillai (p_{Pt} = 1,72 x 10^{-15}) dan probabilidades bajas de que sean la misma especie. Lo mismo ocurre con los análisis MANOVA entre *Pg. minutula* y *Pg. fodina* y entre *Pg. luterbacheri* y *Pg. fodina*, en el que las pruebas lambda de Wilk y traza de Pillai dan respectivamente los siguientes resultados: p_{Wl} = 2,10 x 10^{-16} y p_{Pt} = 3,23 x 10^{-15} entre las dos primeras, y p_{Wl} = p_{Pt} = 1,60 x 10^{-18} entre las dos segundas (Figs. 11b,c).

5. DESCRIPCIÓN SISTEMÁTICA

El tratamiento morfoestadístico de poblaciones del género *Palaeoglobigerina* ha permitido delimitar con suficiente certidumbre 4 especies, una de las cuales no había sido formalmente definida hasta ahora. Esta especie ha sido reconocida en ocasiones bajos los nombres de *Globigerina* cf. *fringa, Parvularugoglobigerina fringa* y *Palaeoglobigerina* cf. *fringa* (Luterbacher y Premoli Silva, 1964; Brinkhuis y Zachariasse, 1988; Arenillas y Arz, 1996, 2000; Arenillas *et al*., 2007). En las Láminas 1 y 2 se muestran imágenes de MEB del holotipo y paratipos de la nueva especie definida, así como de otras especies del Daniense inferior que son citadas en la diagnosis diferencial.

Orden FORAMINIFERIDA Eichwald, 1830
Suborden GLOBIGERINIDA Blow, 1979
Familia EOGLOBIGERINIDAE Blow, 1979
Género *Palaeoglobigerina* Arenillas, Arz y Náñez, 2007

Palaeoglobigerina luterbacheri n.sp
Lám. 1, Figs. 1-15

no 1950 *Globigerina fringa* Subbotina, p. 104, Lám. 5, Figs. 19-21.

1964 *Globigerina* cf. *fringa* Luterbacher y Premoli Silva, p. 118, Lám. 1, Figs.1-5, 9-16.

1973 *"Globigerina" fringa* Subbotina; Krasheninnikov y Hoskins (parte), p. 113, Lám. 8, Figs. 1-2.

?1988 *Globigerina fringa* Subbotina; Keller, p. 256, Lám. 3, Figs. 16-17.

1988 *Parvularugoglobigerina fringa* (Subbotina); Brinkhuis y Zachariasse, p. 158, Lám. 2, Figs. 10-11.

1995 *Parvularugoglobigerina perexigua* Li *et al.* (parte), p. 132, Lám. 2, Figs. 4-5.

2000 *Globoconusa?* cf. *fringa* Arenillas y Arz, Lám. 2, Figs. 6-7.

Derivatio nominis.- Especie dedicada al Prof. Dr. HansPeter Luterbacher.

Ejemplares-tipo.- Depositados en el Museo Paleontológico de la Universidad de Zaragoza - Gobierno de Aragón (España). Holotipo MPZ 2007/1, Lám. 1, Figs 1-4: 1, vista espiral; 2, vista axial; 3, vista umbilical; 4, detalle de la superficie de la pared. Paratipo MPZ 2007/2, Lám. 1, Figs 5-8: 5, vista espiral; 6, vista axial; 7, vista umbilical; 8, detalle de la superficie de la pared. Paratipo MPZ 2007/3, Lám. 1, Figs 9-11: 9, vista umbilical; 10, vista axial; 11, vista espiral. Paratipo MPZ 2007/4, Lám. 1, Figs 12-15: 12, vista umbilical; 13, vista axial; 14, vista espiral; 15, detalle de la superficie de la pared.

Localidad-tipo y nivel-tipo.- Daniense inferior de la Formación El Haria, en el corte de El Kef, Túnez; Muestra KF 15,00 (3 m sobre el límite K/Pg). Zona de *Parvularugoglobigerina eugubina*, Subzona de *Parvularugoglobigerina sabina*.

Diagnosis.- Foraminífero planctónico caracterizado por su pared lisa microperforada (poros cilíndricos < 1 micra), abertura umbilical-extraumbilical, lado espiral generalmente plano y 4 cámaras en la última vuelta de espira (contorno subcuadrado). El holotipo refleja las características promedio de la especie y los paratipos la variabilidad morfológica sobre todo en lo que respecta a: la mayor o menor convexidad del lado espiral (desde plano en paratipos MPZ 2007/2 y MPZ 2007/4 a ligeramente convexo en paratipo MPZ 2007/3), la forma de la abertura (en general, de arco bajo, aunque ligeramente alta en el paratipo MPZ 2007/3) y la forma de la cámara (en general globular-subesférica, aunque algo hemisférica en MPZ 2007/4). El paratipo MPZ 2007/3 muestra características intermedias a *Palaeoglobigerina fodina* (Blow).

Descripción.- Concha pequeña, globosa, con lado espiral plano o ligeramente convexo. Disposición de las cámaras trocoespiralada, con 8 a 10 cámaras distribuidas en 2,5 vueltas de espira, y 4 cámaras en la última vuelta. Crecimiento helicoidal, con una tasa de crecimiento en tamaño de las cámaras alta. Cámaras subesféricas o globulares. Contorno ecuatorial subcuadrado, lobulado, con suturas intercamerales deprimidas. Perfil axial redondeado. Ombligo estrecho. Abertura principal interiomarginal, umbilical-extraumbilical, semicircular o de arco bajo, y rodeada de un fino labio. Pared calcárea hialina, lisa, y microperforada con poros cilíndricos (< 1 micra), a veces con poros en túmulo incipientes y escasas papilas redondeadas irregularmente esparcidas. Tamaño en adulto aproximadamente de 110 (±20) micras en longitud y 70 (±20) micras en altura.

Description.- *Test minute, globose, with spiral side flat or slightly convex. Trochospiral arrangement, with 8 to 10 chambers distributed in 2.5 spiral whorls and 4 chambers in the last whorl. Helicoidal growth, with high rate of chambers enlargement in size. Chambers subspherical or globular. Equatorial outline subsquadrate, lobate, with incised sutures. Axial margin rounded. Umbilicus narrow. Aperture interiomarginal, umbilical-extraumbilical, semicircular or low-arched, and bordered by a thin imperforate lip. Wall calcareous hyaline, smooth, and microperforate with pore-murals (< 1 micron), and sometimes with incipient pore-mounds and scarce blunt papillas, irregularly scattered. Adult size approximately of 110 (±20) microns in length and 70 (±20) microns in height.*

Edad y distribución bioestratigráfica.- Desde la parte

media de la Subzona *de Parvularugoglobigerina longiapertura* (Zona de *Guembelitria cretacea*) a la parte basal de la Subzona *de Eoglobigerina trivialis* (Zona de *Parasubbotina pseudobulloides*), en la parte basal del Daniense (Paleoceno, Cenozoico).

Distribución paleoambiental y paleogeográfica.- Medio pelágico superficial, esencialmente cosmopolita.

Diagnosis diferencial.- *Palaeoglobigerina fodina* (Blow) se diferencia de *Pg. luterbacheri* por tener el lado espiral ligeramente convexo o convexo, contorno ecuatorial subrómbico, y la abertura en posición intraumbilical. *Palaeoglobigerina alticonusa* (Li, McGowran y Boersma) se diferencia por tener el lado espiral muy convexo a turricular, y la abertura en posición intraumbilical. *Palaeoglobigerina minutula* (Luterbacher y Premoli Silva) se diferencia por tener un contorno ecuatorial subtriangular, 3 a 3,5 cámaras en la última vuelta de espira y la abertura en posición generalmente intraumbilical. *Palaeoglobigerina extensa* (Blow) se diferencia por tener el lado espiral ligeramente convexo o convexo, contorno ecuatorial subrómbico y la abertura con forma de arco bajo alargado. *Parvularugoglobigerina eugubina* (Luterbacher y Premoli Silva) se diferencia por tener un contorno ecuatorial subcircular, 4 a 4,5 cámaras en la primera vuelta de espira (estadio neánico) y 5 a 6,5 cámaras en la última vuelta de espira (estadio adulto), y un tamaño ligeramente mayor. *Parvularugoglobigerina sabina* (Luterbacher y Premoli Silva) se diferencia por tener abertura en posición intraumbilical, un contorno ecuatorial subpentagonal, 4 a 4,5 cámaras en la primera vuelta de espira (estadio neánico) y en la última vuelta de espira (estadio adulto), y un tamaño ligeramente mayor. *Parvularugoglobigerina perexigua* Li, McGowran y Boersma se diferencia por tener 4 a 4,5 cámaras tanto en la primera como en la última vuelta de espira (estadios neánico y adulto) y una abertura con forma de arco alto alargado.

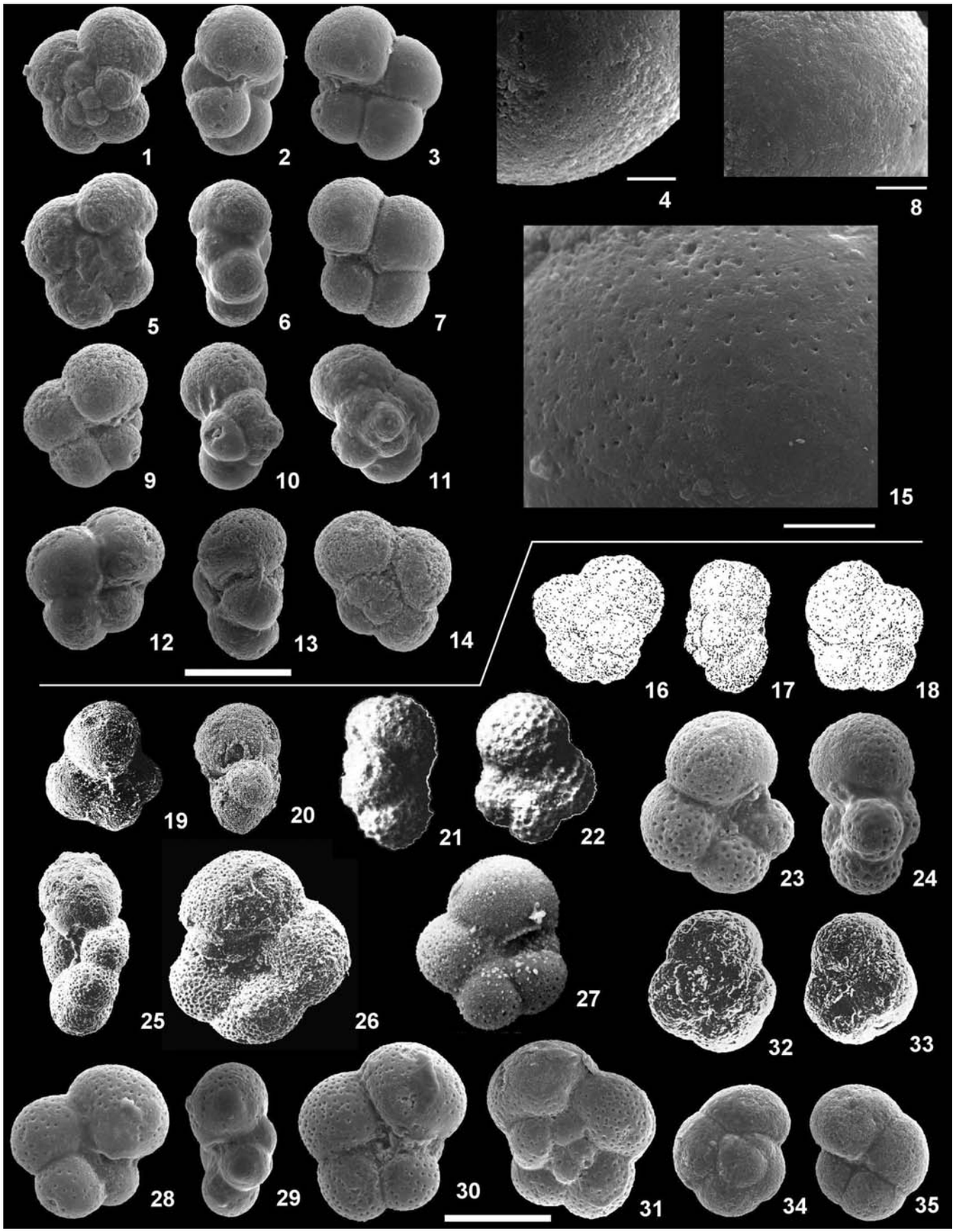
Eoglobigerina fringa (Subbotina) se diferencia por presentar pared espinosa y macroperforada (poros en copa), abertura en posición intraumbilical y rodeada de un labio grueso (a veces tipo solapa), y un tamaño mayor en el estadio adulto. *Eoglobigerina eobulloides* (Morozova) se diferencia por presentar pared espinosa y macroperforada (poros en copa), generalmente reticulada, 4 a 4,5 cámaras en la última vuelta de espira, la abertura en posición intraumbilical y rodeada de un labio grueso (a veces tipo solapa), y un tamaño mayor en el estadio adulto. *Eoglobigerina simplicissima* (Blow) se diferencia por presentar pared espinosa y macroperforada (poros en copa), generalmente reticulada, el lado espiral ligeramente convexo, la abertura en posición intraumbilical y rodeada de un labio grueso (a veces tipo solapa), y un tamaño mayor en el estadio adulto. *Parasubbotina moskvini* (Shutskaya) se diferencia por presentar pared espinosa y macroperforada (poros en copa), generalmente reticulada, y un tamaño mayor en el estadio adulto. *Globanomalina imitata* (Subbotina) se diferencia por presentar pared macroperforada (poros en copa), abertura rodeada de un labio grueso (a veces tipo solapa), y un tamaño mayor en el estadio adulto. *Hedbergella monmouthensis* (Olsson) se diferencia por presentar pared macroperforada (poros en copa) y pustulada, 4 a 5,5 cámaras en la última vuelta de espira, abertura rodeada de un labio grueso (a veces tipo solapa), y un tamaño mayor en el estadio adulto.

Microfotografías de MEB de las especies comparadas con *Pg. luterbacheri* pueden verse en las Láminas 1 y 2, que incluyen algunas imágenes y dibujos originales de holotipos.

Lámina 1. Imágenes de MEB de ejemplares de *Palaeoglobigerina luterbacheri* y otras especies del Daniense basal de morfología externa similar (barras de escala = 100 micras; barras de escala de microfotos de detalle = 10 micras; v.a. = vista axial, v.e. = vista espiral, v.u. = vista umbilical, d.s.p. = detalle de la superficie de la pared); 1-15, *Palaeoglobigerina luterbacheri* n. sp.: 1, 2, 3, 4, Holotipo MPZ 2007/1, v.e., v.a. y v.u. y d.s.p., ejemplar de El Kef, Túnez; 5, 6, 7, 8, Paratipo MPZ 2007/2 v.e., v.a., v.u. y d.s.p., ejemplar de El Kef, Túnez; 9, 10, 11, Paratipo MPZ 2007/3, v.u., v.a y v.e, ejemplar de El Kef, Túnez; 12, 13, 14, 15, Paratipo MPZ 2007/4, v.u., v.a., v.e. y d.s.p., ejemplar de El Kef, Túnez.16-20, *Palaeoglobigerina luterbacheri* n. sp.: 16, 17, 18, v.e., v.a. y v.u., ejemplar de Ceselli, Italia, clasificado como *Globigerina* cf. *fringa* (Luterbacher y Premoli Silva, 1964); 19, 20 v.u. y v.a., ejemplar de DSDP Hole 152, Caribe, clasificado como un paratipo de *Parvularugoglobigerina perexigua* Li, McGowran y Boersma, 1995. 21-24, *Eoglobigerina fringa* (Subbotina, 1950): 21, 22, v.a. y v.u., holotipo de Anapa (Caucaso), Rusia (fotografías de Olsson *et al*., 1999), 23, 24, v.u. y v.a., ejemplar de El Kef, Túnez. 25-31, *Globanomalina imitata* (Subbotina, 1953): 25, 26, v.a. y v.u., holotipo de Kuban River (Caucaso), Rusia (fotografías de Olsson *et al*., 1999); 27, v.u., ejemplar de DSDP Leg 6, Pacífico Sur (Blow, 1979), clasificado como *Globorotalia* (*Turborotalia*) sp., tipo 1; 28, 29 v.u. y v.a., ejemplar de El Kef, Túnez; 30, 31, v.u. y v.e., ejemplar de El Kef, Túnez. 32-35, *Hedbergella? hillebrandti* (Orue-Etxebarría, 1985): 32, 33, v.e. y v.u., holotipo y paratipo de Sopelana, España; 34, 35, v.e. y v.u., ejemplar de El Kef, Túnez.

Plate 1. SEM images of species of Palaeoglobigerina luterbacheri *and other basal Danian species of similar external morphology (scale bar = 100 microns; scale bar of detail microphotos = 10 microns; v.a.= axial view, v.e.= espiral view, v.u.= umbilical view, d.s.p. = detail of wall-texture).*

Lámina 1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Discusión.- Hasta la fecha no se había definido una especie con las características morfológicas de *Pg. luterbacheri*. Los primeros en identificar la especie fueron Luterbacher y Premoli Silva (1964), bajo el nombre de *Globigerina* cf. *fringa* (Lám. 1, figs. 16-18), pero no la definieron formalmente. Ha sido asignada frecuentemente a la especie *Globigerina fringa* Subbotina (Smit, 1982; Brinkhuis y Zachariasse, 1988; Keller y Benjamini, 1991). Sin embargo, no debe ser confundida con la verdadera *Eoglobigerina fringa* (Subbotina), ya que esta especie es un eoglobigerínido de similar forma pero con poros en copa, pared normalmente reticulada en estadio adulto y generalmente de mayor tamaño (Stainforth *et al*., 1975; Toumarkine y Luterbacher, 1985; Canudo *et al*., 1991; Li *et al*., 1995). La especie aquí considerada se encuentra restringida prácticamente a las Zonas de *G. cretacea* y *Pv. eugubina*, biozonas que no fueron reconocidas por Subbotina (1950). Por esta razón, Luterbacher y Premoli Silva (1964) prefirieron denominarla "cf. *fringa*", y este ha sido el nombre utilizado en diversas ocasiones (Canudo y Molina, 1992; Canudo *et al*., 1991; Arenillas y Arz, 1996, 2000; Arenillas *et al*., 2007).

Al igual que el resto de especies de *Palaeoglobigerina*, *Pg. luterbacheri* ha sido identificada o incluida en diversos géneros y especies. Inicialmente fue incluida en los géneros *Globigerina* o *Eoglobigerina* (Luterbacher y Premoli Silva, 1964; Krasheninnikov y Hoskins, 1963; Blow, 1979; Smit, 1982; Keller, 1988; Keller y Benjamini, 1991), y más tarde en *Parvularugoglobigerina* (Brinkhuis y Zachariasse, 1988; Liu y Olsson, 1992; Li *et al*., 1995; Olsson *et al*., 1999) y *Globoconusa* (Arenillas y Arz, 1996, 2000; Arenillas *et al*., 2007). El paratipo de *Parvularugoglobigerina perexigua* (Lám. 1, figs. 19-20) de Li *et al*. (1995) podría representar un morfotipo de *Pg. luterbacheri*, con la abertura en posición umbilical-extraumbilical, pero con el lado espiral ligeramente convexo más semejante al paratipo MPZ 2007/3. Este paratipo muestra características intermedias a *Palaeoglobigerina fodina* (Blow), pero sus proporciones (H/L ≈ 66% y CH/H ≈ 91%) caen dentro de variabilidad morfológica de *Pg. luterbacheri*. Liu y Olsson (1992) incluyeron *Pg. luterbacheri* dentro de la variabilidad intraespecífica de *Parvularugoglobigerina* aff. *eugubina*, y Olsson *et al*. (1999) en la de *Parvularugoglobigerina extensa*. La especie *Globigerina hillebrandti* Orue-Etxebarría (1985) se asemeja a *Pg. luterbacheri*, pero difiere en su contorno menos lobulado, cámaras ovaladas y suturas menos deprimidas (Lám. 1, figs. 32-33). Apellániz *et al*. (2002) incluyeron esta especie en el genero *Hedbergella* Brönnimann y Brown, aunque también podría ser una especie bentónica (Lám. 1, figs. 34-35).

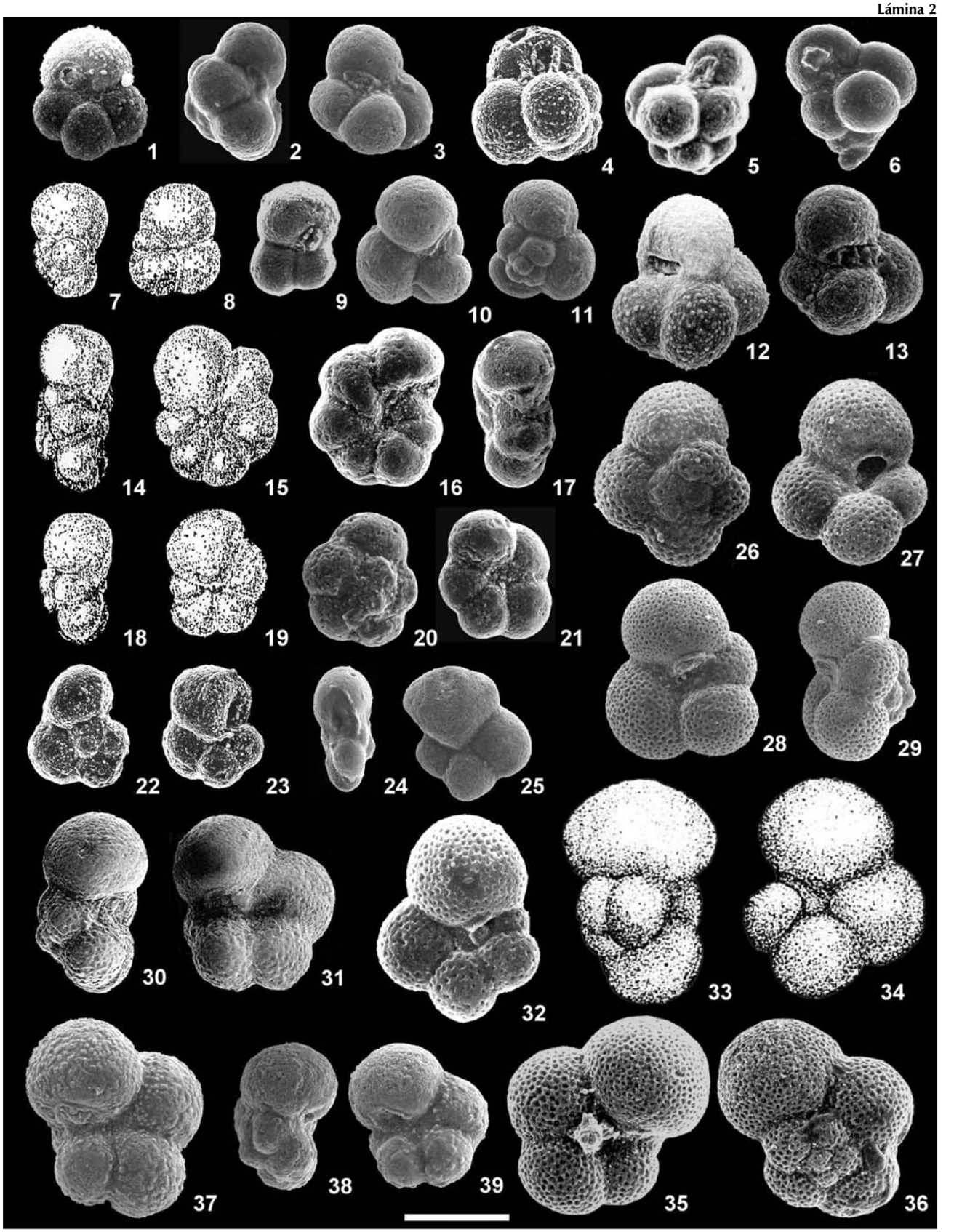
6. CONCLUSIONES

El análisis morfoestadístico de poblaciones del género *Palaeoglobigerina* Arenillas, Arz y Náñez del Daniense basal ha permitido delimitar cuatro especies en este género: *Pg. alticonusa* (Li, McGowran y Boersma), *Pg. minutula* (Luterbacher y Premoli Silva), *Pg. fodina* (Blow) y *Pg. luterbacheri* n. sp. Este análisis se ha basado en medidas biométricas de 90 ejemplares del género procedentes de dos muestras del corte de El Kef (Túnez), a los que se ha aplicado diferentes métodos uni-, bi- y multi-

Lámina 2. Imágenes de MEB de especies de *Palaeoglobigerina, Parvularugoglobigerina, Eoglobigerina, Parasubbotina* y *Hedbergella* del Daniense basal (barra de escala = 100 micras; v.a. = vista axial, v.e. = vista espiral, v.u. = vista umbilical); 1-3, *Palaeoglobigerina fodina* (Blow, 1979): 1, v.u., holotipo de DSDP Leg 6, Pacífico Sur; 2, 3, v.a. y v.u., ejemplar de El Kef, Túnez. 4-6, *Palaeoglobigerina alticonusa* (Li, McGowran y Boersma, 1995): 4, v.u., holotipo de DSDP Hole 152, Pacífico Caribeño; 5, v.a., ejemplar de El Kef, Túnez; 6, v.a., ejemplar de Aïn Settara, Túnez. 7-11, *Palaeoglobigerina minutula* (Luterbacher y Premoli-Silva, 1964): 7, 8, v.a. y v.u., holotipo de Ceselli, Italia (Luterbacher y Premoli-Silva, 1964); 9, v.u., ejemplar de Aïn Settara, Túnez; 10, 11, v.u. y v.e., ejemplar de Elles, Túnez. 12-13, *Palaeoglobigerina extensa* (Blow, 1979): 12, v.u., holotipo de DSDP Leg 6, Pacífico Sur; 13, v.u., ejemplar de Agost, España. 14-17, *Parvularugoglobigerina eugubina* (Luterbacher y Premoli-Silva, 1964): 14, 15, v.a. y v.u., holotipo de Ceselli, Italia; 16, 17, v.u. y v.a., ejemplar de Agost, España. 18-21, *Parvularugoglobigerina sabina* (Luterbacher y Premoli-Silva, 1964): 18, 19, v.a. y v.u., holotipo de Ceselli, Italia; 20, 21, v.e. y v.u., ejemplar de Agost, España. 22-25, *Parvularugoglobigerina perexigua* Li, McGowran y Boersma, 1995: 22, 23, v.e. y v.u., holotipo de DSDP Hole 152, Caribe; 24, 25, v.a. y v.u., ejemplar de Elles, Túnez. 26-29, *Eoglobigerina simplicissima* Blow, 1979: 26, 27, v.e. y v.u., holotipo de DSDP Leg 6, Pacífico Sur; 28, 29, v.u. y v.a., ejemplar de El Kef, Túnez. 30-32, *Eoglobigerina eobulloides* (Morozova, 1959): 30, 31, v.a. y v.u., holotipo de PenFínsula Tarkhankhut (Crimea), Ucrania (fotografías de Olsson *et al*., 1999); 32, v.u., ejemplar de DSDP Leg 6, Pacífico Sur (Blow, 1979). 33-36, *Parasubbotina moskvini* (Shutskaya, 1953): 33, 34, v.a. y v.u., holotipo de Kheu River (Caucaso), Rusia; 35, 36, v.u. y v.e., ejemplar de Aïn Settara, Túnez. 37-39, *Hedbergella monmouthensis* (Olsson, 1960): 37, v.u., ejemplar de El Kef, Túnez; 38, 39, v.a. y v.u., ejemplar de El Kef, Túnez.

Plate 2. SEM images of species of Palaeoglobigerina, Parvularugoglobigerina, Eoglobigerina, Parasubbotina and Hedbergella *from the basal Danian (scale bar = 100 microns; v.a.= axial view, v.e.= espiral view, v.u.= umbilical view).*

Lámina 2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variantes incluyendo pruebas estadísticas para estimar la probabilidad de que el conjunto de poblaciones pertenezcan a la misma especie o no. El resultado es la delimitación de al menos las 4 especies previamente propuestas, sugiriendo que *Pg. fodina* es una especie morfológicamente intermedia entre *Pg. alticonusa* y las otras dos especies, *Pg. minutula* y *Pg. luterbacheri*.

La nueva especie propuesta, *Pg. luterbacheri*, ha sido nombrada en honor al Prof. Dr. HansPeter Luterbacher. Había sido previamente reconocida con el nombre "cf. *fringa*", pero no tenía una definición formal. Las características diagnósticas de esta especie son: 4 cámaras en la última vuelta de espira, lado espiral generalmente plano, contorno ecuatorial subcuadrado y abertura umbilical-extraumbilical. Las otras características son compartidas con el resto de especies de *Palaeoglobigerina*, es decir, concha trocoespiralada muy pequeña (110±20 micras en longitud), cámaras subesféricas o globosas, 3,5 a 4 cámaras en la primera vuelta de espira, y pared calcítica hialina, lisa y microperforada (poros cilíndricos o poros en túmulo incipientes).

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ANEXO

	L	W	H	CL	CW	CH	W/L	H/L	CW/W	CL/L	CH/H
Palaeoglobigerina alticonusa	80,8	79,8	90,8	41,7	52,2	38,6	98,8	112,4	65,4	51,6	42,5
	96,4	89,4	98,8	48,2	67,6	45,9	92,7	102,5	75,6	50,0	46,5
	77,1	77,1	86,7	31,7	49,4	38,8	100,0	112,5	64,1	41,1	44,8
	86,4	92,3	107,6	42,3	63,5	41,7	106,8	124,5	68,8	49,0	38,8
	88,2	85,9	105,9	43,5	58,8	39,4	97,4	120,1	68,5	49,3	37,2
	102,9	101,2	115,8	45,3	57,0	44,4	98,3	112,5	56,3	44,0	38,3
	97,6	92,9	109,4	51,8	65,3	40,5	95,2	112,1	70,3	53,1	37,0
	97,0	92,3	107,6	45,3	61,2	51,2	95,2	110,9	66,3	46,7	47,6
	80,3	73,2	84,1	40,1	50,1	36,4	91,2	104,7	68,4	49,9	43,3
	104,4	100,0	114,4	53,1	83,1	47,2	95,8	109,6	83,1	50,9	41,3
	83,6	77,9	96,8	37,4	60,9	41,1	93,2	115,8	78,2	44,7	42,5
	95,5	100,5	127,0	49,3	71,1	50,8	105,2	133,0	70,7	51,6	40,0
	107,1	97,6	120,4	49,9	64,4	46,7	91,1	112,4	66,0	46,6	38,8
	118,1	125,7	136,3	54,2	69,9	48,2	106,4	115,4	55,6	45,9	35,4
	108,9	100,0	113,3	51,1	63,3	52,2	91,8	104,0	63,3	46,9	46,1
	102,6	106,0	110,9	51,3	71,8	47,9	103,3	108,1	67,7	50,0	43,2
	118,0	107,8	120,6	59,9	73,5	53,0	91,4	102,2	68,2	50,8	43,9
	88,9	95,8	102,3	56,4	56,4	41,0	107,8	115,1	58,9	63,4	40,1
	100,9	85,5	101,8	63,3	58,2	41,3	84,7	100,9	68,1	62,7	40,6
	129,1	118,0	130,0	83,8	77,0	52,4	91,4	100,7	65,3	64,9	40,3
	135,1	128,3	138,5	63,3	68,4	59,8	95,0	102,5	53,3	46,9	43,2
	114,6	107,8	123,1	54,7	70,1	51,3	94,1	107,4	65,0	47,7	41,7
	97,4	87,6	108,1	55,1	56,2	50,6	89,9	111,0	64,2	56,6	46,8
medias	**100,5**	**96,6**	**110,9**	**51,0**	**63,9**	**46,1**	**96,4**	**110,9**	**66,6**	**50,6**	**41,7**

Tabla 1. Medidas biométricas (en micras) sobre ejemplares de *Palaeoglobigerina alticonusa,* e índices biométricos W/L, H/L, CW/W, CL/L y CH/H (en tanto por ciento). Las medidas se han tomado sobre individuos de dos horizontes estratigráficos a 1,75 y 2 m (muestras KF13,75 y KF14) sobre el límite K/Pg de El Kef.

Table 1. Biometric measures (in microns) on specimens of Palaeoglobigerina alticonusa*, and biometric indices W/L, H/L, CW/W, CL/L and CH/H (in percentage). The measures have been taken on specimens of two stratigraphic horizons placed 1.75 and 2 m above the K/Pg boundary of El Kef (samples KF13.75 and KF14).*

	L	W	H	CL	CW	CH	W/L	H/L	CW/W	CL/L	CH/H
Palaeoglobigerina alticonusa	80,7	78,3	62,8	44,9	47,1	47,4	97,0	77,8	60,2	55,6	75,5
	96,1	85,0	83,3	41,6	59,6	60,5	88,4	86,7	70,1	43,3	72,6
	101,2	94,1	74,7	49,4	58,8	61,7	93,0	73,8	62,5	48,8	82,6
	114,0	107,1	83,4	54,2	79,3	71,2	93,9	73,2	74,0	47,5	85,4
	112,8	102,7	82,5	53,5	75,6	69,7	91,0	73,1	73,6	47,4	84,5
	117,8	107,8	80,0	57,8	74,4	63,3	91,5	67,9	69,0	49,1	79,1
	105,3	98,3	77,2	50,2	61,1	66,2	93,4	73,3	62,2	47,7	85,8
	88,4	80,7	70,2	42,2	52,4	54,5	91,3	79,4	64,9	47,7	77,6
	97,2	92,2	80,2	47,2	53,2	60,2	94,9	82,5	57,7	48,6	75,1
	107,2	100,1	78,4	51,0	63,2	59,4	93,4	73,1	63,1	47,6	75,8
	110,2	99,8	79,4	53,2	66,3	61,6	90,6	72,1	66,4	48,3	77,6
	115,3	104,3	81,2	52,2	72,3	62,2	90,5	70,4	69,3	45,3	76,6
	94,1	89,8	83,8	48,7	56,4	64,4	95,4	89,1	62,8	51,8	76,8
	100,1	92,4	78,7	54,7	56,9	61,6	92,3	78,6	61,6	54,6	78,3
	85,5	76,1	61,6	47,9	51,6	47,9	89,0	72,0	67,8	56,0	77,8
	104,3	94,0	71,8	56,4	62,9	61,6	90,1	68,8	66,9	54,1	85,8
	109,5	102,6	85,5	59,9	70,1	61,6	93,7	78,1	68,3	54,7	72,0
	111,2	106,9	86,1	60,7	71,8	71,8	96,1	77,4	67,2	54,6	83,4
	95,8	86,4	68,4	52,2	60,0	53,0	90,2	71,4	69,4	54,5	77,5
	94,1	89,8	71,8	51,3	60,7	54,7	95,4	76,3	67,6	54,5	76,2
	99,2	88,1	75,3	53,0	64,1	60,1	88,8	75,9	72,8	53,4	79,8
	92,4	88,9	70,1	51,3	59,7	58,9	96,2	75,9	67,2	55,5	84,0
medias	**101,5**	**93,9**	**76,7**	**51,5**	**62,6**	**60,6**	**92,6**	**75,8**	**66,6**	**50,9**	**79,1**

Tabla 2. Medidas biométricas (en micras) sobre ejemplares de *Palaeoglobigerina fodina,* e índices biométricos W/L, H/L, CW/W, CL/L y CH/H (en tanto por ciento). Las medidas se han tomado sobre individuos de dos horizontes estratigráficos a 1,75 y 2 m (muestras KF13,75 y KF14) sobre el límite K/Pg de El Kef.

Table 2. Biometric measures (in microns) on specimens of Palaeoglobigerina fodina*, and biometric indices W/L, H/L, CW/W, CL/L and CH/H (in percentage). The measures have been taken on specimens of two stratigraphic horizons placed 1.75 and 2 m above the K/Pg boundary of El Kef (samples KF13.75 and KF14).*

	L	W	H	CL	CW	CH	W/L	H/L	CW/W	CL/L	CH/H
Palaeoglobigerina alticonusa	104,1	92,3	71,7	64,7	73,9	71,7	88,7	68,9	80,1	62,2	100,0
	112,9	87,0	79,3	69,9	72,6	77,3	77,1	70,2	83,4	61,9	97,5
	109,4	79,4	70,6	59,4	73,5	64,5	72,6	64,5	92,6	54,3	91,4
	104,7	91,7	89,4	55,9	73,5	67,0	87,6	85,4	80,2	53,4	74,9
	112,7	91,9	90,1	54,8	90,1	79,3	81,5	79,9	98,0	48,6	88,0
	98,4	84,9	65,9	56,0	71,3	65,9	86,3	67,0	84,0	56,9	100,0
	112,5	91,9	71,2	58,8	74,2	69,7	81,7	63,3	80,7	52,3	97,9
	112,9	85,5	101,2	63,8	72,3	73,5	75,7	89,6	84,6	56,5	72,6
	101,2	86,2	70,2	57,2	77,3	70,2	85,2	69,4	89,7	56,5	100,0
	107,3	82,4	74,3	61,2	79,4	73,2	76,8	69,2	96,4	57,0	98,5
	110,2	87,2	92,2	56,7	82,2	80,2	79,1	83,7	94,3	51,5	87,0
	111,2	88,4	58,1	57,3	71,8	58,1	79,5	52,2	81,2	51,5	100,0
	92,3	87,2	65,8	55,1	80,4	64,9	94,5	71,3	92,2	59,7	98,6
	100,9	86,4	66,7	59,8	69,3	66,7	85,6	66,1	80,2	59,3	100,0
	97,5	84,1	71,8	53,0	67,5	63,2	86,3	73,6	80,3	54,4	88,0
	101,3	76,1	65,0	63,3	70,1	70,1	75,1	64,2	92,1	62,5	107,8
	105,2	83,8	69,3	51,3	78,7	68,4	79,7	65,9	93,9	48,8	98,7
	104,5	85,5	66,7	58,1	69,3	66,7	81,8	63,8	81,1	55,6	100,0
	105,7	92,1	73,5	55,6	75,3	73,5	87,1	69,5	81,8	52,6	100,0
	106,1	85,9	78,7	54,7	71,0	78,7	81,0	74,2	82,7	51,6	100,0
	94,1	81,2	70,1	56,4	68,4	67,6	86,3	74,5	84,2	59,9	96,4
medias	**105,0**	**86,2**	**74,4**	**58,2**	**74,4**	**70,0**	**82,3**	**70,8**	**86,4**	**55,6**	**95,1**

Tabla 3. Medidas biométricas (en micras) sobre ejemplares de *Palaeoglobigerina minu tula*, e índices biométricos W/L, H/L, CW/W, CL/L y CH/H (en tanto por ciento). Las medidas se han tomado sobre individuos de dos horizontes estratigráficos a 1,75 y 2 m (muestras KF13,75 y KF14) sobre el límite K/Pg de El Kef.

Table 3. Biometric measures (in microns) on specimens of Palaeoglobigerina minutula*, and biometric indices W/L, H/L, CW/W, CL/L and CH/H (in percentage). The measures have been taken on specimens of two stratigraphic horizons placed 1.75 and 2 m above the K/Pg boundary of El Kef (sam ples KF13.75 and KF14).*

	L	W	H	CL	CW	CH	W/L	H/L	CW/W	CL/L	CH/H
Palaeoglobigerina luterbacheri	136,2	127,5	92,1	88,2	76,3	88,2	93,6	67,6	59,8	64,8	95,8
	125,9	107,7	70,5	64,2	64,2	70,5	85,5	56,0	59,6	51,0	100,0
	115,3	98,8	78,2	57,6	62,3	74,5	85,7	67,8	63,1	50,0	95,3
	123,7	108,2	80,6	57,1	65,2	79,6	87,5	65,2	60,3	46,2	98,8
	98,8	82,8	63,3	52,2	55,5	60,0	83,8	64,1	67,0	52,8	94,8
	107,6	95,3	64,1	49,4	58,2	62,3	88,6	59,6	61,1	45,9	97,2
	112,7	95,1	73,1	59,8	61,7	68,9	84,4	64,9	64,9	53,1	94,3
	108,8	98,2	84,7	52,9	67,6	84,7	90,3	77,8	68,8	48,6	100,0
	105,0	85,5	67,8	61,1	60,1	65,0	81,4	64,6	70,3	58,2	95,9
	104,3	90,3	67,8	53,7	61,0	65,6	86,6	65,0	67,6	51,5	96,8
	124,4	108,9	66,7	54,4	61,1	64,4	87,5	53,6	56,1	43,7	96,6
	107,9	92,5	68,4	60,2	67,5	63,6	85,7	63,4	73,0	55,8	93,0
	102,6	94,1	64,1	58,2	53,0	64,1	91,7	62,5	56,3	56,7	100,0
	106,0	97,5	59,8	53,9	59,0	59,8	92,0	56,4	60,5	50,8	100,0
	119,7	104,3	72,7	59,8	70,1	72,7	87,1	60,7	67,2	50,0	100,0
	118,5	94,1	78,7	73,0	69,8	78,7	79,4	66,4	74,2	61,6	100,0
	128,3	110,3	82,1	71,8	76,9	76,8	86,0	64,0	69,7	56,0	93,5
	99,2	93,2	68,4	51,3	59,8	68,4	94,0	69,0	64,2	51,7	100,0
	104,3	87,2	70,1	63,3	63,7	69,3	83,6	67,2	73,1	60,7	98,9
	105,2	88,9	65,0	61,6	58,1	65,0	84,5	61,8	65,4	58,6	100,0
	106,0	102,6	73,5	56,4	68,4	70,1	96,8	69,3	66,7	53,2	95,4
	103,5	95,8	61,6	61,6	66,7	57,6	92,6	59,5	69,6	59,5	93,5
	107,8	96,6	71,0	56,5	58,1	66,3	89,6	65,9	60,1	52,4	93,4
	106,9	92,3	78,7	56,4	63,3	78,4	86,3	73,6	68,6	52,8	99,6
medias	**111,6**	**97,8**	**71,8**	**59,8**	**63,7**	**69,8**	**87,7**	**64,4**	**65,3**	**53,6**	**97,2**

Tabla 4. Medidas biométricas (en micras) sobre ejemplares de *Palaeoglobigerina luterbacheri*, e índices biométricos W/L, H/L, CW/W, CL/L y CH/H (en tanto por ciento). Las medidas se han tomado sobre individuos de dos horizontes estratigráficos a 1,75 y 2 m (muestras KF13,75 y KF14) sobre el límite K/Pg de El Kef.

Table 4. Biometric measures (in microns) on specimens of Palaeoglobigerina luterbacheri, *and biometric indices W/L, H/L, CW/W, CL/L and CH/H (in percentage). The measures have been taken on specimens of two stratigraphic horizons placed 1.75 and 2 m above the K/Pg boundary of El Kef (samples KF13.75 and KF14).*

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Palynology of the Paleogene Oshosun Formation in the Dahomey Basin, southwestern Nigeria

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Abstract

A palynological investigation has been conducted on the Paleogene mudstone sequence of the Oshosun Formation encountered in two boreholes (IB10 and IL3) and one surface section (Sagamu Quarry) in the Dahomey Basin, southwestern Nigeria. Among the palynomorphs found during this investigation dinoflagellate cysts are most abundant, but angiosperm pollen typical of Paleogene tropical areas such as *Bombacacidites africanus*, *Proxapertites cursus*, *Retistephanocolpites williamsii*, *Spinizonocolpites baculatus* and *S. echinatus* are also present. Occurrences of age-diagnostic dinoflagellate cysts (e.g. *Apectodinium homomorphum, A. quinquelatum, A. paniculatum*, *Kallosphaeridium* cf. *brevibarbatum*, *Hafniasphaera septata*, *Ifecysta pachyderma*) support a late Paleocene to early Eocene age for the Oshosun Formation. The relative abundance of species of the thermophilic genus *Apectodinium* indicate deposition of this formation during the global Paleocene-Eocene thermal maximum. Changes in the percentages of major palynomorph groups suggest variations in the palaeoenvironmental conditions of the Oshosun Formation. Near-shore and reduced or fluctuating salinity conditions are indicated by an *Apectodinium-Homotryblium-Kallosphaeridium* assemblage which is associated with relatively common land-derived pollen and spores. A relatively strong contribution from a terrestrial source and hence proximity to a land area is noted for the two western localities (boreholes IB10 and IL3). Slightly more open marine (neritic) conditions are indicated by relative abundance of *Spiniferites* and/or *Cleistosphaeridium* and scarcity of terrestrial palynomorphs (upper IB10 and Sagamu section). The rare presence of the green algae *Debarya* and *Ovoidites* in two of the three investigated sections (IB10 and Sagamu Quarry) indicates an occasional influx from freshwater environments. The new name *Triorites takahashii* Schrank, nom. nov. is introduced as a replacement of *Triorites scabratus* Takahashi and Jux 1989, a junior homonym of *Triorites scabratus* Couper 1954.

Keywords: Nigeria, Cenozoic, Tertiary, Paleogene, dinoflagellates, palynomorphs

Resumen

Se ha estudiado, desde el punto de vista palinológico, una serie paleógena de la Formación Oshosun a partir de dos sondeos (IB10 e IL3) y de una sección en superficie (cantera Sagamu) en la Cuenca de Dahomey, suroeste de Nigeria. Entre los palinomorfos encontrados, los más abundantes fueron los quistes de dinoflagelados, si bien también se registró polen de angiospermas típicas de áreas tropicales paleógenas, como *Bombacacidites africanus*, *Proxapertites cursus*, *Retistephanocolpites williamsii*, *Spinizonocolpites baculatus* y *S. echinatus*. La presencia de quistes de dinoflagelados diagnósticos de edad (como por ejemplo, *Apectodinium homomorphum, A. quinquelatum, A. paniculatum*, *Kallosphaeridium* cf. *brevibarbatum*, *Hafniasphaera septata*, *Ifecysta pachyderma*) indican una edad Paleoceno superior a Eoceno inferior para la Formación Oshosun. La reltiva abundancia de especies del género termófilo *Apectodinium* sugiere que la Formación Oshosun se depositó durante el máximo global térmico del Paleoceno-Eoceno. Los cambios en los porcentajes de los grupos de palinomorfos más abundantes indica la existencia de variaciones en las condiciones paleoambientales de la Formación Oshosun. La asociación *Apectodinium-Homotryblium-Kallosphaeridium* apunta a la presencia de un medio costero y de salinidad reducida o fluctuante, asociado a polen y esporas relativamente comunes procedentes de medios

terrestres. Esta influencia terrestre es más acusada en las dos localidades occidentales (sondeos IB10 e IL3). La existencia de unas condiciones más neríticas viene indicada por la relativa abundancia de *Spiniferites* y/o *Cleistosphaeridium* y por la poca frecuencia de palinomorfos terrestres (IB10 superior y sección Sagamu). La escasa presencia de las algas verdes *Debarya* y *Ovoidites* en dos de las tres secciones investigadas (IB10 y cantera Sagamu) indica un influjo ocasional de medios de agua dulce. Se propone *Triorites takahashii* Schrank, nom. nov. para reemplazar a *Triorites scabratus* Takahashi & Jux, 1989, un homónimo anterior de *Triorites scabratus* Couper, 1954.

Palabras clave: Nigeria, Cenozoico, Terciario, Paleógeno, dinoflagelados, palynomorfos

1. INTRODUCTION AND STRATIGRAPHIC FRAMEWORK

The study area is located at the eastern flank of the Dahomey Basin in southwestern Nigeria (Fig. 1). The Oshosun Formation, which is at the focus of the present paper, and the overlying Ilaro Sandstone form the stratigraphic top of the Dahomey Basin (e.g. Idowu *et al*., 1993). The pre-Oshosun stratigraphy of the basin has been summarized by Omatsola and Adegoke (1980, 1981) and Idowu *et al*. (1993). These authors recognized below the Oshosun the following formations:

Ewekoro (limestones, late Maastrichtian to Paleocene), Araromi (shale, Maastrichtian), Afowo (sandstone and shale, Turonian) and Ise (sandstone, Neocomian-Albian). The latter is a pre-rift sequence composed predominantly of continental sands and siltstones which overly the basement complex. Locally (new road cut in Akinjole Village near Abeokuta) the base of the Ise Formation is conglomeratic. The Araromi, Afowo and Ise formations together form the Abeokuta Group (Omatsola and Adegoke, 1981). Other accounts on the stratigraphy of the Dahomey Basin and neighbouring areas have been given by Reyment (1965) and Adegoke (1969).

In the present paper the Oshosun Formation has been investigated palynologically at two subsurface sections (boreholes IB10 and IL3) and one surface section, the Sagamu Quarry (Fig. 1). There are few previous palynological studies on sediments equivalent to the Oshosun Formation. Jan Du Chêne *et al*. (1978b) interpreted palynofloras from the Akinbo Formation (corresponding to the lower part of the Oshosun Formation) as late Paleocene to early Eocene. To the northwest of the study area, the same age was assigned to argillaceous sediments at the top of the section exposed in the Onigbolo Quarry in the neighbouring Benin Republic. This was based on a combined micropalaeontological (ostracods) and palynological (mainly pollen and spores) study (Bio-Lokoto *et al*., 1998).

Ogbe (1972) interpreted the Akinbo Formation to be between latest Thanetian and earliest Ypresian based on the presence of such foraminifera as *Globorotalia convexa*, *G. aequa*, and *G*. aff. *velascoensis* (early to late Paleocene) and some typical Eocene forms such as *Globorotalia aragonensis* and *G. simulatilis*. On the basis of foraminifera and ostracods, Okosun (1990) considered the age of Oshosun Formation to be early to middle Eocene. The work of Gebhardt *et al*. (2005) on foraminifera recovered from the Oshosun Formation at the Sagamu Quarry indicated a late Paleocene to early Eocene age. The same work suggested that the deposition of the Oshosun Formation coincides with the global Initial Eocene thermal maximum (IETM).

The objective of the present study is to document the lateral and vertical distribution of palynomorphs in the Oshosun Formation along an east-west transect based on the three sections mentioned above. Semi-quantitative distribution patterns of major palynomorph groups (marine dinoflagellates and organic-walled microforaminifera, terrestrially-derived pollen and spores, freshwater algae) will be used mainly to interpret vertical and lateral variations of the depositional environments while selected dinoflagellate cyst taxa will be interpreted palynostratigraphically with the view of comparing results with those obtained from previous biostratigraphic studies based on other microfossil groups.

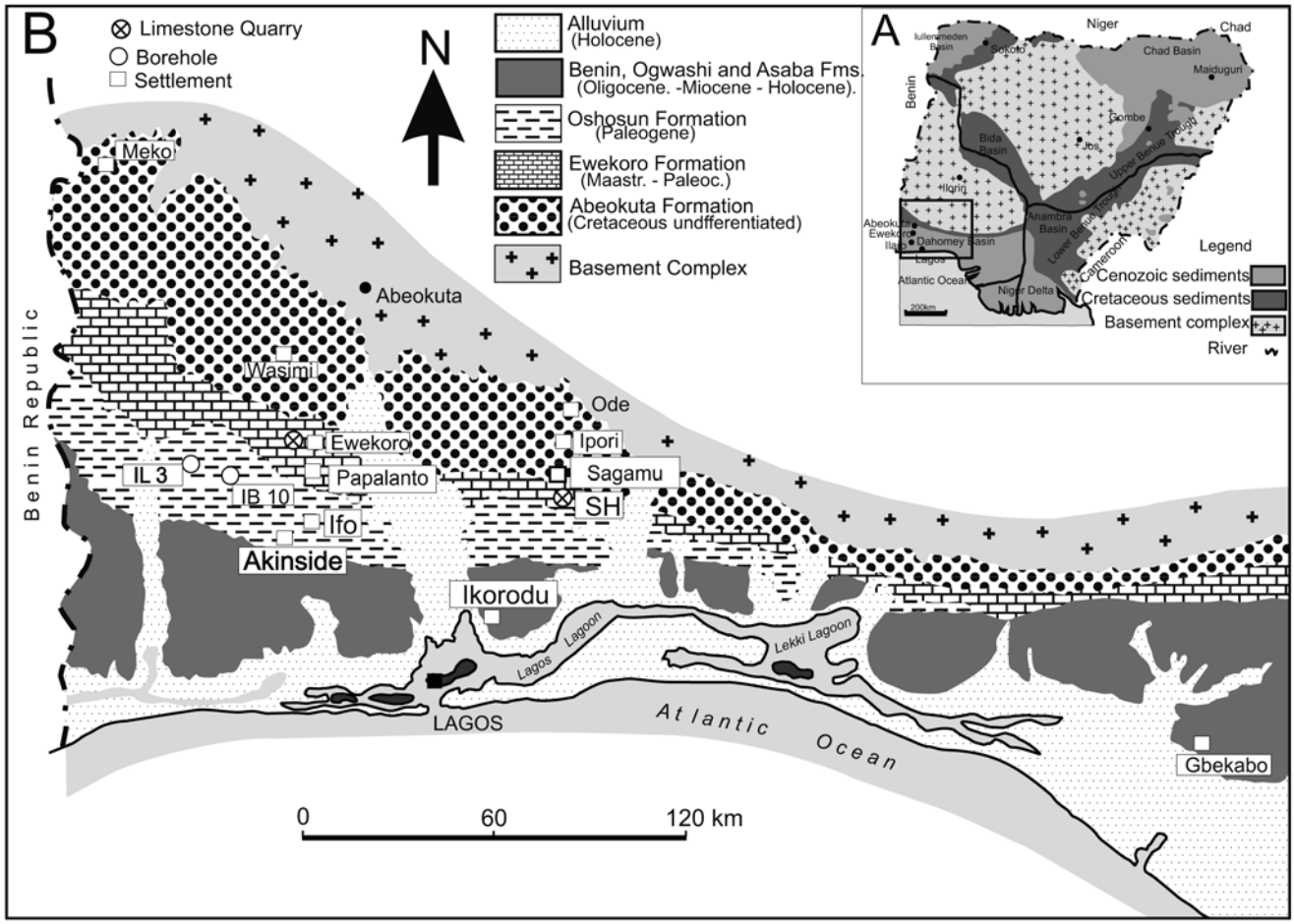


Figure1. (A) Geological sketch map of Nigeria. The rectangle shows the area covered by B. (B) Geological map of the eastern Dahomey Basin with the studied localities IB10, IL3 (boreholes) and the Sagamu Quarry (SH), (modified after the geological map of Nigeria, sheets 67, 68 and 69).

2. MATERIAL AND METHODS

The Oshosun Formation as sampled in the two boreholes (IB10 and IL3) and the Sagamu Quarry (Figs. 2-4) consists mainly of greenish-grey to dark-grey mudstones, but vertical and lateral variations have been observed. In the IL3 borehole (Fig. 3) sandstones are found intercalated in the lower part of the mudstone sequence. The other borehole and the quarry section (Figs. 2 and 4) have continuous mudstone sequences. In all three sections the underlying carbonate deposits of the Ewekoro Formation can be recognized which are exploited in quarries at Ewekoro and Sagamu (and in neighbouring Benin at Onigbolo) for cement production. A thin glauconitic bed is found at the base of the Oshosun Formation in the Sagamu section.

Forty eight samples from the Oshosun Formation (mainly mudstone) were palynologically analysed for this study. Thirty nine were core samples from the two boreholes (IB10 and IL3) whereas the remaining nine were surface samples from the Sagamu Quarry. Two microscope slides per sample were prepared from the >15mm fraction of the unoxidized HCl/HF-resistant residues.

During microscopic examination, 200 palynomorphs were counted for each sample where possible. The slides and other material are housed at the palynological collections of the Institute for Applied Geosciences, Technical University Berlin (Institut für Angewandte Geowissenschaften, TU Berlin).

3. PALYNOLOGICAL RESULTS

The percentages of major palynomorph groups (dinocysts, foraminiferal linings, spores, pollen, algae and inaperturates (*incertae sedis*)) in each of the samples are presented in Figs. 2-4, and range charts depicting the vertical distribution of the most characteristic palynomorph species in all three sections are shown in Fig.5. It can be seen that most assemblages in two of the three sections (IB10 and Sagamu) are characterized by the dominance of dinoflagellate cysts (Figs. 2, 4), which may attain abundances of up to approximately 90% of all palynomorph specimens counted. Terrestrially-derived forms (pollen and spores) are a subordinate elements in the two eastern sections (SH and IB10) but attain up to 69% in one sample of the western section (IL3 borehole). The latter section shows accordingly the strongest fluctuations in the percentages of marine (dinoflagellates plus microforaminerfal linings) vs. non-marine (mainly pollen and spores) palynomorphs. Other components unevenly distributed across the sections include microforaminiferal linings (relatively abundant in the IL3 section), fresh water algae (Zygnemataceae, only in Sagamu and IB10), and unidentified palynomorphs without a well defined aperture (inaperturates). Representatives of the prasinophytes, a group of marine green algae, were encountered exclusively in the SH section (Fig.5).

Among the dinoflagellate cysts are abundant representatives of *Spiniferites*, *Lejeunecysta*, *Homotryblium* and *Apectodinium* (Fig. 5). In addition, high numbers of *Cleistosphaeridium* and *Kallospharidium* contributed significantly to the composition of the studied palynofloras. *Cleistosphaeridium* sp.1 dominates the dinocysts in the SH section (Fig. 5). *Ilexpollenites* and *Bombacacidites africanus* represent major components of the land-derived material in the IB10 and IL3 sections respectively. Other significant contributors include the species *Spinizonocolpites echinatus*, S. *baculatus* and *Mauritiidites crassibaculatus*.

The percentage diagrams of major palynomorph groups will be discussed below in the context of depositional environments while some of the dinoflagellates listed in the range chart are assessed in one of the following sections from a palynostratigraphic perspective. In Appendix 1, a list of the most characteristic palynomorphs, each with author citation and reference to plate illustration is given. Selected forms are pictured in Plates 1 and 2.

Palynological productivity is best in the borehole IB10 where 14 samples out of a total of 20 yielded well preserved palynomorphs. In case of the IL3 borehole and the Sagamu Quarry, six samples each, from a total of 19 and 9 samples respectively, were palynologically productive. Preservation of palynomorphs and productivity seem to be related to lithology and recent weathering. The continuous mudstone sequence encountered in the IB10 borehole proved to be most favourable for palynology, whereas sandstones intercalated in the Oshosun Formation (IL3 borehole) or recent weathering (the two upper samples from the Sagamu Quarry) reduced the preservation potential of palynomorphs.

3.1. Nomenclatural considerations

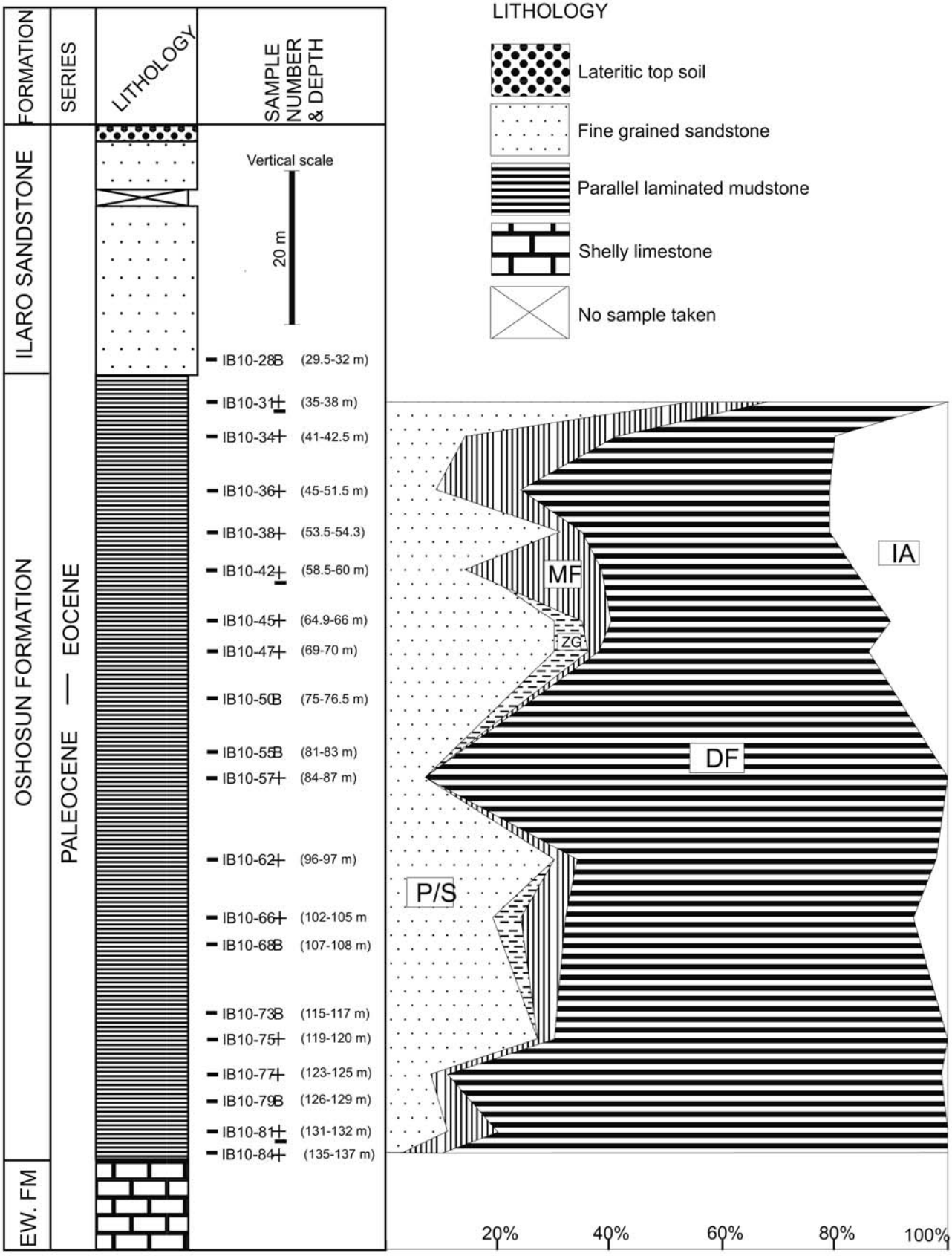
Extensive taxonomical, systematic or nomenclatural considerations are beyond the scope of this paper. In one case, however, a homonymy was noted which necessitated this short nomenclatural note and the introduction of a new name in accordance with the International Code of Botanical Nomenclature (Greuter *et al*., 2000).

Triorites takahashii Schrank, nom. nov.
(Plate 2, fig.15)

1989 *Triorites scabratus* n.sp. – Takahashi and Jux, p. 259, pl. 16, figs. 3-4 (holotype pl. 16, fig. 3, no. GN 5330).

Remarks.- Approximately in the middle part of the section penetrated by the borehole IB10 (samples IB10-47 and 66), a few triporate pollen grains have been found which were identified as *Triorites scabratus* originally described by Takahashi and Jux (1989) from "Middle Tertiary" deposits of the Jos Plateau, Nigeria. A short survey of other species published in the genus *Triorites* showed that a morphologically different pollen species had been

Figure 2. Lithostratigraphy and percentage distribution of major palynomorph groups in the IB10 borehole. B = barren samples. + = ≥ 200 specimens from the first two slides, ± = ≥ 50 specimens from the first two slides. EW FM = Ewekoro Formation. P/S= Pollen/spores, ZG = Zygnemataceae, MF = Microforaminifera, DF = Dinoflagellate cysts, IA = Inaperturates (incertae sedis).


FORMATION
SERIES
LITHOLOGY
SAMPLE NUMBER & DEPTH
ILARO SANDSTONE
OSHOSUN FORMATION
EW. FM
PALEOCENE — EOCENE
Vertical scale
20 m
IB10-28B (29.5-32 m)
IB10-31 (35-38 m)
IB10-34 (41-42.5 m)
IB10-36 (45-51.5 m)
IB10-38 (53.5-54.3)
IB10-42 (58.5-60 m)
IB10-45 (64.9-66 m)
IB10-47 (69-70 m)
IB10-50B (75-76.5 m)
IB10-55B (81-83 m)
IB10-57 (84-87 m)
IB10-62 (96-97 m)
IB10-66 (102-105 m
IB10-68B (107-108 m)
IB10-73B (115-117 m)
IB10-75 (119-120 m)
IB10-77 (123-125 m)
IB10-79B (126-129 m)
IB10-81 (131-132 m)
IB10-84 (135-137 m)
LITHOLOGY
Lateritic top soil
Fine grained sandstone
Parallel laminated mudstone
Shelly limestone
No sample taken
IA
MF
ZG
DF
P/S
20%
40%
60%
80%
100%

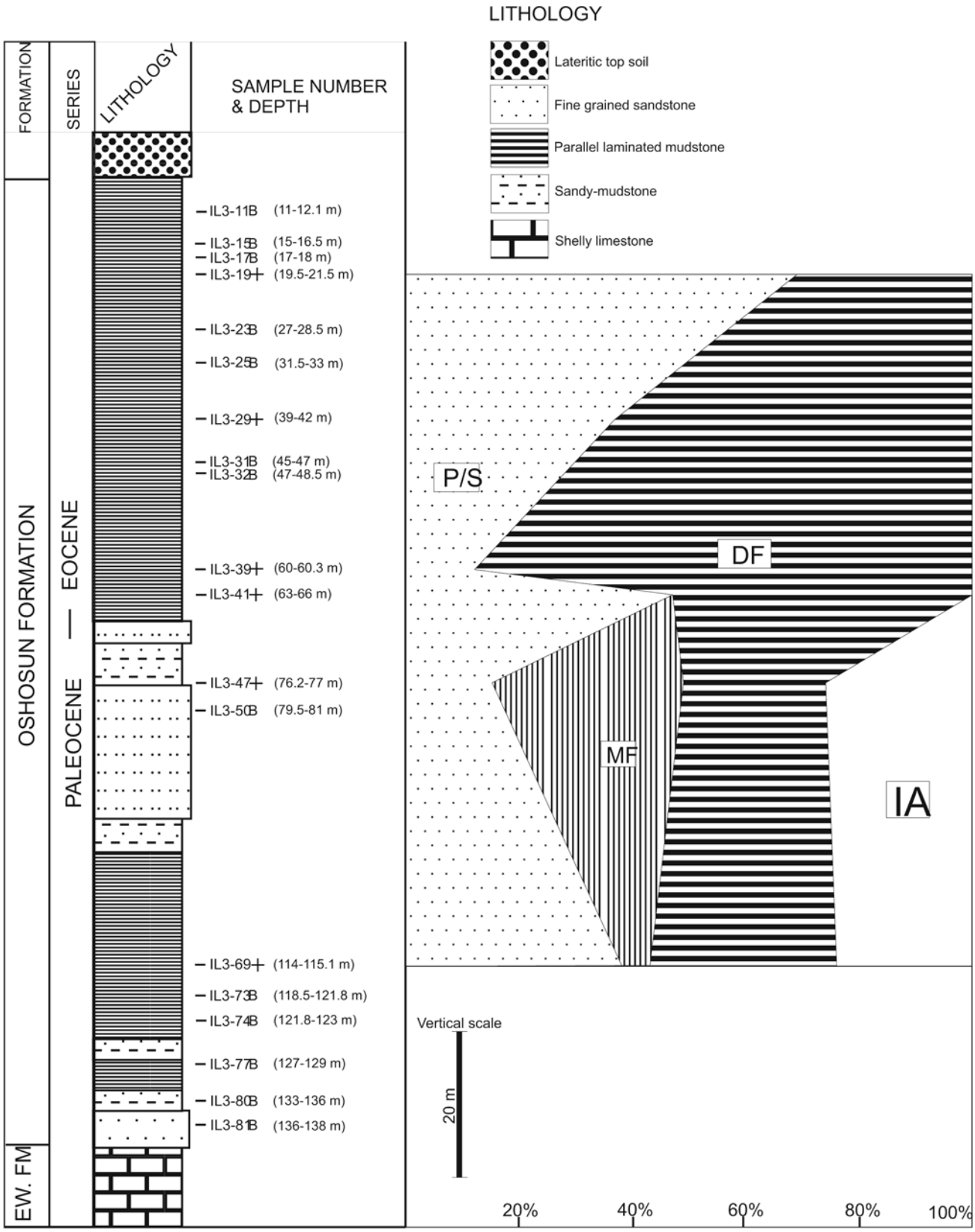


Figure 3. Lithostratigraphy and percentage distribution of major palynomorph groups in the IL3 borehole. B= barren samples. + = ≥ 200 specimens from the first two slides. EW FM = Ewekoro Formation. P/S = Pollen/spores, MF= Microforaminifera, DF= Dinoflagellate cysts, ZG = Zygnemataceae, IA= Inaperturates (incertae sedis).

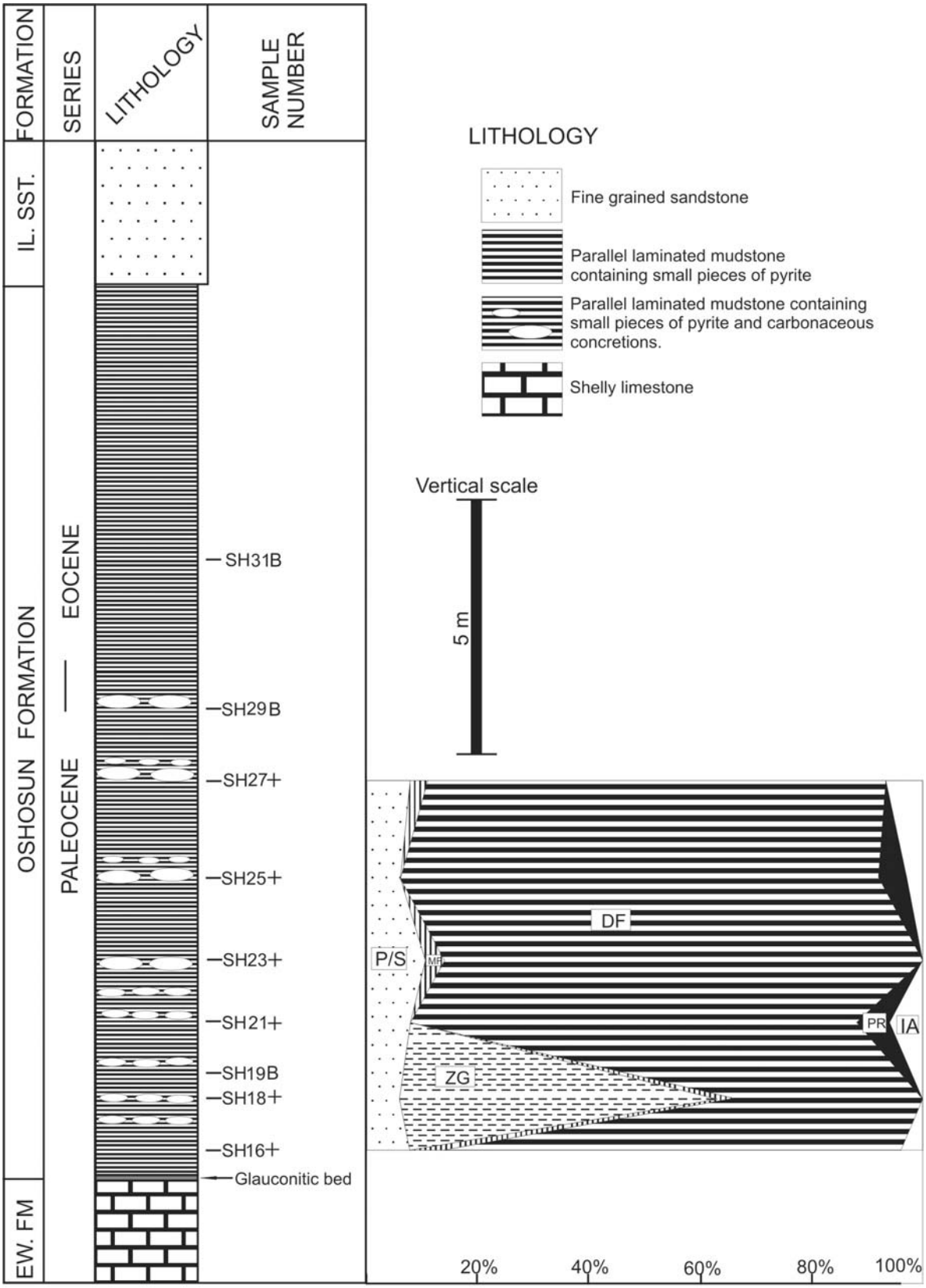


Figure 4. Lithostratigraphy and percentage distribution of major palynomorph groups in the Sagamu Quarry section. B = barren samples. + = ≥ 200 specimens from the first two slides. EW FM = Ewekoro Formation. P/S= Pollen/spores, ZG = Zygnemataceae, MF = Microforaminifera, DF = Dinoflagellate cysts, PR = Prasinophytes, IA = Inaperturates (incertae sedis).

described earlier under the same name from upper Miocene to lower Pliocene deposits of New Zealand by Couper (1954, p. 480, text-fig. 5). Since *Triorites scabratus* Couper (1954) has priority over its junior homonym *Triorites scabratus* Takahashi and Jux (1989) the new name *Triorites takahashii* is proposed here to replace *Triorites scabratus* Takahashi and Jux.

3.2. Palynostratigraphy

In addition to many long-ranging or non-diagnostic palynomorphs, a good number of biostratigraphically relevant dinocysts and pollen were also identified in the studied sections. Important dinocysts include *Apectodinium homomorphum, A. quinquelatum-paniculatum, Eatonicysta ursulae*, *Hafniasphaera septata*, *Kallosphaeridium* cf. *brevibarbatum, Ifecysta pachyderma, Palaeocystodinium australinum, Phelodinium* sp. cf. *P. magnificum* and others. Selected previous records and ranges of these and other dinoflagellate cyst species are summarized in Table 1. Several species found in the Oshosun Formation were previously recorded from other Nigerian localities based on the work of Edet and Nyong (1993), Jan du Chêne and Adediran (1985), Jan du Chêne *et al*. (1978a, b) and Oloto (1989, 1990, 1992). Relevant dinoflagellate ranges outside Nigeria are based on Jan du Chêne *et al*. (1985), Powell (1992), Williams and Bujak (1985), Williams *et al*. (1993, 2004) and Atta-Peters and Salami (2004). It can be seen in Table 1 that most dinoflagellate ranges overlap in the late Paleocene (Thanetian) to early Eocene (Ypresian) interval thus confirming the foraminifera-based age of the Oshosun Formation recently published by Gebhardt *et al*. (2005). It is also noteworthy that a high overall semblance exists between the present assemblage and the late Paleocene to early Eocene dinoflagellate assemblage recorded by Jan du Chêne and Adediran (1985) from the Imo Shale along the Benin-Ore Highway, southwest Nigeria. Rare dinoflagellate cysts of typically Campanian to Maastrichtian age (e.g. *Cerodinium granulostriatum*, see Jain and Millepied, 1973; Beilstein, 1994) may possibly be reworked from older formations.

Pollen and spores from the Oshosun Formation (see Fig. 5; Plate 2, Figs. 5, 7-17 and Appendix 1) are not considered in detail here because they do not allow a more precise age determination than dinoflagellate cysts. It may be mentioned, however, that Nigerian and more general West African ranges of some characteristic forms (e.g. *Spinizonocolpites echinatus*, *S. baculatus*, *Proxapertites cursus* and *Retistephanocolpites williamsii*) are consistent with a Paleocene-Eocene age (Germeraad *et al*., 1968; Salard-Cheboldaeff, 1990).

3.3. Depositional environments and palaeoclimatological implications

The depositional environment of the Oshosun Formation is reconstructed by evaluating the palynological associations encountered in the three sections studied. Environmental factors such as salinity, water temperature, hydrography and proximity to shoreline areas are known to be reflected in the distribution pattern, abundance and morphology of palynomorphs in general and dinoflagellate cysts in particular (e.g. Köthe, 1990; Dale 1996; Sluijs *et al*., 2005). The palynological assemblages in the IB10 and in the Sagamu Quarry section are generally dominated by marine dinflagellate cysts (Figs. 2 and 4). In both sections an *Apectodinium-Homotryblium-Kallosphaeridium* assemblage can be recognized, and is best developed in the lower part of the Oshosun Formation in the IB10 borehole (samples IB10-57 to IB10-84, Fig. 2). The relative abundance of *Apectodinium* is significant because this genus is a well known warm-water genus whose radiation is linked to the late Paleocene or rather Paleocene-Eocene thermal maximum (LPTM of Crouch *et al*, 2001; PETM of Crouch *et al*., 2003 and Sluijs *et al*., 2005). In some studies the PETM is also called Initial Eocene thermal maximum (IETM). This term was used by Gebhardt *et al*. (2005) who recognized the coincidence of the IETM event with the deposition of the Oshosun Formation in a study of foraminifera from the Sagamu Quarry.

Apectodinium and/or *Homotryblium* have also been related to near-shore and reduced salinity conditions (Jain and Garg, 1986; Garg and Khowaja-Ateequzzaman, 2000; Dybkjaer, 2004). In other studies (see review of Sluijs *et al*., 2005), representatives of the latter genus have been interpreted as characteristic of high salinity, lagoonal settings.

Figure 5. Distribution of palynomorphs in the boreholes IB10, IL3 and in the Sagamu Quarry section. • = 1, ❍= 2-9, ■ ≥ 10 specimens.

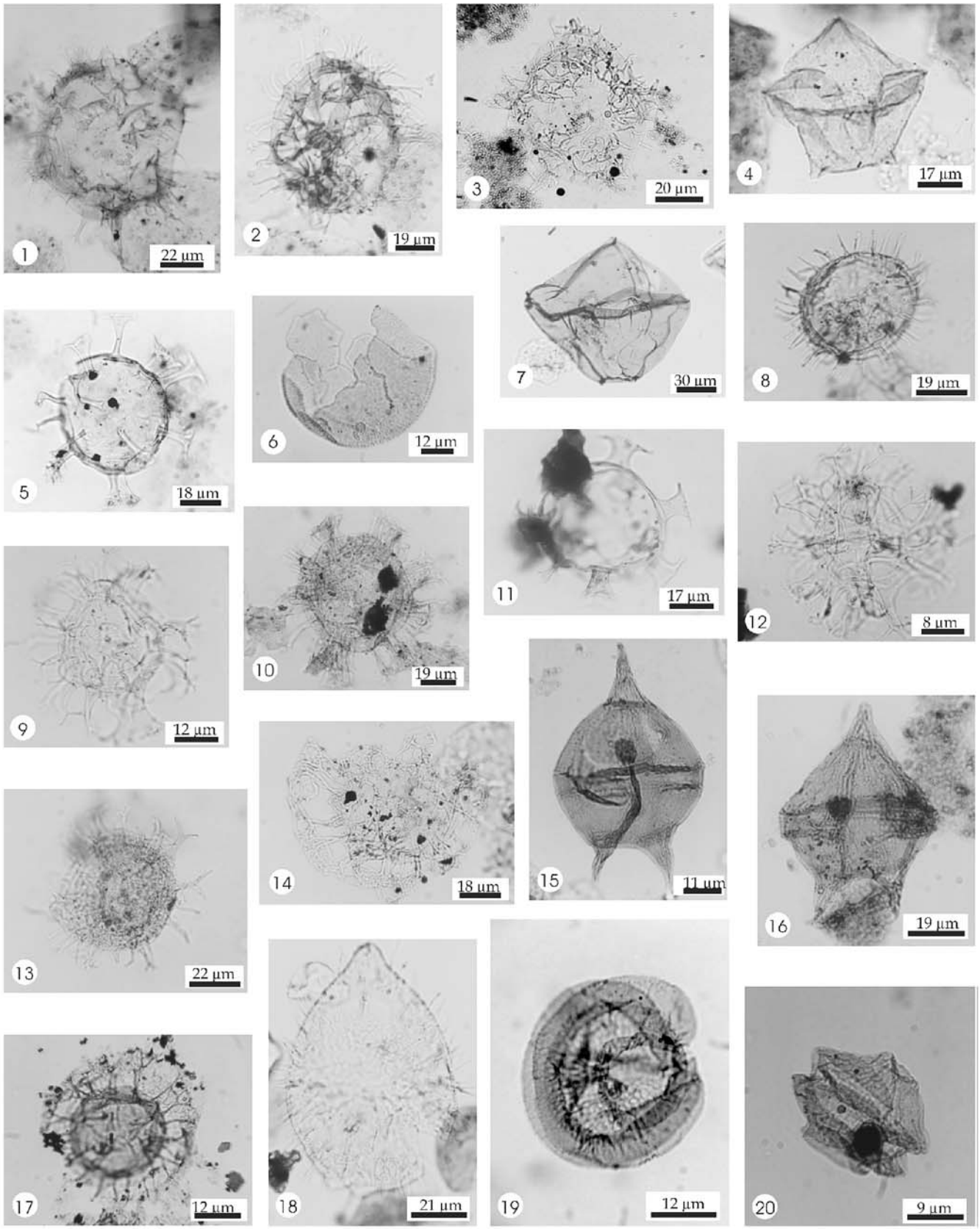
Sample / Taxa	IB10 borehole														IL3 borehole						SH Quarry					
	84	81	77	75	66	62	57	47	45	42	38	36	34	31	69	47	41	39	29	19	16	18	21	23	25	27
Dinoflagellates																										
Adnatosphaeridium multispinosum																			○							
Adnatosphaeridium sp.							○											○								
Apectodinium homomorphum	○		■	■	○	○	■									○					○				○	
Apectodinium quinquelatum																						○			○	
A. quinquelatum-paniculatum																										○
Apectodinium sp. A																							○			
Apectodinium sp. 1																					○	○				
Cerodinium cf. *balticum*		●																								
Cerodinium granulostriatum			●																							
Cleistosphaeridium sp. 1								●													■	■	■	■	■	■
Cleistosphaeridium sp. 2			○	○						○		○										○				
Cordosphaeridium fibrospinosum			○																							
Cordosphaeridium inodes																										●
Eatonicysta ursulae																					○					
Fibrocysta sp. cf. *F. lappacea*																		■								
Hafniasphaera septata													○				○				○	■				
Homotryblium abbreviatum			○			○																				
Homotryblium spp.	■	○	■																							
Homotryblium tenuispinosum	○		○		○	●	○																			
Ifecysta pachyderma																					○				○	
Kallosphaeridium cf. *brevibarbatum*					■	○							○												■	
Kallosphaeridium cf. *capulatum*																							■		○	
Kallosphaeridium spp.				■																						
Lejeunecysta cf. *beninensis*			●																							
Lejeunecysta cf. *cinctoria*									○	○					■											
Lejeunecysta cf. *communis*																									●	
Lejeunecysta cf. *lata*							○	○			■	○														
Lejeunecysta sp. 1											●															
Lejeunecysta sp. 2								○			○															
Operculodinium centrocarpum													○												○	
Palaeocystodinium australinum																						○				
Palaeocystodinium golzowense																									○	
Phelodinium sp. cf. *P. magnificum*	●																									
Polysphaeridium subtile								○									○			○						
Senegalinium orei	○				○																○	○				
Spiniferites membranaceus									○						○											
Spiniferites pseudofurcatus																									●	
Spiniferites spp.			○	■	○		○	■	■		■	■	■		○			○	■		■	■			○	
Prasinophytes																										
Pterospermella australiensis																							○		○	
Zygnemataceae																										
Debarya sp.																						■				
Ovoidites cf. *parvus*					○			○	○																	
Spore																										
Cicatricososporites eocenicus																○										
Dictyophyllidites harrisii						○																				
Dictyophyllidites sp.					○																					
Leiotriletes maxoides					○						●															
Verrucatosporites ornatus									○														○			
Pollen																										
Bombacacidites africanus																	■			■						
Grimsdalea cf. *magnaclavata*													●													
Ilexpollenites sp.				■	○	■	○						■	○										○		
Mauritiidites crassibaculatus			○	○																						
Proxapertites cursus																				○						
Psilatricolporites cf. *crassus*																	●									
Retimonocolpites sp.									●																	
Retistephanocolpites williamsii	●														○											
Retisyncolporites sp.			○																							
Rhoipites sp.						●																				
Spinizonocolpites baculatus																	○									
Spinizonocolpites echinatus														○						○						
Striatopollis nigericus																		○								
Tricolpites cf. *microreticulatus*																	●									
Triorites takahashii					●			○																		

	Lt. Cret.	Paleocene			Eocene			
	Ca-Ma	Dan	Sel	Than	Ypr	Lut	Bar	Pria
1. *Apectodinum homomorphum*	□□□	□□□□□□	□□□□□□	■■■■■■ □□□□□□	■■■■■■ □□□□□□	■■■■■■ □□□□□□	■■■■■■ □□□□□□	■■■■■▶ □□□□□□
2. *Apectodinum paniculatum*				■■■■■■ □□□□□□	■■■■■■ □□□□□□			
3. *Apectodinum quinquelatum*				■■■■■■ □□□□□□	■■■■■■ □□□□□□			
4. *Cordosphaeridium fibrospinosum*	■■■ □□□	■■■■■■ □□□□□□	■■■■■■ □□□□□□	■■■■■■ □□□□□□	■■■■■■ □□□□□□	■■■■■■	■■■■■■	■■■■■▶
5. *Eatonicysta ursulae*					■■■■■■	■■■■■■		
6. *Hafniasphaera septata*		■■■■■■	■■■■■■	■■■■■■	■■■■■■ □□□□□□			
7. *Homotryblium abbreviatum*				□□□□□□	■■■■■■ □□□□□□	■■■■■■	■■■■■■	■■■■■▶
8. *Homotryblium tenuispinosum*				■■	■■■■■■	■■■■■■	■■■■■■	■■■■■▶
9. *Ifecysta pachyderma*				□□□□□□	□□□□□□			
10. *Kallosphaeridium brevibarbatum (cf.)*					■■■■■■			
11. *Palaeocystodinium australinum*	■■■■■■ □□□□□□	■■■■■■ □□□□□□	■■■■■■	■■■■■■				
12. *Phelodinium sp. cf. P. magnificum*				□□□□□□	□□□□□□			
13. *Polysphaeridium subtile*					■■■■■■ □□□□□□	■■■■■■	■■■■■■	
14. *Senegalinium orei*				□□□□□□	□□□□□□			

Table 1. Selected previous records of some dinoflagellate species (or related forms: cf.) from the Oshosun Formation. Nigerian and other West African records (□□□□□□) based on Jan du Chêne *et al*., 1978a, b (1); Oloto, 1989 (11), 1990 (11), 1992 (6, 13); Jan du Chêne and Adediran, 1985 (1-4, 7, 9, 12, 14); Edet and Nyong, 1993 (11); Atta-Peters and Salami, 2004 (1, 4). Non-Nigerian records (■■■■■■) based on Powell, 1992 (1-3, 7); Williams *et al*., 1993 (4, 5); Williams *et al*., 2004 (5, 8); Williams and Bujak, 1985 (6, 7, 11, 13); Jan du Chêne *et al*., 1985 (10).

Plate 1. Sample and slide number and coordinates are given for each of the illustrated specimen. (1) and (2) *Apectodinium homomorphum,* IB10-77, 1, 37.2/99 and IB10-77, 1, 41.2/112 (3) *Apectodinium quinquelatum*, SH18, 1, 34/104.8 (4) *Lejeunecysta* cf. *beninensis*, IB10-77, 2, 47.5/100 (5) *Homotryblium tenuispinosum*, IB10-66, 1, 24.6/104.8 (6) *Kallosphaeridium* cf. *brevibarbatum*, SH25, 1, 40.4/102.6 (7) *Lejeunecysta* cf. *lata*, IB10-57, 1, 42.8/109.9 (8) *Operculodinium centrocarpum*, IB10-34, 1, 44.1/104.1 (9) *Spiniferites membranaceus*, IB10-45, 1, 28.9/102.2 (10) *Cordosphaeridium fibrospinosum*, IB10-77, 2, 32.9/107.9 (11) *Homotryblium abbreviatum*, IB10-62, 1, 40.4/108.3 (12) *Spiniferites* spp., IB10-45, 2, 43.4/96.9 (13) *Hafniasphaera septata*, SH16, 1, 33.4/103.8 (14) *Adnatosphaeridium* sp., IB10-57, 1, 30.2/100.3 (15) *Cerodinium granulostriatum*, IB10-77, 2, 46.5/99 (16) *Senegalinium orei*, SH18, 1, 34.6/100.5 (17) *Eatonicysta ursulae*, SH16, 1, 31/104.3 (18) *Fibrocysta* sp. cf. *F. lappacea* IL3-39, 1, 44.2/107.8 (19) and (20) *Debarya* sp., SH18, 1, 34/106.5 and SH18, 1, 24.8/101.6.

Plate 1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In the IB10 borehole, species of *Spiniferites* become more abundant in the upper part of the section above the *Apectodinium-Homotryblium-Kallosphaeridium* interval. This may signify a shift towards slightly more open marine conditions following previous palaeoecological interpretations of this widely distributed genus (e.g. Williams, 1977; Jan du Chêne and Adediran, 1985; Köthe 1990; Sluijs *et al*., 2005). In the Sagamu section this phase is represented by an association with relatively abundant specimens of *Cleistosphaeridium*, another form with outer neritic preferences (see review in Sluijs *et al*., 2005).

Influx of freshwater into the depositional environment of the Oshosun Formation is sporadically indicated by algae such as *Ovoidites* and *Debarya*. *Ovoidites* cf. *parvus* is a minor element in IB10 (5-7%, samples IB10-66, 47 and 45). Debarya, freshwater alga (Zygnemataceae; see Head, 1992), is dominant in a single sample (about 60% in SH18) in the lower part of the Sagamu section (Fig. 4), perhaps suggesting a relatively short and strong pulse of freshwater influx into a marine shelf environment. It cannot be excluded that additional forms related to freshwater algae are among the inaperturate palynomorphs (IA in Figs. 2-4) that are not specifically identified in the present paper. However, this is not supported by the association of relatively common inaperturates and (marine) foraminiferal linings in the lower part of the IL3 section (Fig. 3).

Terrestrially-derived pollen and spores, which may be wind- and/or water-transported, are relatively rare in the Sagamu section (6-10%, Fig. 4) in the east of the study area. These forms become more common in a westerly direction where they attain 31% in the IB10 borehole (Fig. 2) and up to 69% at the top of the IL3 borehole (Fig. 3). The latter section is also characterized by the strongest fluctuations in the marine/terrestrial ratio. From the distribution of pollen and spores it may be concluded that the two western sections (especially IL3) were closer to a terrestrial source than the Sagamu section during most of the time of deposition of the Oshosun Formation. This is also supported by the lithological composition of the formation which has the highest sandstone contents in the IL3 section.

4. CONCLUSIONS

1. Dinoflagellate cyst associations with *Apectodinium* suggest a late Paleocene to early Eocene (Thanetian-Ypresian) age for the Oshosun Formation corresponding to the global Paleocene-Eocene thermal maximum (PETM).

2. The abundance of *Apectodinium* and *Homotryblium* may be indicative of deposition under reduced or fluctuating salinity conditions suggesting a marginal marine, perhaps estuarine-influenced environment.

3. Influx from freshwater environments led to the occasional inclusion of Zygnemataceae (freshwater algae) such as *Debarya* sp. and *Ovoidites* cf. *parvus* as found in the Sagamu Quarry and the IB10 borehole sections respectively.

4. Along an east-west transect, land-derived pollen and spores become more common in the two western sections (IB10 and IL3 boreholes) suggesting proximity to a terrestrial source area there.

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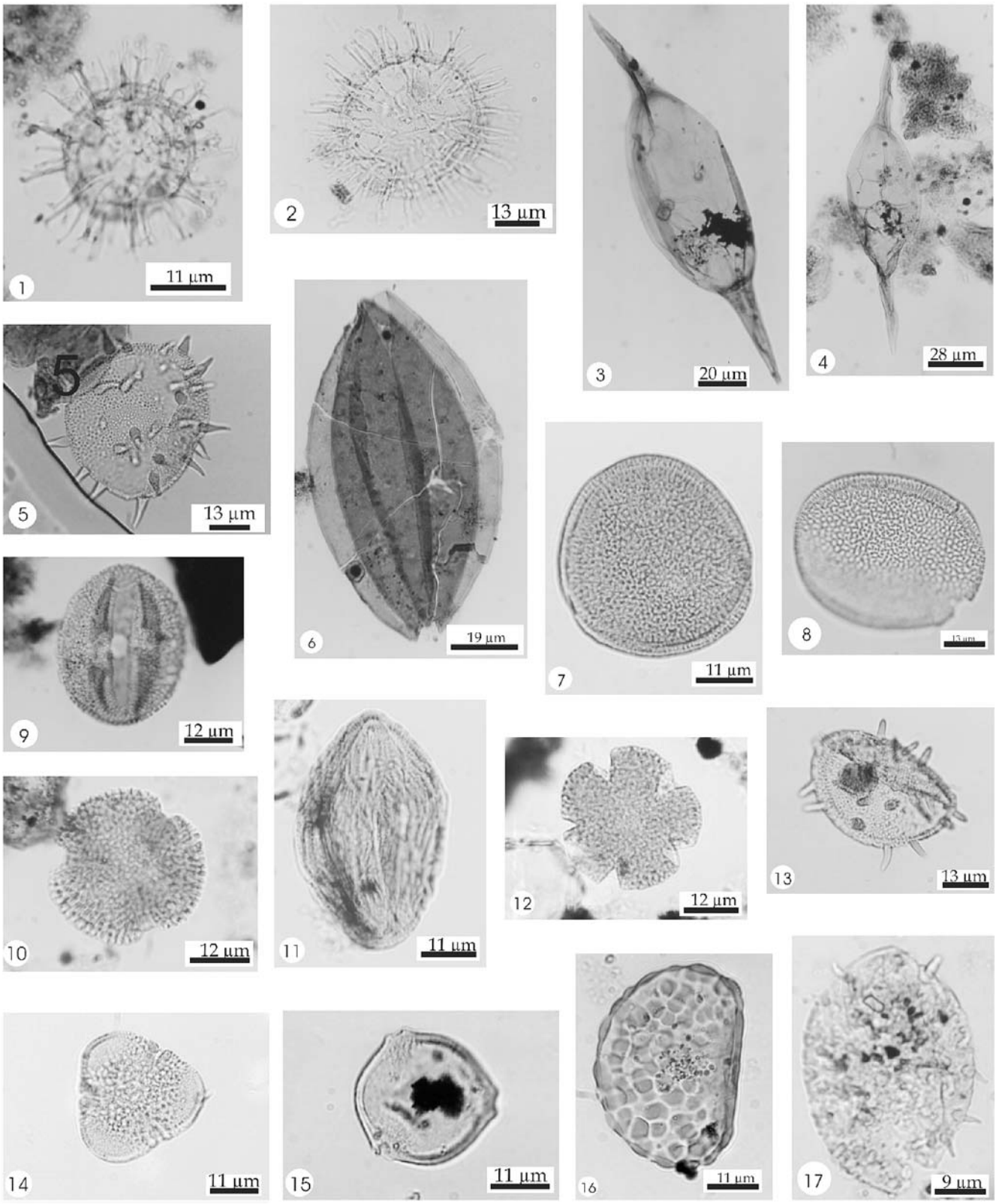
Plate 2. Sample and slide number and coordinates are given for each of the illustrated specimen. (1) *Cleistosphaeridium* sp.1, SH23, 1, 36.4/99.8 (2) *Polysphaeridium subtile*, IL3-19, 1, 42.7/109.5 (3) *Paleocystodinium golzowense*, SH25, 1, 48/102.6 (4) *Paleocystodinium australinum*, SH18, 1, 41.7/97.8 (5) *Spinizonocolpites echinatus*, IL3-19, 1, 49.5/111.6 (6) *Ovoidites* cf. *parvus*, IB10-66, 2, 24.4/104.5 (7) and (8) *Proxapertites cursus*, IL3-19, 1, 34/104 and IL3-19, 1, 47.3/101.5 (9) *Rhoipites* sp., IB10-62, 2, 39.8/100.9 (10) *Ilexpollenites* sp., IB10-66, 2, 43.3/105.2 (11) *Striatopollis nigericus*, IL3-39, 1, 44.3/105.2 (12) *Retistephanocolpites williamsii*, IL3-69, 1, 35/103.2 (13) *Spinizonocolpites baculatus*, IL3-41, 1, 26/110.2 (14) *Bombacacidites africanus*, IL3-19, 1, 35.8/92.5 (15) *Triorites takahashii*, IB10-47, 1, 32.4/106.4 (16) *Verrucatosporites ornatus*, IB10-45, 2, 38.9/102 (17) *Mauritiidites crassibaculatus*, IB10-77, 1, 41/110.2.

Plate 2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APPENDIX 1: LIST OF SPECIES

Dinoflagellate cysts

Adnatosphaeridium multispinosum Williams and Downie in Davey *et al*., 1966

Adnatosphaeridium sp. (Plate 1/14)

Apectodinium homomorphum (Deflandre and Cookson, 1955) Lentin and Williams, 1977 (Plate 1/1-2)

Apectodinium quinquelatum (Williams and Downie 1966) Costa and Downie, 1979 (Plate 1/3)

Apectodinium quinquelatum-paniculatum sensu Jan du Chêne and Adediran, 1985

Apectodinium sp. A Garg and Khowaja-Ateequzzaman, 2000

Apectodinium sp. 1

Cerodinium cf. *balticum* Vozzhennikova, 1967 (Plate 1/15)

Cerodinium granulostriatum (Jain and Millepied, 1973) Lentin and Williams, 1987 (Plate 1/15)

Cleistosphaeridium sp. 1 (Plate 2/1)

Cleistosphaeridium sp. 2

Cordosphaeridium fibrospinosum Davey and Williams, 1966 (Plate 1/10)

Cordosphaeridium inodes (Klump) Eisenack, 1963

Eatonicysta ursulae (Morgenroth, 1966) Stover and Evitt, 1978 (Plate 1/17)

Fibrocysta sp. cf. *F. lappacea* (Drugg, 1970) Stover and Evitt, 1978 (Plate 1/18)

Hafniasphaera septata (Cookson and Eisenack, 1967b) Hansen, 1977 (Plate 1/13)

Homotryblium abbreviatum Eaton, 1976 (Plate 1/11)

Homotryblium spp.

Homotryblium tenuispinosum Davey and Williams, 1966 (Plate 1/5)

Ifecysta pachyderma Jan du Chêne and Adediran, 1985

Kallosphaeridium cf. *brevibarbatum* De Coninck, 1969 (Plate 1/6)

Kallosphaeridium capulatum Stover, 1977 emend. Jan du Chêne *et al*., 1985

Kallosphaeridium spp.

Lejeunecysta cf. *beninensis* Biffi and Grignani, 1983 (Plate 1/4)

Lejeunecysta cf. *cinctoria* (Bujak 1980) Lentin and Williams, 1981

Lejeunecysta cf. *communis* Biffi and Grignani, 1983

Lejeunecysta cf. *lata* Biffi and Grignani, 1983 (Plate 1/7)

Lejeunecysta sp. 1

Lejeunecysta sp. 2

Operculodinium centrocarpum (Deflandre and Cookson, 1955) Wall, 1967 (Plate 1/8)

Palaeocystodinium australinum (Cookson, 1965) Lentin and Williams, 1976 (Plate 2/4)

Palaeocystodinium golzowense Alberti, 1961 sensu Jan du Chêne and Adediran, 1985 (Plate 2/3)

Phelodinium sp. cf. *P. magnificum* (Stanley, 1965) Stover and Evitt, 1978 sensu Jan du Chêne and Adediran, 1985

Polysphaeridium subtile Davey and Williams, 1966 (Plate 2/2)

Senegalinium orei Jan du Chêne and Adediran, 1985 (Plate 1/16)

Spiniferites membranaceus (Rossignol, 1964) Sarjeant, 1970 (Plate 1/9)

Spiniferites pseudofurcatus (Klump, 1953) Sarjeant, 1970

Spiniferites spp. (Plate 1/12)

Prasinophytes

Pterospermella australiensis (Deflandre and Cookson, 1955) Eisenack *et al*., 1973

Zygnemataceae

Debarya sp. (Plate 1/19-20)

Ovoidites cf. *parvus* (Cookson and Dettmann, 1959) Nakoman, 1966 (Plate 2/6)

Spores

Cicatricososporites eocenicus (Selling, 1944) Jansonius and Hills, 1976

Dictyophyllidites harrisii Couper, 1958

Dictyophyllidites sp.

Leiotriletes maxoides Krutzsch, 1962

Verrucatosporites ornatus (Sah, 1967) Kumar and Takahashi, 1991 (Plate 2/16)

Pollen

Bombacacidites africanus Takahashi and Jux, 1989 (Plate 2/14)

Grimsdalea cf. *magnaclavata* Germeraad *et al*., 1968

Ilexpollenites sp. (Plate 2/10)

Mauritiidites crassibaculatus Van Hoeken-Klinkenberg, 1964 (Plate 2/17)

Proxapertites cursus Van Hoeken-Klinkenberg, 1966 (Plate 2/7-8)

Psilatricolporites cf. *crassus* Hammen and Wijmstra, 1964

Retimonocolpites sp.

Retistephanocolpites williamsii Germeraad *et al*., 1968 sensu Bio-Lokoto *et al*., 1998 (Plate 2/12)

Retisyncolporites sp.

Rhoipites sp. (Plate 2/9)

Spinizonocolpites baculatus Muller, 1968 (Plate 2/13)

Spinizonocolpites echinatus Muller, 1968 (Plate 2/5)

Striatopollis nigericus Takahashi and Jux, 1989 (Plate 2/11)

Tricolpites cf. *microreticulatus* Belsky *et al*., 1965

Triorites takahashii Schrank, nom. nov. (Plate 2/15)

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Recent marine Ostracoda from the Solomon Islands. Part 5: Cytheroidea, Leptocytheridae

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Abstract

Nine species, belonging to three genera, of the family Leptocytheridae were encountered in the Solomon Islands. Of these, five are described and illustrated herein as new: *Leptocythere rokuaiensis, Callistocytere parakeiji, C. punctatuberculata, C. scripta* and *Tanella striatopunctata* ssp. nov. Three species, *Leptocythere foveoreticulata* McKenzie, *L. pulchra* Zhao & Whatley and *Tanella ochracea* (Brady) have been previously described from elsewhere in the Indo-Pacific. A rare species of *Leptocythere* is left in open nomenclature. Although numerically, the leptocytherids are not of major significance in terms of abundance or diversity, they form nonetheless a significant and very evident component of the total fauna of 160 species.

Keywords: Solomon Islands, Recent, Marine Ostracoda, Leptocytheridae.

Resumen

Se han reconocido tres géneros y nueve especies de ostrácodos marinos actuales de la familia Leptocytheridae en las islas Salomón. Cinco de estas especies son nuevas y se describen e ilustran aquí: *Leptocythere rokuaiensis, Callistocytere parakeiji, C. punctatuberculata, C. scripta* y *Tanella striatopunctata* ssp. nov. Tres especies, *Leptocythere foveoreticulata* McKenzie, *L. pulchra* Zhao & Whatley y *Tanella ochracea* (Brady), han sido descritas previamente en el Indo-Pacífico. Una especie rara de *Leptocythere* se describe en *nomina aperta*. Aunque los leptocythéridos no son muy abundantes ni diversos, forman un componente significativo de la fauna total de 160 especies en estas islas.

Palabras clave: Islas Salomón, Reciente, ostrácodos marinos, Leptocytheridae.

1. INTRODUCTION

The present work is part of a larger study of the Quaternary and Recent Ostracoda of the Solomon Islands. 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 have been sadly neglected. This is the fifth in a series of publications in which we seek to redress this situation.

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

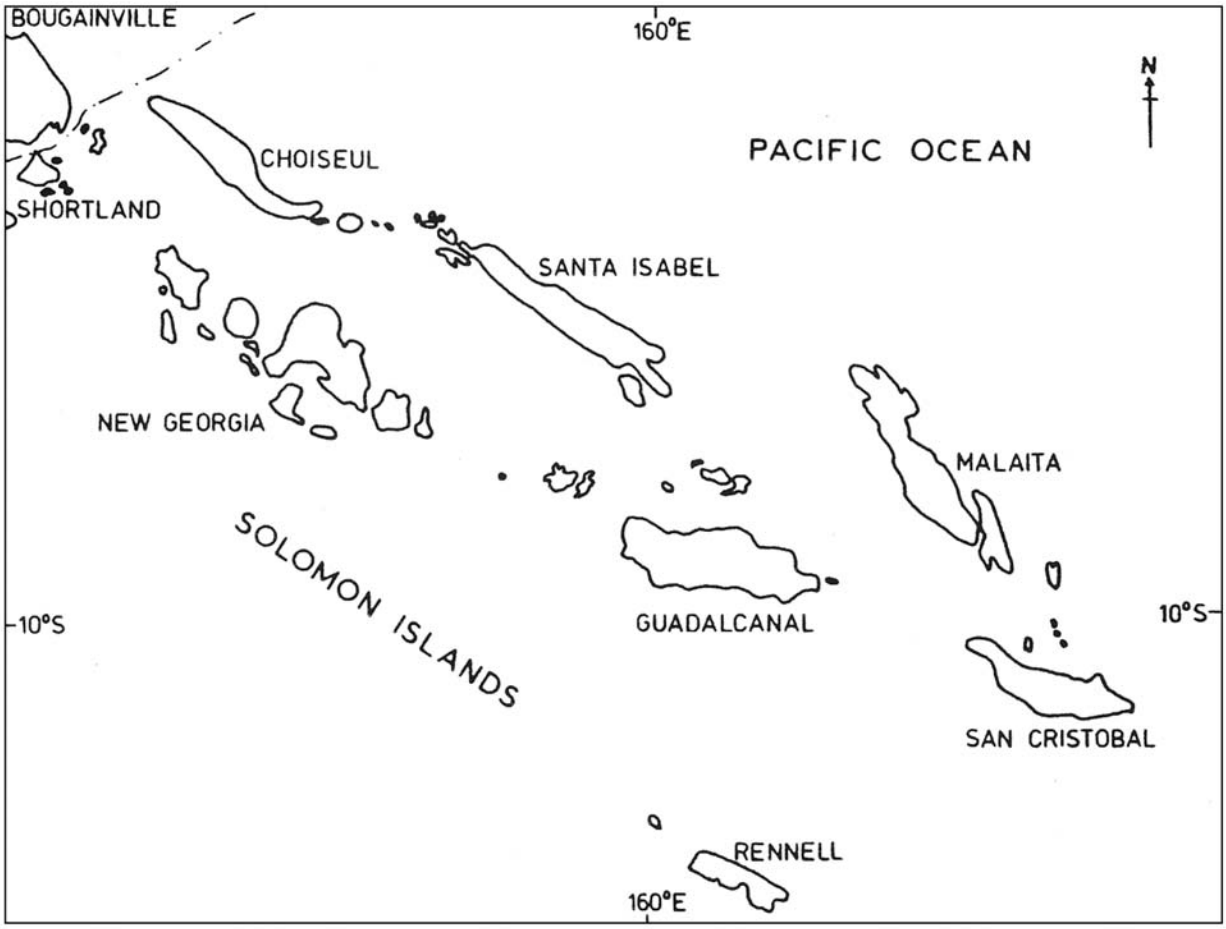


Figure 1. The Solomon Islands.

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 Whatley & Titterton, 1981 and Titterton (1984 MS).

The total ostracod fauna comprises some 160 species belonging to 56 genera. The overwhelmingly dominant group are the cytherids (63%) the remainder are marine cyprids (15%), bairdiids (8%) and platycopids/cladocopids (13%). Within this fauna, 9 species, belonging to three genera, of the family Leptocytheridae were encountered. Five of the 9 are new but only 2 species are endemic to the Solomon Islands. The other species all occur in Indonesia and *L. pulchra* Zhao & Whatley and *C. parakeijii* sp. nov. are even more widely distributed in the Indo-Pacific, occurring as far west as Madagascar, the latter also to as far south as New Caledonia. *Tanella ochracea* (Brady) also occurs in New Caledonia.

There has been a resurgence of studies of Ostracoda in the SW Pacific area. Among the important contributions of the last decades are Behrens (1991a, b; Great Barrier Reef), Cabioch *et al*. (1986; New Caledonia), Dewi (1997; Java Sea), Howe & McKenzie (1989; NW Australia), Jellinek (1993; Kenya), Mostafawi (1992; Malaysia), Whatley *et al*. (1995, 1996; Northern Australia), Whatley & Keeler (1989; Reunion Island), Whatley & Zhao (1987, 1988; Malacca Straits), Whatley & Jones (1999; Easter Island), Whatley *et al*. (2000; Easter Island), Whatley & Roberts (1995; Pitcairn Group), Whatley *et al*. (in press; Pitcairn Group), Yassini *et al*. (1993; Eastern Australia), Yassini & Jones (1995; Eastern Australia), Zhao & Whatley (1989; Malaysia).

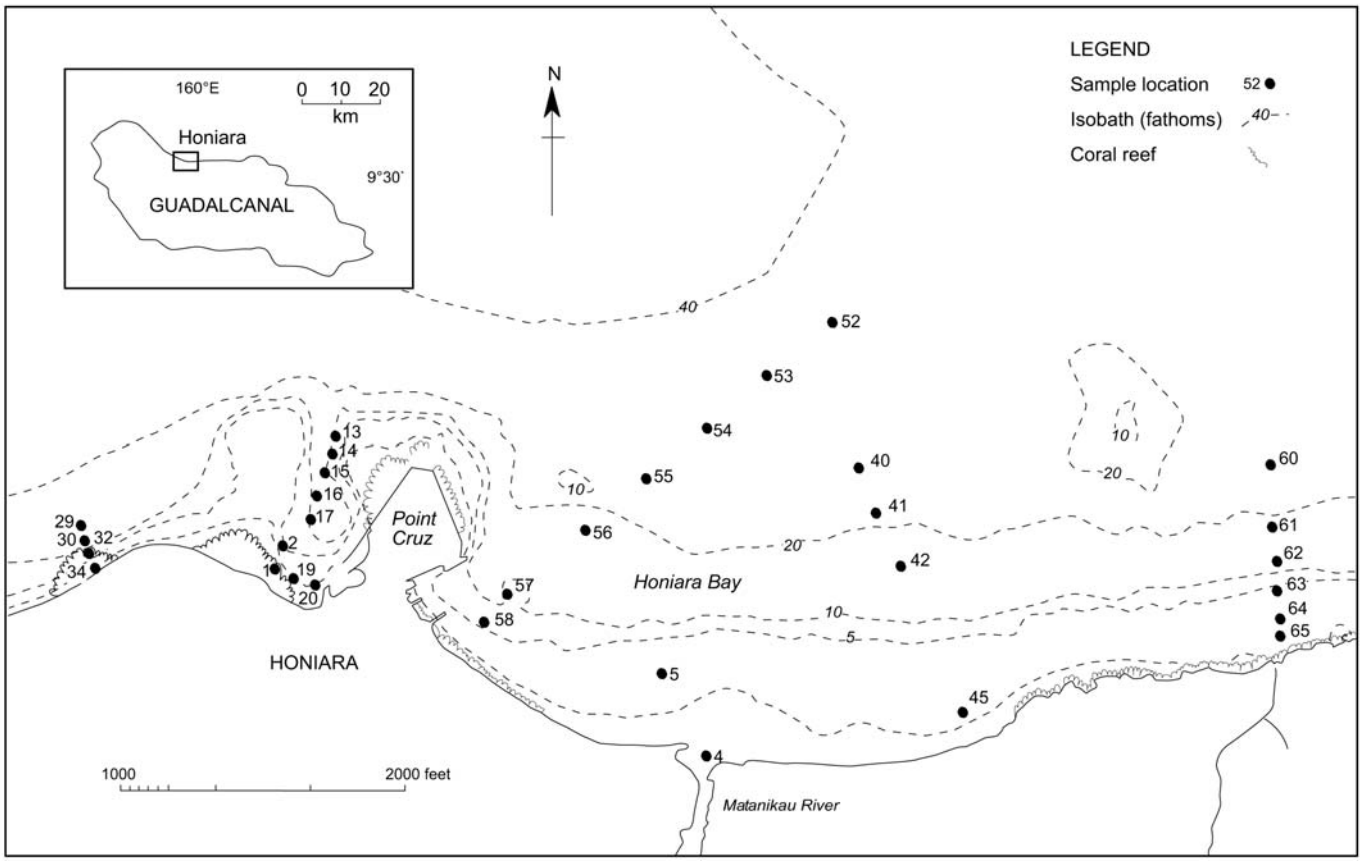


Figure 2. Location of sample stations, Honiara Bay, N. Guadalcanal, Solomon Islands.

The present contribution is the fifth paper in the current series on the Recent marine Ostracoda of the Solomon Islands. Earlier papers deal with the marine Cypridoidea and Cladocopina/Platycopina (Titterton & Whatley, 2006a) the Xestoleberidae (Titterton & Whatley, 2005), the Bythocytheridae to the Cytheruridae (Titterton & Whatley, 2006 b) and the Hemicytheridae and Thaerocytheridae (Titterton & Whatley, in press). Quaternary marine and brackish Ostracoda are the subject of an additional study (Whatley *et al*., in press).

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. 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, rpc=radial pore canal, npc=normal pore canal, LOC= line of concrescence. All new taxa are fully described.

Class OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily CYTHEROIDEA Baird, 1850
Family LEPTOCYTHERIDAE Hanai, 1957
Genus *Leptocythere* Sars, 1925
Leptocythere foveoreticulata (McKenzie & Sudijono), 1981
(Fig. 4, Nos 1-2; Pl. 1, Figs 1-10)

1981 *Ishizakiella foveoreticulata* McKenzie & Sudijono, p. 36, Pl. 1, Fig. 6, Pl. 2, Figs 5, 6.

1982 *Ishizakiella foveoreticulata* McKenzie & Sudijono. McKenzie p. 416, Pl. 7, Figs 2, 3.

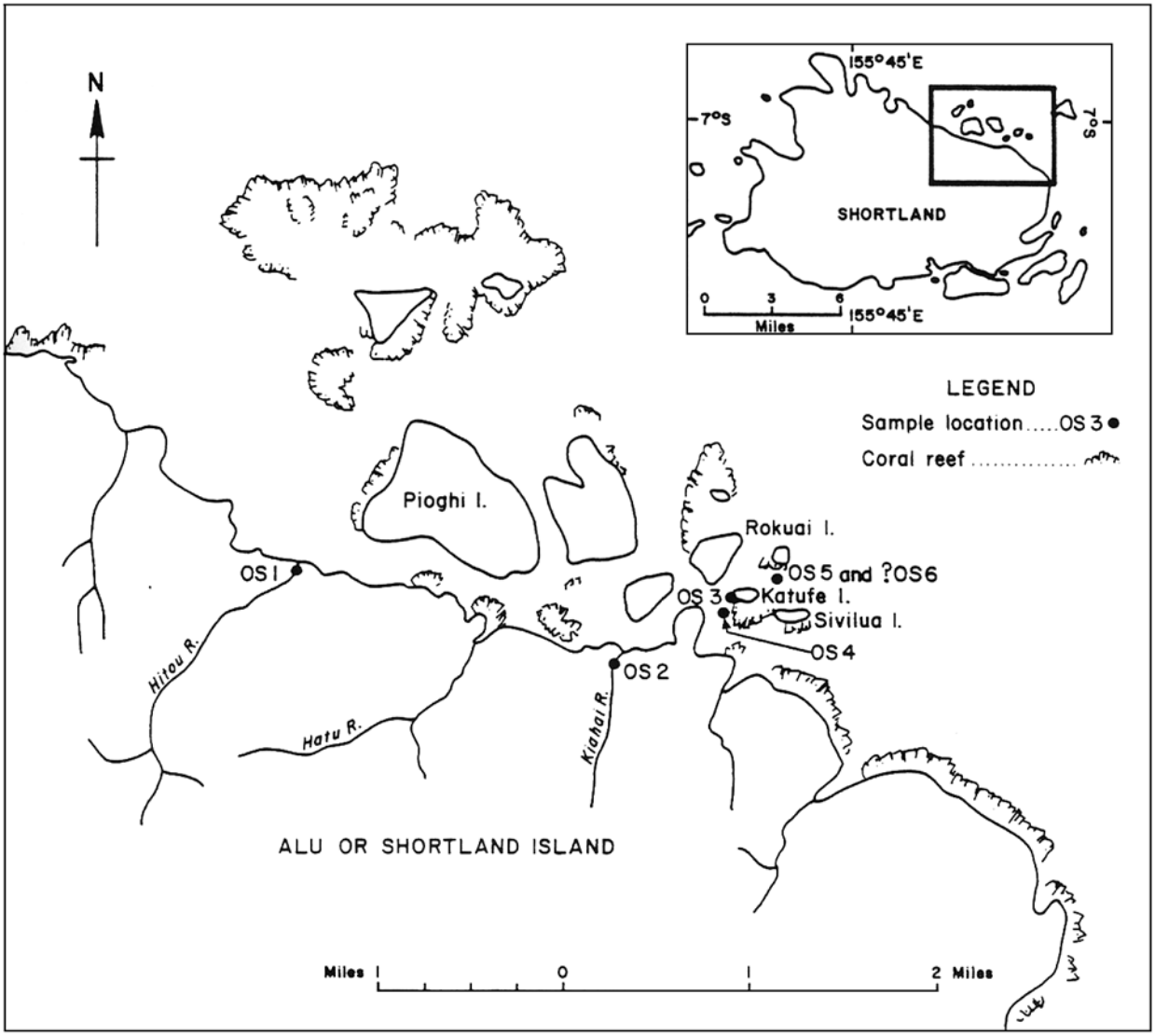


Figure 3. Location of sample stations, Shortland Island, Solomon Islands.

Material.- 9 adult valves and carapaces.

Dimensions.-	Length	Height	Width
Female LV, RT/SIR/355	0.65	0.34	
Female C, RT/SIR/353	0.64	0.33	0.30
Male LV, RT/SIR/354	0.61	0.30	
Male LV, RT/SIR/356	0.64	0.33	
Male RV, RT/SIR/357	0.62	0.31	
Female RV, RT/SIR/359	0.69	0.33	

Distribution.-Samples: 5, OS6 Guadalcanal and Shortland islands. The material figured by McKenzie (1982) is from Late Pliocene sediments from Sangiran, Java.

Remarks.-The present authors do not accept the validity of the genus *Ishizakiella* McKenzie & Sudijono, 1981. At best those taxa attributed to it represent a species group of *Leptocythere*. For example, Maybury & Whatley (1980) have illustrated species of *Leptocythere* from the Pliocene of Cornwall and Brittany, which are very similar in shape and ornament to the present species. McKenzie & Sudijono (1981) also placed the Recent Japanese species *Tanella pacifica* and *T. miurensis* Hanai, 1957 in *Ishizakiella* and was followed in this by Tsukagoshi (1994), who also included *Tanella supralittoralis* Schornikov. We would probably include these species in *Leptocythere*. *Leptocythere (Callistocythere) arenicola* Hartmann, 1964, from

the Recent of the Red Sea, is also similar to the present species, particularly in anterior ornament. The former possesses more strongly developed ribs and differs in ornament medianly and posteriorly. The two species also differ in detail of the marginal pore canals. *Leptocythere rokuaiensis* sp. nov. is very closely related to the present species, particularly the male valve, although the female is more noticeably different. Both species possess a reticulate ornament and an anterior submarginal rib that bifurcates subdorsally and a rib subparallel to the posterior margin. In *L. rokuaiensis* this posterior rib is weaker, particularly posteroventrally, and the posterior margin is less truncate than in the present species. *Cythere ochracea* Brady, 1880, Recent, New Caledonia, lacks the distinctive posterior rib of the present species. One specimen among the present material, RT/SIR/359, differed slightly from the others in that the posterior rib is more prominently developed ventrally.

Leptocythere pulchra Zhao & Whatley, 1989
(Fig. 4, Nos 7-8; Pl. 1, Figs 11-19)

1981 *Leptocythere parafoveata* Keeler MS, p.128, Pl. 7, Figs 7-10.

1987 *Leptocythere* sp. Whatley & Zhao, p. 6, Fig. 4.

1989 *Leptocythere pulchra* sp. nov. Zhao & Whatley, p. 173, Pl. 1, Figs 5-9.

1989 *Leptocythere pulchra* Zhao & Whatley. Whatley & Keeler, p. 71, Pl. 3, Figs 8-11.

non 1995 *Leptocythere pulchra* Zhao & Whatley. Babinot & Kouyoumontzakis, Pl. 2, Fig. 20 [= *Neocyprideis timorensis* (Fyan)].

Material.-12 adult valves and carapaces.

Dimensions.-	Length	Height	Width
RV, RT/SIR/368	0.38	0.19	
LV, RT/SIR/369	0.37	0.19	
RV, RT/SIR/370	0.40	0.20	
LV, RT/SIR/371	0.39	0.20	
RV, RT/SIR/374	0.39	0.19	
C, RT/SIR/372	0.39	0.19	0.18
LV, RT/SIR/373	0.39	0.20	

Distribution.-This species has been recorded from the Malacca Straits (Whatley & Zhao, 1987), Jason Bay off the NE Coast of Malaya (Zhao & Whatley, 1989) and from St. Pierre Harbour, Reunion Island, Indian Ocean (Whatley & Keeler, 1989). Present study samples: 2, 29, 30, OS6, Guadalcanal and Shortland islands.

Remarks.-This is a very distinctive species of *Leptocythere* strongly reticulate, with a broad anterior submarginal, ocular ridge; the anterior vestibule absent but a posterior vestibule may be present; rpc few, very complex and branching. It differs from the other species of *Leptocythere* encountered in that the inner lamella and marginal pore canals resemble *Callistocythere* but an anterior vestibule is absent, while the hinge and muscle scar pattern resemble *Leptocythere*. The ornament is also unusual; however, this strong ornament is also seen in some species of *Leptocythere* described by Maybury & Whatley (1981), from the Pliocene of Cornwall and Brittany and *L. posterobursa* (Doruk) from the Upper Miocene of Turkey. The present species resembles *L. foveata* (Hartmann, 1953), Recent, from Southern France; the reticulate ornament of the former, however, is more strongly developed. Among the present fauna, two distinct ornamental morphotypes occur, just as they did in the type material described by Zhao & Whatley (1989) from Jason Bay. The most common forms are those with rounded or oval puncta (Pl. 1, Figs 12 & 13 and Pl. 1, Fig. 7 in Zhao & Whatley, 1989). Less common are those with cribrose puncta (Pl. 1, Figs 15 & 17 and Pl. 1, Figs 5 & 6 in Zhao & Whatley, 1989).

Leptocythere rokuaiensis sp. nov.
(Fig. 4, Nos 3-4; Pl. 1, Figs 20-26)

Derivatio nominis.-L. With reference to the type locality, near Rokuai Island off the northeast coast of Shortland Island, Solomon Islands.

Holotype.- LV, RT/SIR/362.

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

Material.-10 adult valves and carapaces.

Diagnosis.-A species of *Leptocythere* with a delicately reticulate ornament of randomly arranged, polygonal fossae posteriorly with a distinct secondary reticulate ornament developed within primary fossae posteriorly but which dominate the ornament anteriorly; muri smooth. Anterior marginal rib dividing above mid-height into 2 subparallel ribs. Posterior sub-marginal rib continues a short distance parallel to ventral margin.

Description.-Medium. Moderately thick-shelled. Opaque. Subrectangular in lateral view; subelliptical in dorsal view. Anterior margin broadly rounded with extremity rather below mid-height. Posterior margin narrower, bluntly rounded. Dorsal margin gently arched: anterior cardinal angle rounded; posterior angle obtusely rounded. Ventral margin gently biconvex about broad oral concavity. Greatest length at mid-height; greatest height just posterior to anterior cardinal angle; greatest width median. LV slightly larger than RV, small overlap at cardinal angles. Valves with a very slight median constriction and posteroventral inflation. Posterior ornament of randomly arranged polygonal reticulae with a strong secondary reticulate ornament within fossae; murae smooth. Secondary ornament becoming dominant anteriorly. Anterior submarginal rib divided just above mid-height, 2 branches continue subparallel to anterior margin. Posterior rib distal but subparallel to margin, continues ventrally for a short distance. Npcs few, small, regularly distributed. Inner lamella wide: inner margin sub-parallel to outer margin; LOC diverges from inner margin forming a narrow, crescentic anterior vestibule and even narrower posteroventral vestibule. Rpcs branching, majority into 3 or 4, 31-33 branches anteriorly; 25-27 posteriorly. Selvage peripheral arched over "snap-knob" structure orally. Hinge modified entomodont, typical of genus but rather feebly developed. Central muscle scars comprise a vertical row of 4 adductor scars, dorsal and ventral scars ovate, median scars dumb-bell shaped and frontal scar possibly v-shaped.

Dimensions.-	Length	Height	Width
Holotype LV, RT/SIR/362	0.59	0.30	
Paratype C, RT/SIR/360	0.59	0.29	0.23
Paratype C, RT/SIR/361	0.59	0.30	0.23
Paratype RV, RT/SIR/363	0.58	0.30	
LV, RT/SIR/364	0.56	0.28	
C, RT/SIR/365	0.58	0.29	0.23

Distribution.-Samples: 5, 16, OS6, Guadalcanal and Shortland islands.

Remarks.-This species is most similar to *L. foveoreticulata* (McKenzie) 1982. They differ in surface ornament in that in the present species the primary, polygonal fossae are weakly developed anteriorly, the secondary reticulate ornament being dominant and the valves are slightly inflated posteroventrally. It is possible that only females of the present species were found, as sexual dimorphism was not observed.

Leptocythere sp.
(Fig. 4, Nos 5-6; Pl. 2, Figs 21, 22, 24, 25)

Material.-1 adult carapace (opened).

Description.-Medium. Thick-shelled. Opaque. Subrectangular in shape in lateral view: subelliptical in dorsal view. Anterior margin broadly rounded. Posterior margin bluntly rounded. Dorsal margin gently arched: posterior cardinal angle prominent. Ventral margin, gently convex. Greatest length at mid-height; greatest height through anterior cardinal angle; greatest width at posterior third. Small overlap of LV>RV at cardinal angles and along posterior margin. Valves inflated posterodorsally and posteroventrally; strong, prominent, vertical but slightly curved rib-like swelling posteriorly. Surface of valves strongly punctate with irregular, smooth riblets accentuating lateral swellings and very prominent anterior and posterior submarginal ribs. A short, strong ventro-lateral rib terminates at about 2/3 length in a punctate tubercle. Inner lamella wide, inner margin subparallel to outer margin: LOC divergent from inner margin anteriorly forming a broad crescentic anterior vestibulum, posteriorly and ventrally a narrow, irregular vestibulum. Rpcs branching into 2 or 3 canals except anteroventrally where branch into 4 or 5 and anterodiorsally where canals are simple, short and straight: about 30-31 canal branches anteriorly; 23-26 posteriorly. Hinge modified entomodont and typical of genus, but rather feebly developed.

Dimensions.-	Length	Height
LV, RT/SIR/366	0.63	0.33
RV, RT/SIR/367	0.63	0.33

Distribution.- Sample: 56, Guadalcanal.

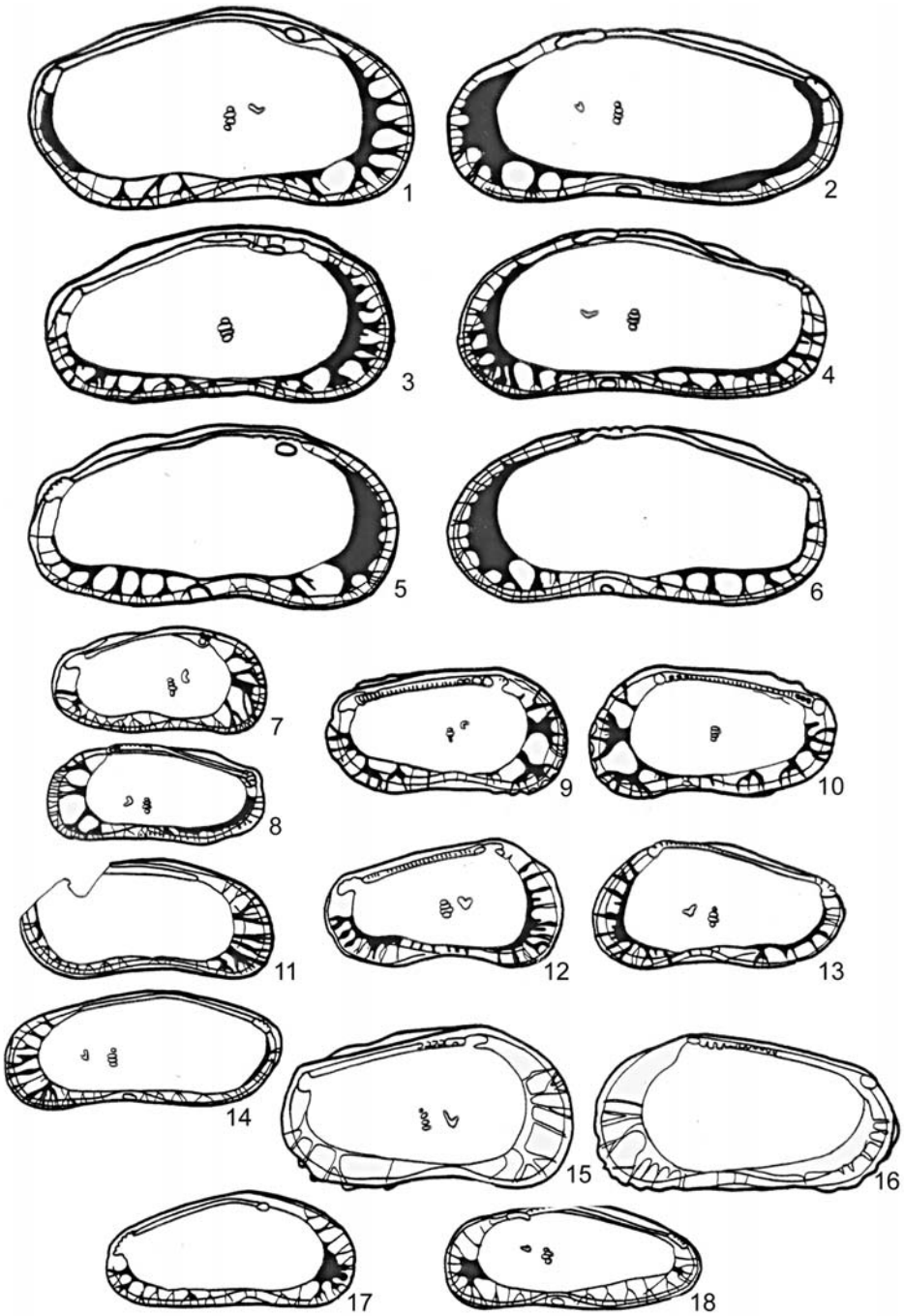


Figure 4. Internal lateral views.*1-2, Leptocythere foveoreticulata* (McKenzie & Sudijono) 1981. *1*, Female left valve RT/SIR/355 x 80.8. *2*, Male right valve RT/SIR/357 x 87.1. *3-4, Leptocythere rokuaiensis* sp. nov., *3*, Holotype left valve RT/SIR/362 x 81.4. *4*, Paratype right valve RT/SIR/363 x 86.2. *5-6, Leptocythere sp., 5*, Left valve RT/SIR/366 x 81.0. *6,* Right valve RT/SIR/367 x 82.5. *7-8, Leptocythere pulchra* Zhao & Whatley, 1989, *7,* Left valve RT/SIR/371 x 74.4. *8,* Right valve RT/SIR/374 x 76.9. *9-10, Callistocythere parakeiji* sp. nov., *9,* Left valve RT/SIR/382 x 86.8. *10,* Right valve RT/SIR/381 x 91.9. *11, 14, Tanella ochracea* (Brady) 1890. *11*, Left valve RT/SIR/402 x 92.1. *14*, Right valve RT/SIR/399 x 84.4. *12-13, Callistocythere punctatuberculata* sp. nov., *12,* Left valve RT/SIR/388 x 91.7. *13,* Paratype right valve RT/SIR/386 x 97.2. *15-16, Callistocythere scripta* sp. nov., *15*, Left valve RT/SIR/395 x 105.3. *16*, Right valve RT/SIR/396 x 110.5. *17-18, Tanella striatopunctata* sp. nov., *17*, Holotype female left valve RT/SIR/411 x 95.1. *18*, Female right valve RT/SIR/410 x 81.4.

*Remark*s.-The present species differs from *L. rokuaiensis* sp. nov. and *L. pulchra* Zhao and Whatley, 1989 in that the primary surface ornament is punctate rather than reticulate. It is also strongly inflated posterodorsally and posteroventrally and the posterior and anterior submarginal ribs are more strongly developed. The present species is believed to be new but because only a single carapace was found it must be left in open nomenclature.

Genus *Callistocythere* Ruggieri, 1953
Callistocythere parakeiji sp. nov.
(Fig. 4, Nos 9-10; Pl. 2, Figs 14, 19, 20, 23, 26)

1966 *Callistocythere* species JA Maddocks, p. 63, Figs 48, 2a, b.

1986 *Leptocythere keiji* Hartmann. Cabioch, Anglada & Babinot, p. 26, Pl. 8, Figs 9-11.

Derivatio nominis.-L. With reference to the overall similarity in ornament of this species to *Callistocythere keiji* (Hartmann), 1978, from the Recent of Western Australia.

Holotype.-RV, RT/SIR/375.

Type locality and horizon.-Sample 57, 850 feet offshore, east of Point Cruz, Honiara Bay. 8 fathoms, Unconsolidated very fine-grained. Sand. Recent.

Material.-16 valves and carapaces, A-1 to adult.

Diagnosis. -A very small species of *Callistocythere* with a surface ornament of strong, irregular ribs forming a rather close reticulate meshwork with deep fossae, which are secondarily micropunctate. Particularly conspicuous is the almost trilobate rib below the posterior cardinal angle. Greatest width of carapace at posterior quarter.

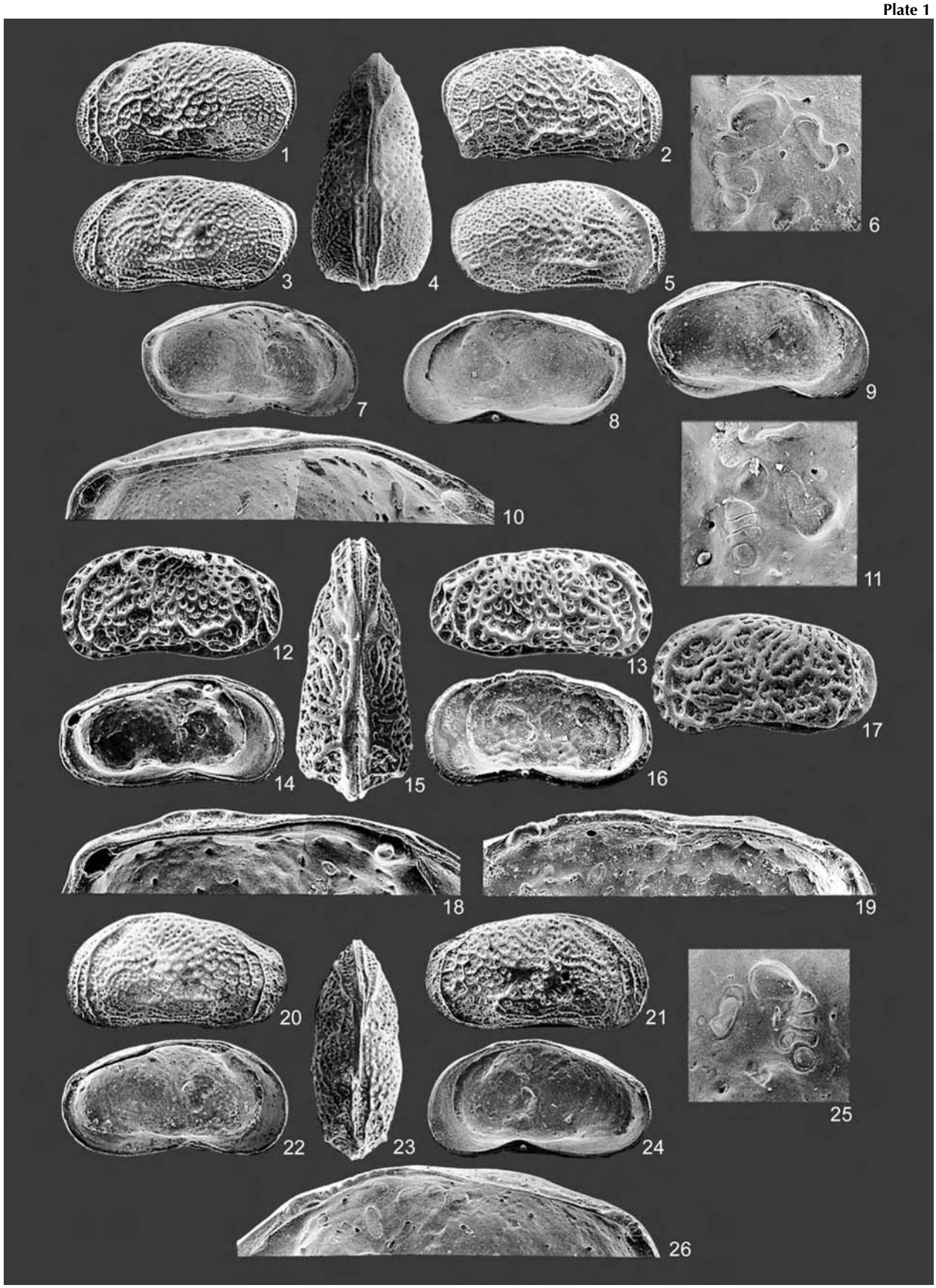
Description.-Very small. Thick-shelled. Opaque. Subquadrate in lateral view: subrectangular in dorsal view. Anterior margin broadly rounded with 7 short, blunt marginal denticles anteroventrally; extremity just below mid-height. Posterior margin narrower, bluntly rounded in RV to subtruncated in LV; extremity at mid-height. Dorsal margin almost straight: cardinal angles obtusely rounded. Ventral margin broadly concave. Greatest length at mid-height; greatest height through anterior cardinal angle; greatest width at posterior quarter. LV> RV, overlap at posterior cardinal angle and on anterior margin. Eye-spot large, obscured by ornament. Valves inflated antero- and posteromedianly. Surface of valves strongly ornamented by irregular ribs forming a rather close reticulate meshwork with deep fossae, which are minutely secondarily punctate. Particularly conspicuous is the almost trilobate rib below the posterior cardinal angle. Some ribs, such as the main subvertical rib in the anterolateral area, are scalloped in parts of their extent. Npcs large, sieve type. Inner lamella broad: LOC and inner margin coincident, subparallel to outer margin. Rpcs few, wide and branching; approximately 6 anterior and 4 posterior canals, widening proximally. "Snap-knob" mechanism developed on flange orally, knob on RV. Hinge pseudoentomodont, robust. Central muscle scars small, sited subcentrally, comprise 4 closely spaced, subovate adductor scars with a large L-shaped frontal scar.

Dimensions.-	Length	Height	Width
Holotype RV, RT/SIR/375	0.39	0.21	
Paratype LV, RT/SIR/377	0.39	0.22	
Paratype C, RT/SIR/376	0.39	0.22	0.19
Paratype RV, RT/SIR/378	0.38	0.22	
Paratype C, RT/SIR/379	0.39	0.23	0.17
Paratype A-1 juv. RV, RT/SIR/380	0.35	0.19	
RV, RT/SIR/381	0.37	0.21	
LV, RT/SIR/382	0.38	0.22	

Plate 1.

1-10, Leptocythere foveoreticulata (McKenzie & Sudijono, 1981), *1, 6, 7, 10,* Female left valve RT/SIR/355, *1,* external lateral view x 60.0. *6,* detail of central muscle scars x 277.8. *7,* internal view x 60.0. *10,* detail of hinge x 153.3. *2,* Female right valve RT/SIR/359, external lateral view x 56.5. *3,* Male left valve RT/SIR/354, external lateral view x 65.6. *4,* Female carapace RT/SIR/353, dorsal view x 67.2. *5, 8,* Male right valve RT/SIR/357, *5,* external lateral view x 62.9. *8,* internal view x 62.9. *9,* Male left valve RT/SIR/356, internal view x 62.5. *11-19, Leptocythere pulchra* Zhao & Whatley, 1989, *11, 14, 18,* Left valve RT/SIR/371, *11,* detail of central muscle scars x 408.6. *14,* internal view x 102.6. *18,* detail of hinge x 215.3. *12,* Left valve RT/SIR/369, external lateral view x 106.8. *13,* Right valve RT/SIR/368, external lateral view x 102.6. *15,* Carapace RT/SIR/372, dorsal view x 120.5. *16, 19,* Right valve RT/SIR/370, *16,* internal view x 100.0. *19,* detail of hinge x 214.1. *17,* Left valve RT/SIR/373, external lateral view x 102.6. *20-26, Leptocythere rokuaiensis* sp. nov., *20,* Holotype left valve RT/SIR/362, external lateral view x 66.1. *21,* Paratype carapace, RT/SIR/361, external lateral view of right valve x 66.1. *22,* Left valve RT/SIR/364, internal view x 67.8. *23,* Paratype carapace RT/SIR/360, dorsal view x 69.6. *24-26,* Paratype right valve RT/SIR/363, *24,* internal view x 67.8. *25,* detail of central muscle scars x 268.1. *26,* detail of hinge x 160.4.

Plate 1



Distribution.-Maddocks (1966) recorded the species from Recent, littoral and sublittoral environments around Nosy Bé, Northern Madagascar. Watson (1988 MS) records it from the Java Sea and Cabioch et al. (1986), from New Caledonia. Present study samples: 1, 2, 14, 17, 19, 29, 30, 42, 57, Guadalcanal.

Remarks.-Specimens of some of the species recorded and illustrated by Maddocks (1966) from the Recent off Nosy Bé, Madagascar, were made available by her to the authors. Of these, *Callistocythere* species JA is conspecific with the present species. The present species is very similar to *Callistocythere keiji* (Hartmann) 1978, from the Recent off Western Australia. The two species differ in details of ornament particularly posterodorsally, and the present species is more quadrate in shape. The present species differs from *Callistocythere scripta* sp. nov. of the present study, in the detail of the surface ornament; the present species possesses a distinctive, almost trilobate rib posterodorsally. *Callistocythere eulittoralis* Hartmann, 1974, from the Recent off Western Africa, *C. purii* McKenzie, 1967, and *Leptocythere* sp. (?*purii*) Hartmann, 1979, both from the Recent eulittoral of Southern Australia, *Leptocythere kaiata* Hornibrook, 1952 from the Eocene of New Zealand and *C. cranekeyensis* (Puri) 1960, of Teeter, 1973, all possess similar ornament to the present species but may be distinguished by detailed examination of that ornament.

Callistocythere punctatuberculata sp. nov.
(Fig. 4, Nos 12-13; Pl. 2, Figs 1-11)

Derivatio nominis.-L. With reference to the conspicuous, punctate tubercles of this species.

Holotype.- LV, RT/SIR/384.

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

Material.-50 valves and. carapaces, A-1 to adult.

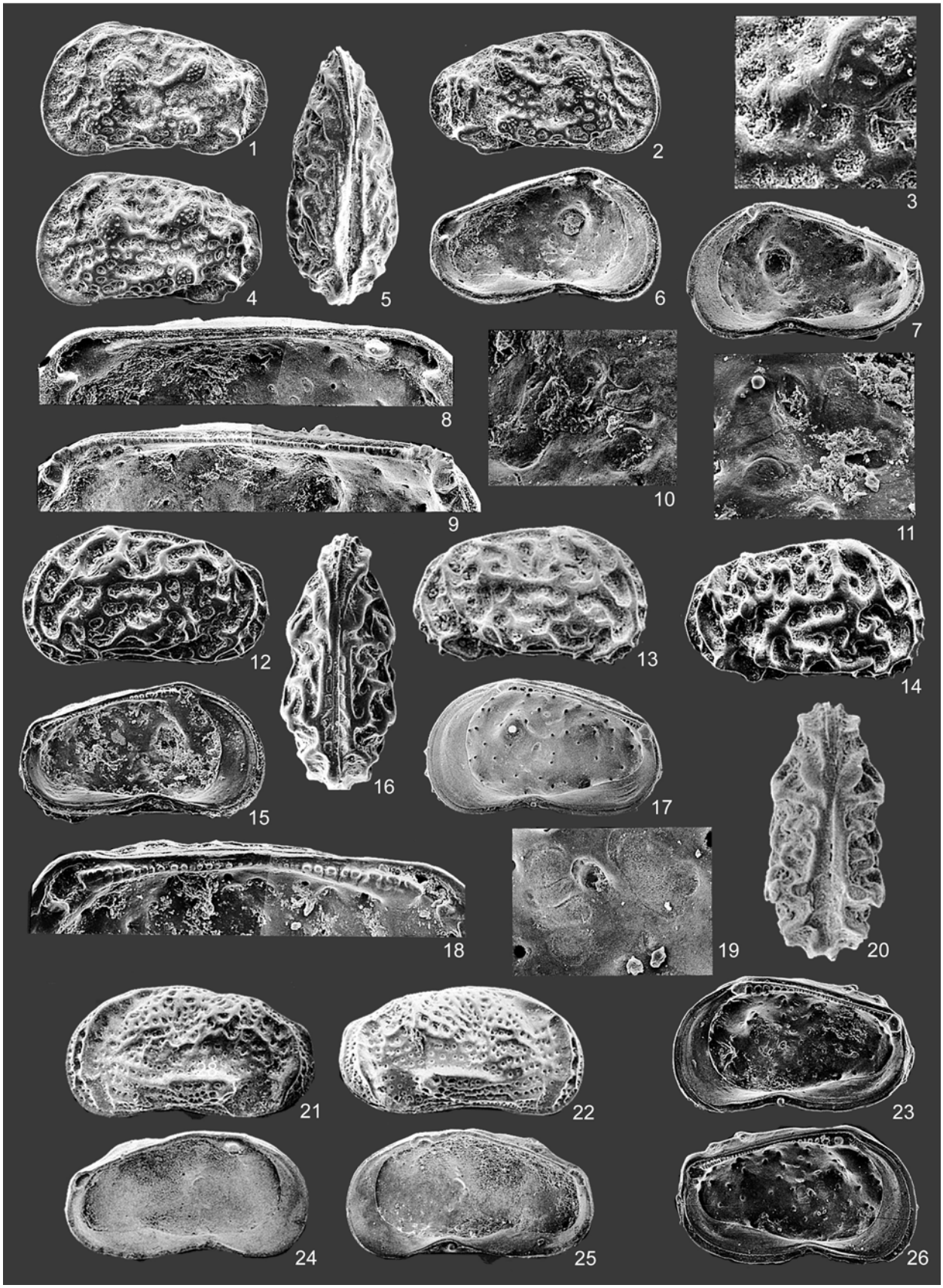
Diagnosis.-A very small species of *Callistocythere* ornamented by small, subovate reticula with 4 or 5 prominent densely punctate lateral tubercles, and an anterior marginal rim like rib. Marginal pore canals few with approximately 12 anterior and 11 posterior canals, some bifurcate. LV anterior median hinge with a single tooth.

Description.-Very small. Thick-shelled. Opaque. Subquadrate in shape in lateral view; subhastate in dorsal view. Male narrower posteriorly. Anterior margin broadly rounded, with apex at mid height in RV but below mid height in LV. Posterior margin narrower, well rounded. Dorsal margin very gently arched, sloping posteriorly; cardinal angles obtusely rounded. Ventral margin concave. Greatest length at mid-height; greatest height through anterior cardinal angle; greatest width at posterior quarter. Valves inflated posteriorly narrowing anteriorly. Eye-spot inconspicuous. Surface of valves reticulate; reticulae small, subovate, irregularly distributed; 3, 4 or 5 lateral tubercles, more or less well developed in each individual; 1 tubercle posterodorsally, 1 directly ventral to this, 1 anterior tubercle at about mid-height, a fourth may be present more anterior to and ventral to anterior tubercle and a fifth posteromedianly. Tubercles with a secondary reticulate ornament of small, ovate fossae. A prominent, marginal anterior rim like rib, peripheral in LV; subperipheral in RV. NPCs few, small, evenly distributed. Inner lamella wide: LOC and inner margin, subparallel to outer margin, divergent anteriorly and posteriorly forming narrow crescentic vestibula. Rpcs few: approximately 12 true anterior and 11 posterior canals some bifurcate, wide, slightly sin-

Plate 2.

1-11, *Callistocythere punctatuberculata* sp. nov., *1,* Paratype left valve RT/SIR/385, external lateral view x 108.1. *2,* Paratype right valve RT/SIR/386, external lateral view x 113.9. *3, 4,* Holotype left valve RT/SIR/384, *3,* detail of lateral ornament x 332.8. *4,* external lateral view x 102.6. *5,* Paratype carapace RT/SIR/383, dorsal view x 127.8. *6, 8*, Left valve RT/SIR/388, *6,* internal view x 117.1. *8,* detail of hinge x 239.2. *7, 9, 10*, Right valve RT/SIR/387, *7,* internal view x 116.7. *9,* detail of hinge x 251.0. *10,* detail of central muscle scars x 493.8. *11-13, 15-18, Callistocythere scripta* sp. nov., *11, 15, 18,* Paratype left valve RT/SIR/391, *11,* detail of central muscle scars x 538.6. *15,* internal lateral view x 115.8. *18,* detail of hinge x 284.0. *12,* Holotype carapace RT/SIR/390, external lateral view of left valve x 115.8. *13,* Right valve RT/SIR/393, external lateral view x 105.1. *16*, Paratype carapace RT/SIR/389, dorsal view x 121.6. *17,* Paratype RT/SIR/392, internal view x 113.5. *14, 19, 20, 23, 26, Callistocythere parakeiji* sp. nov., *14*, Holotype right valve RT/SIR/375, external lateral view x 107.7. *19, 23*, Paratype left valve RT/SIR/377, *19,* detail of central muscle scars x 505.1. *23,* internal view x 113.2. *20,* Paratype carapace RT/SIR/379, dorsal view x 117.9. *26,* Right valve RT/SIR/378, internal view x 110.3. *21, 22, 24, 25*, *Leptocythere* sp., *21, 25*, Left valve RT/SIR/366, *21,* external lateral view x 69.8. *25,* internal lateral view x 68.3. *22, 24*, Right valve RT/SIR/367, *22,* external lateral view x 69.0. *24,* internal lateral view x 68.3.

Plate 2



uous, short, simple, straight in oral region. "Snap-knob" formed by outer margin of RV orally; complementary socket in LV. Hinge modified pseudoentomodont, with single anterior tooth on median element of LV. Central muscle scars situated subcentrally; 4 small, subovate, closely spaced adductor scars in vertical row; v-shaped frontal scar open dorsally, anterior arm shortest.

Dimensions.-	Length	Height	Width
Holotype LV, RT/SIR/384	0.39	0.23	
Paratype C, RT/SIR/383	0.36	0.22	0.17
Paratype L, LT/SIR/385	0.37	0.22	
Paratype RV, RT/SIR/386	0.36	0.20	
RV, RT/SIR/387	0.35	0.19	
LV, RT/SIR/388	0.36	0.22	

Distribution.-Watson (1988 MS) records this species from the Java Sea. Present study samples: 1, 2, 13, 14, 17, 19, 30, 55-58, Guadalcanal.

Remarks.-The present species differs from *C. parakeiji* sp. nov. and *C. scripta* sp. nov. of the present study in that the rpcs are less polyfurcate and, unlike most species of *Callistocythere*, the LV possesses only a single anterior tooth of the median element of the hinge. This species is probably closely related to *C. dorsotuberculata* Hartmann, 1979, Recent, Southern Australia, which also possesses lateral tubercles in similar positions, a similar hinge, muscle scar pattern and ventral "snap-knob" mechanism but differs considerably in detail of the ornament. Other species with similar lateral tubercles are *C. crenata* (Brady) 1890, illustrated by Holden, 1976, from the Miocene to Pleistocene of Midway Island and a morphological variety of *C. hartmanni* McKenzie, 1967 illustrated by Hartmann (1981) Recent, eastern Australia. The lateral tubercles observed may be phenotyoic. Three tubercles, 1 anteromedianly, 1 posterodorsally and 1 posteroventrally, are present in all but may vary in strength of development. Strongly developed tubercles are reflected by a depression internally. Other specimens possess four or five tubercles. Tubercles seem to be symmetrical on both valves of the same individual. Individuals with 3 and those with more than 3 tubercles may occur in the same sample.

Callistocythere scripta sp. nov.
(Fig. 4, Nos 15-16; Pl. 2, Figs 11-13, 15-18)

Derivatio nominis.-L. With reference to the resemblance of the surface ornament to primitive writing.

Holotype.- C RT/SIR/390.

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

Material.-56 valves and carapaces, A-1 to adult.

Diagnosis.-A very small species of *Callistocythere* characterised by a strong ornament of irregular ribs forming an open meshwork somewhat resembling primitive written script and with deep fossae. The most conspicuous rib extends laterally, dorsal to mid-height, becoming inflated where other ribs meet it. Greatest width at posterior third.

Description.-Very small. Thick-shelled. Opaque. Sexual dimorphism not observed. Subquadrate in shape in lateral view: subelliptical in dorsal view. Anterior margin broadly rounded with 7 blunt marginal denticles anteroventrally. Posterior margin narrower, almost angularly rounded with 3 blunt marginal denticles posteroventrally. Dorsal margin straight, overhung by ornament so appears gently arched in lateral view: cardinal angles obtusely rounded. Ventral margin biconvex about strong oral concavity. Greatest length at mid-height; greatest height through anterior cardinal angle; greatest width at posterior third. LV > RV, slight overlap at cardinal angles. Eye-spot obscured by lateral ribs. Valves gently inflated antero- and posteromedianly. Surface of valves strongly inflated by irregular ribs forming an open meshwork somewhat resembling primitive written script, and with deep fossae. The most conspicuous rib extends laterally, dorsal to mid-height and becomes inflated where other ribs meet it. Inner lamella broad: LOC and inner margin coincident, subparallel to outer margin. Rpcs few, broad: approximately 6 anteriorly and 5 posteriorly, widening proximally and branching distally. "Snap-knob" mechanism present in oral concavity, knob developed in RV. Hinge pseudoentomodont: RV anterior and posterior terminal elements a polygonal boss; median element a bar dorsally with locellae ventrally which increase in size anteriorly and posteriorly and are open ventrally. Central muscle scars comprise a vertical row of 4 small, ovate adductor scars with a large, almost

L-shaped frontal scar; deep fulcral point between dorsal 2 adductor scars and frontal scar.

Dimensions.-	Length	Height	Width
Holotype C, RT/SIR/390	0.38	0.20	0.17
Paratype LV, RT/SIR/391	0.38	0.21	
Paratype C, RT/SIR/389	0.37	0.20	0.17
Paratype RV, RT/SIR/392	0.37	0.20	
RV, RT/SIR/393	0.39	0.22	
LV, RT/SIR/394	0.36	0.20	
LV, RT/SIR/395	0.38	0.21	
RV, RT/SIR/396	0.38	0.21	

Distribution.-This was the most abundant species recorded by Williams (1980 MS) in Quaternary brackish water sediments from the Indespensable Reefs but it did not occur in the offshore Quaternary marine sediments from Guadalcanal. Watson (1988 MS) also records this species from the Java Sea. Present study samples: OS3, OS5, OS6, Shortland Island.

Remarks.-The present species, like *Callistocythere parakeiji* sp. nov., can be distinguished from other species of the genus by the detail of the ornament. The most conspicuous rib of the present species extends laterally; dorsal to mid-height, becoming swollen where other ribs meet it. The only species known to the authors than resembles this species is *Callistocythere* sp. C. of Jellineck (1993) from the coast of Kenya. The resemblance is superficial, however, as there are many differences in the ornamentation when the two species are compared in detail.

Genus Tanella Kingma, 1948

Remarks.-McKenzie (1982) discussed the problems of the diagnosis of this genus which had arisen because of inadequate illustration and/or description of the type material. He suggested that *Tanella* should be confined to the tropical and subtropical Indopacific. Species assigned to *Tanella* which have been described from the Caribbean probably belong to *Mesocythere* Hartmann, 1956 or *Minicythere* Ornellas, 1974. The present authors consider *Mesocythere*, which was established on soft parts, to be synonymous with *Tanella*. The type species of the genus, *T. gracilis* Kingma, is very variable and, as Witte (1993) has demonstrated, many subspecies of *T. gracilis* and several species of *Tanella* should be subsumed within the type species. Keij, 1979 figured a lectotype of *T. gracilis* from the Indonesian Pliocene, illustrating the characteristic shape and reticulo/costate ornament. *Tanella gracilis*, notwithstanding the occurrence of a number of morphotypes, occurs in the Pacific, Indian and Atlantic oceans and also in the Caribbean. However, the three species that occur in the Solomon Islands seem to fall beyond the limits of size, shape and ornament that would allow them to be considered variants of *T. gracilis*.

Tanella ochracea (Brady), 1890
(Fig. 4, Nos 11-14; Pl. 3, Figs 1-10)

1890 *Cythere ochracea* Brady, p. 498, Pl. 2, Figs 8, 9.

1986 *Tanella ochracea* (Brady). McKenzie, Pl. 1, Fig. 17 (lectotype).

Material.-10 adult valves and carapaces.

Dimensions.	Length	Height	Width
C, RT/SIR/397	0.46	0.20	0.20
C, RT/SIR/398	0.45	0.19	0.19
RV, RT/SIR/399	0.45	0.20	
RV, RT/SIR/400	0.47	0.20	
LV, RT/SIR/401	0.43	0.19	

Distribution.-Brady (1890) described the species from Noumea and Watson (1988 MS) records it in the Java Sea. In the present study it occurs only in Honiara Bay, Guadalcanal.

Remarks.-The present species is a member of the *T. gracilis* group but is more elongate and reniform in shape, has much more delicate ornament in which, while the anterior ribs are of a similar pattern, the nature and distribution of the reticulation and of the posterior ribs, is very different. *Tanella gracilis* is highly variable in surface ornament. Hartmann, 1981 illustrated three morphotypes, one of which is *T. gracilis* morphotype 3 and may represent a halfway point between *T. gracilis* and *T. ochracea*.

Tanella striatopunctata sp. nov.
(Fig. 4, Nos 17-18; Pl. 3, Figs 11-24)

Derivatio nominis.-L. with reference to the nature of the surface ornament of longitudinal ribs with intercostal puncta.

Holotype.- Female LV, RT/SIR/411.

Type locality and level.-Sample 40, 5,100 feet offshore east of Point Cruz, Honiara Bay. 20 fathoms. Unconsolidated, medium-grained sand. Recent.

Material.-34 valves and carapaces, A-2 to adult.

Diagnosis.-A species of *Tanella* with an ornament of oblique lateral ribs with parallel intercostal puncta arranged usually in single rows. Lateral ribs merge or end anteriorly and posteriorly where submarginal ribs are developed almost at right angles.

Description.-Small, moderately thick-shelled. Opaque. Sexual dimorphism conspicuous; female more laterally inflated, broader posteriorly and slightly larger than male. Elongate, subrectangular in lateral view; subelliptical in dorsal view. Anterior margin broadly rounded, becoming obliquely sloping anterodorsally; extremity just below mid-height. Posterior margin narrower, male narrower than female; margin bluntly rounded in female, obliquely sloping posteroventrally in male; extremity at mid-height. Dorsal margin gently arched; anterior cardinal angle rounded, posterior angle obtusely rounded. Ventral margin almost straight with broad oral concavity. Greatest length at mid-height; greatest height just anterior of mid-length; greatest width median in male, just posterior of mid-length in female. LV slightly larger than RV, with overlap at anterior cardinal angle and on posterior margin. Eye tubercle absent. Valve surface strongly ornamented by a series of longitudinal ribs with distinct intercostal reticulation. Lateral ribs merge or end towards anterior and posterior where they are cut off by marginal ribs extending at right angles. A submarginal anterior rib extends from the anterior cardinal angle to the anteroventral angle. A strong posterior rib develops dorsally from a lateral rib and curves to extend straight and obliquely, some distance from posterior margin and continues as a lateral rib parallel to ventral margin, not quite meeting anterior rib. Intercostal reticulae subovate, deep, usually 1 row between ribs, but two parallel rows occur where the distance between ribs increases. A broad rim of reticulae occurs anteriorly and posteriorly. Inner lamella wide: inner margin subparallel to outer margin. LOC and inner margin divergent anteriorly forming a subquadrate vestibulum and posteroventrally a small pocket-like vestibulum. Rpcs branching, usually into 2 or 5 canals: about 21 anterior and 16 posterior branches. "Snap-knob" mechanism well developed. Hinge pseudoentomodont. RV anterior terminal element an arched dentate ridge of 4 denticles; median element a long, smooth bar, gently arched anteriorly and straight posteriorly; posterior terminal element an arched dentate ridge of 5 denticles; LV complementary and with a strong ovate tooth anteriorly below median groove, accommodated by arched posterior terminal element of RV. Central muscle scars situated slightly towards anterior, adductor scars on posterior edge of shallow depression, small, subovate, closely spaced on anterior edge of depression a large v-shaped frontal scar, open anterodorsally.

Dimensions.-	Length	Height	Width
Holotype Female LV, RT/SIR/411	0.41	0.20	
Paratype Male C, RT/SIR/403	0.41	0.19	0.15
Paratype Female C, RT/SIR/404	0.43	0.21	0.17
Female C, RT/SIR/405	0.44	0.20	0.19
Female RV, RT/SIR/406	0.43	0.20	
Male LV, RT/SIR/407	0.42	0.19	
Paratype Male RV, RT/SIR/408	0.42	0.19	
Male RV, RT/SIR/409	0.42	0.19	
Female RV, RT/SIR/410	0.43	0.20	

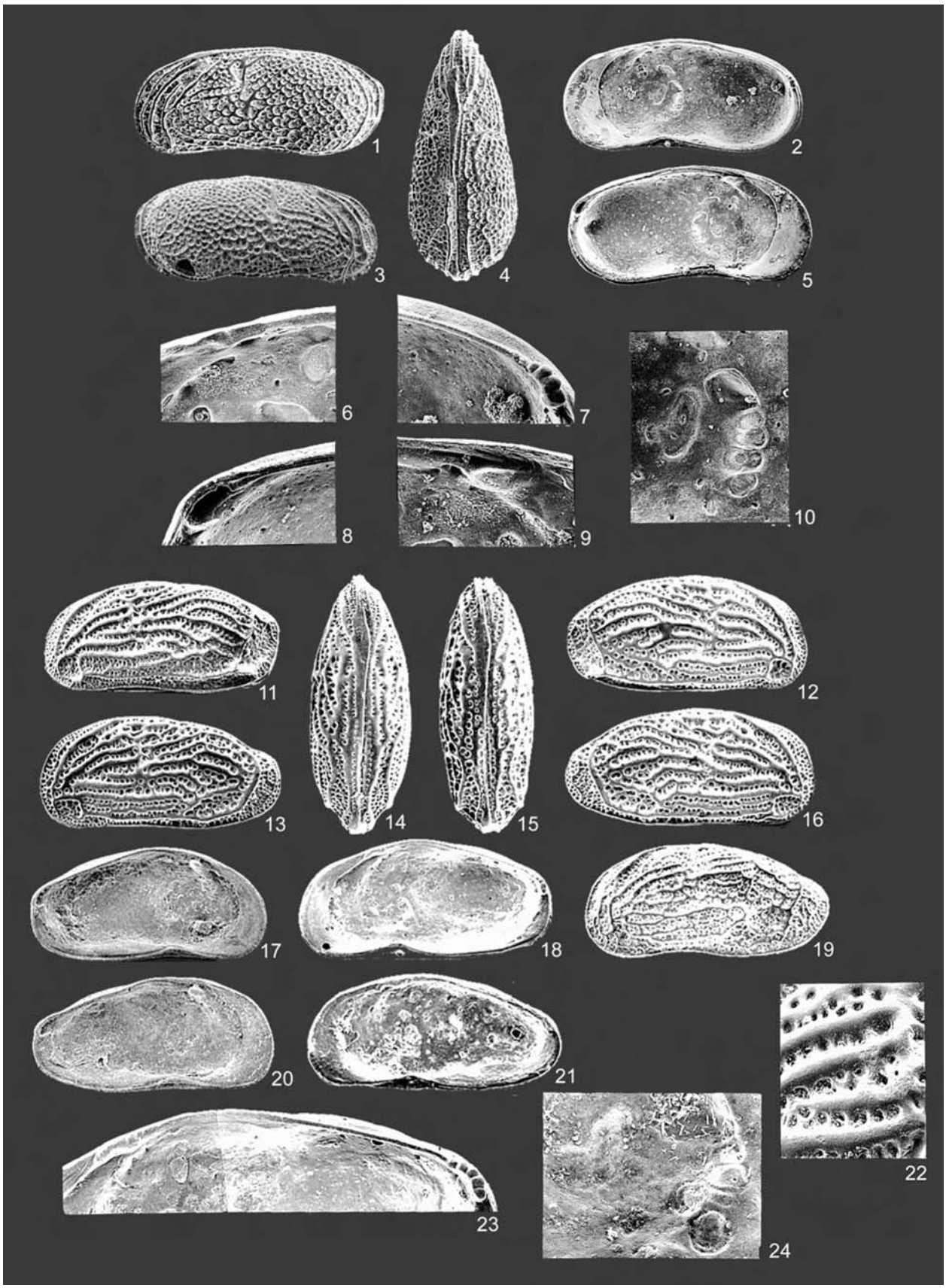
Distribution.-Samples: 5, 13-15, 40, 41, 53, 55-58, Guadalcanal.

Remarks.-The present species possesses a distinctive ornament of oblique lateral ribs with intercostals puncta.

Plate 3.

1-10, Tanella ochracea (Brady), 1890, *1, 2, 5-10* Carapace RT/SIR/398, *1,* external lateral view of left valve x 98.9. *2,* internal view of right valve x 94.4. *5,* internal view of left valve x 97.8. *6,* detail of right anterior hinge x 369.0. *7,* detail of right posterior hinge x 372.2. *8,* detail of left anterior hinge x 364.7. *9,* detail of left posterior hinge x 356.3. *10,* detail of central muscle scars x 378.4. *3*, Carapace RT/SIR/400, external lateral view of right valve x 91.5. *4,* Carapace RT/SIR/397, dorsal view x 95.7. *11-24, Tanella striatopunctata* sp. nov., *11*, *22,* Female carapace RT/SIR/405, *11,* external lateral view of left valve x 95.5. *22,* detail of lateral ornament x 338.6. *12*, Female right valve RT/SIR/406, external lateral view x 101.2. *13,* Male left valve RT/SIR/407, external lateral view x 102.4. *14,* Female carapace RT/SIR/404, dorsal view x 107.0. *15,* Male carapace RT/SIR/403, dorsal view x 109.8. *16,* Paratype, male right valve RT/SIR/408, x 104.8. *17,* Female left valve RT/SIR/411, internal view x 102.4. *18, 23, 24,* Female right valve RT/SIR/410, *18,* internal view x 104.7. *23,* detail of hinge x 229.0. *24*, detail of central muscle scars x 314.5. *19,* A-1 left valve RT/SIR/412 external lateral view x 113.2.*20,* Male left valve RT/SIR/407 internal view x 102.4. *21*, Male right valve RT/SIR/409 internal lateral view x 107.1.

Plate 3



Apart from the ornament this species can be distinguished from *T. ochracea* by its shape, in being narrower and more bluntly rounded posteriorly and in the presence of an anterior vestibule.

3. ACKNOWLEDGEMENTS

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The distribution of foraminifera in surface sediments of the Clyde River Estuary and Bateman's Bay (New South Wales, Australia)

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Abstract

Foraminifera were analysed in 32 samples collected from surface sediments of the Clyde River Estuary and Bateman's Bay, NSW, Australia. Six foraminiferal assemblages have been recognised, two of which are likely to represent local geomorphological factors, including a tidal-delta front. The remaining assemblages appear to reflect downstream increase in salinity, from low salinity *Ammonia beccarii* dominated assemblages, to a more diverse higher salinity (normal marine) *Elphidium* spp. dominated assemblage in the bay. The recognition of these assemblages offers potential for reconstructing Holocene estuary development, and for distinguishing the mode of emplacement of high-energy deposits that may be due to tsunami or storm events.

Keywords: Benthic Foraminifera, Recent, Estuary, New South Wales, Australia

Resumen

Se analizaron 32 muestras de foraminíferos recogidas en sedimentos superficiales del estuario del Río Clyde y en la Bahía de Bateman (Nueva Gales del Sur, Australia). Se han reconocido seis asociaciones de foraminíferos, de las cuales dos parecen reflejar factores geomorfológicos, incluido un frente deltaico mareal. El resto de las asociaciones parecen indicar un incremento de la salinidad, desde la asociación con *Ammonia beccarii* de baja salinidad, hasta una salinidad mayor (de tipo marino normal) dominada por *Elphidium* spp. El conocimiento de estas asociaciones permite la reconstrucción del desarrollo del estuario durante el Holoceno, así como la carecterización de depósitos de alta energía debidos probablemente a tsunamis o tormentas.

Palabras clave: Foraminíferos bentónicos, Reciente, Estuario, Nueva Gales del Sur, Australia

1. INTRODUCTION

The evolution of estuaries, embayments and deltas along the southeast coast of Australia is currently a subject of debate. Some authors state that coastal evolution here is dominated by gradual processes of wave and tidal deposition (*e.g.* Umitsu *et al.,* 2001), whilst other authors suggest that catastrophic events, such as tsunami, have strongly influenced coastal development (*e.g.* Bryant *et al.,* 1996; Bryant, 2001). Discriminating between these two modes of coastal development is difficult, but has been addressed in some cases by developing sedimentological techniques, such as using parameters of boulders moved by waves, to establish the likely mode of transport, whether storm wave or tsunami (Bryant, 2001). The potential exists to use other forms of evidence to help establish causal mechanisms, such as the analysis of finer sediment and also microfossils preserved in the sediment. The latter may be particularly useful as certain microfossil species indicate quite specific ecological requirements

(Haslett, 2002) that enable sediment provenance and transport pathways to be deduced (Haslett *et al*., 2000). For example, foraminifera are wholly marine organisms that possess quite robust tests that may often be preserved, and when displaced are able to indicate provenance and transport of the sediment from which they have been recovered. It would be expected that sediments deposited onshore by tsunami or storms might contain species from beyond the immediate coast, however, in order to use foraminifera in this way, their distribution in the modern coastal environment needs to be established.

The purpose of this study is to provide a preliminary map of the distribution of foraminifera taxa in a major estuary/bay complex along the New South Wales coast that has not previously been investigated. Recently, a number of other studies of Holocene nearshore foraminifera in Australia have been undertaken, including Haslett (2001), Wang and Chappell (2001), Cann *et al*. (2002), Horton *et al*. (2003), and Woodroffe *et al*. (2005), and the present study contributes to this growing database but along a stretch of the coastline not yet investigated. The study area comprises the Clyde River Estuary and Bateman's Bay, where Bryant (2001) has identified onshore deposits that he suggests may have been deposited by tsunami. Foraminifera have been recovered from samples of these suspected tsunami deposits (S. K. Haslett and D. M. Everett, unpublished data), but it is not known whether the species encountered normally inhabit the estuary (*i.e*. autochthonous) or live on the shelf and have been transported into the estuary (*i.e*. allochthonous), making a high energy event a more likely agent for their deposition.

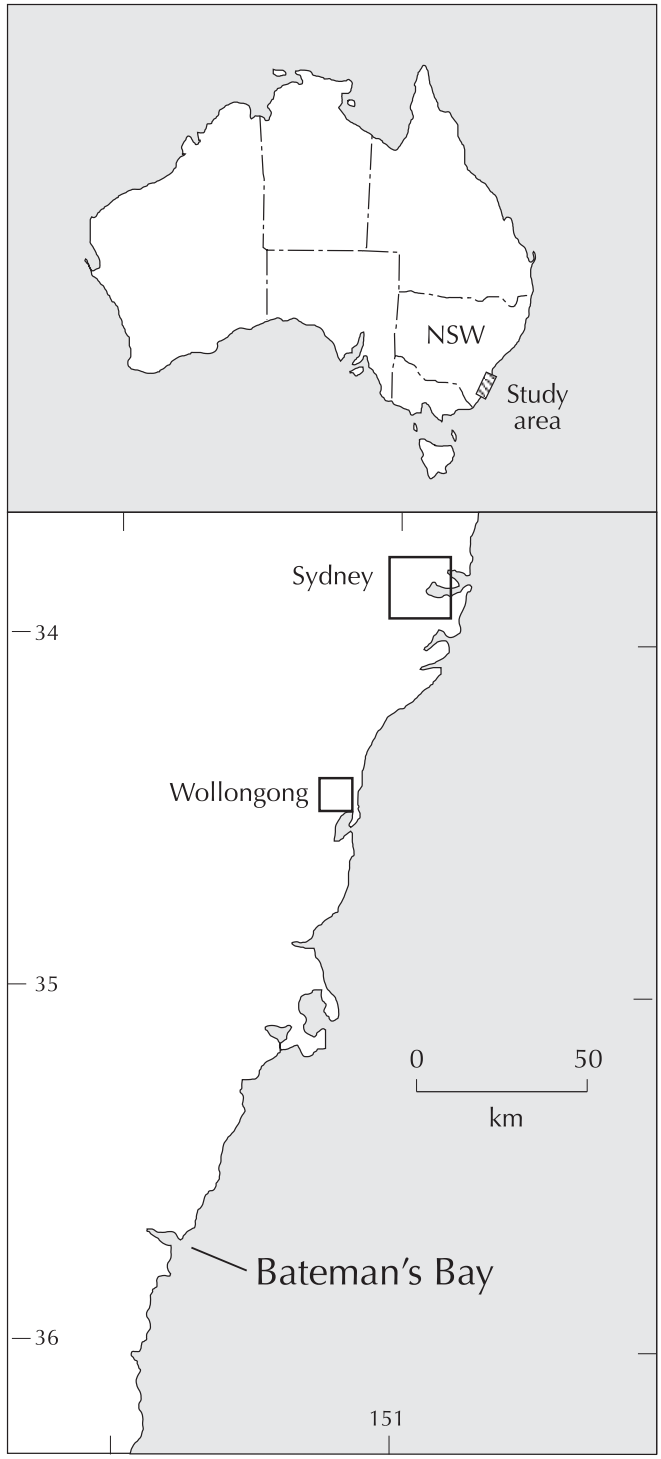

Figure 1. Location of Bateman's Bay in eastern New South Wales (NSW), Australia.

2. REGIONAL SETTING

The Clyde River Estuary and Bateman's Bay are located approximately 215 km south of Sydney along the southeast Australian coastline (Fig. 1). The Clyde River catchment extends from the Southeast Australian Highlands, comprising a major active component in the complex development of the regional landscape (Brown, 2000). The estuary and bay open out into the Tasman Sea in the southwest Pacific Ocean. The coast is generally microtidal, with a mean range of 1.6 m (relatively small tidal prism with minimal tidal currents). Offshore, the continental shelf is deep but relatively narrow, experiencing considerable wave energy, dominated by southeasterly swell with wave periods of 12-16 seconds and a mean wave height of 1-2.5 m. The area experiences

a temperate climate with January mean temperatures of 21ºC, and July means of 11ºC. Mean annual rainfall is 1029 mm, with a range of 690-1660 mm (Umitsu *et al.*, 2001).

3. METHODS

Samples were collected using a boat and grab sampling equipment for the molluscan study by Switzer (2005), who recorded water depth and facies in the field. The sample locations are given in Figure 2. Subsamples of untreated sediment were supplied to the author and processed for foraminifera by washing over a 63 μm sieve and searching the >63 μm fraction under a reflected light microscope. Samples were not stained to distinguish live specimens as some time had elapsed between collection and processing of the sediment. Specimens were dry-picked and are curated in the Quaternary Research Centre at Bath Spa University, UK.

Identification of taxa is based on Yassini and Jones (1995). However, some grouping of genera and species has been performed in order to provide taxonomic counting groups that negate the time-consuming need to identify some specimens to below either suborder or generic levels. These taxonomic counting groups have only been established where, based on Yassini and Jones (1995) and Murray (1991), it is anticipated that little or no environmental information would be lost. Consequences of establishing counting groups include the combination of sometimes rare species to produce higher counts, and the reduction in the number of taxa of a foraminiferal assemblage. The taxonomic counting groups established are defined as follows:

– *Cibicides* group include species in the genera *Cibicides* (*i.e. C. refulgens*) and *Cibicidoides* (mainly *C. floridanus*).

– *Cornuspira* group include species in the genera *Cornuspira* (*i.e. C. foliaceus*) and *Cornuspiroides* (*i.e. C. striatolus*).

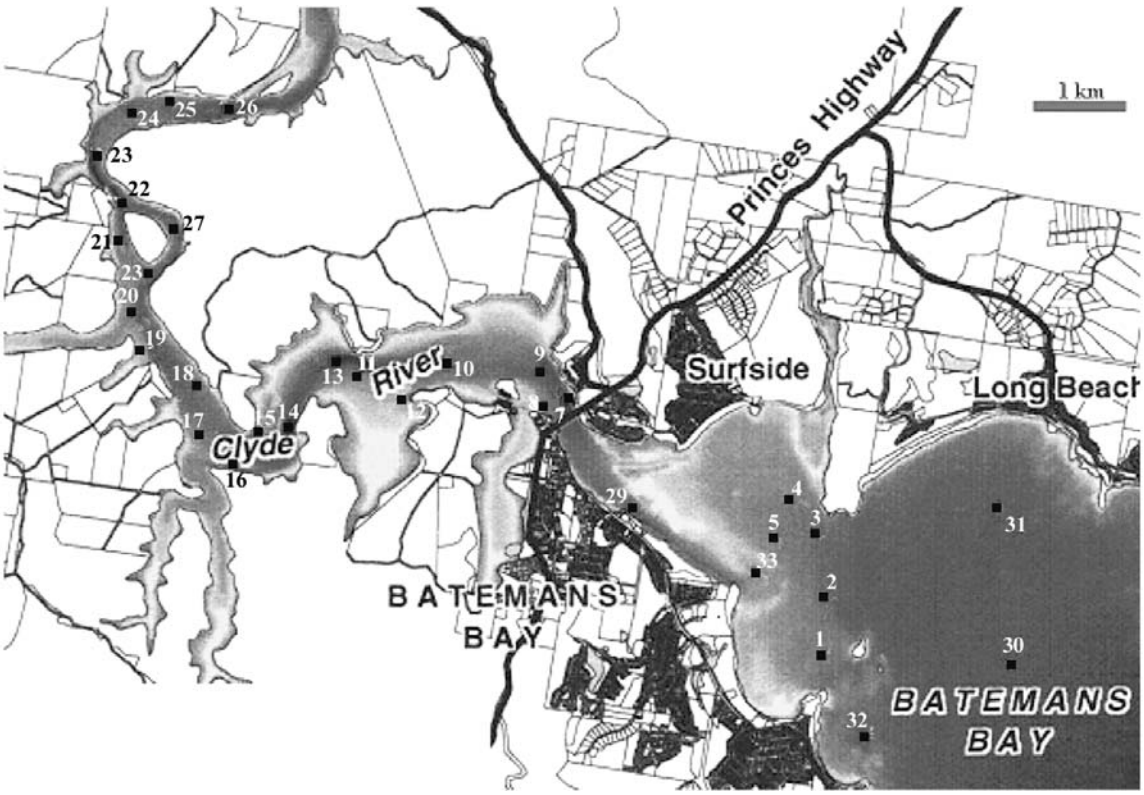

Figure 2. Location of samples in the Clyde River Estuary and Bateman's Bay, New South Wales, Australia (kindly supplied by Adam Switzer).

– *Cribrononion* spp. includes all species in this genus, but mainly *C. simplex* and *C. sydneyensis*.

– *Elphidium* spp. includes all species in this genus, but in this study the main species are *E. crispum*, *E. macellum*, and *E. advenum*.

– *Glabratella-Rosalina* group include all species in these closely-related and ecologically similar genera, mainly *G. australensis*, *G. patelliformis*, *R. australis*, and *R. bradyi*.

– Miliolid group include all species belonging to genera of the Miliolina Families Spiroloculinidae and Hauerinidae, but mainly *Quinqueloculina*.

– Planktonic spp. includes all planktonic foraminifera species, mainly *Globigerina* spp. and *Turborotalia inflata*.

– Other extra-estuarine species include all other taxa encountered that are not estuarine species and do not fall within any of the other taxonomic counting groups.

3.1. Results

The preliminary results are given in Table 1. The % sand (>63μm) data indicate that the estuary-bay system is dominated by sand-grade sediments, with values typically >90% in the estuary, but decreasing to generally <90% in the bay. Although the amount of sediment searched in this preliminary study varies, foraminifera are encountered in the majority of samples, however, a number appear to be barren. The number of specimens picked ranges up to 123 and in some cases is dependent on the amount of sediments searched, however, the concentration of specimens per gram of sediment (total/g) also varies greatly, with the highest concentration being estimated at 2650 per gram. Preservation of foraminifera tests is generally good, however, some specimens do show signs of abrasion. The number of taxa counted per sample (*cf.* diversity) is quite low, with some monospecific assemblages (1 taxon only), but does vary up to a high of nine taxa. *Ammonia beccarii* is the most frequently encountered taxa being found in all but one sample that yielded any foraminifera. *Elphidium* spp. are also widespread, but are more frequent in the more seaward samples. Miliolid group, *Trochulina dimidiata*, *Haynesina depressula*, and *Cibicides* group are also frequently encountered.

4. DISCUSSION

From the preliminary data given in Table 1, fossiliferous samples have been submitted to cluster analysis (CONISS) which identifies difference/similarity between samples based on their microfossil content (Dale and Dale, 2002). The results are plotted in Figure 3 and indicate that six distinct foraminifera assemblages (FA) may be recognised (Table 2) that characterise the various depositional environments present:

– *FA1 - inner estuary assemblage*. This assemblage is represented by six samples (Table 1), five of which did not yield any foraminifera and are preliminarily considered barren. One sample (BBGS-26) yielded an *Ammonia beccarii* monospecific assemblage. The field facies interpretation considered these samples to represent a mixed estuarine/fluvial to estuarine depositional environment, suggesting low salinity at the transition from freshwater to marine conditions. The FA1 characteristics given in Table 2 support this interpretation.

– *FA2 – high energy assemblage*. This assemblage is represented by two adjacent samples collected in a stretch of the estuary that opens upstream, with a sizeable midstream island that bifurcates the flow. Foraminifera are abundant and diverse in this assemblage, and many of the constituent taxa are non-estuarine suggesting transport up-estuary from normal marine conditions during a high energy event, such as a storm (or tsunami). The estuary constricts upstream to this point and it is likely that sudden energy dissipation here (as funnelled flow enters the broader channel) resulted in the deposition of the transported sediment as a bar or delta. *Ammonia beccarii* dominates the assemblage, but five other taxa are also found in the two samples (Tables 1 and 2).

– *FA3 – middle estuary assemblage*. This assemblage is represented by 10 samples, one of which is barren, but all others are dominated by *Ammonia beccarii*. The number of taxa encountered is generally low to moderate, but *Elphidium* spp. occurs in seven of the samples as a subdominant taxa. The two most downstream samples both contain *Elphidium discoidalis multiloculum*, which Yassini and Jones (1995) consider characterise tidal inlet channels. The assemblage is similar to the *Ammonia beccarii* lagoon association of Murray (1991) found elsewhere along the east Australian coast and

Assemblage	Sample	CONISS No.	Water Depth (m)	Facies	>63µm (g)	% sand (>63µm)	Searched weight (g)	% examined	*Ammonia beccarii*	*Cibicides* group	*Cornuspira* group	*Cribrononion* spp.	*Elphidium discoidalis multiloculum*	*Elphidium* spp.	*Glabratella-Rosalina* group	*Haynesina depressula*	*Miliolid* group	*planktonic* spp.	*Trochulina dimidiata*	Other extra-estuarine species	TOTAL	Total/g	Number of species
(upstream)	BBGS-26	1	8,5	Mixed estuarine/fluvial	32,59	93,35	25,17	77,2	3												3	0,12	1
	BBGS-25		8	Mixed estuarine/fluvial	29,93	95,71	1,58	5,3	barren sample												0	0,00	0
	BBGS-24		5	Mixed estuarine/fluvial	38,83	91,26	6,37	16,4	barren sample												0	0,00	0
FA1	BBGS-23		8	Estuarine facies	28,71	92,20	6,08	21,2	barren sample												0	0,00	0
	BBGS-22		11	Estuarine facies (Deep)	37,20	no data	0,91	2,4	barren sample												0	0,00	0
	BBGS-21		6	Estuarine facies	31,41	92,55	6,08	19,4	barren sample												0	0,00	0
	BBGS-27	2	7,5	Estuarine facies	25,53	92,63	0,97	3,8	55	1	1	4	2	32			12		13	3	123	126,80	9
FA2	BBGS-28	3	6	Estuarine facies	31,85	88,69	6,26	19,7	19	1	2	1		7	3				7	1	41	6,55	8
	BBGS-20	4	5	Estuarine facies	15,74	86,20	2,83	18,0	40					10							50	17,67	2
	BBGS-19	5	5	Estuarine facies	46,57	97,80	18,69	40,1	3					1							4	0,21	2
	BBGS-18		6	Estuarine facies	32,14	94,25	8,59	26,7					barren sample								0	0	0
	BBGS-17	6	6,5	Estuarine facies	13,66	81,02	0,38	2,8	18					5		6				4	33	86,84	4
FA3	BBGS-16	7	4	Estuarine facies	21,63	no data	6,21	28,7	1												1	0,16	1
	BBGS-15	8	5	Estuarine facies	27,98	no data	16,14	57,7	2												2	0,12	1
	BBGS-14	9	12	Estuarine facies (Deep)	11,83	61,45	0,04	0,3	96					9		1					106	2650,00	3
	BBGS-12	10	6	Estuarine facies	26,22	89,31	5,93	22,6	7					3							10	1,69	2
	BBGS-11	11	6	Estuarine facies	39,95	96,75	23,88	59,8	38				2	9			1				50	2,09	4
	BBGS-10	12	4	Estuarine facies	27,2	98,16	8,63	31,7	30				2	17		1					50	5,79	4
	BBGS-9	13	8,5	Tidal delta front (flood)	20,18	96,60	12,9	63,9	22												22	1,71	1
FA4	BBGS-8	14	5	Tidal delta front (flood)	34,40	96,09	10,89	31,7	3												3	0,28	1
	BBGS-6	15	3,5	Inner bay facies	14,27	no data	0,46	3,2	1												1	2,17	1
	BBGS-7	16	8	Tidal delta front	45,94	92,10	0,76	1,7	6												6	7,89	1
	BBGS-29	17	10	Channel facies	38,70	86,91	18,2	47,0	14		1	1		2			1		5		24	1,32	6
FA5	BBGS-33	18	7	Tidal delta front (ebb)	43,42	95,58	4,23	9,7	56	5				25			11		3	1	101	23,88	6
	BBGS-5	19	3	Inner bay facies	20,95	87,62	1,82	8,7	4					15		3	7			4	33	18,13	5
	BBGS-4	20	2	Inner bay facies	25,30	90,10	2,01	7,9	7					13			1				21	10,45	3
	BBGS-3	21	6,5	Mid bay facies	19,93	89,73	1,57	7,9	14	8				49			12			8	91	57,96	5
FA6	BBGS-2	22	4,5	Mid bay facies	38,96	no data	0,72	1,8	2	1				5	1	2	8	1	1		21	29,17	8
	BBGS-1	23	3,5	Mid bay facies	48,05	95,30	2,84	5,9	10	1				79					8		98	34,51	4
	BBGS-32	24	11	Outer bay facies	26,10	79,91	5,27	20,2	1					6					2		9	1,71	3
	BBGS-31	25	14	Outer bay facies	3,53	42,53	0,17	4,8						1		2					3	17,65	2
(downstream)	BBGS-30	26	11	Outer bay facies	32,43	no data	0,02	0,1	3					2	8	1	8	1	1		24	1200,00	7

Table 1. Sample details ordered from upstream to downstream (kindly supplied by Adam Switzer), sedimentological and micropalaeontological data, and interpretive foraminifera assemblages (FA). The CONISS No. refers to the sample number used in the cluster analysis and shown in Figure 2.

other western Pacific locations. At these other locations the association indicates shallow water deposition and intermediate salinity.

– *FA4 – tidal delta front assemblage*. This assemblage is represented by four adjacent samples all of which yield a low abundance *Ammonia beccarii* monospecific assemblage. It is unlikely that the low number of taxa indicates low salinity, which might be the usual interpretation. Given the transitional location between middle and outer estuary, and the geomorphological field interpretation as a tidal delta front, it is much more likely that the monospecific assemblage reflects local factors, such as preferential size sorting, concentrating specimens of *Ammonia beccarii*.

– *FA5 – outer estuary assemblage*. This assemblage is represented by two samples in which foraminifera are relatively abundant and diverse. *Ammonia beccarii* dominates, but *Elphidium* spp. is also significant, as are a number of normal marine taxa that occur, including the Miliolid group and *Trochulina dimidiata*. This assemblage is similar to the *Ammonia beccarii* shelf association of Murray (1991), found in locations around the western Pacific coast. This association is indicative of normal salinity and water depths down to 25m, parameters consistent with the outer estuarine environment in question here.

– *FA6 – bay assemblage*. This assemblage is represented by eight samples all yielding *Elphidium* spp., which is the dominant taxa in all but two samples, where the

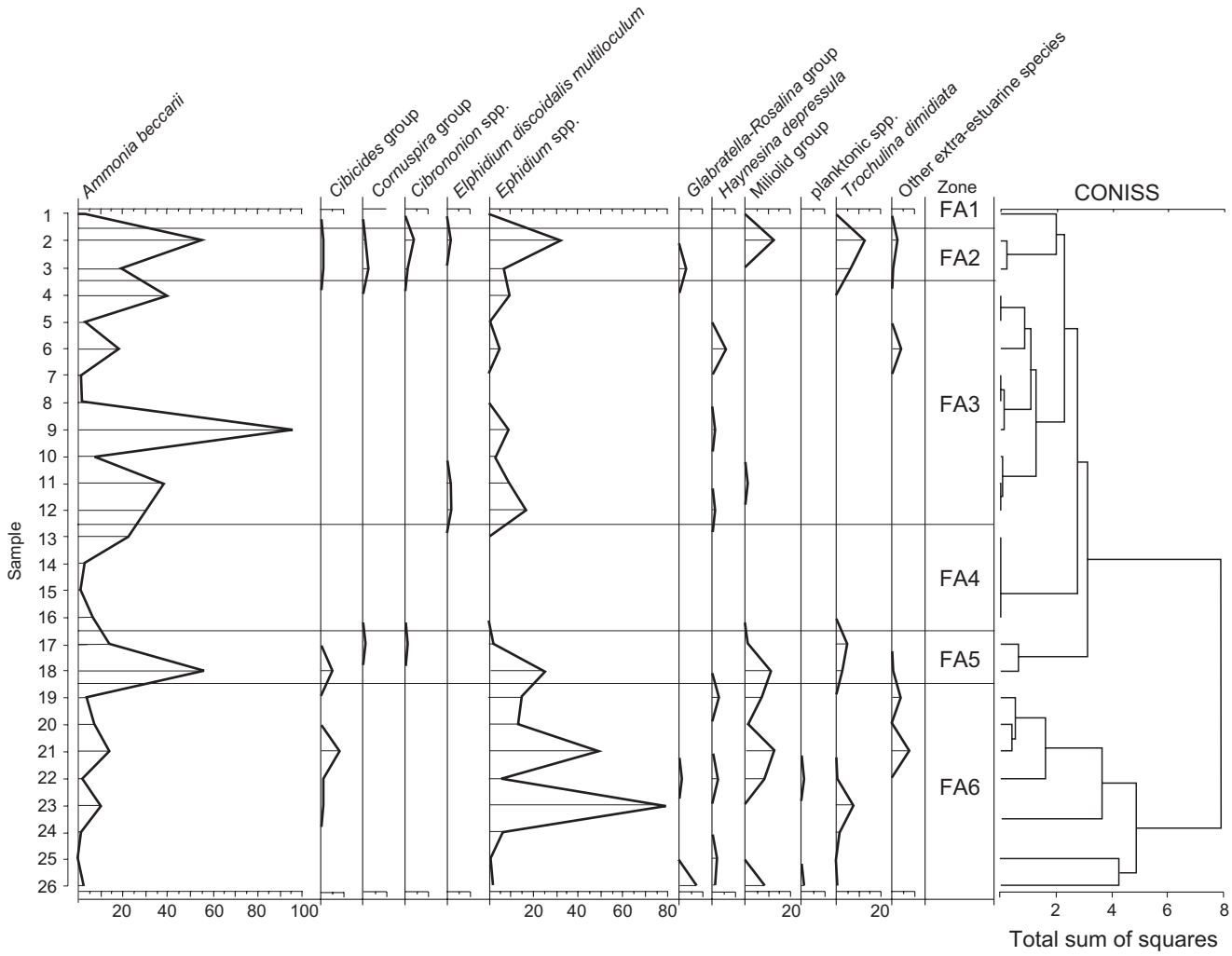

Figure 3. Cluster analysis of fossiliferous samples from Table 1 and assignment of foraminiferal assemblage (FA) zones. The key to the sample numbers are given in Table 1 as CONISS No.

Foraminifera assemblage (FA)	Characteristic taxa	Other important taxa	Diversity range	Murray's (1991) association	Environmental parameters
1 - inner estuary	Barren of foraminifera	*Ammonia beccarii*	0-1	none	<12‰ salinity
2 – high energy	*Ammonia beccarii*	• *Elphidium* spp. • *Trochulina dimidiata* • *Cribrononion* spp. • *Cornuspira* group • *Cibicides* group	8-9	none	Emplacement by storm surge or tsunami (?)
3 - middle estuary	*Ammonia beccarii*	*Elphidium* spp.	0-4	*Ammonia beccarii* lagoon association	• 12-35‰ salinity • 0-15m water depth
4 - tidal delta front	*Ammonia beccarii*	*none*	1	none	not known
5 - outer estuary	*Ammonia beccarii*	• *Elphidium* spp. • Miliolid group • *Trochulina dimidiata*	6	*Ammonia beccarii* shelf association	• 31-35‰ salinity • 0-25m water depth
6 - bay	*Elphidium* spp.	• *Ammonia beccarii* • Miliolid group • *Trochulina dimidiata*	2-5	*Elphidium crispum* association	• 30-35‰ salinity • 0-25m water depth

Table 2. Summary of foraminifera assemblages (FA's) interpreted for the Clyde River Estuary and Bateman's Bay.

Miliolid group dominate. *Ammonia beccarii* also occurs along with a number of normal marine taxa. Foraminifera abundance and the number of taxa encountered are moderate to high. This assemblage is similar to the *Elphidium crispum* association of Murray (1991), encountered at global locations, including the western Pacific. This association is indicative of normal salinity and water depths down to 25m, parameters consistent with the environment of Bateman's Bay.

Of the assemblages established two of them (FA2 and FA4) reflect local geomorphological factors, whereas the remaining assemblages appear to reflect salinity change along the estuary-bay transect, with FA1 representing low salinity (<12‰) and FA6 probably representing normal salinity around 35‰. FA3 and FA5 indicate transitional salinity conditions between these two extremes. It is likely that these salinity controlled assemblages have counterparts in other NSW estuaries. Indeed, Albani (1968) in studying foraminifera from the estuary of Port Hacking near Sydney established that *Ammonia beccarii* occurred throughout the estuary, but that normal marine species, including *Elphidium crispum* and *Trochulina dimidiata*, only occur in the middle to outer parts of the estuary. This correlates well with the downstream shift of dominance from *Ammonia beccarii* to *Elphidium* spp. dominated assemblages in the present study. Therefore, the present study contributes to a developing consistent foraminiferal distribution pattern for NSW estuary-bay depositional environments in Australia and may enable wider comparison with studies in New Zealand (Hayward *et al.*, 2004). Furthermore, in examining beach sand samples from the open NSW coast, Haslett *et al.* (2000) found that these normal marine foraminiferal assemblages were dominated by *Trochulina dimidiata*.

5. CONCLUSION

This preliminary study of foraminiferal distribution in the surface sediments of the Clyde River Estuary and Bateman's Bay indicate that:

1. the depositional environments of the modern estuarine-bay sediments are characterised by six distinct

foraminiferal assemblages, two of which are thought to represent local geomorphological factors only, whilst the others appear to reflect a downstream increase in salinity. Lower salinity assemblages dominated by *Ammonia beccarii* and with low diversity occur upstream, whilst a higher salinity (normal marine) assemblage dominated by *Elphidium* spp. and with higher diversity occurs in the bay;

2. the recognition of these foraminiferal assemblages shows great potential for using foraminifera as palaeoenvironmental tools in reconstructing the evolution of NSW estuaries;

3. the use of foraminifera in distinguishing between onshore sediments deposited by tsunami or storms is greatly advanced, in that it is now known which foraminiferal assemblages occur under normal conditions within the estuary. FA2 reported here appears anomalous and may be due to deposition of sediment high up the estuary during a storm and, therefore, will provide a comparison for future investigations studying high energy sediments.

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New ostracod species from the non-marine Cretaceous of Mongolia

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Abstract

Within the non-marine Cretaceous formations of Mongolia ostracods are one of the most important groups in stratigraphical terms. The following new species of the superfamily Cypridoidea are described: *Trapezoidella hornei* n. sp. from the Shinekhudag Formation (Hauterivian-Barremian), *Ilyocyprimorpha gobiensis* n. sp. from the Khukhteeg Formation (Aptian-Albian), *Talicypridea neustruevae* n. sp. from the Bayanzag/Djadokhta Formation (Coniacian to Santonian) and *Clinocypris solongiinensis* n. sp. from the Baruungoyot Formation (Campanian).

***Keywords*:** Non-marine Cretaceous, Ostracoda, Mongolia, Central Asia

Resumen

Desde el punto de vista estratigráfico, el grupo más importante en las formaciones cretácicas continentales de Mongolia es el de los ostrácodos. Se describen las siguientes especies nuevas de la superfamilia Cypridoidea: *Trapezoidella hornei* n. sp., de la Formación Shinekhudag (Hauteriviense-Barremiense); *Ilyocyprimorpha gobiensis* n. sp., de la Formación Khukhteeg (Aptiense-Albiense); *Talicypridea neustruevae* n. sp., de la Formación Bayanzag/Djadokhta (Coniaciense a Santoniense) y *Clinocypris solongiinensis* n. sp., de la Formación Baruungoyot (Campanianense).

***Palabras clave*:** Cretácico continental, Ostracoda, Mongolia, Asia Central

1. INTRODUCTION

The Cretaceous of Mongolia is unique with regard to its palaeontology, palaeobiogeography and taphonomy, largely because of an unusual abundance of fossilised animal and plant remains in non-marine deposits of varied genesis. These include dinosaurs, mammals, turtles, crocodiles, lizards, birds, fishes, molluscs, phyllopods, insects, plant macrofossils, pollen and spores, and ostracods.

Non-marine Cretaceous deposits are widespread and well developed in southern and southeastern Mongolia (Khand *et al.,* 2000). Ostracods are very abundant within these sediments. The Mongolian Cretaceous is subdivided into eight formations (see Fig. 1). The Lower Cretaceous is composed of the Tsagaantsav (Berriasian-Valanginian), Shinekhudag (Hauterivian-Barremian) and Khukhteeg (Aptian-Albian) formations. The Upper Cretaceous consists of the Baruunbayan (Albian-Cenomanian), Bayanshiree (Cenomanian-Turonian), Bayanzag (= Djadokhta) (Coniacian-Santonian), Baruungoyot (Campanian) and Nemegt (Maastrichtian) formations.

In the mid-1950s the study of Mongolian ostracods started with geological investigations in the southeast of the country in conjunction with petroleum exploration (Galeeva,

System	Series	Stage	Formations in Mongolia
Cretaceous	Upper	Maastrichtian	Nemegt Formation
		Campanian	Baruungoyot Formation
		Santonian ↑ Coniacian	Bayanzag (=Djadokhta) Formation
		Turonian ↑ Cenomanian	Bayanshiree Formation
		Cenomanian ↑ Albian	Baruunbayan Formation
	Lower	Albian ↑ Aptian	Khukhteeg Formation
		Barremian ↑ Hauterivian	Shinekhudag Formation
		Valanginian ↑ Berriasian	Tsagaantsav Formation

Figure 1. Stratigraphic terms of Cretaceous non-marine formations in Mongolia (modified from Khand, 2000).

1955; Lyubimova, 1956). A second period in the study of Mongolian Cretaceous ostracods is connected with the Polish-Mongolian and Mongolian-Russian palaeontological expeditions from the late 1960s to 1971. The findings of the explorations mentioned above resulted in the publication of numerous articles by Polish, Russian and Mongolian scientists (Szczechura & Blaszyk, 1970; Szczechura, 1978, 1982; Neustrueva, 1974, 1977; Stankevitch, 1974; Stankevitch & Khand 1976; Khand, 1974, 1976, 1977, 1979, 2000, 2001, Khand *et al.,* 2003). Detailed studies of shell morphology were conducted on some representatives of Cretaceous and Palaeogene ostracods by the Polish ostracodologist J. Szczechura (1978, 1982). On the basis of all these studies, nine successive assemblages of ostracods have been determined, three of them of Early Cretaceous and six of Late Cretaceous age. The whole fauna comprises 160 species, 45 genera and 3 superfamilies.

During the Cretaceous, representatives of the superfamily Cypridoidea were widespread and common in nonmarine environments, whereas those of the Cytheroidea were less widely distributed and those of the Darwinuloidea comparatively rare. Regarding the evolution of Mesozoic and early Cenozoic nonmarine ostracods of Mongolia, the senior author had previously noticed possible connections between Cretaceous and early Palaeogene lineages (Khand, 2000), postulating Cretaceous ancestry of some modern genera.

2. SYSTEMATIC SECTION

All specimens are housed at the Palaeontological Centre, Mongolian Academy of Sciences (PC, MAS), Ulaanbataar. The degree of curvature of the anterior and posterior margins is described adopting the terminology proposed by Lüttig (1962): "equicurvate" stands for equally rounded, "infracurvate" stands for ventrally more strongly curved, "supracurvate" stands for dorsally more strongly curved. The position of the working area within Mongolia is shown in Figure 2.

Figure 2. Map of Mongolia with geographic position of the working area. The localities lie in the district of Middle Govi (Gobi) within an area south to southwest of Mandalgovi as marked by the dotted rectangle.

Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily CYPRIDOIDEA Baird, 1845
Family TRAPEZOIDELLIDAE Sohn, 1979
Subfamily TRAPEZOIDELLINAE Sohn, 1979
Genus *Trapezoidella* Sohn, 1979

Trapezoidella hornei n. sp.
(Plate 1, Figs. A-B)

Derivation of name.- In honour of the British ostracodologist David John Horne.

Holotype.- N5/300, PC MAS.

Type locality and horizon.- Bayanerkhet, Mongolia (103°30′ N, 46°48′ E); mudstone layers in upper member of Shinekhudag Formation (Hauterivian–Barremian).

Material.-10 complete carapaces.

Dimensions (in mm).-

	N5/300, PC MAS	N5/301, PC MAS
Length:	1.13	1.13
Height:	0.80	0.78

Diagnosis.- Carapace with strongly convex dorsal margin and distinct, gently curved ventrolateral ridges on both valves.

Description.- Carapace large with subtriangular lateral outline. Maximum height at about middle length, maximum length at one third of height. Left valve larger than and overlapping the right one, overreaching it along dorsal margin. Hinge margin gently convex. Anterior margin more broadly rounded than posterior margin. Ventral margin straight to slightly concave at middle length. Both valves with gently curved ventrolateral and smaller ventrodorsal ridges that overreach the ventral carapace in dorsal view. Internal features unknown.

Remarks.- *Trapezoidella hornei* n. sp. shows some similarities to *Trapezoidella rothi* Sohn, 1979 from the Lower Cretaceous (?Valanginian to ?Middle Albian) Lakota Formation (Black Hills, South Dakota and Wyoming, USA) in general shape and the occurrence of ventrolateral and smaller ventrodorsal ridges. However, the taxon described here is more triangular in shape. This difference can be recognized especially on the smaller right valve. Its ventrolateral ridges are much stronger than those of *T. rothi*. Also in contrast to *T. rothi,* these ridges distinctly overreach the ventral margin in dorsal view.

There are also similarities with representatives of *Dongyingia* Boije, 1978 [Li & Lai, 1988, see Hou *et al*. (1988)], from the Paleogene of China, concerning general outline and the development of ventrolateral ridges. *Trapezoidella*, however, differs from *Dongyingia* in also having dorsolateral ridges with adjoining shallow sulci.

Occurrence.- Known only from the type locality and horizon.

Subfamily ILYOCYPRIMORPHINAE Sinitsa, 1999
(in Nikolaeva, I. & Neustrueva, I.Y., 1999)
Genus *Ilyocyprimorpha* Mandelstam in Galeeva, 1955

Ilyocyprimorpha gobiensis n. sp.
(Plate 1, Figs. C-D)

Derivation of name.- After the Gobi desert.

Holotype.- N5/302, PC MAS.

Type locality and horizon.- Khukhteeg, Mongolia (108°10' N, 44°40' E); clay and limestone, upper part of the Khukhteeg Formation (Aptian-Albian).

Material.- 30 complete carapaces and valves.

Dimensions (in mm).-

	N5/302, PC MAS	N5/303, PC MAS
Length:	1.02	1.01
Height:	0.71	0.63

Diagnosis.- Surface coarsely reticulated, with nodes and tubercles. Right valve larger than left one.

Description.- Carapace medium sized, angularly ovate to subtrapezoidal in lateral outline. Maximum height at about one fifth of length, maximum length at middle height. Right valve larger than left and overlapping it along the entire margin except the dorsal one. Dorsal margin straight, ventral margin almost straight to slightly concave. Anterior margin broadly infracurvate, posterior margin more narrowly infracurvate. Cardinal angles noticeable. Surface covered with strong conical nodes. Inner margin follows the line of outer margin.

Variation.- Insignificant variations concerning sizes and number of tubercles.

Remarks.- The specimens described show similarities to *Ilyocyprimorpha binoda* Gou & Wang 1986 (Gou *et al*., 1986) in lateral view, outline and ornamentation, described from the Lower Cretaceous Saihan Tal Formation of the Eren Basin in Nei Mongol (China). In comparison with the Chinese species, the Mongolian one is distinctly smaller sized, more coarsely ornamented with stronger nodes and tubercles.

Occurrence.- Known only from the type locality and horizon.

Family CYPRIDIDAE Baird, 1850
Subfamily TALICYPRIDEINAE Hou, 1982

Remarks.- The subfamily name Talicyprideinae has been used in different spellings by various authors: Talicyprideidinae (Hou, 1982), Talicypridinae and Talicyprideinae. Since it derives from *Talicypridea*, not "*Talicypris*", the root is "Talicypride" plus the subfamily suffix "–inae", and thus the subfamily name has to be Talicyprideinae following the International Code for Zoological Nomenclature (fourth edition).

Genus *Talicypridea* Khand, 1977
Syn. *Cristocypridea* Hou, 1977 (in: Ye *et al.,* 1977)
Syn. *Nemegtia* Szczechura, 1978

Talicypridea neustruevae n. sp.
(Plate 1, Figs. E-F)

Derivation of name.- In honour of the Russian ostracodologist Irina Yurievna Neustrueva.

Holotype.- N5/306, PC MAS.

Type locality and horizon.- Bayanzag, Mongolia (103°44' N, 44°12' E); red clay of the upper part of the Bayanzag Formation (Coniacian-Santonian).

Material.- 8 complete carapaces.

Dimensions (in mm):

	N5/306, PC MAS	N5/307, PC MAS
Length:	0.90	0.84
Heigth:	0.54	0.54

Diagnosis.- A medium-sized species of *Talicypridea*, subovate in outline. Surface covered with wave-like ornamentation trending to the anterior end and on the lip-like extension with weakly noticeable spines.

Description.- Subovate in lateral outline. Left valve larger than right, overlaps the latter along the entire margin except for the dorsal margin and the lip-like anteroventral extension. Anterior margin equicurvate to slightly infracurvate, posterior margin slightly infracurvate. Dorsal margin almost straight or weakly convex, ventral margin slightly concave. Anteroventral, the right valve bears a lip-like extension with a few indistinct lateral spines. The valve's surface is covered with an indistinct wavy ornamentation.

Variation (dimorphism).- The holotype and paratype N5/307 PC MAS (pl. 1, figs. E and F, respectively) are both very similar in general shape, but differ in proportions (the paratype is more compressed). In comparison to the paratype the holotype's anterior margin tends to be more equicurvate and its posterior margin is infracurvate, while the opposite is true for the paratype (i.e. its anterior margin is infracurvate and the posterior margin nearly equicurvate). A sexual dimorphism may be considered here.

Remarks.- The described specimens show similarities to *Talicypridea biformata* described by Szcechura & Blaszyk (1970) from the Upper Cretaceous of Mongolia. *T. neustruevae* n. sp., however, is different in being smaller and more subovate. In addition, the anterodorsal overlap of the left valve is regular and the position of the rostrum-like process is lower than that of *T. biformata*.

Occurrence.- Known only from the type locality and horizon.

Subfamily CLINOCYPRIDINAE Mandelstam, 1960
Genus *Clinocypris* Mandelstam, 1956

Remarks.- *Clinocypris* shows similarities to *Mongolianella* Mandelstam, 1956 and, even more, to *Eoparacypris* Anderson, 1971. *Mongolianella*, however, is much less acute posteriorly and the anterior margin is more infracurvate.

Clinocypris has striking similarities with *Eoparacypris* Anderson, 1971 from the Purbeck and Wealden of England, and could possibly be differentiated from the latter by the muscle-scar pattern. Unfortunately, Mandelstam (in Schneider et al., 1956, p.114) only notes that the muscle-scar pattern in *Clinocypris* is typical for representatives of the family Cyprididae, and the muscle-scars in *Clinocypris solongiinensis* n. sp. have not been observed. Therefore, this problem has to be postponed as subject to future research.

Clinocypris solongiinensis n. sp.
(Plate 1, Figs. G-H)

Derivation of name.- After the locality Solongiin Tsav.

Holotype.- N5/304, PC MAS.

Type locality and horizon.- Solongiin Tsav, Mongolia (103°09′ N, 44°31′ E); dark gray clay in the upper part of the Baruungoyot Formation (Campanian - Early Maastrichtian).

Material.- More than 100 carapaces, well preserved.

Dimensions (in mm).-

	N5/300, PC MAS	N5/301, PC MAS
Length:	1.18	1.60
Height:	0.54	0.53

Diagnosis.- Carapace large, with elongate-oval to reniform lateral outline, tapering towards posterior end. Dorsal margin slightly convex, ventral margin very distinctly concave at a position slightly anterior of middle length.

Description.- Large carapace, elongate-oval and reniform in lateral view tapering towards posterior end. Left valve larger than right, overlapping the latter along the entire margin except the dorsal one (hinge margin region). Anterior margin broad and weakly infracurvate, posterior margin narrower infracurvate. Hinge margin straight. Cardinal angles noticeable but strongly rounded. Surface smooth. Duplicature along anterior and posterior inner margins, distinctly wider anterior. Marginal pore canals rather straight.

Variation.- Variation within this species mainly concerns the size of the carapace and the degree of convexity of the ventral margin.

Remarks.- *Clinocypris solongiinensis* n. sp. shows some similarity to *Mongolianella palmosa* Lyubimova 1956,

from the Lower Cretaceous of Mongolia. However, *C. solongiinensis* n. sp. differs in being more elongate and reniform (concave ventral margin) in lateral outline, smaller in size and having a different overlap.

Occurrence.- Known only from the type locality and horizon.

3. PALAEOGEOGRAPHICAL DISTRIBUTION OF THE GENERA

The four genera of which representatives are described here differ significantly in their geographical distribution and the total number of species known to date. The numbers of species were taken from the database of E. G. Kempf, at the status of 1997 (Kempf, 1980, 1997) and partially completed based on some newer publications.

Ilyocyprimorpha (22 species determined, plus 2 questionably belonging to the genus) and *Talicypridea* (130 species determined, 64 of these belonging to the synonymous genus *Cristocypridea*, 3 to the synonymous genus *Nemegtia*) are only known from the northern hemisphere with reasonable certainty. Both genera are mainly distributed in Central Asia (Mongolia and China). While the genus *Talicypridea* is restricted to Central Asia (Lower to Upper Cretaceous of Mongolia and China) and India (Whatley & Bajpai, 2005, Upper Cretaceous), the genus *Ilyocyprimorpha* (limited to the Lower Cretaceous in Central Asia) also occurs in Lower Cenozoic (Paleocene) deposits of North America (Swain, 1999, one species). However, Khand (2000) discussed the possibility that the Talicyprideinae represent a transition between Mesozoic and Recent Cyprididae. Admittedly, Musacchio (1989, "*Cypridea*" sp., pl. 3, figs. 7-8) and Musacchio & Simeoni (1989, "*Cypridea*" *vistaalegrensis*, pl. 3, fig. 2) picture specimens from the Upper Cretaceous (pre-Maastrichtian, Anacleto Formation, Neuquén Basin, Argentina) that very much resemble *Talicypridea* and, along with other species reported therein (*Altanicypris*? sp. 1, assigned to *Bogdocypris* Khand, 1994 by Khand [2000], and *Altanicypris*? sp. 2), provide evidence for a South American occurrence of representatives of the subfamily Talicyprideinae. Cabral *et. al* (2005) report 2 species of a new genus of the Talicyprideinae from Portugal, SW Europe and therewith confirm the occurrence of its representatives already known from the Barremian to Aptian of northern Spain (cf. Brenner, 1976, pl. 9, figs. 1-7, *Mantelliana uniensis* sp. nov. therein).

The genera *Trapezoidella* and *Clinocypris* are, in addition to their occurrence in the northern hemisphere, also known from the southern hemisphere. Representatives of *Trapezoidella* (4 species named) occur in the Upper Jurassic (Kimmeridgian sensu gallico, Schudack, 1995, Schudack *et al*. 1998) and Lower Cretaceous of North America (Sohn, 1979, 2 species), the Upper Jurassic (Kimmeridgian) of Tanzania, East Africa (Sames, 2002, Schudack & Schudack, 2002, two indetermined species) and the Lower Cretaceous of Asia (Nikolaeva & Neustrueva, 1999; 2 species). Including this paper, 3 of 5 named species occur in the Lower Cretaceous Central Asia (Mongolia), although the Late Jurassic occurrence in Africa and North America implies an origin outside Central Asia. *Clinocypris* (38 species determined plus 9 questionably belonging to the genus; ocurring from Early Triassic to Cretaceous) is mainly known from China (Cretaceous), Mongolia and Transbaikalia (Nikolaeva & Neustrueva, 1999) but also occurs in the Precaspian Depression, the Triassic of Poland, and the Lower Cretaceous of Brazil, South America (Krömmelbein, 1965).

Plate 1

Scale bar = 200μm

A-B. *Trapezoidella hornei* n. sp., locality Bayanerkhet, Shinekhudag Formation, Early Cretaceous. A: right lateral view of carapace, specimen N5/300 PC MAS, holotype. B: dorsal view, anterior end to the right, specimen N5/301 PC MAS.

C-D. *Ilyocyprimorpha gobiensis* n. sp., locality Khukhteeg, Kukhteeg formation, Early Cretaceous. C: right valve, specimen N5/302, holotype. D: dorsal view, anterior end to the right, specimen N5/303 PC MAS.

E-F. *Talicypridea neustruevae* n. sp., locality Bayanzag, Bayanzag (=Djadokhta) Formation, Late Cretaceous. E: right lateral view of carapace, specimen N5/306, PC MAS, holotype. F: right lateral view, specimen N5/307, PC MAS, paratype.

G-H. *Clinocypris solongiinensis* n. sp., locality Solongiin Tsav, Baruungoyot Formation, Late Cretaceous. G: right lateral view of carapace, specimen N5/304 PC MAS, holotype. H: right lateral view of carapace, specimen N5/305 PC MAS.

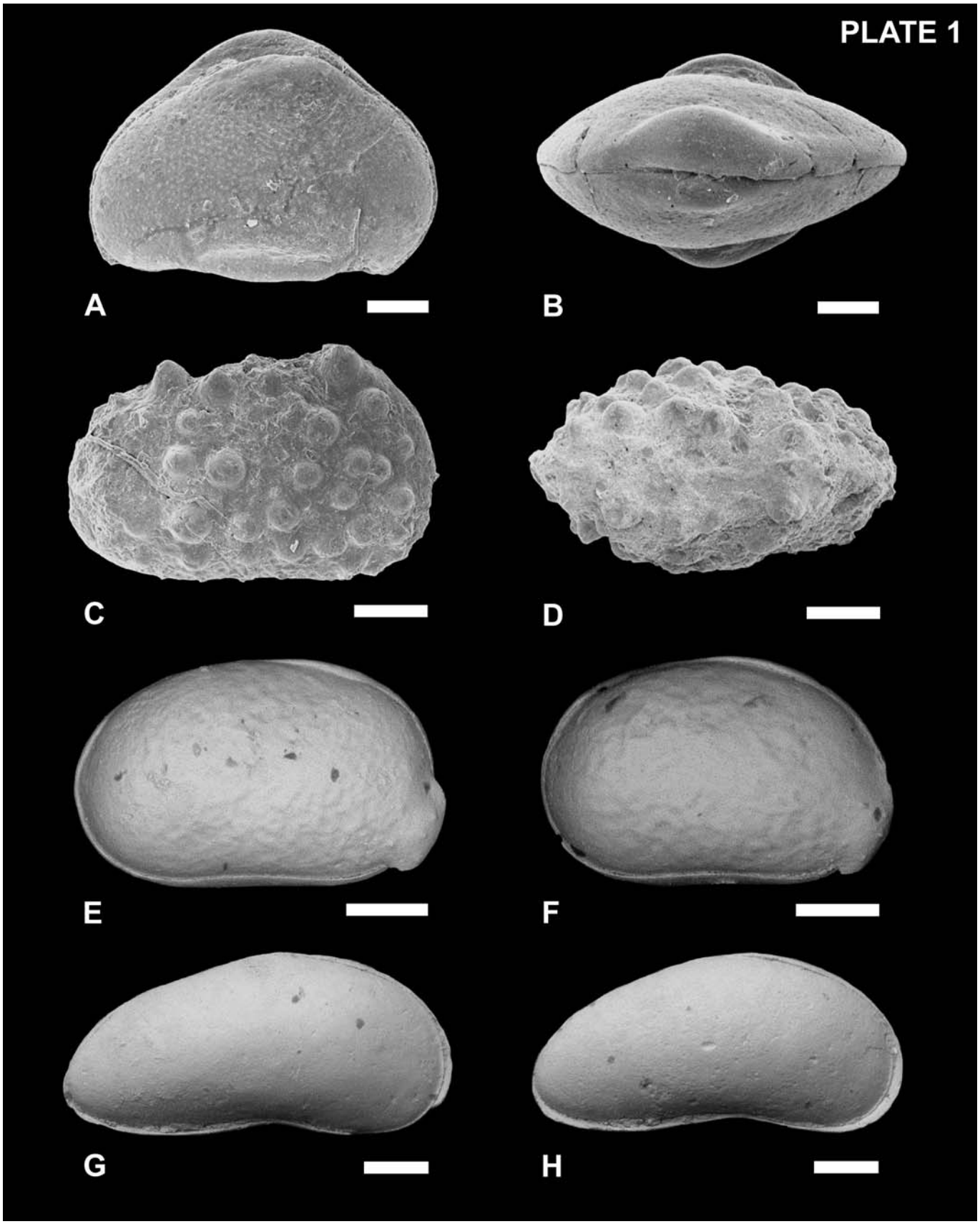
PLATE 1
A
B
C
D
E
F
G
H

4. CONCLUSIONS

The four new species described here belong to cypridoidean genera of particular importance in the nonmarine Cretaceous of Central Asia. However, studies of nonmarine Upper Jurassic to Lower and Upper Cretaceous ostracods conducted within the last 20 years have shown the importance of taxonomic and stratigraphical comparisons in a global context. Endemism of nonmarine ostracod taxa at the genus level, as well as at the species level in part, seems to have been overestimated in the past. Comparisons on a global scale are likely to allow and improve a supraregional biostratigraphical application of Late Jurassic and Cretaceous nonmarine ostracods. A regionally and temporally separated occurrence of *Ilyocyprimorpha*, for example (cf. chapter above) or the detection of *Trapezoidella*, which at first was only known from the Lower Cretaceous of North America and Mongolia before, in the Kimmeridgian of SE Tanzania (Schudack & Schudack, 2002; Sames 2002) and North America (Schudack, 1995; Schudack *et al.*, 1998), demonstrates the incompleteness of our knowledge and necessity of further research. That applies especially for the southern hemisphere (Gondwana).

For future research, and the reconstruction of origin, evolution and spreading directions of nonmarine ostracods in particular, it is essential to take distributional mechanisms, plate tectonics and paleoclimate into consideration, beyond the taxonomic work. As has been presumed by Schudack & Sames (2003) for the genus *Cypridea* for example, an origin of some important nonmarine taxa and lineages on the Gondwana continent and a subsequent migration to the northern hemisphere is probable.

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Chlorophyta de los Valles Calchaquíes (Mioceno Medio y Superior), Argentina

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Resumen

Las Formaciones San José y Chiquimil del Grupo Santa María (Mioceno Medio y Superior) y la Formación Palo Pintado del Grupo Payogastilla (Mioceno Superior,) afloran en los Valles Calchaquíes, provincias de Salta, Tucumán y Catamarca, en el noroeste de la República Argentina. Estas unidades sedimentarias representan principalmente sistemas fluviales con varios episodios lacustres. Se presentan e ilustran 14 especies de cigosporas, cenobios y colonias de Chlorophyta que provienen de asociaciones palinológicas de origen continental. Entre ellas *Botryococcus braunii* Kützing es común y frecuente en otras asociaciones de Argentina; *Oedogonium cretaceum* Zippi, *Coelastrum* sp., *Lecaniella korsoddensis* Batten, Koppelhus & Nielsen, *Ovoidites spriggi* (Cookson & Dettmann) Zippi y *Schizosporis* sp. son mencionadas por primera vez para el Terciario Superior de Argentina; y *Cymatiosphaera* sp. ya ha sido registrada en el Oligoceno de este país. Se crea una especie nueva, *Sphaeroplea miocenica* sp. nov., y se enmienda *Lecaniella korsoddensis*. Al comparar los fósiles con los análogos modernos de Chlorophyta se deduce que integraron cuerpos de agua dulce, temporales, poco profundos, eutróficos a mesotróficos, con temperaturas primaverales entre 20-21 ºC. *Sphaeroplea miocenica* sp. nov. y *Ovoidites* sp. 2 son exclusivas de Formación San José; mientras que *Ovoidites grandis* (Pocock) Zippi, *Pediastrum simplex* (Meyen) Lemmermann, *Pediastrum boryanum* var. *longicorne* Reinsch y *Ovoidites* sp. 1 caracterizan a la Formación Palo Pintado. La Formación Chiquimil no tiene elementos exclusivos. *Lecaniella korsoddensis, Ovoidites parvus, Ovoidites spriggi y Botryococcus braunii* son comunes a las tres asociaciones.

Palabras clave: Palinología, algas de agua dulce, Chlorophyta, Mioceno, Valles Calchaquíes, Argentina

Abstract

[Chlorophyta from the Middle and Late Miocene of Argentina]. The San Jose and Chiquimil Formations of the Santa Maria Group (Middle and Upper Miocene) and Palo Pintado Formation of the Payogastilla Group (Upper Miocene) outcrop in the Calchaqui Valleys, Salta, Tucumán and Catamarca provinces, in the Northwest of Argentina. These sedimentary units represent mainly fluvial systems with several lacustrine episodes. Fourteen fossil species of zygospores, coenobia and chlorophyta colonies that integrate from palynological associations of continental origin are presented and illustrated. Among them *Botryococcus braunii* Kützing is common and frequent with other associations in Argentina; *Oedogonium cretaceum* Zippi, *Coelastrum* sp., *Lecaniella korsoddensis* Batten, Koppelhus & Nielsen, *Ovoidites spriggi* (Cookson & Dettman) Zippi and *Schizosporis* sp. are mentioned for the first time in the Upper Tertiary period in Argentina; and *Cymatiosphaera* sp. has already been registered in the Oligocene period in this country. A new species is created, *Sphaeroplea miocenica* sp. nov. and *Lecaniella korsoddensis* is emended. When comparing the fossils with modern analogous ones of Chlorophyta, it can be deduced that they integrated freshwater, temporal, not very deep, eutrophic to mesotrophic bodies, with spring temperatures about 20-21° C. *Sphaeroplea miocenica* sp. nov. and *Ovoidites* sp. 2 are exclusive of San José Formation while *Ovoidites grandis* (Pocock) Zippi, *Pediastum simplex* (Meyen) Lemmermann, *Pediastrum boryanum* var. *longicorne* Reinsch and *Ovoidites* sp. 1 characterize Palo Pintado Formation. Chiquimil Formation does not have exclusive elements. *Lecaniella korsoddensis, Ovoidites parvus, Ovoidites spriggi* and *Botryococcus braunii* are common to the three associations.

Keywords: Palynology, freshwater algae, Chlorophyta, Miocene, Calchaquíes Valleys, Argentina

1. INTRODUCCIÓN

Las algas dadas a conocer en este trabajo integran asociaciones palinológicas de origen netamente continental constituídas en orden decreciente de abundancia, por magnoliófitas, pinófitas, pteridófitas y briófitas (Acevedo *et al.*, 1997; Anzótegui & Cuadrado, 1996; Cuadrado & Anzótegui, 1992; Herbst *et al*. 2000; Mautino, 2003; Mautino & Anzótegui, 1998, 2000, 2002 a, b, c, 2004).

En el registro fósil palinológico es habitual encontrar cigosporas, colonias y cenobios de Chlorophyta; no obstante, las cigosporas están muy pobremente estudiadas, de tal manera que las de Zygnemataceae, fueron confundidas, en repetidas ocasiones, con propágulos de hongos, esporas monoletes de pteridófitas o polen monosulcado de ciertas pinófitas o magnoliófitas (van Geel, 1976 y 1978; Jarzen, 1979; van Geel & Grenfell, 1996). Es así que Graham (1971) considera que las cigosporas tienen valor potencial en las investigaciones palinológicas.

La importancia de esta contribución radica en que por primera vez se ha logrado identificar una gran diversidad de cigosporas, colonias y cenobios de Chlorophyta en formaciones del Terciario argentino. De los porcentajes relativos de la asociación polínica se destaca la frecuencia de las especies de algas y se analizan las condiciones paleoambientales para su producción. Se determinaron los taxones comunes y/o exclusivos al comparar su distribución estratigráfica en cada una de las formaciones (Formaciones San José, Chiquimil y Palo Pintado).

En este trabajo se dan a conocer las siguientes especies: *Pediastrum boryanum* var. *longicorne* Reinsch, *Pediastrum simplex* (Meyen) Lemmermann, *Oedogonium cretaceum* Zippi, *Coelastrum* sp., *Ovoidites parvus* (Cookson y Dettman) Nakoman*, Ovoidites spriggi* (Cookson & Dettmann) Zippi, *Ovoidites grandis* (Pocock) Zippi, *Ovoidites* sp. 1, *Ovoidites* sp. 2, *Schizosporis* sp., *Botryococcus braunii* Kützing y *Cymatiosphaera* sp. Entre las novedades de este aporte se crea la especie *Sphaeroplea miocenica* sp. nov. y se enmienda *Lecaniella korsoddensis* Batten, Khoppelhus y Nielsen la cual es, además, primera cita para el Mioceno de Argentina junto a *Oedogonium cretaceum*, *Coelastrum sp.*, *Ovoidites spriggi* y *Schizosporis* sp. *Pediastrum boryanum* var. *longicorne* y *Pediastrum simplex*, tienen un registro escaso en sedimentos del Terciario argentino (Zamaloa y Tell, 2005) al igual que *Cymatiosphaera* sp. que solo fue citada previamente por Barreda (1997a) para la Formación San Julián (Oligoceno de la cuenca austral). En cambio es conocido el amplio registro cosmopolita de *Botryococcus brauni* (Barreda, 1997b) que aparece desde el Precámbrico (Cookson, 1953; Guy-Ohlson, 1992).

Actualmente, las clorofitas son más frecuentes en aguas dulces que en marinas; muchas de ellas son planctónicas aunque se encuentran bentónicas y litorales (Margalef, 1983). La productividad de las clorofitas se relaciona en forma directa con la luz, nutrientes y transparencia del agua.

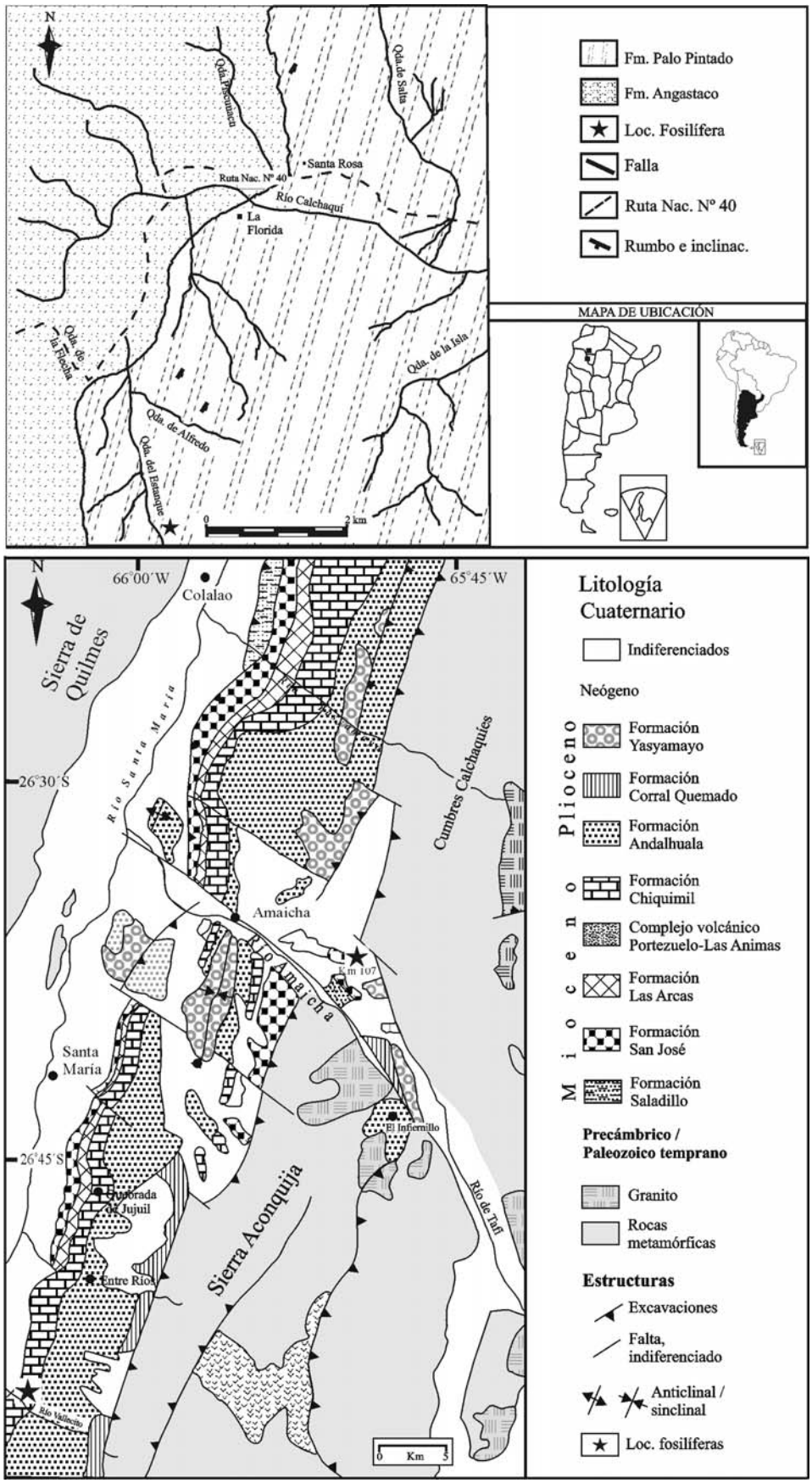
Las Zygnemataceae, familia a la que pertenecen la mitad de las especies de este trabajo, se reproducen en forma asexual formando aplanosporas y sexual produciendo cigosporas, a través de un proceso especial de conjugación. El cigoto, al principio del ciclo vital, puede tener movilidad, pero luego se rodea de una membrana formando una cigospora, mediante la cual resiste a la desecación y soporta condiciones desfavorables. Esta pared o membrana gruesa es resistente a la oxidación, debido a la presencia de esporopolenina, que favorece su fosilización. En cambio no ocurre lo mismo con los filamentos que normalmente no fosilizan debido a que las paredes celulares contienen celulosa y pectina, y se cubren de una vaina de mucílago (Head, 1992; van Geel & Grenfell, 1996; Zippi, 1998).

1.1. Marco geológico y geográfico

Las Formaciones San José, Chiquimil y Palo Pintado afloran en los valles Calchaquíes, en las provincias de Tucumán (noroeste), Catamarca (centro-este) y Salta (centro-sur). Las Formaciones San José y Chiquimil integran la base del Grupo Santa María, entre las que se encuentra la Formación Las Arcas. La Formación Palo Pintado, en cambio, es parte del Grupo Payogastilla (Diaz & Malizzia, 1983) junto a las Formaciones Angastaco y San Felipe que provienen del centro-sur de la provincia de Salta (Figura 1).

Figura 1. Mapa geológico (Modificado de Diaz & Malizzia, 1983; Kleinert & Strecker, 2001 y Anzótegui, 2006).

Figure 1. Geological map (Modified from Diaz & Malizzia, 1983; Kleinert & Strecker, 2001 and Anzótegui, 2006).


N
Qda. Pucumucu
Qda. de Salta
Santa Rosa
Ruta Nac. Nº 40
Río Calchaquí
La Florida
Qda. de la Florida
Qda. de la Isla
Qda. de Alfredo
Qda. del Estanque
0
2 km
Fm. Palo Pintado
Fm. Angastaco
Loc. Fosilífera
Falla
Ruta Nac. Nº 40
Rumbo e inclinac.
MAPA DE UBICACIÓN
N
66°00´W
Colalao
65°45´W
Sierra de Quilmes
Río Santa María
26°30´S
Cumbres Calchaquíes
Amaicha
Río Amaicha
Km 107
Santa María
El Infiernillo
26°45´S
Quebrada de Jujuil
Sierra Aconquija
Río de Tafí
Entre Ríos
Río Vallecito
0 Km 3
Litología
Cuaternario
Indiferenciados
Neógeno
Plioceno
Formación Yasyamayo
Formación Corral Quemado
Formación Andalhuala
Mioceno
Formación Chiquimil
Complejo volcánico Portezuelo-Las Animas
Formación Las Arcas
Formación San José
Formación Saladillo
Precámbrico / Paleozoico temprano
Granito
Rocas metamórficas
Estructuras
Excavaciones
Falta, indiferenciado
Anticlinal / sinclinal
Loc. fosilíferas

Los palinomorfos provienen de las siguientes localidades fosilíferas: Km 107 (San José), Río Vallecito (Chiquimil) y Quebrada del Estanque (Palo Pintado). Km 107, en la quebrada de Amaicha, está ubicada al noroeste de la provincia de Tucumán, sobre la ruta provincial 307; Río Vallecito se encuentra en la provincia de Catamarca, al sur de la ciudad de Santa María, próxima a El Desmonte. Finalmente, Quebrada del Estanque aflora sobre ambas márgenes del río Calchaquí entre las localidades de Angastaco y San Carlos en la provincia de Salta.

La Formación San José es asignada al Mioceno Medio (Bossi *et al.,* 1998) mediante datos estratigráficos, de facies, radimétricos en tobas y por estudios paleontológicos (Bossi *et al*., 1998). En cambio las Formaciones Chiquimil y Palo Pintado corresponden al Mioceno Superior (Bossi *et al.,* 1998; Diaz & Malizzia, 1983; Diaz, 1985; Herbst *et al*., 1987; Morton, 1992; Starck & Anzótegui, 2001). La Formación Chiquimil fue datada mediante una asociación faunística y la Formación Palo Pintado por estudios estratigráficos y restos de mamíferos.

Las formaciones estudiadas, de acuerdo al análisis de facies, representan sistemas fluviales con episodios lacustres (Bossi *et al*., 1998; Diaz & Malizzia, 1983 y Jalfin, en Herbst *et al*., 1987). Para la localidad Río Vallecito, Herbst (1984) señala que el ambiente de sedimentación se produjo bajo condiciones fluviales de tipo entrelazado donde hay depósitos de pequeñas lagunas abandonadas dentro de la planicie aluvial.

El perfil realizado en la localidad Río Vallecito abarca un espesor de 360 metros. Sedimentológicamente está constituído por areniscas medianas a finas, de color predominantemente amarillo, con intercalaciones de conglomerados, limolitas verdes o rojizas. Las facies de limolitas son portadoras de palinomorfos e impresiones de hojas (magnoliófitas y pteridófitas) y pelecípodos, las que se encuentran especialmente en la sección inferior y media de la secuencia (Figura 2).

En la Quebrada del Estanque, el perfil de la Formación Palo Pintado tiene una potencia de 400 metros y está constituído por areniscas, limolíticas y conglomerádicas (Jalfin en Herbst *et al*. 1987). Las areniscas se distribuyen homogéneamente, con distintos tipos de estratificación: planar, linguoide, fina o maciza y con ondulitas. Los niveles polínicos están concentrados principalmente en la parte media de la secuencia y esporádicamente en la base y tope (Figura 2).

En la localidad Km 107, el perfil abarca aproximadamente 70 metros de espesor y los palinomorfos proceden de capas pelíticas sucesivas dispuestas muy próximas entre sí principalmente de la parte basal (15 m) del afloramiento. La secuencia sedimentaria está compuesta por areniscas muy finas a finas; en menor proporción pelitas, areniscas medianas y calizas organógenas, en las capas inferiores y conglomerados en las secciones cuspidales (Figura 2).

2. MATERIALES Y MÉTODOS

Las algas se encuentran en buen estado de preservación y provienen de muestras obtenidas en perfiles realizados en cada localidad; en Río Vallecito se obtuvieron 22 muestras fértiles; 20 del Km 107 y 40 de la localidad Quebrada del Estanque (cedidas por L. M. Anzótegui).

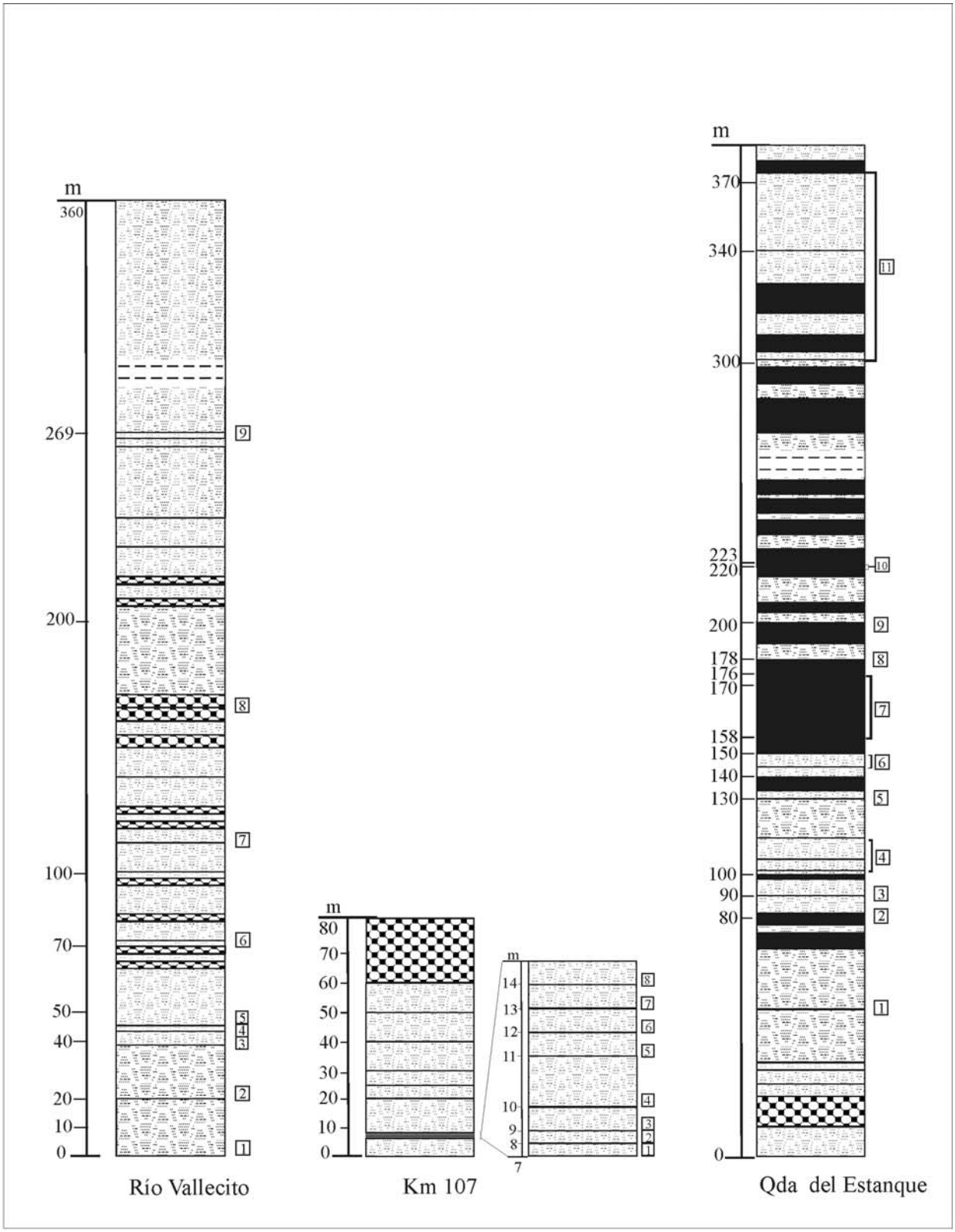
Para la obtención de los palinomorfos, se han eliminado los silicatos con ácido fluorhídrico, se empleó ácido nítrico para la oxidación y el montaje se realizó en glicerina-gelatina.

Los preparados palinológicos están depositados en la colección de la Facultad de Ciencias Exactas Naturales y Agrimensura de la Universidad Nacional del Nordeste bajo la sigla CTES-PMP (Corrientes Preparados Micropaleontológicos).

Los palinomorfos se analizaron con un microscopio óptico Leitz Diaplan y las fotomicrografías fueron obtenidas con Cámara digital Canon Power Shot 550; las del microscopio electrónico de barrido fueron tomadas en un equipo Jeol ISM-580 OLV de Universidad Nacional del Nordeste.

Figura 2. Columna estratigráfica esquemática de las localidades con los niveles polínicos.

Figure 2. Stratigraphic column of the studied area with fossiliferous levels.



REFERENCIAS

LIMOLITA CONGLOMERADO ARENISCA Nivel con palinomorfos

En la columna estratigráfica de la localidad Km 107 se establecieron 8 niveles palinológicos, 7 en Río Vallecito y 11 en Quebrada del Estanque (Figura 2).

Los porcentajes relativos de los palinomorfos obtenidos por nivel se realizó sobre la base del conteo de 200 ejemplares por cada uno de ellos.

Se describen únicamente las especies nuevas, las primeras citas y las que permanecen con nomenclatura abierta. Para las demás sólo se consignan dimensiones y comentarios (cuando son necesarios).

Para las descripciones taxonómicas se emplea un sistema mixto, prefiriéndose, en la medida de lo posible, el sistema morfogenérico en detrimento del sistema natural.

3. PALEONTOLOGÍA SISTEMÁTICA

División CHLOROPHYTA Pascher, 1914
Clase CHLOROPHYCEAE Kützing, 1843
Orden CHLOROCOCCALES Marchand, 1895
Familia BOTRYOCOCCACEAE Wille, 1909
Género *Botryococcus* Kützing, 1849

Especie tipo.- *Botryococcus braunii* Kützing, 1849

Botryococcus braunii Kützing, 1849
Lám. 2, Fig. 11

Dimensiones.- Colonias de 25-75 µm de diámetro, células de 3-4 µm de ancho y 6-9 µm de alto.

Comentarios.- La forma y tamaño de estas colonias mucilaginosas depende del grado de fragmentación de las mismas. Con el microscopio electrónico de barrido, se observan los espacios vacíos que corresponden al lugar que ocupaban las células y puede inferirse la disposición en par que tenían.

Material estudiado.- CTES-PMP Río Vallecito 1695a: 46-98,5; Km 107: 1945b; 38,2/104; 40,9/100,5; 2266c: 39,5/108,2; 1926e: 40,5/97,8; 1942c: 35/103,5 y Quebrada del Estanque: 2021a: 49,2/106,2; 2021c: 40,7/110,6; 36,8/101,5.

Localidades.- Río Vallecito, Km 107 y Quebrada del Estanque.

Procedencia estratigráfica y edad.- Formación San José, Mioceno Medio. Formación Chiquimil y Formación Palo Pintado, Mioceno Superior.

Registros previos.- Alga cosmopolita de biocrón amplio desde el Precámbrico al Holoceno (Cookson, 1953; Guy-Ohlson, 1992); otros autores (Batten & Grenfell, 1996; Clausing, 1999) consideran que aparece después del Ordovícico. En Argentina, son numerosos los trabajos que registran esta especie; entre otros se citan en el Carbonífero, Gutiérrez & Limarino (2001); di Pasquo *et al.* (2001); en el Triásico, Ottone *et al.* (2005); en el Jurásico, Martínez *et al*. (2001); en el Cretácico, Papú (2002); en el Terciario: Barreda (1997b), Barreda & Palamarczuk (2000 a y b), Barreda *et al.* (1998), Barreda *et al*. 2003, Mautino *et al*. (1997), Palamarczuk & Barreda (2000), Papú & Sepúlveda (1997); Prámparo *et al.* (1996) y en el Holoceno, Borel *et al*. (2003).

Ambiente en que se desarrollan los taxones actuales afines.- *Botryococcus* spp. es un alga cosmopolita, de agua dulce, planctónica, aunque puede ser bentónica o estar asociada a los vegetales, como epífita (Komárek & Fott,1983); Fernández (1993) considera que prefiere condiciones lénticas tales como pequeñas lagunas, lagos y zonas pantanosas. *Botryococcus* es característico de aguas oligotróficas aunque también se encuentra en aguas mesotróficas (Tyson, 1995 y Rodríguez Amenábar, 2003).

Familia HYDRODICTYACEAE (Gray) Dumortier 1829
Género *Pediastrum* Meyen, 1829

Observaciones al género.- El género *Pediastrum* junto a *Botryococcus* son habituales en depósitos lacustres y fluviales del Cretácico al Holoceno, aunque *Botryococcus* ya se registra desde el Precámbrico y a través del Fanerozoico (Guy-Ohlson, 1992; Stanley, 1965; Mildenhall & Pocknall, 1989; Bold & Wynne 1985).

Pediastrum agrupa algunas especies de distribución cosmopolita, otras endémicas o bien restringidas a regiones templadas, frías o cálidas (Komárek & Jankovká 2001; Zippi, 1998).

Komárek y Jankovká (2001), en su revisión del género *Pediastrum*, establecen que el mismo, en la actualidad, cuenta con 24 especies y algunas variedades.

En el Terciario de Argentina, los registros de *Pediastrum* son frecuentes, entre otros pueden citarse: en el Paleógeno, Formación Pachaco, (Prámparo *et al*. 1996); Mioceno de la Cuenca del Colorado (Guerstein, 1990); Oligoceno-Mioceno, Formación Chenque (Barreda, 1997b); Oligoceno-Mioceno de la Plataforma Continental Argentina (Palamarczuk & Barreda, 2000); Oligoceno-Mioceno, Formación Centinela (Guerstein *et al*. 2001); Mioceno, Formación La Ollita (Barreda *et al*., 1998); Mioceno, de la Formación Monte León (Barreda & Palamarczuk, 2000a) y Neógeno de la Cuenca del Colorado (Guler *et al*. 2002). La mayoría de estos taxones se encontraban con nomenclatura abierta hasta que Zamaloa y Tell (2005) determinan estas formas en revisión de las especies fósiles de *Pediastrum* en Argentina.

Especie tipo.- *Pediastrum duplex* Meyen, 1829

Pediastrum simplex (Meyen) Lemmermann, 1897
Lám. 2, Figs. 13, 14

Dimensiones.- Diámetro del cenobio, 52-100 µm; diámetro de las células, 5-14 µm; diámetro de los clatros, 7-14 y µm; longitud de las proyecciones, 10,5-14,7 µm.

Material estudiado.- CTES-PMP Quebrada del Estanque 1975b 57,9/98,6; 1973a: 49/106,5; 42/105; 46/104,1; 2032a: 46,9/103,6; 34,5/103; 1897a: 42,6/104,6.

Localidad.- Quebrada del Estanque.

Procedencia estratigráfica y edad.- Formación Palo Pintado, Mioceno Superior.

Registro previo.- Dueñas (1979) relaciona a *Pediastrum* tipo A con *Pediastrum simplex* (Meyen) Lemmermann, 1897. Este registro corresponde al Holoceno-Pleistoceno de Bogotá. En Argentina ya es mencionado por Starck & Anzotegui (2001) en la Formación Palo Pintado.

Ambiente en que se desarrollan los taxones actuales afines.- Esta especie se desarrolla en regiones templadas a cálidas y está ausente en regiones frías. En Argentina, estas características concuerdan con la distribución geográfica de la especie (Tell, 2004).

Pediastrum boryanum var. *longicorne* Reinsch, 1867
Lám. 2, Fig. 15

Dimensiones.- Diámetro, 52-84 µm; número aproximado de células, 16-32; diámetro de las células, 7-10 µm; longitud de las proyecciones, 7-8,4 µm.

Comentarios.- Este cenobio se caracteriza porque la superficie de las células es granular y las células marginales o externas presentan dos prolongaciones agudas.

Material estudiado.- CTES-PMP Quebrada del Estanque: 1793a: 49,5/103,5; 46/102; 99,8/103; 2050a: 36,4/111,7; 2032a 38/103,5; 36/100 y 39,5/101,7.

Localidad.- Quebrada del Estanque.

Procedencia estratigráfica y edad.- Formación Palo Pintado, Mioceno Superior.

Registro previo.- Formación Palo Pintado, Mioceno superior (Starck & Anzotegui, 2001).

Ambiente en que se desarrollan los taxones actuales afines.- Se desarrolla en cuerpos de agua dulce eutróficos a mesotróficos, con temperatura templadas a frías (Tell, 2004 y Zamaloa y Tell, 2005).

Familia SPHAEROPLEACEAE Kützing, 1849
Género *Sphaeroplea* Agardh, 1824

Especie tipo.- *Sphaeroplea annulina* Agardh, 1824

Sphaeroplea miocenica sp. nov.
Lám. 1, Figs. 1-5

Diagnosis.- *Zygospores 12-14 µm in diameter, subspheroidal-polygonal in shape, inaperturate, wall 1 µm thick, surface dividen in 9-15 polygonal to irregular fields of 3-4 in diameter.*

Holotipo.- PMP-CTES 2268c: 41,4/99,5.

Paratipo.- PMP-CTES 2268b: 45/100.

Localidad y estrato tipo.- Km 107 (26º37'S y 66º 30' W), Quebrada de Amaicha, provincia de Tucumán, Formación San José.

Edad.- Mioceno Medio.

Material estudiado.- CTES-PMP Km 107 2387a: 39,5/1005; 36/100,5; 40,5/108,6; 36,2/98,4; 49,8/100,7;

35/101,4; 33,6/101,4; 2387b: 42/95,8; 42,2/96; 42,8/107,3; 45,2/103; 54,6/108,3; 45,3/102,8; 45,8/110; 47,1/103; 37,5/107; 36,1/104,9; 46,5/103,2; 46/108; 47,1/103,2; 34,8/103,7; 45/104,1; 47,3/104,2; 40/104,1; 2268b: 39,5/100,5; 36/100,5; 40,5/108; 49,8/100,7; 45,7/100,4; 2268c: 44/100; 46,4/102,5; 36/102,8; 44,2/104; 44,5/107; 43/41,8; 2265c: 45,3/102,5; 43,6/100,4; 41,8/100,7; 46,6/102; 43,9/100,8; 40/101,5; 45/102; 40,9/102,8; 48,7/107,3; 47/107,5; 42,3/107,5; 39/107,4; 41,2/107,6; 1946e: 42,8/106; 2267c: 43,2/96,4; 41,8/100,7; 46,6/102; 43,9/100,8.

Derivatio nominis.- El nombre de la especie está referido a la edad de los sedimentos en los que se encuentran las cigosporas.

Descripción.- Cigosporas de 12-14 µm de diámetro; subesferoidales a poliédricas, inaperturadas. Pared de 1 µm de espesor formando crestas bajas, aladas y romas de 2-3 µm de alto, que delimitan 9 a 15 espacios poligonales irregulares de 3-4 µm de diámetro, imitando a un retículo. El microscopio electrónico de barrido permite confirmar la estructura observada al microscopio óptico y, además, revela que la superficie de los espacios poligonales es suavemente granulada a lisa.

Comparaciones.- *Sphaeroplea fenestrata* Zippi (1998) del Cretácico inferior de Canadá se diferencia porque es mayor tanto diámetro general de la espora es mayor (18-26 µm) como el número de espacios poligonales (20-25); las membranas son visiblemente ruguladas en los sectores poligonales y las crestas presentan costillas.

Al comparar *Sphaeroplea miocenica* sp. nov. con especies actuales se hallaron similitudes con *Sphaeroplea wilmani* Fritsch & Rich (Tracanna, 1979 y Parodi & Cáceres, 1986) tanto con *S. wilmani* Fritsch & Rich var. *wilmani* como con *S. wilmani* var. *tucumanensis* Tracanna (Parodi & Cáceres, 1986 y Tracanna, 1979), especialmente por la disposición de las crestas. Sin embargo, *S. miocenica* sp. nov. se diferencia porque posee un tamaño menor y escultura más suave con respecto a las especies actuales, que presentan un tamaño de 25-30 µm y una marcada granulación entre las crestas.

Este es el primer hallazgo del género en sedimentos del Terciario argentino y el segundo registro en sedimentos fósiles de todo el mundo, según se desprende del estudio de Zippi (1998).

Comentarios.- La taxonomía de estas algas está basada en la estructura de las cigosporas (Ramanathan, 1964). Durante el desarrollo del cigoto bentónico o cigospora se produce la síntesis de una pared compleja con ornamentación característica para cada especie (Parodi & Cáceres, 1986).

Actualmente, en este grupo se produce un elevado número de cigosporas, lo que poodría explicar la abundancia de esta forma, en la localidad Km 107.

Ambiente en que se desarrollan los taxones actuales afines.- *Sphaeroplea* es de hábitat planctónico, de aguas dulces o salobres, con moderadas temperaturas (21º C) y ph neutro (Sarma, 1974). También se conoce en suelos inundados sujetos a rápidas desecaciones. El género *Sphaeroplea* es cosmopolita y reúne ocho especies. A pesar de ser más común en el hemisferio sur, en Argentina *Sphaeroplea* es raramente citada (Ramanathan, 1964; Tell, com. pers.).

En condiciones de laboratorio, las cigosporas de *Sphaeroplea wilmani* Fritsch & Rich var. *wilmani* germinan a 20-21 ºC de temperatura (Parodi & Cáceres, 1986). *Sphaeroplea wilmani* var. *tucumanensis* se encuentra en ambientes de pH alcalino (8-10) en la provincia de Tucumán (Tracanna & Couté, 1982).

Familia COELASTRACEAE (West) Wille, 1909
Género *Coelastrum* Nägelli en Kützing, 1849

Observaciones al género.- El género *Coelastrum* actualmente comprende un total de 18 especies, algunas restringidas a regiones tropicales y templadas, y otras cosmopolitas (Komárek & Fott, 1983). En Argentina se registran 9 especies (Tell, 2001).

Especie tipo. *Coelastrum sphaericum* Nägelli en Kützing 1849.

Coelastrum sp.
Lám.1, Fig. 7

Descripción.- Cenobios de 32-35 µm de diámetro, tridimensionales y huecos. Células huecas presumiblemente sub-esferoidales, de 2,5-3,5 µm de diámetro; cantidad de

las mismas difícil de estimar debido al estado de conservación; interconectadas entre sí a través de cinco o seis procesos (prolongaciones de la pared celular) aplanados y/o redondeados de 4-5 µm largo por 0,7-1 µm de ancho, donde uno o dos de ellos son truncos. Pared lisa.

Material estudiado.- CTES-PMP Km 107 2268b: 35,6/108,7; 35,9/101; 1946c: 37,5/99,4. Quebrada del Estanque 2021a: 38,5/105; 56,7/109; 2043a: 42,5/102,5.

Localidades.- Km 107 y Quebrada del Estanque.

Procedencia estratigráfica y edad.- Formación San José, Mioceno Medio. Formación Palo Pintado, Mioceno Superior.

Comparaciones.- En *Coelastrum* sp. cf. *C. reticulatum* var. *cubanum* Komárek en Zippi 1998 del Cretácico de Canadá, el tamaño de las células es mayor (5 µm de diámetro), los procesos de las mismas son menores (2 µm de largo) y el número de células es conocido (aproximadamente 32), en cambio en *Coelastrum* sp., descrito aquí, es imposible contabilizarlas. Ambas especies tienen similar tamaño del cenobio.

Registros previos.- Los registros fósiles del género son escasos. Zippi (1998) lo encontró en sedimentos del Cretácico de Canadá y Hooghiemstra (1984) en el Holoceno de Colombia (como *Coelastrum reticulatum*). Este es el primer registro del género en el Mioceno de Argentina.

Afinidad botánica.- Chlorophyta, Coelastraceae, *Coelastrum*.

Ambiente en que se desarrollan los taxones actuales afines.- El género *Coelastrum* es común en el plancton de agua dulce en lagos y pequeñas lagunas (Prescott, 1962). En la Argentina se registra en todo el país, principalmente en regiones templadas y algunas especies en regiones cálidas (Tell, 2001).

Orden OEDOGONIALES Blakman & Tansley ex West, 1904
Familia OEDOGONIACEAE De Bary, 1854
Género *Oedogonium* Link, 1820

Especie tipo *non designatum*

Oedogonium cretaceum Zippi, 1998
Lám. 1, Fig. 6

Descripción.- Cigosporas de 18-20 µm de diámetro, esferoidales a subesferoidales, inaperturadas. Pared externa lisa a verrucosa, en el interior de la cigospora hay cavidades o poros, que hacia la parte más externa dan a la pared un contorno ondulado.

Material estudiado.- CTES-PMP Km 107 1926c: 36,9/103,5; 36,1/104; 42/101,3; 1948b: 39,3/104,3; 1949b: 45,6/101,3. Quebrada del Estanque 2021a: 46,5/106,5; 43/106,5; 49/105 y 38/103.

Localidades.- Km 107 y Quebrada del Estanque.

Procedencia estratigráfica y edad.- Formación San José, Mioceno Medio. Formación Palo Pintado, Mioceno Superior.

Registros previos.- Los registros de este tipo de alga son raros (Tappan, 1980); entre los más antiguos del mundo se cita a *Paleoedogonium micrum* Baschnagel 1966 para el Devónico Medio de Nueva York (no obstante Zippi, 1998 opina que es una cianobacteria), *O. cretaceum* Zippi, 1998 hallado en sedimentos del Cretácico inferior de Canadá y *Oedogonium* sp. en el Eoceno de la India (Rao, 1957). La especie aquí descripta es la primera cita de estas formas para sedimentos del Mioceno de Argentina.

Afinidad botánica.- Chlorophyta, Oedogoniaceae, *Oedogonium* (Zippi, 1998).

Ambiente en que se desarrollan los taxones actuales afines.- *Oedogonium* es un género cosmopolita, la mayoría de las especies se desarrollan en agua dulce, algunas están vinculadas a aguas salobres y se desconocen especies marinas. La reprodución sexual es estacional y ocurre una o dos veces en el año (Tyffany, 1930; Zippi, 1998).

Orden ZYGNEMATALES Borge & Pascher, 1931
Familia ZYGNEMATACEAE Kützing, 1898

Comentarios.- Las cigosporas de la actual familia Zygnemataceae poseen un largo registro fósil, que se inicia en el Carbonífero del Paleozoico superior (van Geel & Grenfell, 1996); cuentan con una pared diferenciada en tres capas: una externa o exosporio, una media o mesosporio y una interna o endosporio. La capa externa y la interna están compuestas de celulosa y sustancias pécticas y,

usualmente no se preservan; en cambio, la esporopolenina presente en la capa media, contribuye a la fosilización. Esta capa puede ser lisa o presentar una variada ornamentación (van Geel & Grenfell, 1996).

Género *Lecaniella* Cookson & Eisenack, 1962

Especie tipo.- *Lecaniella margostriata* Cookson & Eisenack, 1962

Lecaniella korsoddensis Batten, Koppelhus & Nielsen, 1994 *emend*.

Lám. 1, Figs. 8-13

Enmended diagnosis.- Zygospores 44-126 µm in diameter, subspheroidal-ellipsoidal in shape with two symmetrical halves detached by equatorial dehiscence suture. Halves may retain unfolding or two opposing sides may curl inward to form a canoe-shaped specimen. Each hemisphere divided into a polar and equatorial zone by a circumpolar ridge in polar view. Circumpolar ridge rather subcircular in form, sometimes incompletely developed and scalloped appearance. Wall 0,75-2,5 µm in uniformly thickness, weakly sculptures with low rugulae and in minor porportion lumina isodiametric or incomplete reticulum. Rugulae of 1 µm in width and 0,5-2 µm in high, and lumina 2-5 µm in diameter. Ornament in the central area is slighter or smooth. Marginal region weakly sculptured with rugulae and muri orientated mainly normal to equator.

Diagnosis enmendada.- Cigosporas de 44-126 µm de diámetro; de forma circular a elipsoidales, con dos hemisferios o mitades simétricas separadas por una sutura ecuatorial, mitades desplegadas o bien dobladas sobre sí mismas en forma de canoa. En cada hemisferio, se distingue una zona polar y otra ecuatorial delimitadas por un engrosamiento circumpolar ("*circumpolar ridge*") discontinuo, débil y de forma subcircular, en vista polar. Este engrosamiento, algunas veces tiene desarrollo incompleto y apariencia festoneada. Pared de 0,75-2,5 µm de grosor uniforme, débilmente esculturada con rúgulas definidas, bajas y en menor proporción lúmenes isodiamétricos o ciegos. Las rúgulas miden aproximadamente 1 µm de espesor y 0,5-2 µm de alto; los lúmenes 2-5 µm de diámetro. En la region marginal la pared está débilmente esculturada con rugulas y muros de orientacion normal.

Material estudiado.- Palo Pintado 1973a: 37,3/107,7; 36/107,4; 36,2/107; 45,9/107; 41,8/106; 2111b: 2111b: 42,7/106,5; 37/105; 35/98,5; 37,5/97,6; 35,6/99,8; 38/95,3; 94/102; 37,9/99,5; 38/105,2; 39/102,3; 35,4/106; 2111c: 39/102; 35,6/101,2; 2111a: 35/100.38,2/107; 42/102; 36,4/100,5; 34,7/102,5; 37,3/101,3; 40,9/101; 35/102; 37/99,4; 34,9/101,2. Río Vallecito: 1796d: 42,8/97,7; 1801a: 41,3/109,4; 38,7/101; 1801c: 34,4/101; 1799a: 33/105; 1799b: 44,6/102,9; 34,9/110. 1799a: 27,5/100; 28/99,6; 33/105; 38,4/98; 1799b: 44,6/102,9; 34,9/110; 1801a: 35,9/101,5; 38,7/101; 41,3/109,4. Km 107: 2267c: 40,3/96; 2268c: 42,8/103; 2387a: 49,5/102; 1949b: 45,8/100,7; 1951b: 38,2/98,3; 1942b: 36,9/104,3; 1952a: 46,2/101; 1948b: 41,5/108,5; 2267: 40,3/96.

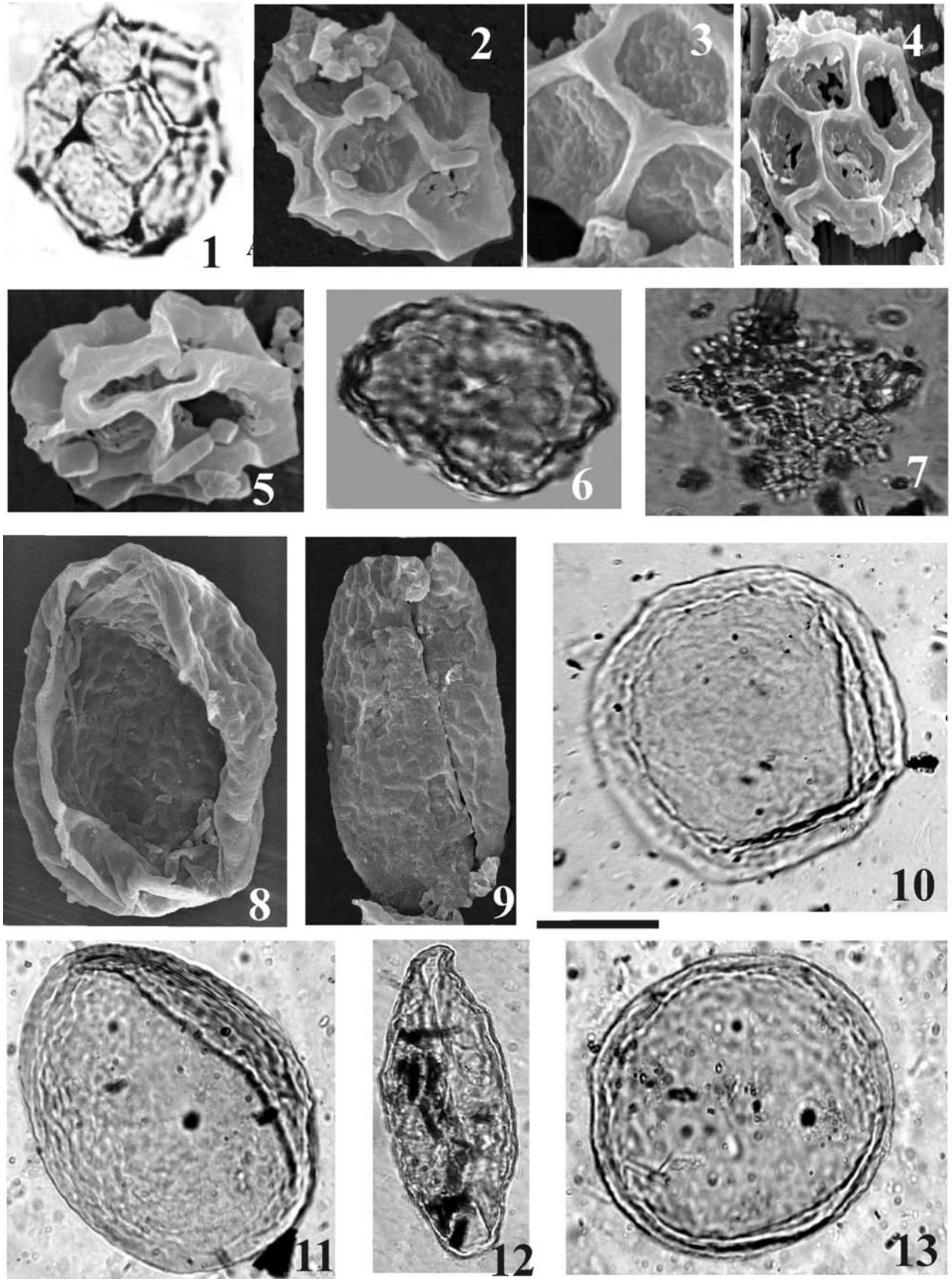
Comentarios.- En esta enmienda se amplia el rango de variabilidad del tamaño de las cigosporas, dado que el resto de los caracteres permanecen invariables con respecto a la descripción original (Batten *et al*. 1994). Estos autores incluyen cigosporas de 44 a 62 µm de diámetro. En cambio las formas halladas en este trabajo tienen dimensiones mayores desde 91 a 126 µm.

Es necesario aclarar que en la descripción original de esta especie, los autores utilizan el término engrosamiento subecuatorial (*subequatorial ridge*). En cambio aquí, para el mismo carácter, se prefiere usar engrosamiento circumpolar (*circumpolar ridge*).

Lámina 1. *1-5*, *Sphaeroplea miocenica* sp. nov. *1*, MO. CTES-PMP 2268c 41,4/99,5. Holotipo. Escala gráfica = 7 µm. *2-5*, MEB. CTES-PMP 2268. *2,3,5*. Escala gráfica = 5 µm. *3*, detalle de la superficie de los espacios poligonales. *4*, escala gráfica = 7 µm. *6*, *Oedogonium cretaceum* Zippi. MO. CTES-PMP 1926c 45,6/101,3. Escala gráfica = 8,5 µm. *7*, *Coelastrum* sp. MO. CTES-PMP 1946c 37,5/99,4. Escala gráfica = 17,5 µm. *8-13*, *Lecaniella korsoddensis* Batten, Koppelhus & Nielsen. *8-9*, MEB. CTES-PMP 2268. Escala gráfica = 13 µm. *10-13,* MO. *10*, CTES-PMP 2111a 35/100. Escala gráfica = 36 µm. *11*, CTES-PMP 2111a 40/101,4. Escala gráfica = 34 µm. *12*, CTES-PMP 2111b 42,7/106,5. *13*, CTES-PMP 2111a 38/101,3. *12, 13*. Escala gráfica = 40 µm.

Plate 1. *1-5*, *Sphaeroplea miocenica* sp. nov. *3,* detail of the polygonal spaces surface. *1*, MO. CTES-PMP 2268c 41,4/99,5. Holotype. Graphic scale = 7 µm. *2-5*, MEB. CTES-PMP 2268. *2,3,5*, graphic scale = 5 µm. *4*, graphic scale = 7 µm. *6*, *Oedogonium cretaceum* Zippi. MO. CTES-PMP 1926c 45,6/101,3. Graphic scale = 8,5 µm. *7*, *Coelastrum* sp. MO. CTES-PMP 1946c 37,5/99,4. Graphic scale = 17,5 µm. *8-13*, *Lecaniella korsoddensis* Batten, Koppelhus & Nielsen. MEB. *8-9*, CTES-PMP 2268. Graphic scale = 13 µm. *!0-13,* MO. *10*, CTES-PMP 2111a 35/100. Graphic scale = 36 µm. *11*, CTES-PMP 2111a 40/101,4. Graphic scale = 34 µm. *12*, CTES-PMP 2111b 42,7/106,5. *13,* CTES-PMP 2111a 38/101,3. *12, 13*. Graphic scale = 40 µm.

Lámina 1



Registros previos.- Dinamarca: Triásico-Jurásico (Batten *et al*. 1994). Primera cita de la especie para el Mioceno de Argentina.

Afinidad botánica y ambiente en que se desarrollan los taxones actuales afines.- Chlorophyta, Zygnemataceae, *Debarya* Wittrock (Transeau). Varios autores (Batten *et al*. 1994; Head, 1992; Hoshaw & McCourt 1988; van Geel & van der Hammen 1978; van Geel & Grenfell, 1996; entre otros) sostienen que el morfogénero *Lecaniella* es afín al género actual, *Debarya*. En cambio Zippi (1998) relaciona a *Lecaniella* con el género *Zygogonium*. Ambos géneros pertenecen a la familia Zygnemataceae.

El género *Debarya* cuenta con 10 especies que tienen una distribución cosmopolita, aunque su registro no es frecuente (Ellis & van Geel, 1978; Kadlubowska, 1984).

El ambiente en que se desarrollarían las especies de *Lecaniella* puede ser deducido de la afinidad con la familia Zygnemataceae, a la que se la relaciona con sistemas de agua dulce (Zippi, 1998). Las cigosporas pueden requerir condiciones de sequía repetidas para iniciar su germinación (Zippi, 1998).

Género *Ovoidites* Potonié 1951 *ex* Thomson & Pflug, 1953 *emend*. Krutzsch, 1959

Especie tipo.- *Ovoidites ligneolus* Potonié *ex* Krutzsch, 1959

Ovoidites parvus (Cookson y Dettman) Nakoman, 1966
Lám. 2, Figs. 5, 6

Dimensiones.- Cigosporas de 35-45 µm de largo por 44-60 µm de ancho, pared de 0,5-1 µm de espesor.

Comentarios.- La línea de dehiscencia puede ser de recorrido recto o sinuoso y en algunas ocasiones estar delimitada por pliegues, especialmente cuando la espora está dividida en dos mitades.

Cigosporas similares han sido ilustradas por van Geel *et al*. (1980, 1981), tipo 315: *Spirogyra* sp. (lámina 6, figuras 315a y 315b); *Schizosporis parvus* Cookson & Dettmann (en Barnett, 1989) en lámina 1, figura 6, *Spirogyra* sp. en lámina 1, figura 10 (Medeanic *et al*. 2000); *Ovoidites* sp. en Rich *et al*. 1982 (lámina 1, figura 1). Se han hallado características similares con *Spirogyra* sp. Tipo A (Zamaloa, 1996; lámina 1, figuras 17-19) en cuanto al contorno de la cigospora, sutura y tipo de ornamentación aunque esta última es de mayor tamaño general (47-71 µm x 102-142 µm) y el espesor de la pared es ligeramente superior (1,5 µm). También son parecidas, aunque de mayor tamaño *Spirogyra* sp. tipo C (van Geel, 1976; lámina 1, figuras 5-10) con 52-110 µm x 26-37 µm; tipo 407: *Spirogyra* (Hooghiemstra, 1984) cuyo tamaño es 23-63 µm x 69-119 µm; *Spirogyra* tipo 1 (van Geel & van der Hammen, 1978) con 40-97 µm x 18-38µm y *Ovoidites* aff. *O. parvus* (Yamamoto, 1995) con 45-127 µm x 26-52,5 µm.

Dada la abundancia de taxones con morfología semejante, los mismos deberían someterse a una exhaustiva revisión.

Material estudiado.- CTES-PMP Río Vallecito 1695e: 38/98,7; 1698f: 30/98,2; 1794a: 46,8/103,3; 43,7/96,4; 37/97,3; 45,4/99,7; 42,8/99,8; 36/107,8; 1801a: 38,8/99; 36/99,4; 1801b: 44,3/98,1; 35,2/102,2; 47/104,3; 1801d: 31,5/107,3; 1799a: 28,4/102,2; 43/98,5; 39,3/97,4; 39,4/97,8; 28,2/98,4; 37,3/100,6; 48,1/102; 1794c: 32,4/100. Km 107: 1942c: 39,5/99,1; 2268b: 41/110; 39,4/111,8; 2387b: 38,7/101,1; 1944c: 32/103; 1946d: 41/97,5; 1948b: 44,3/108,8; 42/106,6; 39,8/103,4; 45,8/103,7; 1948c: 40,8/108; 1948a: 45,7/109,1; 2265c: 42,2/110,5; Quebrada del Estanque: 1793a: 39/110,1; 2111a: 35/101; 39,5/100.

Localidades.- Río Vallecito, Km 107 y Quebrada del Estanque.

Procedencia estratigráfica y edad.- Formación San José, Mioceno Medio. Formación Chiquimil y Formación Palo Pintado, Mioceno Superior.

Registros previos.- Argentina: Triásico (Jain, 1968); Cretácico (Prámparo & Volkheimer, 2002; Prámparo *et al*. 2005); Australia: Jurásico (Filatoff, 1975); Jurásico-Cretácico (Backhouse, 1988); Cretácico (Cookson & Dettmann, 1959); Brasil: Cretácico (Lima, 1989); Terciario (Lima *et al*. 1985, 1991); Canadá: Cretácico (Pocock, 1962; Burden & Hills, 1989; Zippi, 1998); Egipto: Cretácico (Schrank & Mahmoud, 1998); Estados Unidos: Cretácico-Paleoceno (Stanley, 1965); Paleoceno (Elsik, 1968);

Eoceno (Wingate, 1983); Mioceno (Barnett, 1989); Corea: Cretácico (Sangheon, 1997); Turquía: Terciario (Nakoman; 1966).

Afinidad botánica.- Chlorophyta, Zygnemataceae, *Spirogyra* Link 1820.

Ambiente en que se desarrollan los taxones actuales afines.- El morfogénero *Ovoidites* es afín a especies actuales de *Spirogyra* (van Geel & Grenfell, 1996). Este taxón es cosmopolita, de clima tropical, templado a frío (García, 1994). Su preferencia a ambientes dulceacuícolas abiertos lo señala como indicador diagnóstico de condiciones locales. Las cigosporas de Zygnemataceae se forman en primavera, en pequeñas lagunas o bien en ríos de escasa pendiente, de aguas quietas y ricas en oxígeno. Indican que, por lo menos durante una parte del año, el agua registró temperaturas moderadamente calientes que permitieron la formación de cigosporas. Las temperaturas óptimas para el crecimiento de *Spirogyra* están entre 20 y 25 ºC, son las alcanzadas en cuerpos de agua someros que reciben radiación directa del sol por lo menos durante la estación favorable (van Geel & van der Hammen, 1978; van Geel, 1976).

Ovoidites spriggii (Cookson y Dettmann) Zippi, 1998

Lám. 2, Fig. 4

Descripción.- Cigosporas de 47-60 µm de diámetro, forma subesferoidal, con línea de dehiscencia media longitudinal. Pared de 0,5 µm de grosor con ornamentación punctada a psilada.

Material estudiado.- CTES-PMP Río Vallecito 1695c: 31/98,5; 36,9/95; 1695d: 34,6/98,2; 34/100; 1696e: 32/101,9; 1698f: 38/105,4; 1801b: 47/103,6; 35,5/107,3; 1794e: 42,7/91,4; 35/107,3; 34,6/105,5; 45,7/99.7; 1798c: 30,5/100; 1799a: 43/98,5; 1804a: 34/104,5; 31,6/103,4; 36/107; 1804b: 35,9/110,8; 45,3/102; 46,2/99,2; 34,8/102; Km 107: 2387b: 36,9/107; 2267c: 39/96,4; 2266d: 44,5/98,6; 2265c: 42,5/98,5; 1942c: 36,4/102,3; 2268b: 34,5/108,7. Quebrada del Estanque: 2111a: 42/99,5; 37,5/105.

Localidades.- Río Vallecito, Km 107 y Quebrada del Estanque.

Procedencia estratigráfica y edad.- Formación San José, Mioceno Medio. Formación Chiquimil y Formación Palo Pintado, Mioceno Superior.

Registros previos.- Australia: Cretácico (Cookson & Dettmann, 1959; Dettmann, 1963); Brasil: Cretácico (Lima, 1989); Canadá: Cretácico (Pocock, 1962; Zippi, 1998; Burden & Hills, 1989); Estados Unidos (Wingate, 1983); Corea: Cretácico (Sangheon, 1997). Primera cita para el Mioceno de Argentina.

Afinidad botánica.- Chlorophyta, Zygnemataceae, *Spirogyra*.

Ambiente en que se desarrollan los taxones actuales afines.- Ver más arriba en *O. parvus*.

Ovoidites grandis Zippi, 1998

Lám. 2, Figs. 8, 10

Dimensiones.- Cigosporas de 105-140 µm de largo por 45-49 µm de ancho; pared 0,7 µm de espesor.

Comentarios.- Estas cigosporas son de contorno elipsoidal a fusiforme con línea de dehiscencia longitudinal que con frecuencia las divide en dos partes o valvas. *Spirogyra* sp. Tipo A en Zamaloa (1996) es semejante a *Ovoidites grandis* por el tamaño, forma y disposición de la sutura; la diferencia de *Spirogyra* sp. Tipo A está en el espesor de la pared que es ligeramente mayor (1,5 µm). Las cigosporas de *Spirogyra* (lámina 1, figura 10) del Mioceno de la India (Sarkar *et al.*, 1993) son ejemplares semejantes a *O. grandis*.

Los especímenes agrupados bajo el nombre de ?*Leiosphaeridia* sp. Wood & Clendening 1985 en el Devónico de Estados Unidos son similares en algunos rasgos como la pared psilada y la línea de dehiscencia aunque superan a *Ovoidites grandis* en el tamaño general (163-297 µm) y espesor de la pared (4-10 µm).

Material estudiado.- CTES-PMP Quebrada del Estanque: 1715 a: 37,5/100,5; 2111b: 39/105,3; 36/104,1. 41,2/101,5; 43,5/100,2; 2111a: 35/100; 46,2/100 y 39/103,7.

Localidad.- Quebrada del Estanque.

Procedencia estratigráfica y edad.- Formación Palo Pintado, Mioceno Superior.

Registro previo.- Argentina: Terciario (Zamaloa, 1996); Canadá: Jurásico-Cretácico (Pocock, 1962); Cretácico (Zippi, 1998); China: Eoceno-Oligoceno (Song & Liu, 1982); Estados Unidos: Cretácico (Hedlund 1966); India: Mioceno (Sarkar *et al*., 1993).

Afinidad botánica.- Chlorophyta, Zygnemataceae, *Spirogyra*.

Ambiente en que se desarrollan los taxones actuales afines.- Ver más arriba en *O. parvus*.

Ovoidites sp. 1
Lám. 2, Figs. 7, 9

Descripción.- Cigosporas de 64-66 µm de largo por 18-19,6 µm de ancho, de contorno elipsoidal con ápices agudos. Sutura longitudinal media. Pared de 0.7-1 µm de espesor, supracorrugada en sentido del eje longitudinal. Las fotografías al microscopio electrónico de barrido permiten corroborar la escultura observada al microscopio óptico.

Comparaciones.- *Spirogyra* sp. Tipo C en Zamaloa (1996) es similar a *Ovoidites* sp. 1 en particular por la ornamentación de la pared, aunque aquella especie tiene mayor tamaño general (25-38 µm x 60-107 µm). Igual situación se presenta con *Spirogyra* sp. 3 del Holoceno de Argentina (Borel *et al*. 2003) que posee dimensiones de 47-59 µm x 100-103 µm. *Ovoidites* sp. (Prámparo *et al*. 2005) del Cretácico de Argentina es similar a estos palinomorfos, por las dimensiones del largo de la cigospora y escultura de la pared, aunque aquella especie presenta un ancho mayor (42 µm).

Material estudiado.- CTES-PMP Quebrada del Estanque: 1973a: 47/104,1; 48,9/102; 68,4/98,2; 1715: 45,6/98.

Localidad.- Quebrada del Estanque.

Procedencia estratigráfica y edad.- Formación Palo Pintado, Mioceno Superior.

Afinidad botánica.- Chlorophyta, Zygnemataceae, *Spirogyra*.

Ambiente en que se desarrollan los taxones actuales afines.- Ver más arriba en *O. parvus*.

Ovoidites sp. 2
Lám. 2, Fig. 3

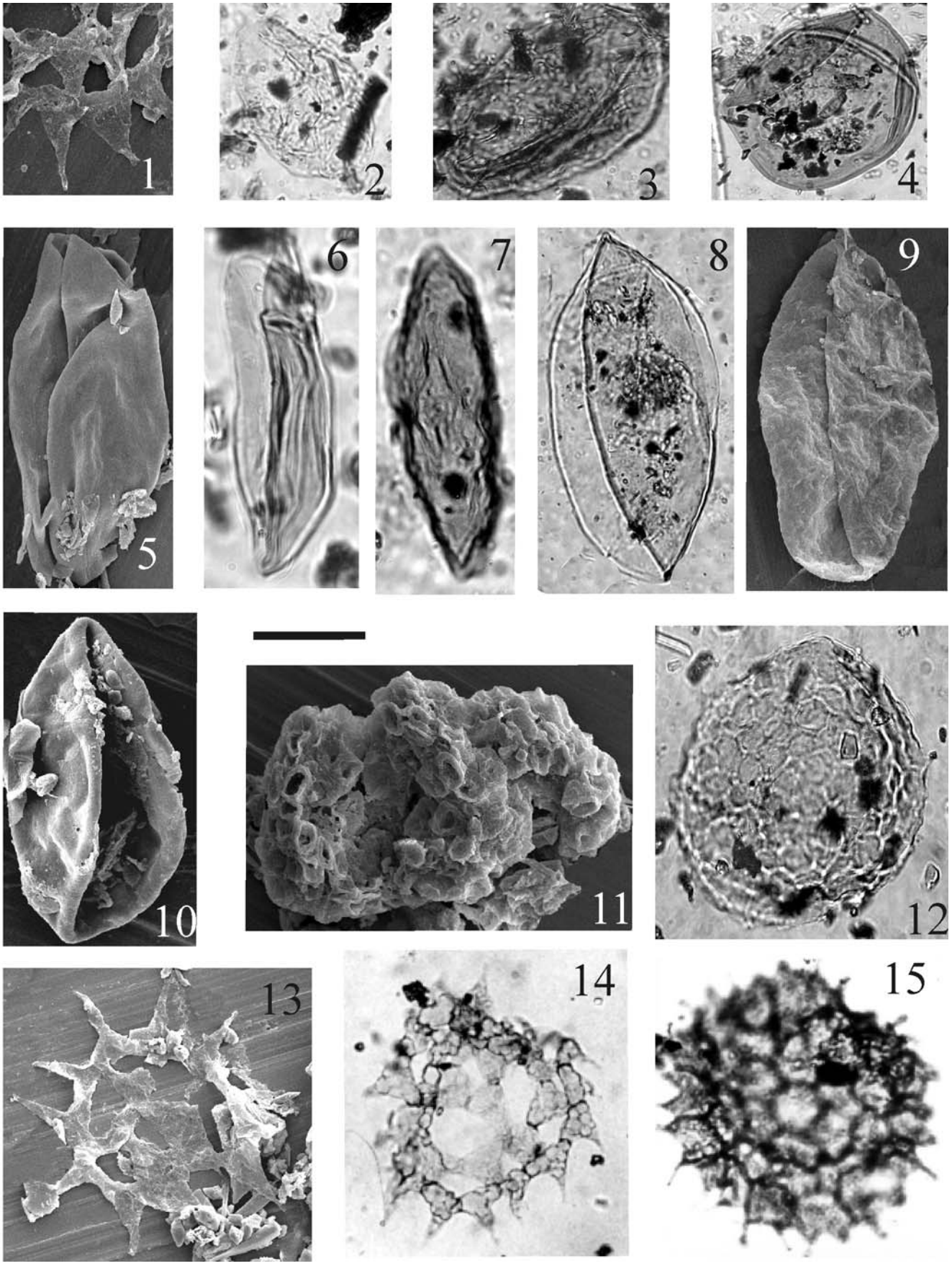
Descripción.- Cigosporas de 67-70 µm de largo por 35-46 µm de ancho, de contorno ovalado. Sutura longitudinal. Pared engrosada de 3 µm de espesor, con un retículo de lúmenes ciegos, muros de 1-2 µm de grosor de recorrido algo sinuoso.

Comparaciones.- Similar a *Spirogyra* sp. Tipo B (Zamaloa 1996) por el tamaño general de las cigosporas, aunque esa especie posee un retículo más definido y completo que las formas aquí descriptas. *Ovoidites ligneolus* (Potonié) Thomson & Pflug 1953, en Stanley 1965, tiene tamaño semejante (72 µm de largo x 36 µm de ancho) y posee como estos palinomorfos, un retículo incompleto, pero se diferencia porque los muros están más próximos entre sí y son más notorios.

Lámina 2. *1, 13,14 Pediastrum simplex* (Meyen) Lemmerman. *1, 13*, MEB. CTES-PMP 1795. Escala gráfica = 40 µm. *14*, MO. CTES-PMP 1795b 57,9/98,6. Escala gráfica = 44 µm. *2*, *Cymatiosphaera* sp. MO. CTES-PMP 1948c 41/109,6. Escala gráfica = 35 µm. *3*, *Ovoidites* sp. 2. MO. CTES-PMP 1948b 44,1/106,4. Escala gráfica = 25 µm. *4*, *Ovoidites spriggi* (Cookson & Dettmann) Zippi. MO. CTES-PMP 2387b 36,9/107. Escala gráfica = 30 µm. *5-6*, *Ovoidites parvus* (Cookson & Dettman) Nakoman. *5*, MEB. CTES-PMP 2021. *6*, MO. CTES-PMP 2268c 39,4/101,5. *5-6*, Escala gráfica = 40 µm. *7,9, Ovoidites* sp.1. *7*, MO. CTES-PMP 1793a 47/104,1. *9*, MEB. CTES-PMP 1715. *7,9,* Escala gráfica = 22 µm. *8, 10*, *Ovoidites grandis* Zippi. *8*, MO. CTES-PMP 2111b 44,5/106. *10*, MEB. CTES-PMP 1715. *8, 10,* Escala gráfica= 46 µm. *11*, *Botryococcus braunii* Kützing. MEB. CTES-PMP 2265. Escala gráfica = 23 µm. *12*, *Schizosporis* sp. MO. CTES-PMP 2021a 39,9/105. Escala gráfica = 39 µm. *15*, *Pediastrum boryanum* var. *longicorne* Reinsch. MO. CTES-PMP 2032a. Escala gráfica= 30,5 µm.

Plate 2. *1, 13,14 Pediastrum simplex* (Meyen) Lemmerman. *1, 13*, MEB. CTES-PMP 1795.Graphic scale = 40 µm. *14*, MO. CTES-PMP 1795b 57,9/98,6. Graphic scale = 44 µm. *2*, *Cymatiosphaera* sp. MO. CTES-PMP 1948c 41/109,6. Graphic scale = 35 µm. *3*, *Ovoidites* sp. 2. MO. CTES-PMP 1948b 44,1/106,4. Graphic scale = 25 µm. *4*, *Ovoidites spriggi* (Cookson & Dettmann) Zippi. MO. CTES-PMP 2387b 36,9/107. Graphic scale = 30 µm. *5-6, Ovoidites parvus* (Cookson & Dettman) Nakoman. *5*, MEB. CTES-PMP 2021. *6*, MO. CTES-PMP 2268c= 39,4/101,5. *5-6,* graphic scale = 40 µm. *7,9, Ovoidites* sp.1. *7*, MO. CTES-PMP 1793a 47/104,1. *9*, CTES-PMP 1715. *7,9, graphic scale* = 22 µm *8, 10*, *Ovoidites grandis* Zippi. *8*, CTES-PMP 2111b 44,5/106. *10*, CTES-PMP 1715. *8, 10, graphic scale* graphic scale = 46 µm *11*, *Botryococcus braunii* Kützing. CTES-PMP 2265. Graphic scale = 23 µm *12*, *Schizosporis* sp. CTES-PMP 2021a 39,9/105. Graphic scale = 39 µm. *15*, *Pediastrum boryanum* var. *longicorne* Reinsch. CTES-PMP 2032a. Graphic scale = 30,5 µm.

Lámina 2



Material estudiado.- CTES-PMP Km 107 1948b: 44,1/106,4; 44,6/100,2; 1948c: 42/109,4; 2268c: 40,5/103; 44/105; 1841c: 40/104,3.

Localidad.- Km 107.

Procedencia estratigráfica y edad.- Formación San José, Mioceno Medio.

Afinidad botánica.- Chlorophyta, Zygnemataceae, *Spirogyra*.

Ambiente en que se desarrollan los taxones actuales afines.- Ver más arriba en *O. parvus*.

Género *Schizosporis* (Cookson & Dettmann) Pierce, 1976

Especie tipo.- *Schizosporis reticulatus* Cookson & Dettmann, 1959

Schizosporis sp.
Lám. 2, Fig. 12

Descripción.- Cigosporas de 70-98 µm de diámetro, ámbito subcircular a elipsoidales, con sutura. Pared de 3 µm de espesor, dividida en lúmenes o sectores bien delimitados levemente poligonales, de 4-7 µm de diámetro de disposición regular y muros de 1 µm de espesor.

Comparaciones.- *Schizosporis reticulatus* Cookson & Dettmann 1959 del Cretácico de Australia, posee tamaño y pared de mayores dimensiones (90-135 µm y 7-11 µm, respectivamente) aunque tienen lúmenes de diámetros similares.

Schizosporis complexus Stanley 1965 tiene tamaño menor (36-60 µm) y los lúmenes son ligeramente más pequeños (3 µm), pero difiere principalmente porque presenta muros duplibaculados.

Material estudiado.- CTES-PMP Km 107: 1952c: 40/105,9; 38,2/105,9; 40/104,2; 1948b: 44,9/100; 45/101,1; 45,8/102; 43/104,5; 42,3/105,5. Quebrada del Estanque: 2021a: 46,9/100; 39,9/105.

Localidades.- Km 107 y Quebrada del Estanque.

Procedencia estratigráfica y edad.- Formación San José, Mioceno Medio. Formación Palo Pintado, Mioceno Superior.

Afinidad botánica.- Chlorophyta, Zygnemataceae, probablemente *Spirogyra*. (Martin-Closas 2003; Head, 1992).

INCERTAE SEDIS
Género *Cymatiosphaera* (O. Wetzel) Deflandre, 1954

Especie tipo.- *Cymatiosphaera radiata* O. Wetzel, 1933

Cymatiosphaera sp.
Lám. 2, Fig. 2

Descripción.- Esporas de 66-75 µm de diámetro, inaperturadas, ovoides a esferoidales. En algunas formas se observa línea de sutura. Pared de 0,7-1 µm de espesor, superficie externa dividida en campos poligonales por membranas delgadas, lisas, rectas a ligeramente sinuosas, de 1 µm de alto. Campos poligonales irregulares, de 4-8 µm de diámetro (algunos de ellos son ciegos).

Comparaciones.- *Cymatiosphaera* sp. ilustrada en Barreda (1997a) posee menor tamaño (22 µm), aunque es bastante similar al material de este trabajo. *Cymatiosphaera* sp. Wood & Clendening 1985 del Devónico de Estados Unidos tiene el mismo diámetro, aunque difiere por su contorno circular, campos poligonales de mayor tamaño (12-18 µm) y muros de espesores superiores (2-3 µm). *Cymatiosphaera pachyteca* Eisenack 1957 en Davies (1985) del Jurásico de Portugal posee semejante estructura en comparación a estas formas aunque sólo se halla ilustrada. *Cymatiosphaera* sp. 1 del Jurásico de Argentina (Martínez *et al.,* 2005) es similar en el tamaño general, membranas rectas a levemente sinuosas y pared lisa, aunque esta última tiene mayor espesor (3 µm) y los polígonos son de diámetros superiores (13-25 µm) comparándolos con los ejemplares aquí descriptos.

Material estudiado.- CTES-PMP Río Vallecito 1695a: 36,4/96,4; 46,6/92; 1799a: 98/45; Km 107: 2268b: 37/100; 1948a: 33,5/103,7; 1948b: 47/103,4; 45,5/108,8; 40/106; 1948c: 41/109,6; 1839c: 36/102,5; Quebrada del Estanque: 1992a: 67/89; 2921a: 51,4/100,7; 2020a: 37,6/97,5; 2035b: 43,7/99,6; 2051a: 47,8/102,4.

Localidades.- Río Vallecito y Quebrada del Estanque.

Procedencia estratigráfica y edad.- Formacion Chiquimil y Formación Palo Pintado, Mioceno Superior.

4. DISCUSIÓN Y CONCLUSIONES

En los niveles palinológicos diferenciados en las 3 localidades estudiadas se estableció la frecuencia relativa de las algas con respecto a los restantes integrantes de las asociaciones polínicas (magnoliófitas, pinófitas, pteridófitas, algas y briófitas) (Tabla 1).

En Quebrada del Estanque (Formación Palo Pintado) los 11 niveles reconocidos (Acevedo *et al*. 1998) se los agrupó en 3 grandes secciones: sección con algas (cuando la frecuencia de algas supera o llega a los 90%), sección con vegetales terrestres (el conjunto de briófitas, pteridófitas, pinófitas y magnoliófitas experimenta el mismo aumento) y secciones mixtas (cuando la presencia de algas llega al 30 % y el resto son elementos terrestres). De ellos, 5 pertenecen a la seción con vegetación terrestre, 4 a la sección con algas y 2 son mixtos. Cuando la proporción de vegetación terrestre domina, las algas son escasas y en niveles mixtos su contenido se equilibra. En los niveles donde las algas son muy abundantes la presencia casi excluyente de las especies *Pediastrum simplex* (Meyen) Lemmermann y *Pediastrum boryanum* var. *longicorne* Reinsch permitió inferir el carácter eutrófico de los cuerpos dulceacuícolas con elevado aporte de nutrientes.

En la localidad Km 107 no se aprecian variaciones verticales entre los 8 niveles y las algas tienen un registro continuo, con valores relativos bajos que oscilan entre el 5 al 13% del espectro palinológico. Solamente en los niveles 2, 6 y 8, la especie más frecuente entre las algas es *Sphaeroplea miocenica* sp. nov. seguida de *Ovoidites parvus* (Cookson & Dettmann) Nakoman y *Lecaniella korsoddensis* Batten, Koppelhus & Nielsen.

Por último en Río Vallecito el porcentaje de algas muestra variaciones verticales. En los niveles 2,5 y 7 la frecuencia de algas es abundante donde las especies más representadas son *Ovoidites parvus y O. spriggi* (Cookson & Dettmann) Zippi; que tambien están en el nivel 4 a las que se suma *Lecaniella korsoddensis*. Uno de ellos (nivel 3) registra bajo porcentaje y los demás niveles muestran ausencia de algas.

Desde el punto de vista paleoambiental, y de acuerdo a las características sedimentológicas de las localidades analizadas, unidas al requerimiento ecológico de las especies actuales afines a los palinomorfos estudiados se infiere que estos taxones de Chlorophyta, integraban comunidades dulceacuícolas situadas en lagunas o charcas someras, efímeras, con disponibilidad significativa de luz, pocos sólidos en suspensión, y oligotróficos a eutróficos. Estos cuerpos de agua se ubicaban en las planicies de inundación de ríos de escasa corriente. Las temperaturas en primavera habrían sido moderadas (20-25ºC), como lo señalan las condiciones para el desarrollo de la formación de las cigosporas tanto de Zygnemataceae como de Sphaeropleaceae. Las condiciones ambientales

Niveles / Localidades		1	2	3	4	5	6	7	8	9	10	11
Km 107		<15	<15	<15	<15	<15	<15	<15	<15			
Qda. del Estanque	%	<15	70-100	15-30	<15	15-30	70-100	<15	70-100	<15	70-100	<15
Río Vallecito		0	15-30	<15	15-30	30-70	0	30-70	0	0		

Tabla 1. Porcentajes relativos de las algas en los niveles polínicos de cada localidad estudiada.
Referencias: 0=ausente, menos del 15%=escaso, 15-30%= medio, 30-70%= abundante, 70-100%= muy abundante.

Table 1. Relative percentages of alga at pollinic level in every studied location .
References : 0 = absent, less than 15 %= scanty, = 15 –30 %= average, 30-70 % =abundant, 70 – 100 %=very abundant.

Taxones \ Formaciones	San José	Palo Pintado	Chiquimil
Sphaeroplea sp.nov.	+	–	–
Ovoidites sp. 2	+	–	–
Oedogonium cretaceum	+	+	–
Coelastrum sp.	+	+	–
Schizosporis sp.	+	+	–
Lecaniella korsoddensis	+	+	+
Botryococcus braunii	+	+	+
Ovoidites parvus	+	+	+
Ovoidites spriggi	+	+	–
Cymatiosphaera sp.	+	+	+
Ovoidites sp.1	–	+	–
Pediastrum simplex	–	+	–
Pediastrum boryanum var. *longicorne*	–	+	–
Ovoidites grandis	–	+	–

Tabla 2. Distribución de las especies de Chlorophyta en la Formación San José, Palo Pintado y Chiquimil. Referencias: += presencia, – = ausencia .

Table 2. Distribution of Chlorophyta species in San José, Palo Pintado and Chiquimil Formations. += presence; – = absence.

óptimas favorecieron la abundancia y diversidad de las especies de algas.

Desde el punto de vista de la distribución vertical de las especies, en el cuadro 2, se destaca que *Sphaeroplea miocenica* sp. nov. y *Ovoidites* sp. 2 están registradas únicamente en la Formación San José. En tanto que *Ovoidites grandis* Zippi, *Ovoidites* sp 1, *Pediastrum boryanum* var. *longicorne* y *Pediastrum simplex* son exclusivas de la Formación Palo Pintado. La Formación Chiquimil carece de elementos exclusivos. En cambio, las especies comunes en las tres formaciones son: *Lecaniella korsoddensis, Botryococcus braunii* Kutzing, *Ovoidites parvus* y *O. spriggi*. (Tabla 2).

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Coprophilous fungi as a source of information of anthropic activities during the Prehistory in the Amblés Valley (Ávila, Spain): The archaeopalynological record

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Abstract

Ever since the Neolithic, pastoral activities have a long record at all the sites studied in the Amblés Valley, with arable agriculture being plausible throughout the 3rd millennium cal. BC. All sites show evidence forest clearance with associated agricultural expansion in the Chalcolithic. Comparing the palynological record of eleven archaeological sites shows it is suggested that pastoralism played a major role in prehistorical economy. This contrasts with the evidence for pastoral activity where the pollen and non-pollen palynomorphs evidence is consistent. Coprophilous fungi assemblages of the Prehistory from the Amblés Valley (Ávila, Spain) are described.

***Keywords*:** Palynology, coprophilous fungi, Quaternary, Prehistory, Amblés Valley, Spain

Resumen

Las actividades pastorales tienen un registro muy amplio en los sitios estudiados en el Valle Amblés, desde el Neolítico, documentándose agricultura a partir del III milenio cal. BC. En los yacimientos calcolíticos se denota la deforestación del bosque asociada a la expansión de la agricultura. El registro palinológico de los once yacimientos arqueológicos estudiados confirma que el paisaje inferido estuvo determinado por actividades pastorales, las cuales jugaron un papel fundamental en la economía prehistórica. Estos datos contrastan con la evidencia palinológica y de microfósiles no polínicos que atestiguan tal tipo de actividad. Se describen los cortejos de hongos coprófilos del Valle Amblés (Ávila, España) durante la Prehistoria.

***Palabras clave*:** Palinología, hongos coprófilos, Cuaternario, Prehistoria, Valle Amblés, España

1. INTRODUCTION

In prehistoric times human activity frequently had a profound effect on the vegetation landscape. It therefore registered in the pollen rain and hence, today, can be recognised in pollen diagrams (Behre, 1988). The value of the pollen diagram in elucidating the human role in vegetational changes was first clearly demostrated by the classic works of Iversen (1941, 1949), who, at the same time, distinguished those pollen taxa which reflect human occupation and economy. In conclusion, human impact on the vegetation in the past can be deduced from the presence of anthropogenic indicators in the records of pollen and by studying botanical macro-remains from archaeological sites (López García *et al.*, 1997).

Nevertheless, the development of anthropic activities, especially of the cattle raising and the shepherding, are difficult to specify only keeping in mind the pollen indicators, since some of them (e.g. *Plantago* sp, *Rumex*

sp, *Urtica* sp, Chenopodiaceae) can be at the same time indicators of areas shepherded as of habitats or nitrophilous pierces for the man (Behre, 1981; Carrión, 2001). For instance, the presence of *Urtica* pollen has been interpreted usually as the reflect of pastoral activities (Galop, 1998); hovewer relatively high values of *Urtica* are also characteristic in some "regional" phenomenon where the dying-off of the birches enriched the soil with nitrate, which could have been favourable for the growth of *Urtica* (van Geel *et al.*, 1981: 404). In these cases, the use of other more precise indicators (non-pollen palynomorphs), at the microhabitat level, can help us firmly to elucidate the origin and development of such activities (van Geel, 1986, 2001; van Geel *et al.*, 2003; Carrión & Navarro, 2002).

2. COPROPHILOUS FUNGI

Herbivorous animals grazing on vegetation ingest many fungal spores along with their food. Coprophilous (dung-loving) fungi are uniquely adapted to herbivore dung. They are deposited with dung, and they grow and reproduce there. They disperse their spores from the heap to a location from which they will be consumed by a herbivore, pass through its gut, and again be deposited with the dung heap (Bell, 2005). Some of the fungi will be coprophilous, and these usually have thick-walled, pigmented spores that require passage through the gut of an animal to germinate (Bell, 1983). The high temperature and enzymes in the digestive tract of the animal will kill most of the other fungal spores they ingest. Once the dung is voided, the viable fungal spores will germinate, grow and fruit on the dung. The spores are usually forcibly discharged into the vegetation surrounding the dung; another grazing animal comes along, eats the vegetation and the cycle is repeated.

Dung consists of the macerated and undigested remains of plant food plus vast quantities of bacteria (mostly dead) as well as animal waste products, such as broken-down red blood cells and bile pigments (Richardson, 2001). The nature of herbivore dung depends on the efficiency of the digestive tract, which, in turn, depends on the animal's digestive anatomy and its microflora. Rumiants produce a fine-textured dung of fibrous plant material whereas horses, with a less efficient system, produce much coarser dung (Bell, 1983, 2005). Dung decomposes rapidly because the macerated material has a high nitrogen content, available aeration, and a high water content that is protected from fluctuations. Although there is little available protein in dung, many other undigested food components are present. Dung is rich in water-soluble vitamins, growth factors, and mineral ions, some of which are metabolic by-products of the microbes in a herbivore's gut. For example, coprogen, an organo-iron compound found in dung, is necessary for the growth and reproduction of the fungus *Pilobolus crystallinus* (Bruce *et al.*, 1960). Dung also contains a large amount of readily available carbohydrates.

Considering the great variation in the feeding habits, habitats, and digestive systems of herbivores, it is surprising how universal coprophilous fungi are (Webster, 1970; Bell, 1983). Some species are restricted to a particular herbivore; for example, *Lasiobolus cainii* is found only on porcupine dung (Webster, 1970). However, many coprophilous fungi grow indiscriminately on any herbivore dung (Bell, 2005). The greatest variety of fungi have been reported on cow, rabbit, and horse dung, but this could be because the majority of research has focused on these animals. Coprophilous fungi are highly specialized for growth on dung, and some never occur elsewhere. While some dung fungi show few modifications peculiar to their habitat, most do have some unique features. Many exhibit some very specialized structures to ensure survival in their unique habitat (Richardson, 2001; Bell, 2005).

The analysis of fossil fungal spores is a rather unexplored field in archaeopalynology. Fungal remains and other non-pollen palynomorphs present in the microscope slides normally are not recorded in palynological studies (van Geel, 2001; Carrión & Navarro, 2002). However, during the last years the possible paleo-environmental indicator value of fungal spores and various other extra palynomorphs from archaeological and natural sites of the Iberian Peninsula was studied (López Sáez *et al.*, 1998, 2000; Carrión, 2001; Carrión & Navarro, 2002). Not all fungal spores do preserve as fossils, just only some taxa can be distinguished and recorded and preservation depends on the thickness of wall of spores and mycelium. As a consequence, only spores of thick-walled Ascomycetes and Dematiaceae are normally preserved (van Geel,

1992). In fact, Graham (1962) has remarked that if the fossil fungi are sufficiently diagnostic to allow precise identification, they can serve as index fossils and environmental indicators, placing one more group of organism to the disposal of the stratigrapher and paleoecologist (Taylor & Osborn, 1996).

Although only some of the fungal taxa can preserve, the records show that some fungi represent a new category of secondary anthropogenic indicators (López Sáez *et al.*, 1991, 1998, 2000; Galop & López Sáez, 2002; van Geel *et al.*, 2003). Among the recorded fungal spores were representatives of the Sordariaceae (Ascomycetes), most of them are coprophilous and often so specialized that they only grow on the dung of a single or of only a few species of animals (van Geel, 1992). In several studies of settlement sites palynological indications were found for the presence of fungi related with animal or human dung (van Geel, 1978). Sordariaceae presently comprises 7-10 genera (Eriksson *et al.*, 2004). These fungi have primarily been differentiated on ascospore morphology and ornamentation (Lundqvist, 1972), but their intergeneric relationships are, however, unclear (Cai *et al.*, 2006).

In the present paper we analysed the fossil record of Sordariaceae (*Cercophora*, *Sordaria*, *Sporormiella*) in the palynological record of archaeological sites from the Amblés Valley (Ávila, Central Spain). Other non-pollen palynomorphs, like the types 169 (*Tripterospora* type, ascospores) or 386 (*Podospora* type, ascospores), which sordariaceous origin seems likely, have been also related with the presence of man or cattle providing dung as a substrate (van Geel *et al.*, 1981, 2003; van Geel, 1986, 2001), but they have been not recorded yet.

Fossil ascospores of the coprophilous *Cercophora* type (type 112) were first recognized by van Geel (1978). They are very scarce in the early Holocene deposits of central and western Europe, but its spores occur regularly with low percentages from the start of forest disturbance onwards (Lundqvist, 1972; van Geel *et al.*, 1981). This may be related to increased populations of large wild, and possible also domesticated, herbivores in the different studied areas (Ralska-Jasiewiczowa & van Geel, 1992). The fungi of the *Cercophora* type take advantage of an increased dung production. The species of the genus *Cercophora* occur also on decaying wood, culms, stems and leaves (Lundqvist, 1972; van der Wiel, 1982). In conclusion, the fossil record shows circumstantial evidence that the presence of ascospores of the *Cercophora* type can often be used as an indicator for dung in the surroundings of the sample site (van Geel, 2001: 106; van Geel *et al.*, 2003).

The type 55, corresponding probably an ascospore from a sordariaceous species, has been described as an indicator of grazing activities (López Sáez *et al.*, 2000). However, the ascospores of *Neurospora* sp (type 55C) indicate the incidence of a local bob fire (van Geel, 1986: 503, 2001: 107). Most species of *Neurospora* have been reported from soil and none occur on dung (Cai *et al.*, 2006). Fungal ascospores of the type 55A (*Sordaria* type) have been described by van Geel (1978), and divided into two subtypes (55A1 and 55A2) by van Geel *et al.* (1981: 418) according its different size and their presence in different sediments, but sometimes it appeared to be impossible to split up the sordariaceous type 55A spores (van Geel *et al.*, 1983). *Sordaria* species have ascospores that are smooth-walled with a basal germ pore and gelatinous sheath (Guarro & Arx, 1987). The ocurrence of type 55A and 55B is conceivably attributable to the presence of dung as a substrate, and its high values have been related to a relatively important anthropogenic influence on the landscape (van Geel *et al.*, 1981: 418-419). They are both coprophilous taxa usually found in settlements (van Geel *et al.*, 2003). Most *Sordaria* species are strictly coprophilous (Guarro & Arx, 1987).

Ascospores of extant *Sporormiella* species (type 113) are common on the dung of domestic herbivores such as sheep, cows, goats, burros, and horses, and on the dung of living megaherbivores including moose, wild sheep, deer, elk, and caribou (Davis, 1987: 290; Burney *et al.*, 2003). They are also common on rabbit dung, are occasionally found on the dung of other animals, and have been found on decaying wood (Ahmed & Cain, 1972). The distinctive dark brown spores of the genus have a pronounced sigmoid germinal aperture and are divided by three to many septa, the spores separating into individual cells at the septa. In the fossil record this non-pollen palynomorph has been recorded usually only as individual cells (van Geel *et al.*, 2003). *Sporormiella* spores have been directly linked to extinct megaherbivores by their abundance in mammoth dung from Late Pleistocene sediments in Utah, and presumably, the spore percentages

during the late-glacial reflect population densities of herbivores equivalent to those of modern grazing mammals (Davis, 1987; Davis & Shafer, 2006). The previously mentioned data can help us to conclud that increased quantities of the spores can be used as indicators of dung, produced by relatively high density populations of domestic herbivores (van Geel, 2001: 107). In conclusion, most *Sporormiella* species are coprophilous.

3. THE STUDIED AREA

The Amblés Valley is bounded to the north by the bulk of Ávila Range, which rise to an altitude of *ca.* 1700 m, and to the south by Parameras Range (*ca.* 2200 m) (Fig. 1). With an extension of 374 km2, a longitude of 42 km from southeast to northwest, and a width that it oscillates between 3 and 10 km, is a graben formed by several blocks of the sunken baseboard defined by the alignment of Serrota Range, Paramera Range and Cuerda de los Polvisos Range by the south, and in tectonic contact for the north with the southern Ávila Range.

In terms of both archaeology and history, the Amblés Valley and the narrow passage at Gredos Range have always functioned as a principal trade route between the North Plateau and the South Plateau including Extremadura. Its position has been pivotal to the development not only of the Gredos Range, but also of significant parts of Spanish Central System. Although surveyed from an archaeological point of view (Fabián García, 1995, 2003), the area

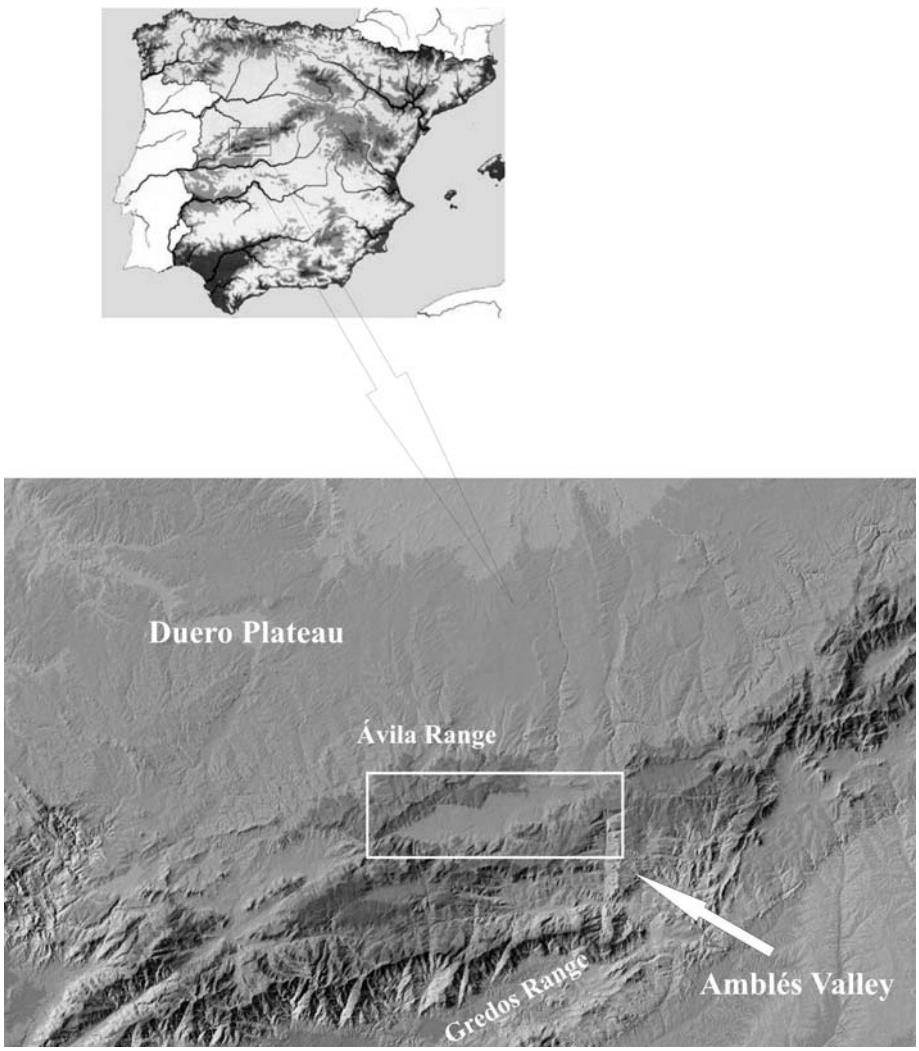

Figure 1. Location of the study area.

has never been the subject of a major academic landscape and environmental archaeology research programme, despite its long chronology of habitation, almost from the Neolithic to recent history.

Current vegetation is a mosaic formed by a great variety of plant communities. This diversity is due to important environmental differences in altitude, aspect, topography and human usage. The vegetation in the valley is dominated by *Quercus ilex and Fraxinus angustifolia* forest while slopes are dominated by *Quercus pyrenaica*. However, most of the area has been cleared and open lands influenced by agropastoral activities are the predominant landscape types in the valley. Agriculture is intensively developed on fluvioglacial deposits.

4. THE FOSSIL RECORD

Eleven archaeological sites were selected in the area for pollen analysis, one from the Neolithic and ten from the Chalcolithic. Table I shows a list of coprophilous fungi, their incidence of occurrence (percentages), and distribution among archaeological sites from the Amblés Valley during two cultural periods (Neolithic and Chalcolithic).

The pollen diagram of the 11 archaeological sites are presented in Figures 2 to 12. The diagrams, including all the components of the different vegetation strata, gives information about reciprocal influences between AP (arboreal pollen) and NAP (non-arboreal pollen).

5. DISCUSSION AND CONCLUSIONS

During the Late Neolithic (4th millennium cal. BC) the pollen diagram of the archaeological site of Dehesa Río Fortes (Fig. 2) show the increase of meadow and ruderal-land communities that provides evidence of the increased human pressure (pastoralism) on the landscape (López Sáez, 2002). It is notable that traces of crop cultivation are not represented.

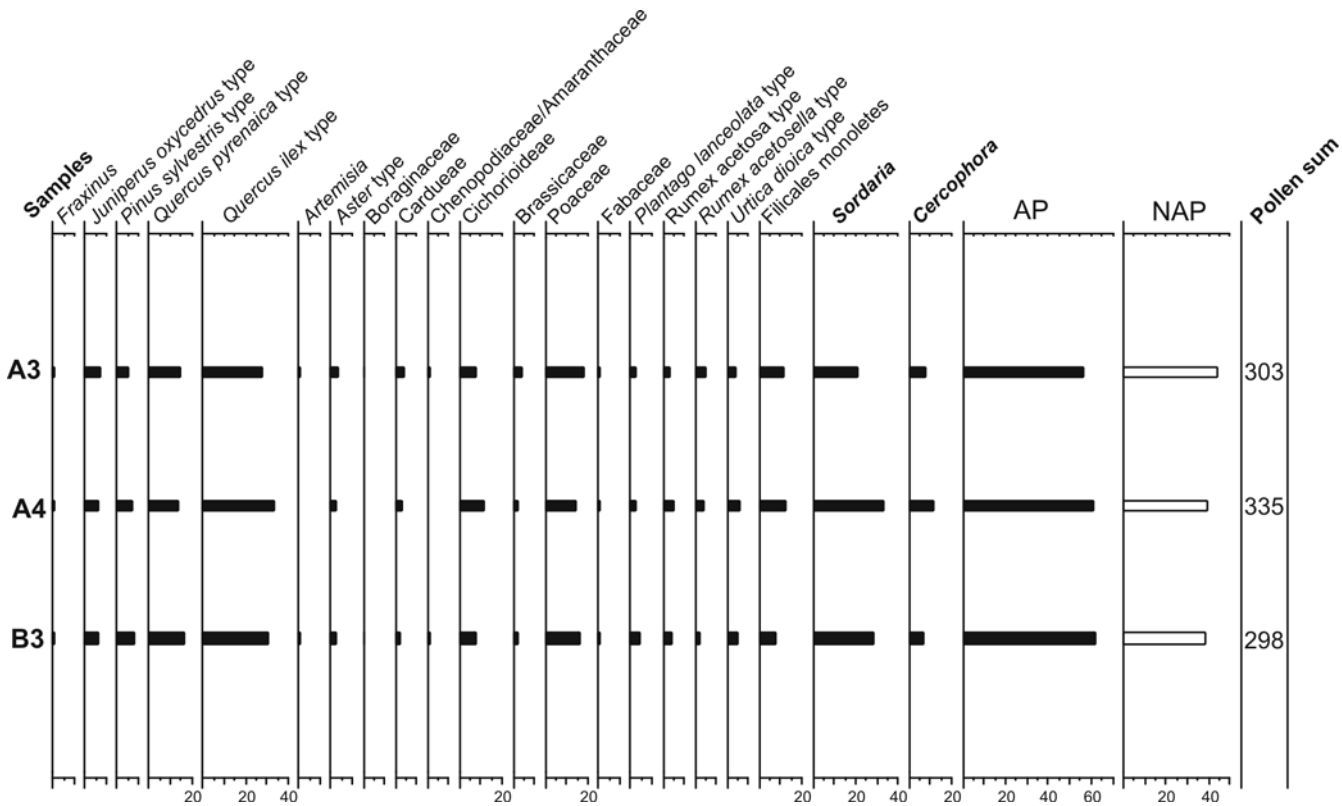

Figure 2. Pollen diagram from the neolithic site of Dehesa Río Fortes.

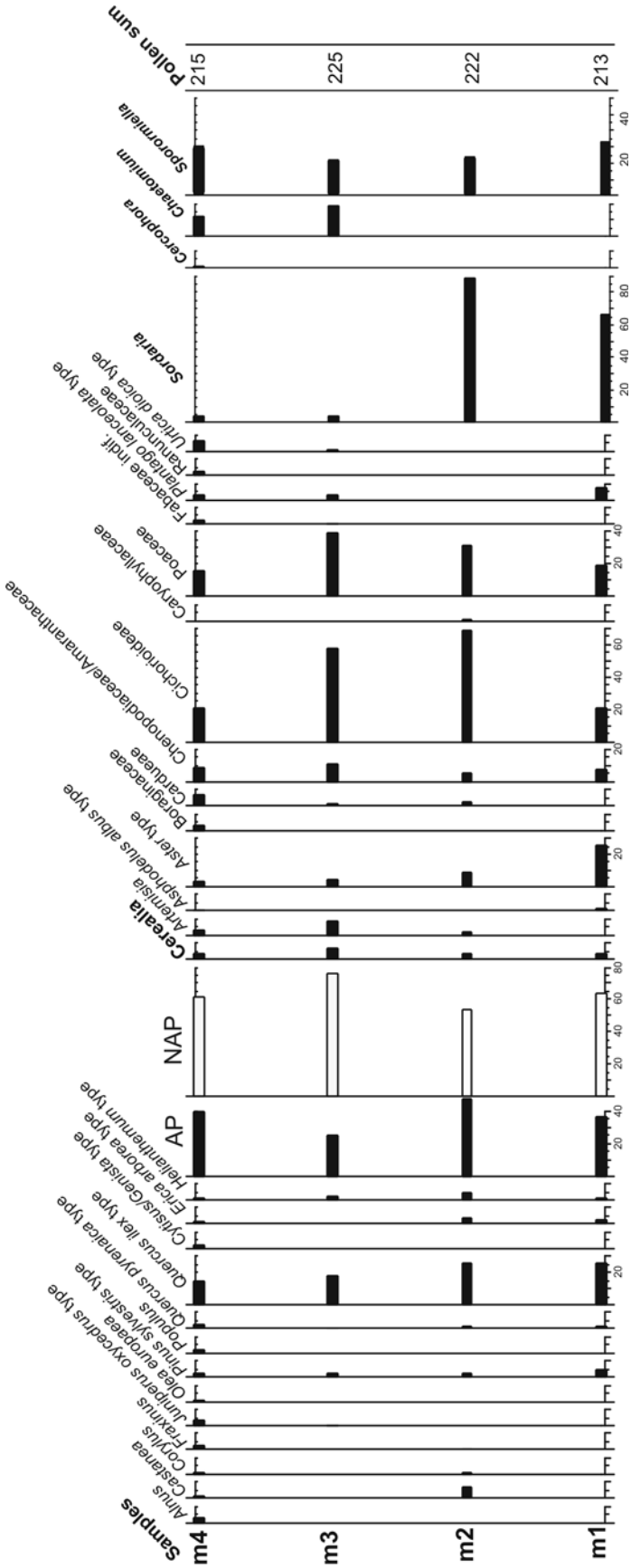

Figure 3. Pollen diagram from the chalcolithic site of Aldeagordillo.

The landscape at the 3rd millennium cal. BC (Chalcolithic) is characterized by open evergreen oak forests (Figs. 3-12). At this time, an increase in farming activity occurs, led by pastoralism. Pollen diagrams from archaeological sites of this period (Aldeagordillo Fig. 3, Cerro de la Cabeza Fig. 4, Cerro Hervero Fig. 5, Fuente Lirio Fig. 6, El Picuezo Fig. 9, Tiro de Pichón Fig. 11 and Valdeprados Fig. 12) show the occurrence of Cerealia pollen type. Throughout most of the 3rd millennium crop farming seems to have played a major role in the agricultural activities near archaeological sites. The values for arboreal taxa fall associated with farming and pastoralism activities. We can also conclud that fire was used ad a means of clearing the landscape since values of carbonicolous fungi (*Chaetomium* sp) are high (López Sáez *et al.*, 1998), specially at Cerro Hervero (20%, Fig. 5), El Picuezo (>30%, Fig. 9) and Los Tiesos (*ca.* 20%, Fig. 10) pollen diagrams. The curves of Poaceae, Chenopodiaceae/Amaranthaceae, *Plantago lanceolata* type and *Urtica dioica* type expand, indicating pastoral activities (Behre, 1981) in the surroundings of archaeological sites (López Sáez *et al.*, 2003).

Most of the three coprophilous fungi recorded were very common and were found in less than 10% of sediment examided (Table I). The taxa that were extremely common (>25%) were *Sporormiella* and *Sordaria*. Other common fungal taxa found in 7-11% in the samples was *Cercophora*. Some fungi were found only in some sites (*Cercophora*) while others were distributed in all sites (*Sordaria*, *Sporormiella* excluding the Neolithic site of Dehesa Río Fortes).

During the Neolithic (Dehesa Río Fortes), *Cercophora* (7-11%) and *Sordaria* (21-33%) are present while *Sporormiella* is absent. During the Chalcolithic the three coprophilous fungi are identified, although *Cercophora* is absent in most of the sites being very abundant on the other hand *Sporormiella*.

We could relate a higher diversity of coprophilous fungi during the Chalcolithic as the result of increased grazing pressure from the Neolithic. In this respect, those archaeological sites with more pastoral pressure are those that show bigger diversity and quantity of coprophilous fungi

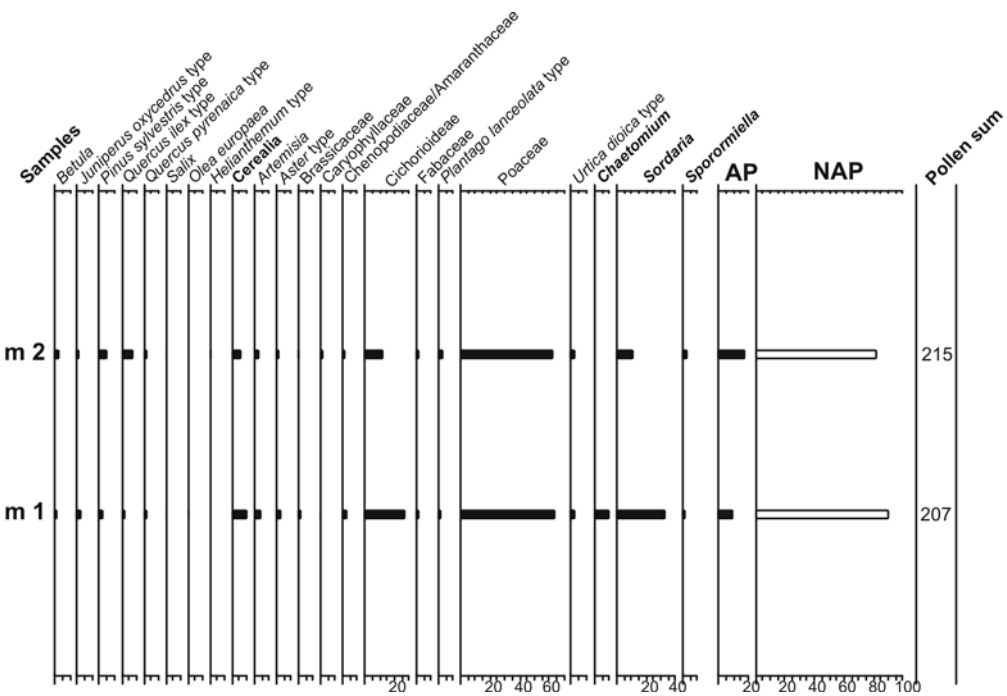

Figure 4. Pollen diagram from the chalcolithic site of Cerro de la Cabeza.

SITES / Spore taxa	*Cercophora*	*Sordaria*	*Sporormiella*
Neolithic			
Dehesa Río Fortes	7-11	21-33	0
Chalcolithic			
Aldeagordillo	1	67-89	25-33
Cerro de la Cabeza	0	11-32	3-4
Cerro Hervero	2	4-7	2-4
Fuente Lirio	0	2	7
Los Itueros	3-6	13-32	15-21
El Morcuero	0	9-19	1-3
El Picuezo	0	11-13	3-7
Los Tiesos	0	7-13	2
Tiro de Pichón	2-3	6-29	5
Valdeprados	0	5,3-9	8-11

Table I. Spore percentage of coprophilous fungi identified in this study

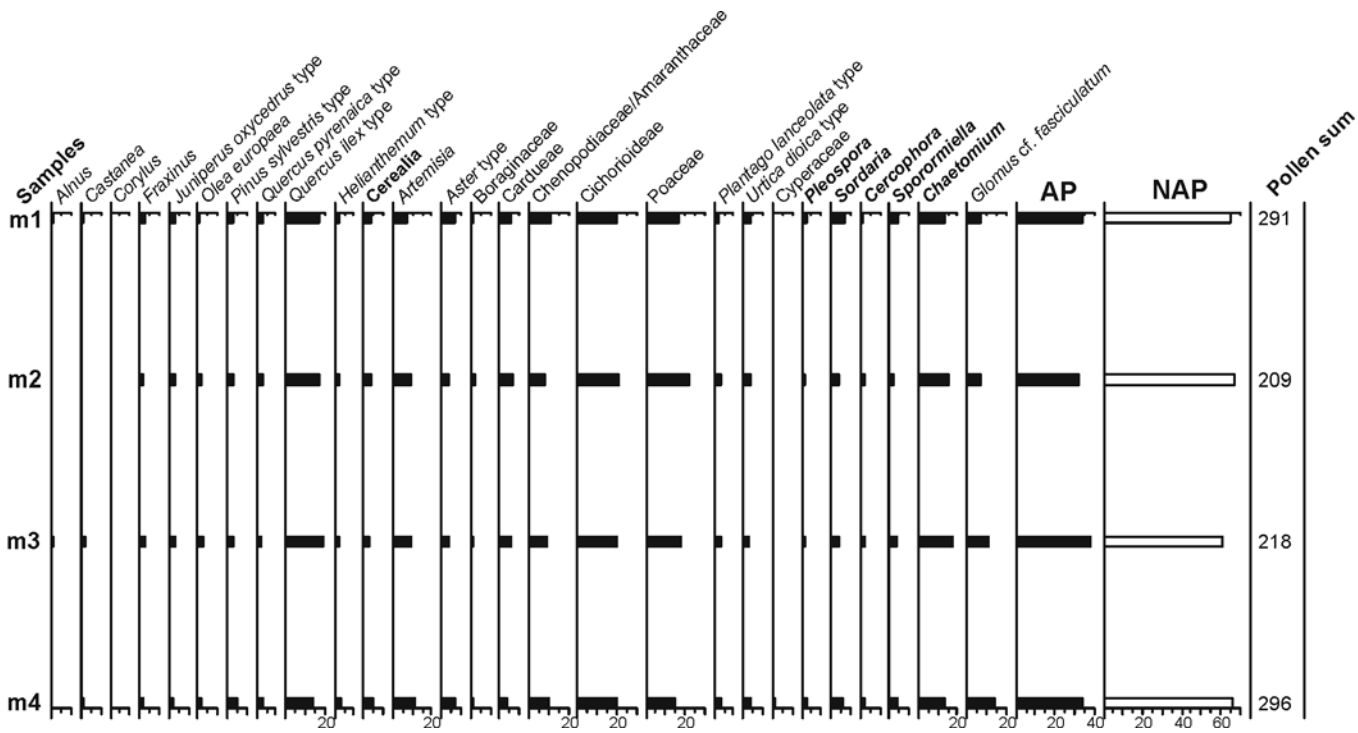

Figure 5. Pollen diagram from the chalcolithic site of Cerro Hervero.

(Aldeagordillo, Los Itueros, La Ladera, Tiro de Pichón); others would suffer a half or low pastoral pressure, that which is reflected in the absence of some of the taxa or in their low percentages (Valdeprados, Fuente Lirio, El Picuezo, Cerro Hervero). The case of Cerro de la Cabeza is very significant because it is a metallurgist town.

It is curious to point out the identification of coprophilous fungi in the next environment of two funeral tumulus (Los Tiesos, El Morcuero), that which would indicate, besides their sacred character, the possible symbolism of the area like area in passing for the livestock.

Our results from the Amblés Valley indicated a gradual change of the species composition and importance values of the fungi on the dung substrates over time. The association of different coprophilous fungal species could be ascribed to the ability of the species involved to toler-

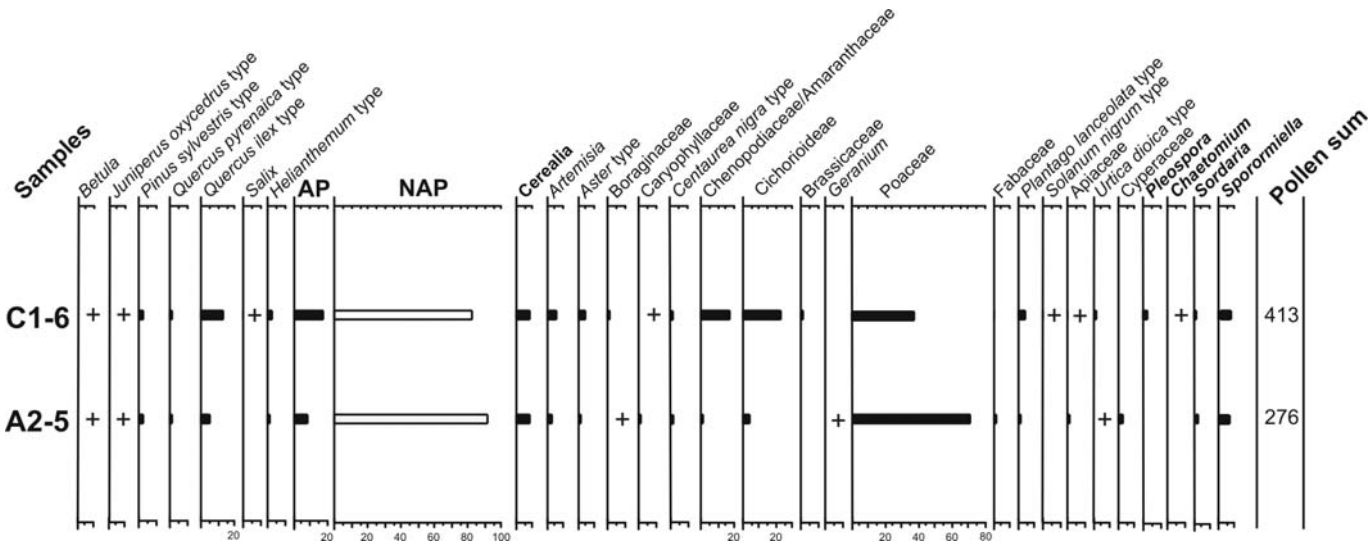

Figure 6. Pollen diagram from the chalcolithic site of Fuente Lirio.

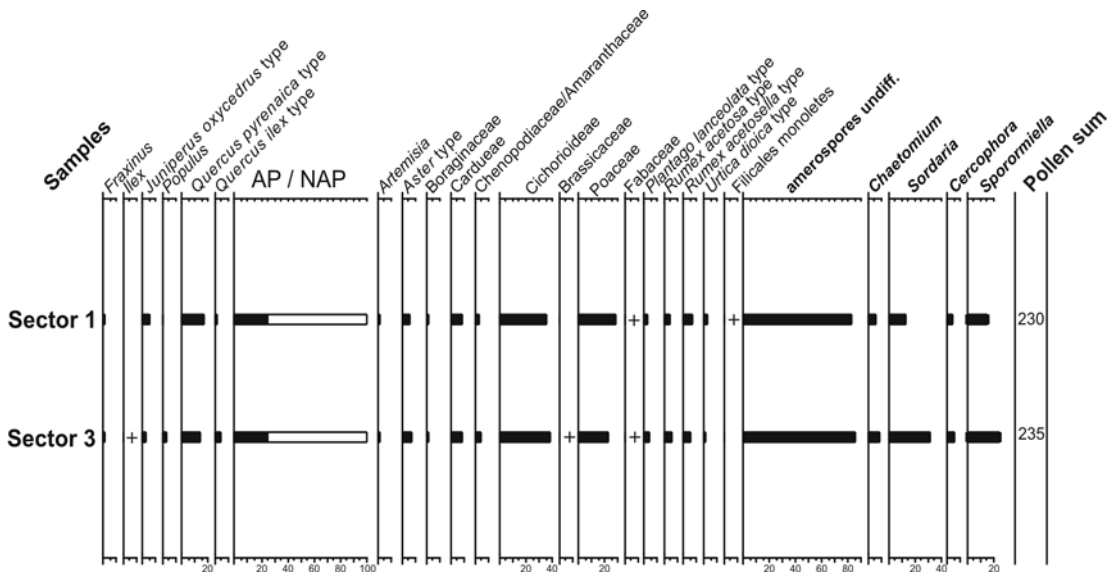

Figure 7. Pollen diagram from the chalcolithic site of Los Itueros.

ate the presence of each other or to benefit from the presence of each other, as opposed to antagonistic interactions.

Environmental factors such as temperature fluctuations, photoperiodicities, water potential of the substrates, the availability of nutrients, the role of other dung-inhabiting organisms, and interspecific fungal species competition, will definitely influence the species composition of any substrate (Webster, 1970). Man and domesticated animals will have been responsible for a range of new habitats, and also the mycoflora of settlement sites and the sur-

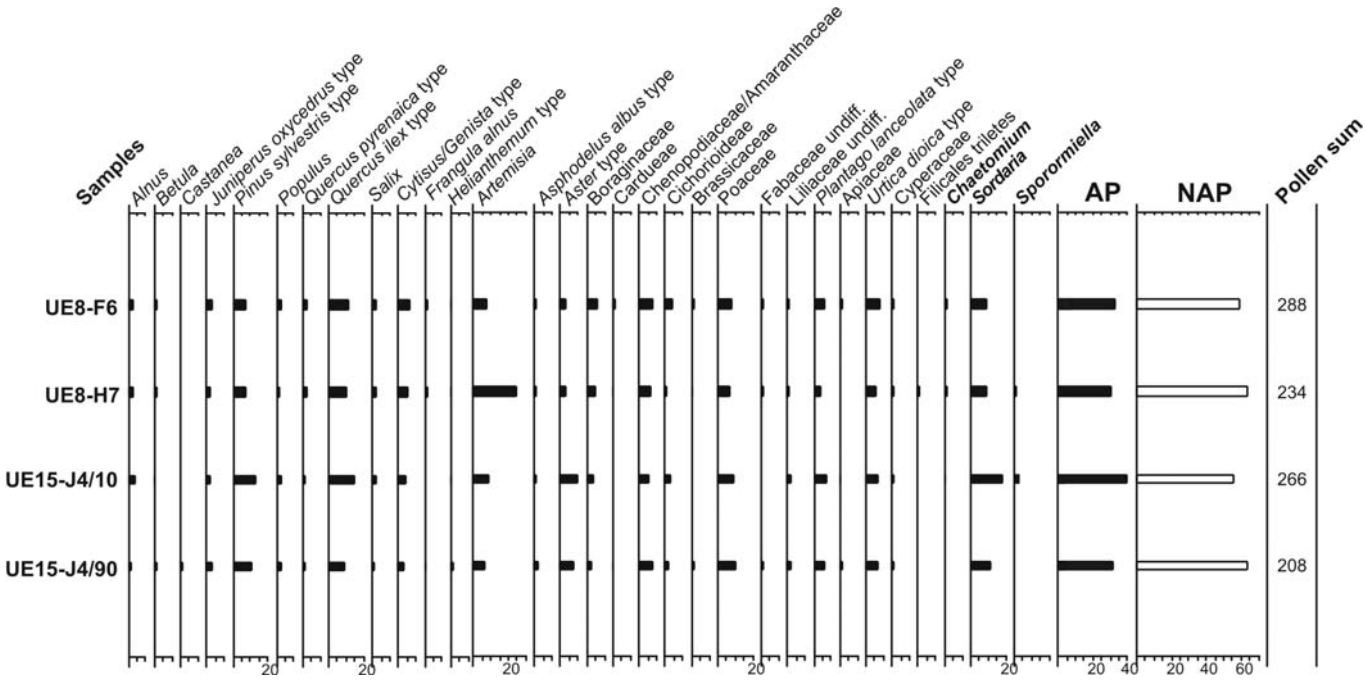

Figure 8. Pollen diagram from the chalcolithic site of El Morcuero.

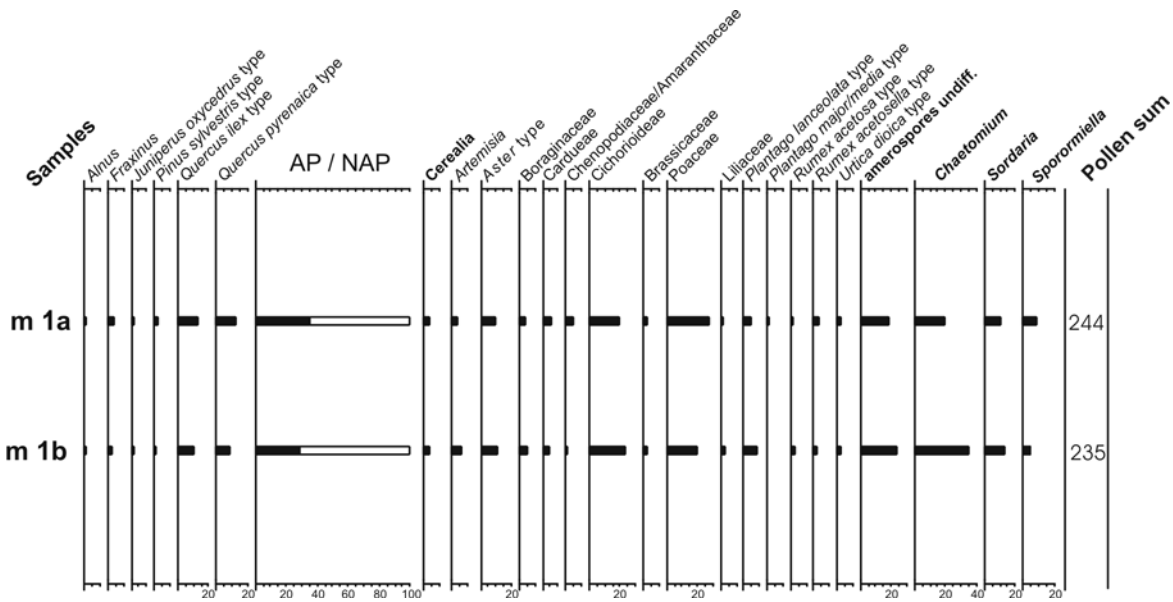

Figure 9. Pollen diagram from the chalcolithic site of El Picuezo.

rounding arable land, pastures and hay-meadows will have been different from the fungal assemblages of undisturbed habitats in natural ecosystems (van Geel, 1992). This is the case in the Amblés Valley during the Chalcolithic. The excrements of herbivorous animals represent an excellent substrate for many micromycete fungi, especially coprophilous fungi, because they possess a rich supply of nutrients. Ascospores of coprophilous Sordariaceae are often restricted to one or few king of dung. This renders the Sordariaceae interesting in palynological inquiry, especially when applied to archaeology (van Geel, 1986: 503; van Geel *et al.*, 2003).

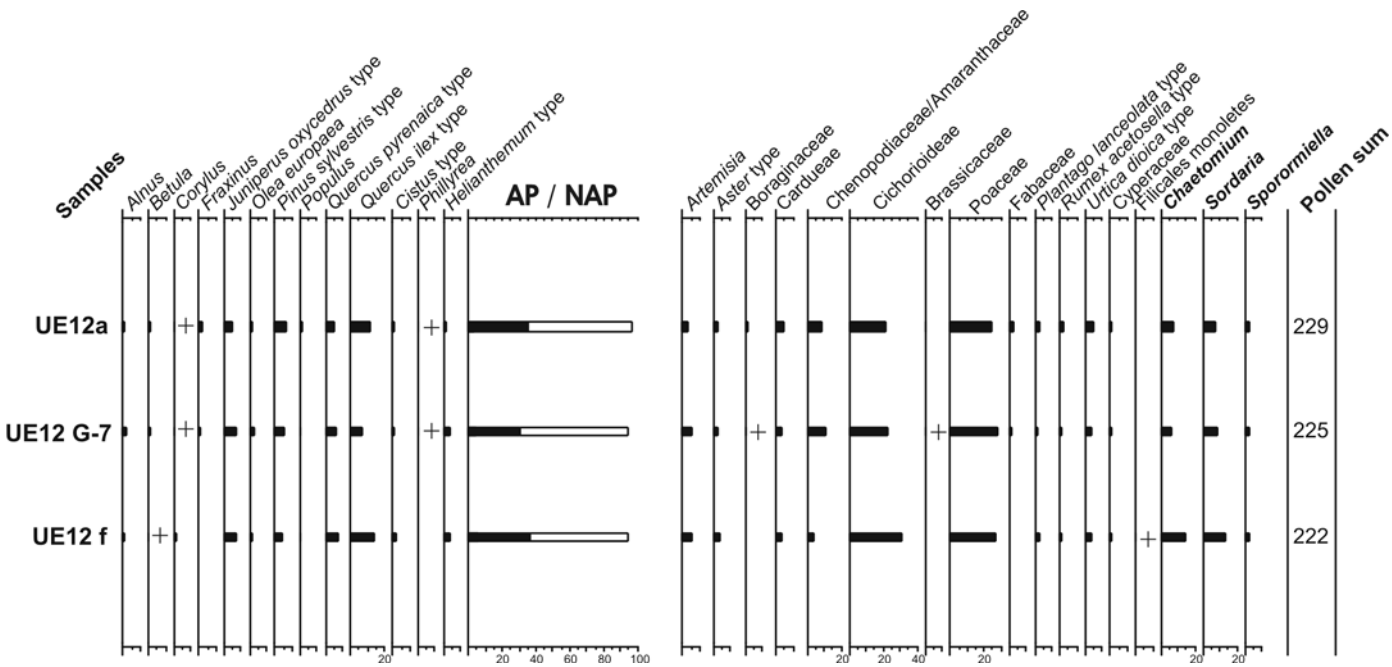

Figure 10. Pollen diagram from the chalcolithic site of Los Tiesos.

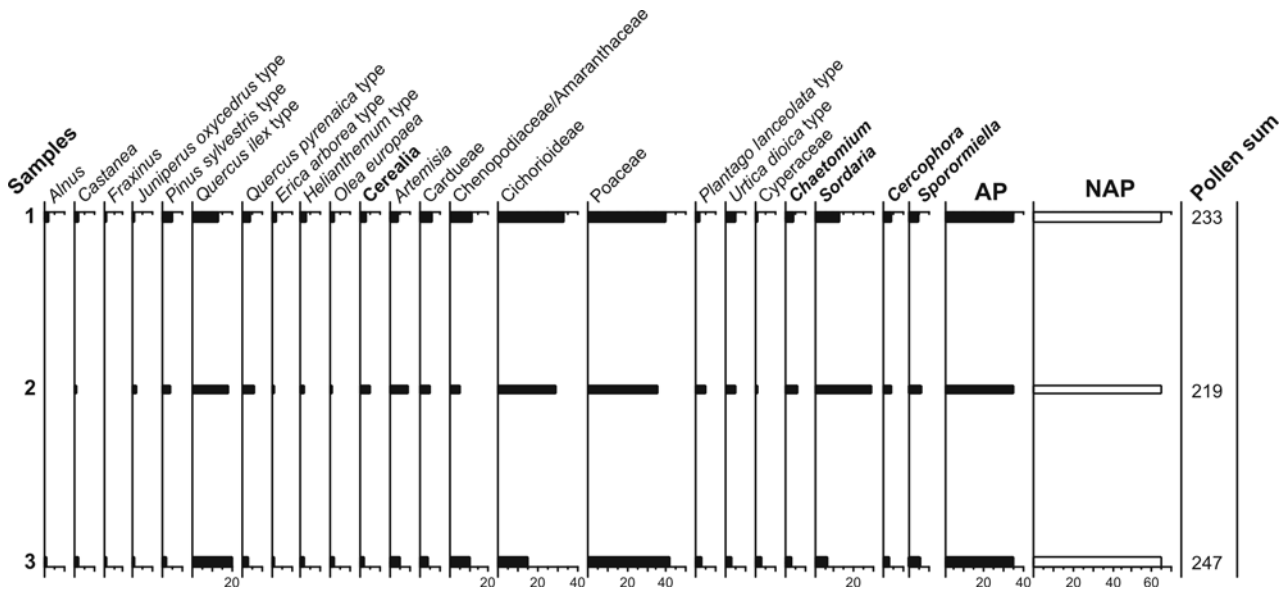

Figure 11. Pollen diagram from the chalcolithic site of Tiro de Pichón.

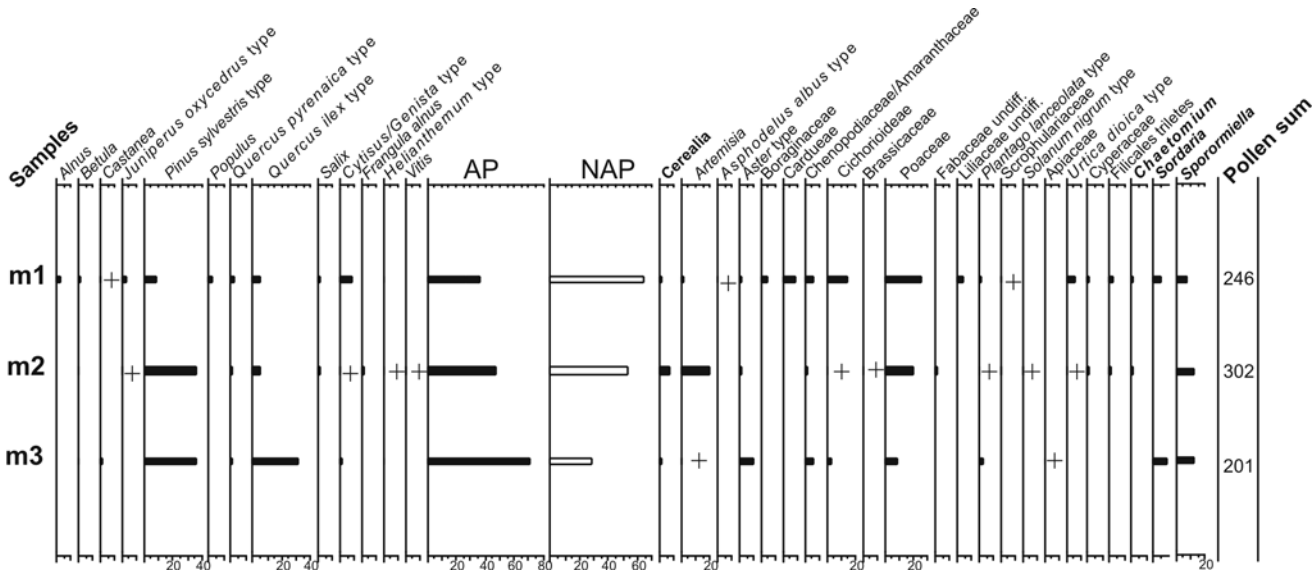

Figure 12. Pollen diagram from the chalcolithic site of Valdeprados.

Fungal species interactions comprise different interactions between the coprophilous fungal species and can be of a positive or negative nature. Competition effects and interference phenomena can play an important role in limiting the time of appearance, as well as the duration and intensity of fruting (Ebersohn & Eicker, 1997). All classes of the Kingdom Fungi are found on dung, with the Zygomycetes usually appearing first, followed by the Ascomycetes, and finally the Basidiomycetes. Unfortunately, fungal succession on dung in the fossil record is very difficult to attemp, because chronological control of the classical succesional pattern could not be stablished. However, from a palaeoecological point of view, it was important to determine the abundance value of each taxa over a specific period of time, as this could give a reliable indication of the ecological importante of the species in question. Thus worth emphasizing that the distribution of coprophilous fungi is influenced locally by the number of herbivores in an area.

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Palynology of a Danian warm climatic wetland in Central Northern Patagonia, Argentina

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Abstract

The study area is located north of the Chubut River, near Las Plumas locality (Chubut province, Argentina). The Danian age of the microfossiliferous Cerro Bororó Formation here studied was established elsewhere. The objective of this contribution is to explain the paleoenvironmental and paleoclimatic significance of the palynologic assemblage of extremely high specific diversity found in a single bed of 15 cm thickness, of an organic rich carbonaceous mudstone. The characteristics of the diversity of this microbiota of excellent preservation and specially the investigation of the scarcely studied group of aquatic species, which have been unknown up to the moment for this Formation, made necessary an intensive and exhaustive use of scanning electron microscopy, in order to achieve an exact taxonomic analysis of the material, composed of 36 form-species of angiosperm pollen, 10 species of gymnosperms (bi- and trisaccate pollen), four forms of *Botryococcus*, massulae of *Azollopsis* spp., four species of zygnematacean algae, prasinophyceans and unfrequent dinoflagellates. The sampling point was a freshwater paleoenvironment (swamp) with abundant hydrophile forms (Chlorococcales, Salviniaceae, Sphagnaceae) and Zygnematacea, surrounded by a hygrophile community of Filicales, Bryophyta, Lycopodiaceae and Selaginellaceae, separated from the sea by brackish swamps with a subtropical community of prevailing Arecaceae (palms): *Proxapertites*, *Longapertites*, *Spinizonocolpites*. The presence of monospecific agglomerates of pollen grains indicates, together with the state of preservation of the palynomorphs, a strong predominance of local (parautochthonous) material.- Proteacean pollen (11 species) is a mayor element of the palynoflora. Proteaceans may have been the most conspicuous floral elements of the subhumid to semiarid lowlands located between the near-coast wetlands and the Podocarpacean forests of the hinterland. Gymnospermous pollen (10.5% of the total spectrum) is represented mainly by podocarpacean pollen, reflecting the existence of a nearby "Conifer-Forest". The megafloral register of a similar Conifer Forest from this Formation is known from earlier studies published elsewhere.

***Keywords*:** Paleogene, Patagonia, Palynology, wetland, paleoclimate, paleocommunities

Resumen

En Chubut extraandina, Patagonia, Argentina, aflora la Formación Cerro Bororó, cuya edad daniana está controlada por estudios micropaleontológicos previos. El objetivo de este estudio es demostrar el significado paleoambiental y paleoclimático de una asociación palinológica muy diversa, excelentemente preservada, hallada en una fangolita carbonosa de la parte inferior de esta Formación. Se realizó un estudio intensivo y exhaustivo del material al microscopio electrónico de barrido, con especial consideración de las especies acuáticas hasta ahora no ilustradas para esta Formación. Se distinguieron 36 morfoespecies de polen de angiospermas, 12 de gimnospermas, 4 formas de *Botryococcus*, másulas de *Azollopsis*, 4 especies de zygnematáceas, prasinofíceas y escasos dinoflagelados. El lugar de muestreo fue un pantano dulceacuícola daniano con palinomorfos correspondientes a una paleocomunidad hidrófila (Botryococcaceae, Zygnemataceae, Salviniaceae, Sphagnaceae), rodeada por una comunidad higrófila ecotonal, reflejada por

esporas de Filicales (22 especies), Lycopodiaceae, Selaginellaceae y Hepaticae. Entre estos humedales y el mar abierto se intercalaron pantanos salobres con una paleocomunidad de palmeras (indicada por la gran frecuencia del grupo de *Proxapertites*, *Longapertites* y *Spinizonocolpites*). El polen de Proteaceae (11 especies) es un elemento mayoritario en la palinoflora. La flora de proteaceas puede haber constituido los elementos más conspicuos de los llanos subhúmedos a semiáridos ubicados entre los humedales cercanos a la costa y los bosques de podocarpáceas de las áreas más elevadas y más húmedas tierra adentro. La presencia de aglomerados monoespecíficos de granos de polen, junto con el excelente estado de preservación de los palinomorfos, indican el gran predominio del material local (parautóctono).

***Palabras clave*:** Paleógeno, Patagonia, Palinología, humedales, paleoclima, paleocomunidades

1. INTRODUCTION

The objective of this contribution is to present the study of an extremely diverse Danian palynologic assemblage, to increase the knowledge of the paleovegetation of the studied area and to reconstruct the Danian paleocommunities. The quality of preservation of the material is excellent. Many of the forms were already known through previous studies; the forms which are new at this locality are marked, in the chapter "TAXA RECORDED", with an asterisk.

The study of the Protoctists and associated aquatic forms are the object of another, complementary study by Scafati *et al*. (2006) (complete version in preparation).

The sampling locality is Puesto Fernández, front of Cerro Bororó (67º 45′ W; 43º 40′ S), approximately 35 km to the northwest of Las Plumas locality, Chubut province (Fig. 1).

The Bororó Formation is known through earlier palynologic, paleobotanic, micropaleontologic and sedimentologic studies by Archangelsky *et al*. (1969), Petriella (1972), Andreis *et al*. (1973), Bertels (1973), Archangelsky (1973, 1976), Archangelsky and Romero (1974), Arguijo (1979), Archangelsky and Zamaloa (1986) and Durango de Cabrera and Romero (1988). A paper of Petriella and Archangelsky (1975) on the vegetation and environment during the Paleocene in Chubut is of special interest for our study, as it presents the first analysis of the life conditions of the elements of the earliest Paleogene paleoflora from four localities of Chubut, through comparison with the life conditions of the modern vegetation, at the family level, arriving (on their figure 1) to a general vegetational zonation. An interesting contribution to the regional context of the lowermost Paleogene stratigraphy and biota is that of Bellosi *et al*. (2000).

The present study allowed the identification of new palynologic and paleoenvironmental evidences for this Formation.

Geologic setting.- The stratigraphic section at Puesto Fernández locality is presented on Fig. 1. (adapted from Petriella, 1972). The Danian age of the Cerro Bororó Formation at this locality was established by Bertels (1973), who identified the forams *Cibicides succedens* Brotzen and *Discorbis* sp. aff. *D. newmanae* Plummer in the upper member of the Formation, allowing a correlation with the upper Danian of Europe and with the Salamanquiano Stage of the San Jorge Basin in central eastern Patagonia.

2. MATERIAL AND METHODS

For extraction of the palynologic samples the standard methods (HCl 10% and HF 70%) were used for removing carbonates and silicates, respectively. The extracted kerogen was sieved (10 µm mesh) with sodium hexametaphosphate 0.3%. The palynologic material was oxidized with nitric acid (30%).

The study was done with optical microscopes (Leitz Dialux 20 with interference contrast, and Leitz Ortholux; the relative abundance was calculated on a universe of 300 specimens. Studies with an SEM Phillips XL Serie 30 were done at the Museo "B. Rivadavia". The photomicrographs were taken with Agfapan APX25 and Kodak Profesional

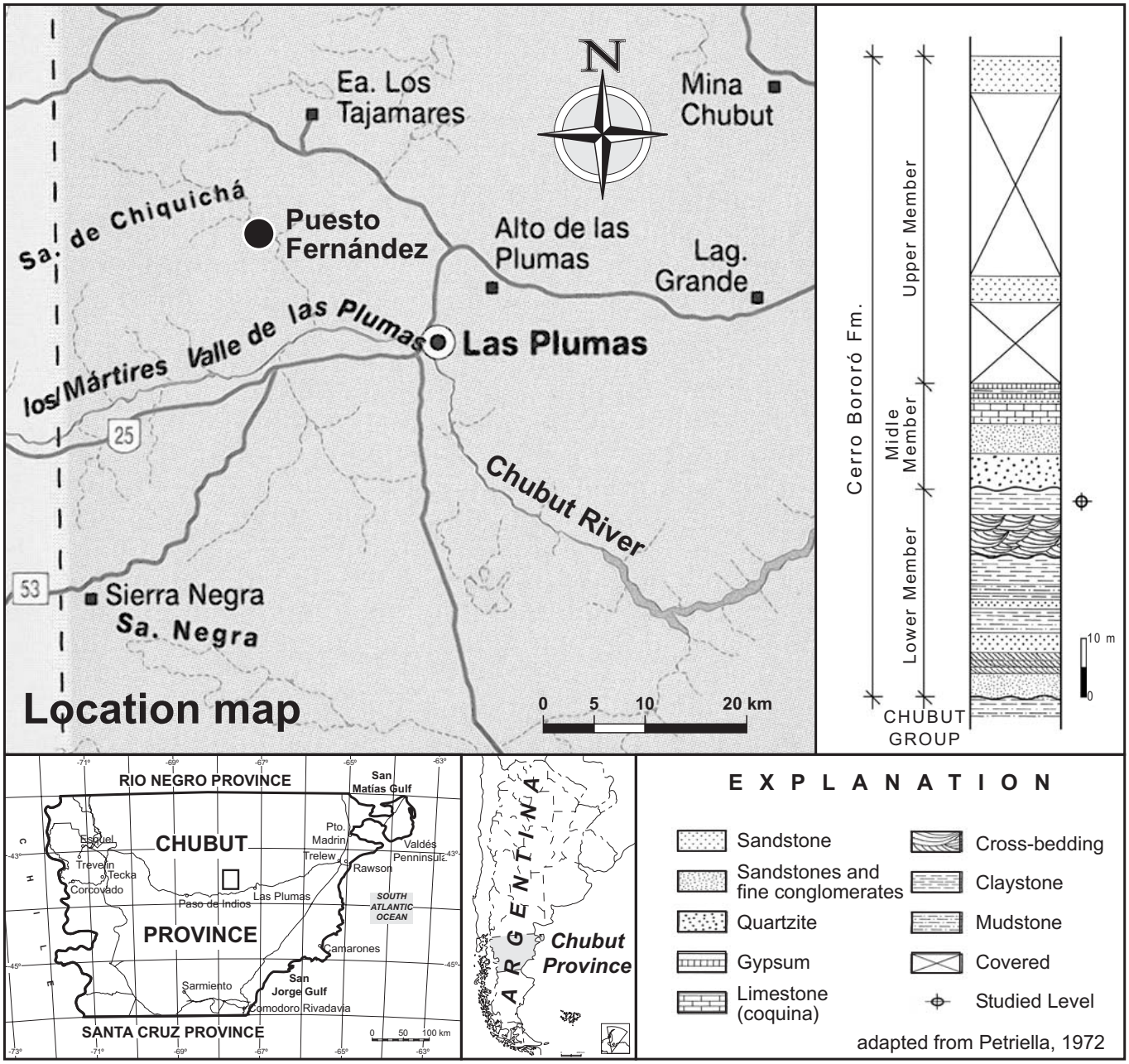


Figure 1. Location of the studied area and stratigraphic location of the assemblage of palynomorphs studied.

100 TMAX film. The illustrated material is stored under the numbers 4994 (SEM numbers 1-4) and 7124 (SEM numbers 1-4) of the paleopalynologic collection of IANIGLA (CRICYT- Mendoza).

For the systematic classification of the material at a suprageneric level, the classification of Whittaker in five kingdoms was used, considering the modifications by Margulis and Schwartz (1982) and Margulis (1988, 1996).

3. TAXA RECORDED

The list includes all taxa identified during the present study. The aquatic species integrating the Kingdom Protoctista and other aquatic forms are treated in detail in Scafati, Melendi and Volkheimer (in preparation).

* species not previously identified in this Formation.

** genus not previously identified in this Formation.

Kingdom Plantae

Taxa	***Biologic Affinity***
Pteridophytes / Bryophytes	
** *Aequitriradites spinulosus* (Cookson & Dettmann) Cookson & Dettmann 1961	Sphaerocarpaceae/ Selaginellaceae
** *Antulsporites clavus* (Balme) Filatoff 1975	Sphagnaceae
** *Azollopsis (Azollopsis) tomentosa* Hall 1968	Salviniaceae
** *Azollopsis (Spiralopsis) intermedia* Sweet & Hill 1974	Salviniaceae
* *Baculatisporites comaumensis (*Cookson) Potonié 1956	Hymenophyllaceae
Biretisporites sp. B (in Archangelsky 1973)	*(Lygodium-type)* Schizaeaceae
** *Camarozonosporites ambigens* (Fradkina) Playford 1971	Lycopodiaceae/Selaginellaceae
** *Ceratosporites equalis* Cookson & Dettmann 1958	Selaginellaceae
** *Cingutriletes australis* (Cookson) Archangelsky 1972	*(Sphagnum*) Sphagnaceae
** *Clavifera triplex* (Bolkhovitina) Bolkhovitina 1966	Gleicheniaceae
Cyathidites patagonicus Archangelsky 1972	Cyatheaceae / Matoniaceae?
Deltoidospora minor (Couper) Pocock 1970	Cyatheaceae/Dicksoniaceae ?
** *Densoisporites velatus* (Weyland & Krieger) Krasnova 1961	Selaginellaceae
* *Dictyophyllidites harrisii* Couper 1958	*(Phlebopteris)* Matoniaceae
** *Distaverrusporites* cf. *simplex* Muller 1968	(*Cyathea*–type ?) Cyatheaceae?
** *Foveosporites* cf. *lacunosus* Partridge 1973	Lycopodiaceae/Ophioglossaceae?
** *Gabonisporis vigourouxii*	Boltenhagen 1967
** *Gleicheniidites senonicus* Ross emend. Skarby 1964	Gleicheniaceae
** *Klukisporites variegatus* Couper 1958	Schizaeaceae
Laevigatosporites ovatus Wilson & Webster 1946	Polypodiaceae/Schizaeaceae ?
Leiotriletes cf. *regularis* (Pflug) Krutzsch 1972	Schizaeaceae / Matoniaceae?
* *Matonisporites crassiangulatus* (Balme) Dettmann 1963	Matoniaceae
* *Matonisporites equiexinus* Couper 1958	(*Phlebopteris?)* Matoniaceae
** *Neoraistrickia* sp.	Selaginellaceae
** *Pityrogramma* sp	Pteridaceae
** *Polypodiaceoisporites* sp.	(*Pteris*-type*)* Pteridaceae
** *Polypodiisporites irregularis* Pocknall & Mildenhall 1984	Polypodiaceae / Psilotaceae
** *Polypodiidites sp.*	*(*Pteris-*type)* Polypodiaceae
Retitriletes austroclavatidites (Cookson) Döring, Krutzsch, Mai & Schulz 1963	(*Lycopodium*) Lycopodiaceae
** *Retitriletes rosewoodensis* (de Jersey) de Jersey 1963	Lycopodiaceae
** *Ricciopsis* sp	Ricciaceae
** *Rugulatisporites chubutensis* Baldoni 1992	Osmundaceae
** *Selaginella perinata* (Krutzsch et al.) Frederiksen 1980	Selaginellaceae
** *Stereisporites antiquasporites* (Wilson & Webster) Dettmann 1963	(*Sphagnum*) Sphagnaceae
Trilites parvallatus Krutzsch 1959	(*Dicksonia*) Dicksoniaceae
** *Trilobosporites* sp.	Dicksoniaceae ?
Tuberculatosporites parvus Archangelsky 1972	Polypodiaceae
Gymnosperms	
Cycadopites spp.	Cycadales
** *Dacrycarpites australiensis* Cookson & Pike 1953	(*Dacrycarpus*) Podocarpaceae
Lygistepollenites florinii (Cookson & Pike) Stover & Evans 1973	(*Dacrydium*) Podocarpaceae
Microcachryidites antarcticus Cookson 1947	(*Microcachrys*) Podocarpaceae
* *Podocarpidites elegans* Romero 1977	Podocarpaceae
* *Podocarpidites exiguus* Harris 1965	Podocarpaceae
Podocarpidites marwickii Couper 1953	Podocarpaceae

Taxa	***Biologic Affinity***
Gymnosperms	
Podocarpidites microreticuloidatus Cookson 1947	Podocarpaceae
* *Podocarpidites rugulosus* Romero 1977	Podocarpaceae
* *Podocarpidites verrucosus* Volkheimer 1972	Podocarpaceae
Trisaccites microsaccatus (Couper) Couper 1960	(*Trisacocladus*) Podocarpaceae
Angiosperms	
Monocotyledons	
** *Clavatipollenites* sp.	Chloranthaceae
Liliacidites regularis Archangelsky 1973	Liliaceae / Arecaceae
Liliacidites variegatus Couper 1953	Liliaceae / Arecaceae
** *Monogemmites gemmatus* (Couper) Krutzsch 1970 emend. Mildenhall 1984	Arecaceae
Monosulcites minutiscabratus McIntyre 1968	*(Manicaria-type*) poss. Arecaceae
Monosulcites sp.	poss. Arecaceae
Longapertites andreisii Archangelsky 1973	Arecaceae
Longapertites patagonicus Archangelsky 1973	Arecaceae
Proxapertites spp.	Arecaceae / Araceae
* *Sparganiaceaepollenites barungensis* Harris 1972	Sparganiaceae / Typhaceae
Spinizonocolpites spp.	Arecaceae
** *Trichotomosulcites subgranulatus* Couper 1953	Liliaceae / Arecaceae
Dicotyledons	
** cf. *Beaupreaidites* sp.	Proteaceae
Ericipites scabratus Harris 1965	Ericaceae / Epacridaceae
Ericipites microtectatum Archangelsky & Zamaloa 1986	Ericaceae / Empetraceae
Gemmatricolpites subsphaericus Archangelsky 1973	(*Ilex*-type) Aquifoliaceae?
** *Integritetradites* sp. (compare with *I. porosus* Schrank & Mahmoud, 2000).	
** *Momipites dilatus* (Fairchild) Nichols 1973	Juglandaceae?
Peninsulapollis gillii (Cookson) Dettmann & Jarzen 1988	(*Beauprea)* Proteaceae
** *Plicatopollis cretacea* Frederiksen & Christopher 1978	*(Engelhardtia)* Juglandaceae
** *Propylipollis lateflexus (*Archangelsky) Baldoni & Askin 1993	(Alfaroa complex) Proteaceae
** *Proteacidites* cf. *asperatus* McIntyre 1968	Proteaceae
** *Proteacidites granulatus* Cookson 1953	Proteaceae
** *Proteacidites stipplatus* Partridge (in Stover & Partridge 1973)	Proteaceae
** *Proteacidites tenuiexinus* Stover (in Stover & Partridge 1973)	Proteaceae
** *Proteacidites* sp.	Proteaceae
Retidiporites camachoi Archangelsky 1973	Proteaceae?
Rhoipites minusculus Archangelsky 1973	Rutaceae / Araliaceae
* *Rhoipites romeroi* Baldoni 1987	Araliaceae?
** *Rousea patagonica* Archangelsky 1973	Adoxaceae
Rousea sp.	
* *Tricolpites lilliei* Couper 1953	
*Tricolpites reticulatus (*Couper) Jarzen & Dettmann 1989	*(Gunnera*) Gunneraceae
* *Tricolpites* cf. *perlongicolpus* Pocknall & Mildenhall 1984	
** *Triporopollenites* cf. *ambiguus* Stover (in Stover & Partridge 1973)	*(Telopea)* Proteaceae
** *Triporopollenites parviannulatus* Frederiksen 1994	Proteaceae

Kingdom Protoctista

Taxa	*Biologic Affinity*
***Chlorophyta* Chlorococcales**	
** *Botryococcus* sp 1 In Scafati et al. 2006	Botryococcaceae
** *Botryococcus* sp 2 In Scafati et al. 2006	Botryococcaceae
** *Botryococcus* sp 3 In Scafati et al. 2006	Botryococcaceae
** *Botryococcus* sp 4 In Scafati et al. 2006	Botryococcaceae
** *Coelastrum* sp.	Coelastraceae
***Chlorophyta* Zygnematales**	
** *Gelasinicysta vangeelii* Head 1992	Zygnemataceae
** *Ovoidites* spp..	Zygnemataceae
** *Schizosporis reticulatus* (Cookson & Dettmann) Pierce 1976	Zygnemataceae
** *Pseudoschizaea circula* (Wolf) emend. Christopher 1976	probably Zygnemataceae
Prasinophyta	
** *Leiosphaeridia hyalina* (Deflandre) Downie 1957	
Dinophyta	
** *Peridinium* sp. aff. *P. limbatum* (Stokes) Lemmermann 1899	Peridiniaceae
** *Dinocyst* indet.	

3. COMPOSITION AND SIGNIFICANCE OF THE PALYNOLOGIC ASSEMBLAGE

The palynologic assemblage studied is integrated by palynomorphs belonging to the kingdoms Plantae and Protoctista.

Within the Kingdom Plantae, the Bryophytes and Pteridophytes are represented with 23.6%; the Gymnosperms with 10.5% and the Angiosperms with 55.3%. The Protoctists represent 10.6 % (Fig. 2).

The Bryophytes/Pteridophytes are represented by the families Sphagnaceae, Salviniaceae, Schizaeaceae, Lycopodiaceae, Selaginellaceae, Gleicheniaceae, Cyatheaceae / Dicksoniaceae?, Matoniaceae, Pteridaceae, Polypodiaceae, Ricciaceae, among others, with an important diversity of aquatic and terrestrial taxa (mainly *Azollopsis* (Plate 2, figs. 1, 2), *Selaginella* (Plate 3, fig. 1), *Dictyophyllidites* (Plate 3, fig. 2), *Ricciopsis* (Plate 3, fig. 3), *Ceratosporites* (Plate 3, fig. 4), *Polypodiisporites* (Plate 3, fig. 6) and *Aequitriradites, Camarozonosporites, Clavifera, Foveosporites, Gabonisporis, Gleicheniidites, Laevigatosporites, Matonisporites, Retitriletes, Stereisporites* and *Trilites* (not illustrated).

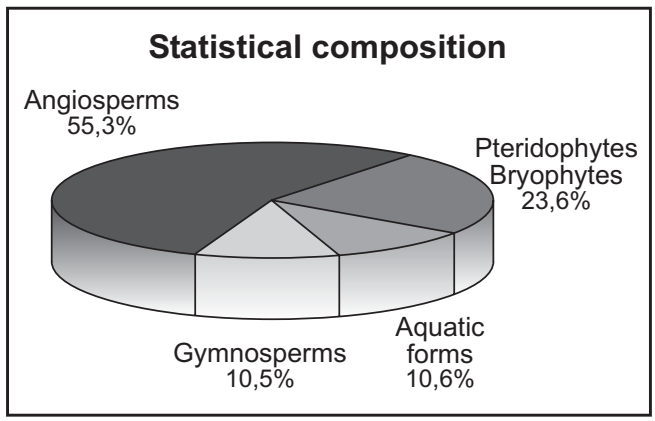


Figure 2. Statistical composition of the palynobiota studied. Cerro Bororó Formation. Puesto Fernández locality. Chubut Province.

The Gymnosperms are a minority, represented by the Podocarpaceae (Plate 6, figs. 1 to 6) and a few representatives of the Cycadales. Generally only low values of the coniferous pollen types, which represent montane vegetations, have been described from the Tertiary in tropical areas (Muller, 1968).

Plate 1

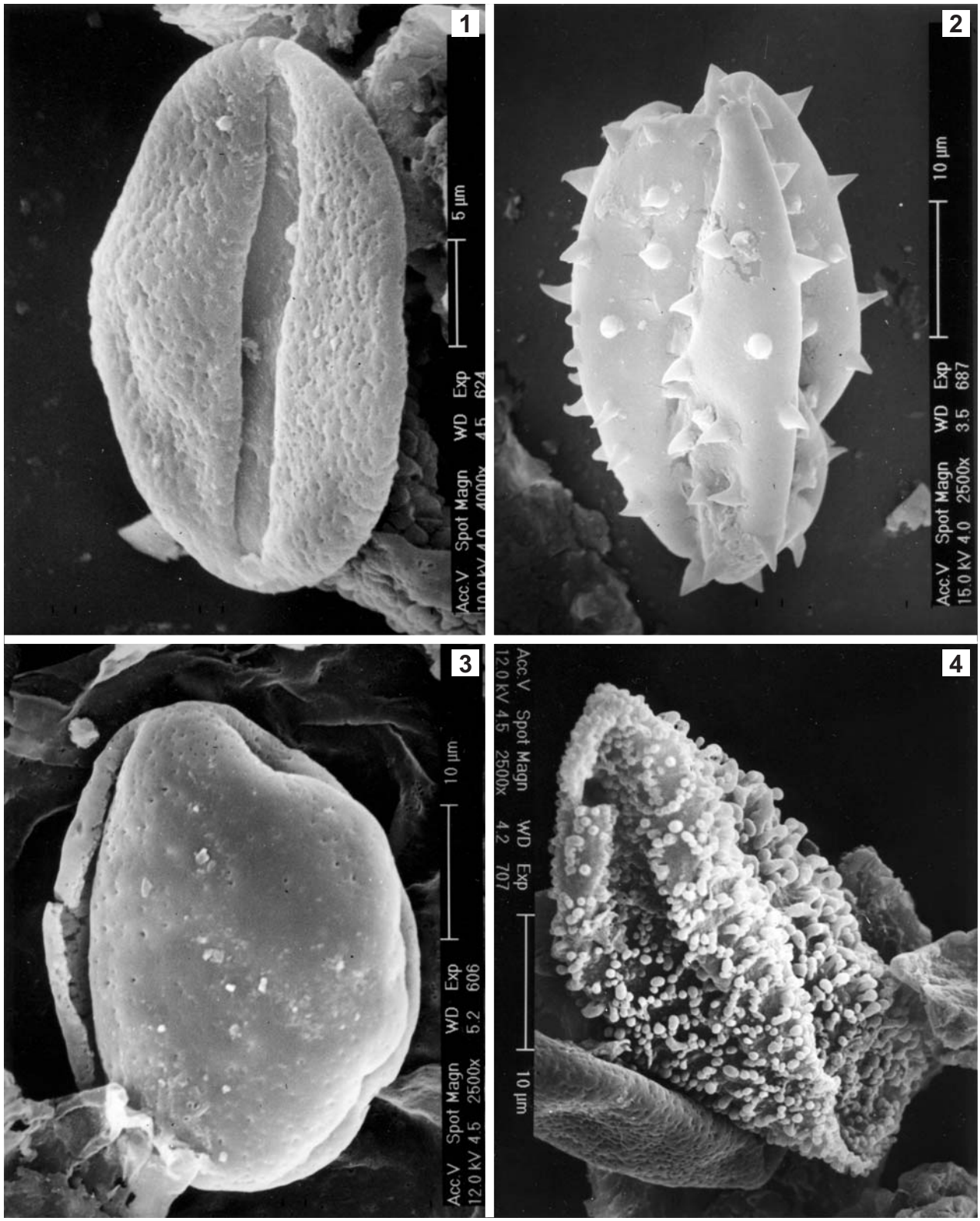


Plate 1**.** Palynomorphs characteristic for Community 1: Brackish palm-swamps near the coast. 1, *Monosulcites minutiscrabratus* McIntyre 1968. 2, *Spinizonocolpites* spp. 3, *Proxapertites* spp. 4, *Monogemmites gemmatus* (Couper) Krutzsch 1970 emend. Mildenhall 1984.

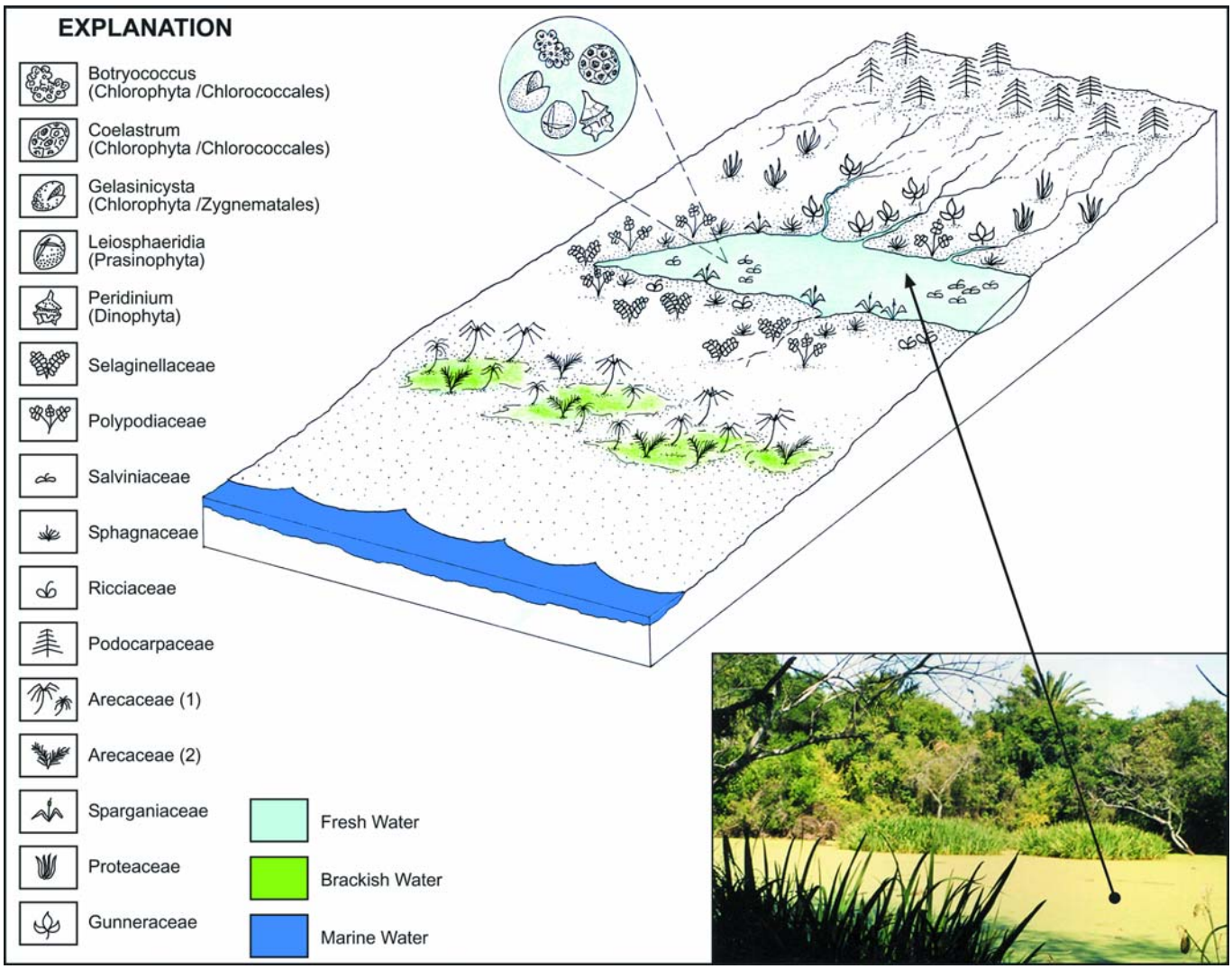


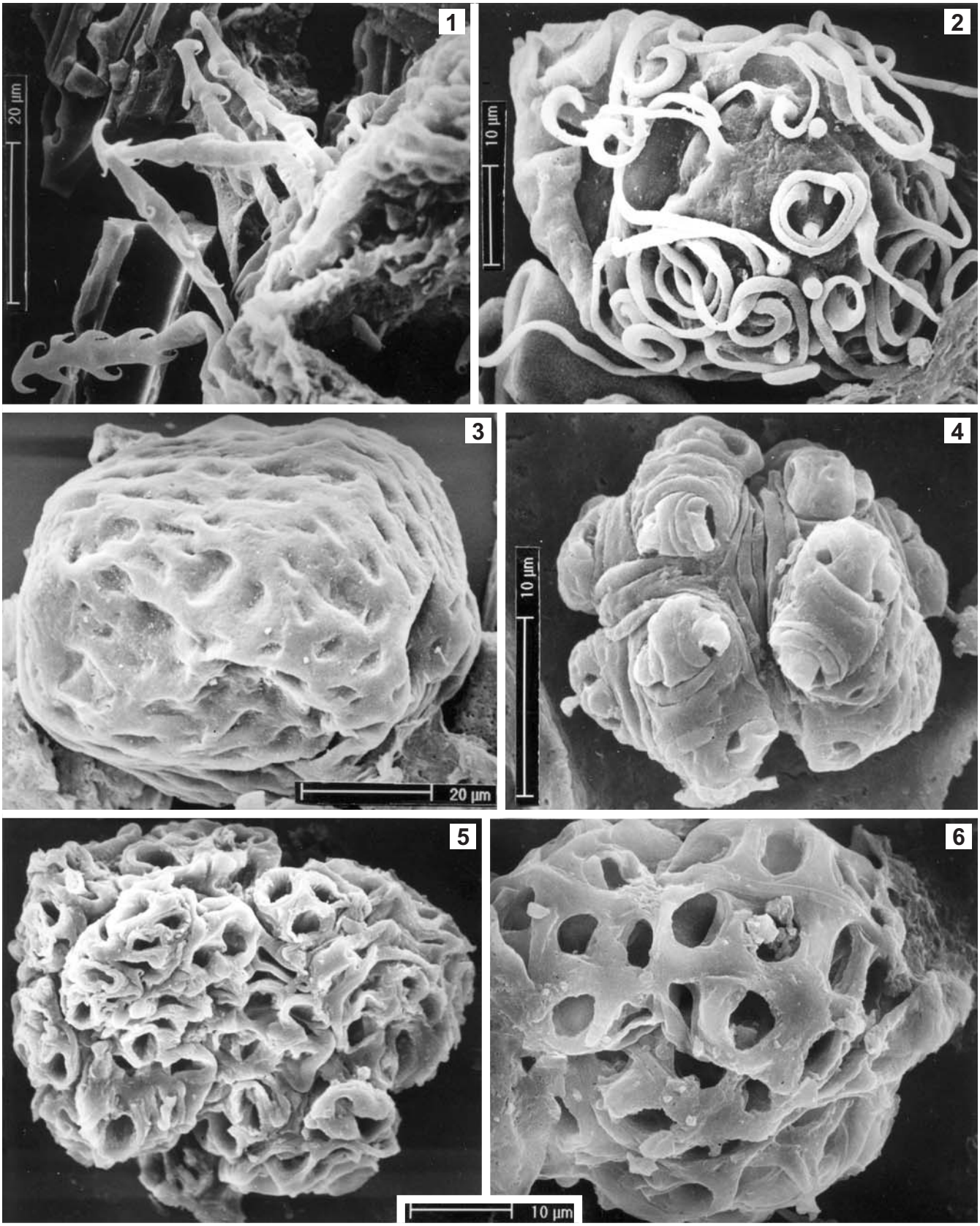
Figure 3. Blockdiagram showing a schematic paleotopography and approximate areal distribution of five paleovegetational communities as indicated by the assemblage of palynomorphs (palynobiota) studied. Cerro Bororó Formation. Danian. Puesto Fernández locality. Chubut Province. 1) Brackish palm-swamps near the coast. 2) Hydrophile community of Salviniaceae and associated protoctists of shallow swampy freshwater bodies. 3) Hygrophile ecotonal community of ferns, Selaginellaceae/Lycopodiaceae and Hepaticae, surrounding the freshwater bodies. 4) A subhumid to semiarid lowland community with prevailing proteaceans. 5) A conifer forest reflected by nine formspecies of podocarpacean pollen.

The Angiosperms are the dominant group, with high frequencies of Monocotyledons (Arecaceae (Plate 1, figs. 1 to 4) and Sparganiaceae/Typhaceae, Liliaceae, Chloranthaceae (not illustrated)) and a relatively low proportion of Dicotyledons: Ericaceae (not illustrated), Juglandaceae (Plate 4, fig. 6), Gunneraceae (Plate 5, fig. 2), with the exception of the Proteaceae, with a high generic and specific diversity in the palynologic register: *Triporopollenites* (Plate 4, figs. 1, 2), *Triatriopollenites* (Plate 4, fig. 3), *Proteacidites* (Plate 4, fig. 4) (5 species), cf. *Beaupreaidites* (Plate 4, fig. 5) and *Peninsulapollis*, *Propylipollis* and *Retidiporites* (not illustrated).

According to Jacobs (2004) palms are the earliest angiosperms thought to be specifically associated with a brackish shoreline setting, and the first plants known to occur in this ecologic role since the Mesozoic conifer family Cheirolepidiaceae.

Plate 2. Palynomorphs characteristic for Community 2: Hydrophile community of Salviniaceae and associated Algae. 1, *Azollopsis (Azollopsis) tomentosa* Hall 1968. 2, *Azollopsis (Spiralopsis) intermedia* Sweet & Hill 1974. 3, *Gelasinicysta vangeelii* Head 1992. 4, *Botryococcus* sp. 1. 5, *Botryococcus* sp. 3. 6, *Botryococcus* sp. 4.

Plate 2



The Protoctists constitute a novel group of taxa mentioned here for the first time for this Formation. The presence of this hydrophile group is environmentally important and they are represented by the Chlorophyta (Chlorococcales (Plate 2, figs. 4 to 6) and Zygnematales (Plate 2, fig. 3)) and, in a lower proportion, by Prasinophyta and Dinophyta (not illustrated). All these forms correspond to a freshwater environment.

The occurrence of unknown forms, difficult to be identified and compared, constitute a limitation, but at the same time a challenge to increase our knowledge about them. (Plate 7, figs. 3 to 6).

5. PALEOCOMMUNITIES

The block diagram of Fig. 3 is an essay of a schematic sketch of the five principal paleocommunities represented by the palynologic assemblage under study.

1) Immediately behind the coastal line (the latter characterized by a coarse sandstone with shark teeth) developed brackish palm swamps (Plate 1) with abundant Arecaceae/Araceae, Sparganiaceae/Typhaceae and Liliaceae. In the palynologic register, this group of monocots is represented *by Liliacidites* spp.*, Monogemmites gemmatus, Monosulcites minutiscabratus, Longapertites andreisii*, *L. patagonicus*, *Proxapertites* spp., *Sparganiaceaepollenites barungensis*, *Spinizonocolpites* spp. and *Trichotomosulcites subgranulatus*. (For details of biologic affinity see the list: Taxa recorded).

2) A hydrophile (sensu Remy and Remy, 1977, p.18) community of shallow, swampy fresh water bodies (Plate 2) follows upcountry. The sampling locality is placed within one of these water bodies characterized by a diverse assemblage of aquatic palynomorphs treated elsewhere (Scafati *et al.*, 2006). The most conspicuous groups which are composing this hydrophile community are the Zygnematacean algae (*Gelasinicysta vangeelii, Ovoidites* sp., *Schizosporis reticulatus, Pseudoschizaea*), the Chlorococcales (*Botryococcus* spp., *Coelastrum* sp.), the Salviniaceae (water ferns), which are forming extended systems of floating macrophytes covering the water surfaces: *Azollopsis (Azollopsis*) *tomentosa* and *Azollopsis (Spiralopsis) intermedia* are frequent in the palynologic register, together with spores of Sphagnaceae (*Stereisporites antiquasporites*, *Cingutriletes australis*).

3) A hygrophile ecotonal community (Plate 3) was surrounding the fresh water bodies. This was by far the most diversified community of the wetland. A highly diversified assemblage of ferns (see the chapter Taxa recorded), belonging to the families Osmundaceae, Schizaeaceae / Matoniaceae, Cyatheaceae / Dicksoniaceae, Polypodiaceae and Pteridiaceae, is represented by 21 formspecies of palynomorphs and is associated with 9 formspecies of Lycopodiaceae/ Selaginellaceae and scarce Bryophyta (Hepaticae), completing the scenario of this warm -climatic Danian wetland.

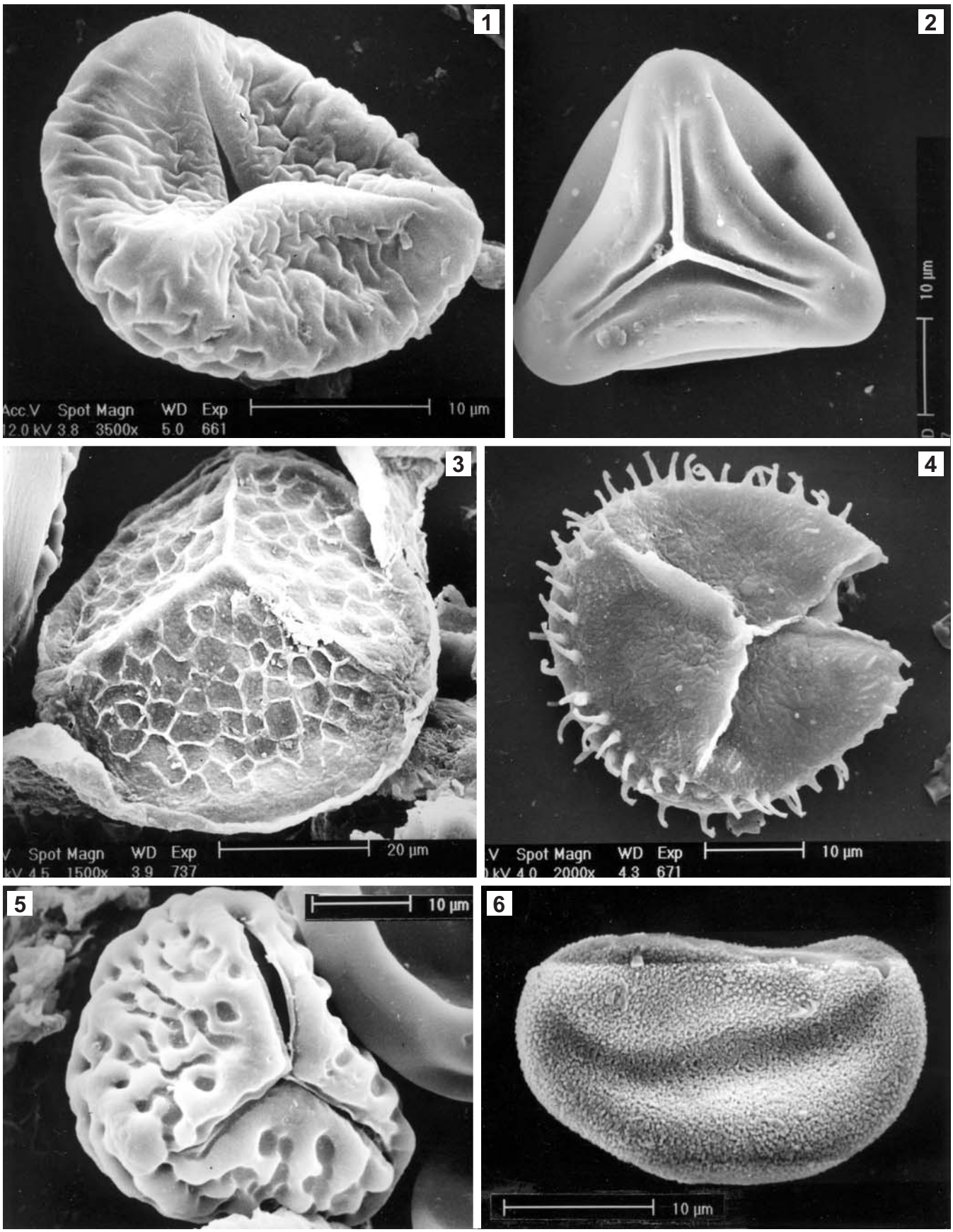
4) A subtropical subhumid to semiarid lowland community (Plates 4 and 5) characterized by a low size arboreal (?) and arbustive stratum, mainly composed by different species of Proteaceae, represented in the palynologic register by *Peninsulapollis gillii, Propylipollis lateflexus, Triporopollenites* cf. *ambiguus, Triporopollenites parviannulatus, Proteacidites granulatus, P.* cf. *asperatus, P. stipplatus, P. tenuiexinus, P*. sp., *Retidiporites camachoi* and cf. *Beaupraidites* sp., as well as Gunneraceae (*Tricolpites reticulatus,* Plate 5), which also indicate warm and (locally) moist conditions. In addition, some Gleicheniaceae (represented by *Gleicheniidites senonicus*) and Ericaceae (*Ericipites scabratus, E. microtectatum*) may have integrated the community.

Plate 3. Palynomorphs characteristic for Community 3: Hygrophile ecotonal community of ferns, Selaginellaceae/Lycopodiaceae and Hepaticae. 1, *Selaginella perinata* (Krutzsch *et al.*) Frederiksen 1980. 2, *Dictyophyllidites harrisii* Couper 1958. 3, *Ricciopsis* sp. 4, *Ceratosporites equalis* Cookson & Dettmann 1958. 5, *Klukisporites variegatus* Couper 1958. 6, *Polypodiisporites irregularis* Pocknall & Mildenhall 1984.

Plate 4. Palynomorphs characteristic for Community 4: Subhumid to semiarid lowland community with prevailing proteaceans. 1-2, *Triporopollenites* cf. *ambiguus* Stover (in Stover & Partdrige 1973). 3, *Triatriopollenites* sp. 4, *Proteacidites* cf. *asperatus* McIntyre 1968. 5, cf. *Beaupreaidites* sp. 6, *Plicatopollis cretacea* Frederiksen & Christopher 1978.

Plate 5. Palynomorphs characteristic for Community 4 (continued): 1, *Rousea patagonica* Archangelsky 1973. 2, *Tricolpites reticulatus* (Couper) Jarzen & Dettmann 1989. 3-4, *Rousea* sp. (picture 4 shows details of picture 3; observe collumelae of intercolpium and the diminution of size of the lumina of the reticulum towards the poles).

Plate 3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12.0 kV 3.8 3500x 5.0 661
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3
Spot Magn WD Exp
1500x 3.9 737
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4
V Spot Magn WD Exp
kV 4.0 2000x 4.3 671
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6
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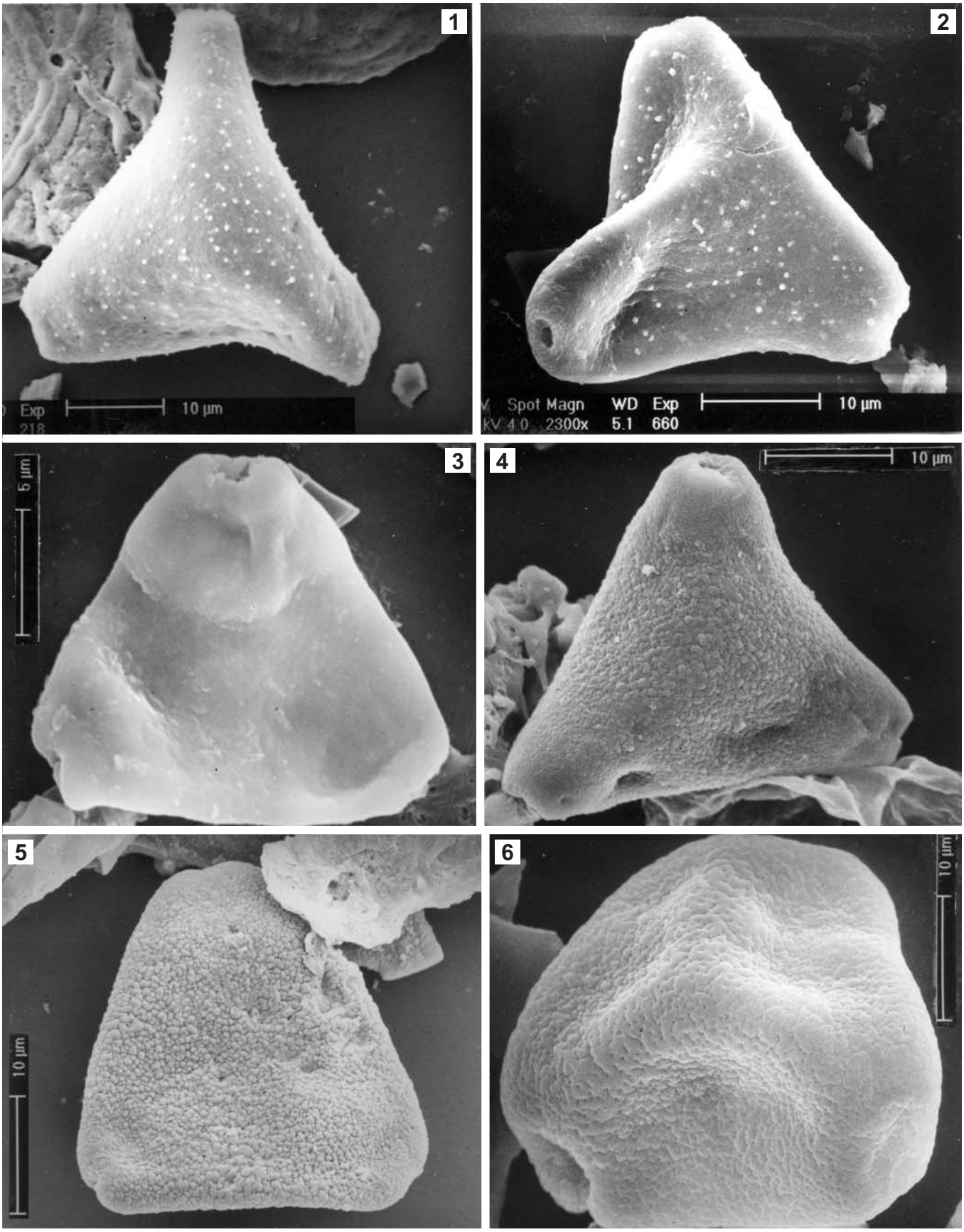
Plate 4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Exp
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KV 4.0 2300x 5.1 660
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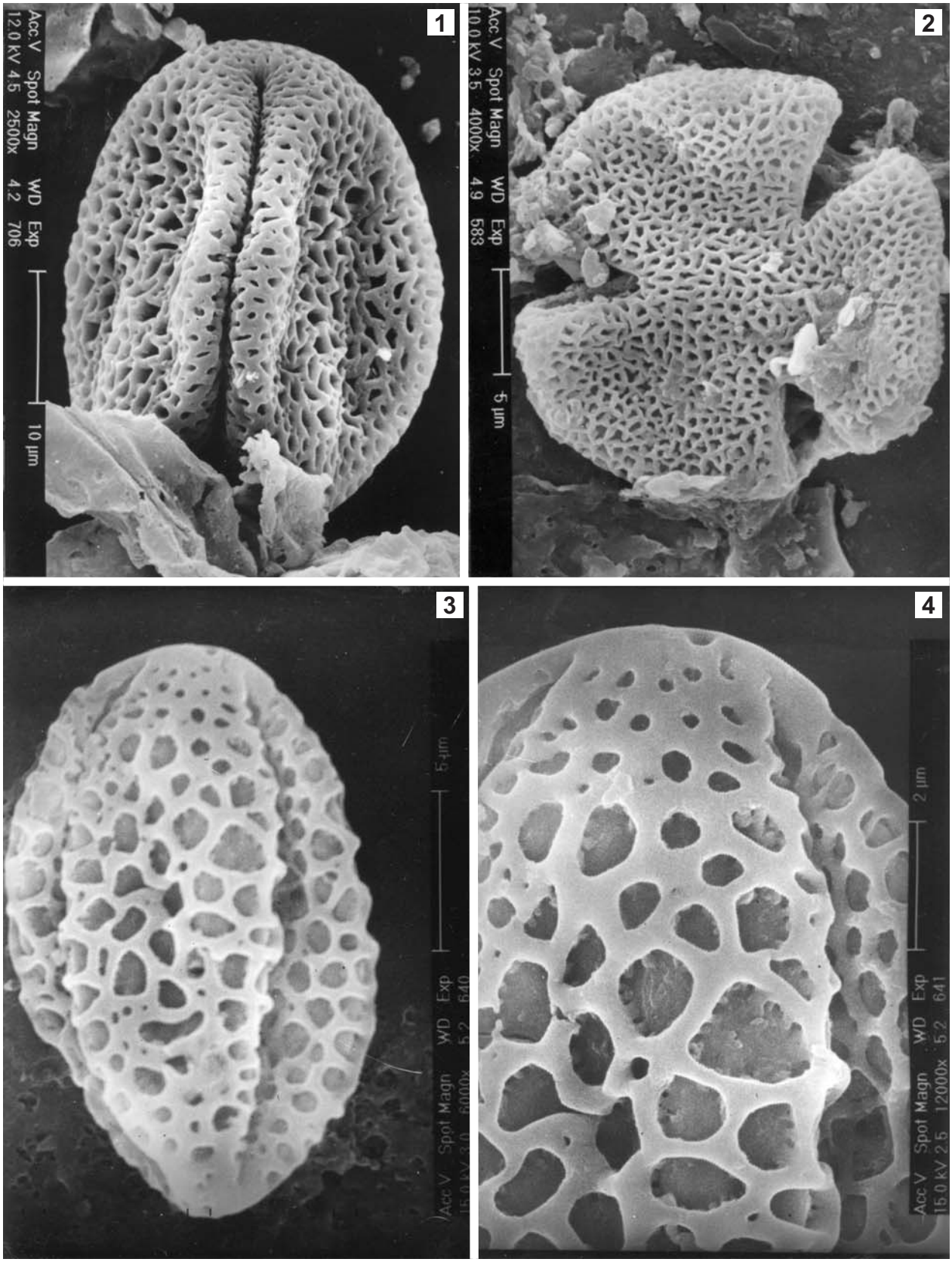
Plate 5


1
Acc.V Spot Magn WD Exp
12.0 kV 4.5 2500x 4.2 706
10 µm
2
Acc.V Spot Magn WD Exp
10.0 kV 3.5 4000x 4.9 583
5 µm
3
Acc.V Spot Magn WD Exp
5 µm
4
Acc.V Spot Magn WD Exp
15.0 kV 2.5 12000x 5.2 641
2 µm

At present we do not know which of the proteacean taxa mentioned are arboreous and which are arbustive, but it seems reasonable to think about an arboreous stratum of Proteaceae and Gunneraceae along the river courses and arbustive proteacean steppes on the interfluvial plains.

5) In the background, at somewhat higher topographic levels, was growing a nearly pure conifer forest (Plate 6). Permineralized trunks of a similar forest from the same member of the Cerro Bororó Formation have been studied in the PhD Thesis of B. Petriella (1972), who found nearly 100 trunks of 4 to 10m of length and up to more than 60 cm of diameter, including numerous stumps. He described the podocarpacean organ-species *Mesembrioxylon mazzonii*.

The complete palynologic register corresponding to a conifer forest reflected by our palynologic assemblage is composed by the nine formspecies of podocarpacean pollen grains mentioned on the list "Taxa recorded".

6. CONCLUSIONS

1) The Danian age of the palynologic assemblage studied is controlled by stratigraphic data from calcareous microfossils (Bertels, 1973).

2) The extremely high taxonomic diversity of the palynologic assemblage (96 species) allows to extend considerably the knowledge on the coexisting paleoenvironments near the coast in the studied area of central Patagonia during Danian times.

3) The depositional environment inferred from this study is continental, with a body of freshwater located relatively near the marine coast line, behind a brackish palm-swamp developed near-shore. A similar spatial distribution of biotopes is found today along thousands of km of the North American Atlantic and the Gulf of Mexico coasts between 38º and 26º of latitude.

4) The elements which compose the palynologic assemblage and allow the definition of five paleocommunities are showing that the climatic conditions were subtropically warm, with the following sequence of changing humidity along a profile extending from a sandy coastal plain towards the interior: 1: brackish palm swamps, 2: a hygrophile flora of a highly diverse community of ferns and associated lycopods and selaginellales, which is bordering 3: a wetland covered by aquatic ferns (*Azollopsis* spp.) and with a shallow water column colonized by abundant planktonic microalgae (principally Botryococcaceae and Zygnemataceae), 4: a piedmont plain characterized by a subhumid to semiarid population of proteaceans and finally, 5: a topographically elevated hinterland covered by coniferous forests.

5) The absence of three important groups of palynomorphs is calling the attention:

   a) No *Nothofagidites* pollen is present. This genus is characteristic for temperate and cool temperate environments. From Danian deposits it is only known in southernmost Patagonia and the Antarctic Peninsula (Paleophytogeoprovince of *Nothofagidites*: Quattrocchio and Volkheimer, 2000).

   b) The genus *Classopollis* is absent too. This thermophile Mesozoic and early Paleogene genus can be found in warm climatic areas. Its mother plants (Cheirolepidiaceae) grew on well drained soils. The latter characteristic was obviously not present in the swampy depositional environment inferred for the sampling point located within the Danian wetland of Puesto Fernández.

   c) No pollen of Ulmaceae (*Verrustephanoporites, Ulmoideipites*) is present.

6) The characteristics of the studied palynologic assemblage and its paleoenvironment denote a marked similarity with the palynologic assemblage described by Palma-Heldt (1978, 1980) and Collao *et al.* (1987) from the Tertiary of Arauco-Concepción (Curanilahue Formation, Lota member), Chile. Their information was

Plate 6. Palynomorphs characteristic for Community 5: Conifer forest, composed mainly by podocarpaceans. 1, *Lygistepollenites florinii* (Cookson & Pike) Stover & Evans 1973. 2, *Podocarpidites verrucosus* Volkheimer 1972. 3-4, *Podocarpidites rugulosus* Romero 1977. 5, *Dacrycarpites australiensis* Cookson & Pike 1953. 6, *Podocarpidites elegans* Romero 1977.

Plate 6

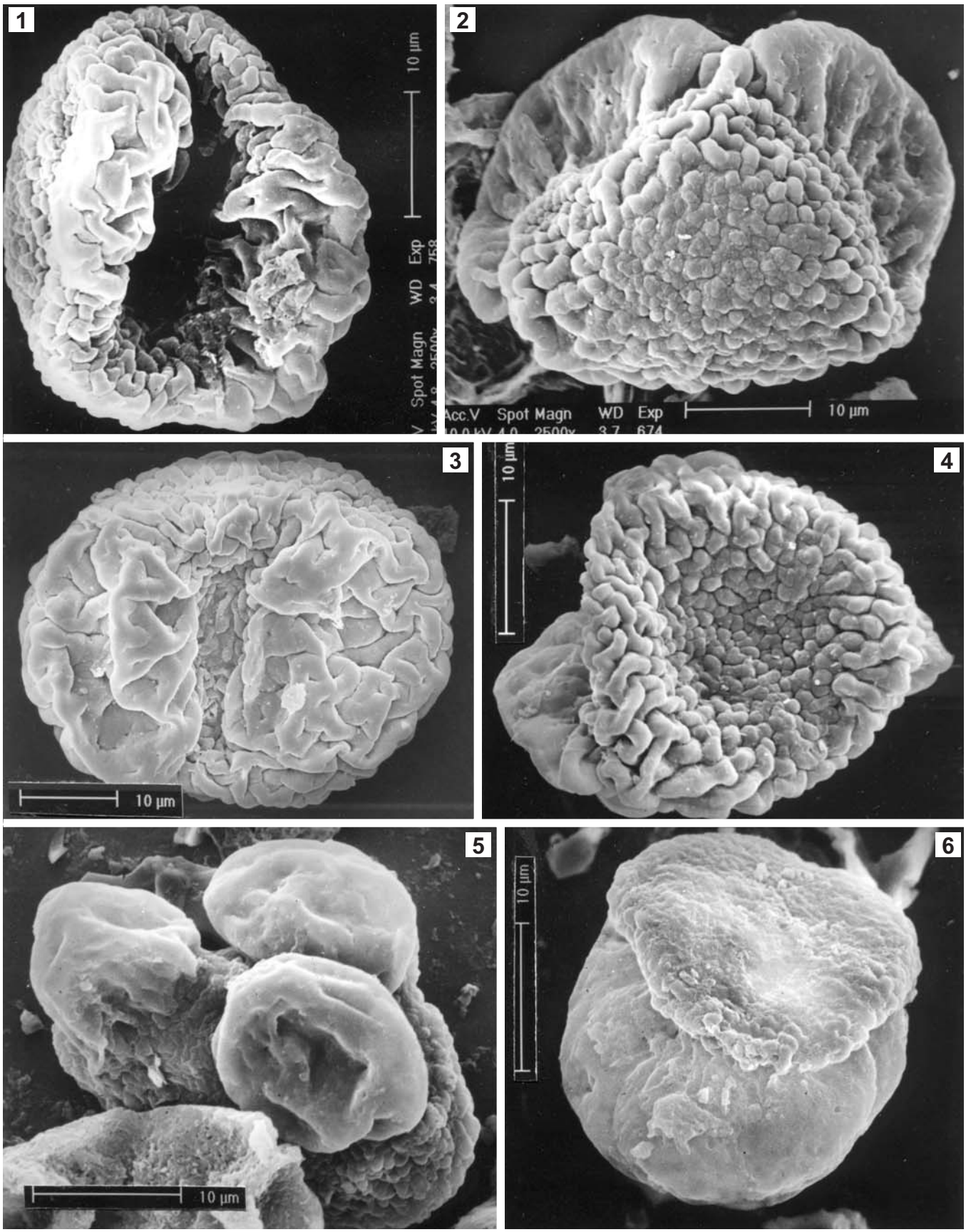
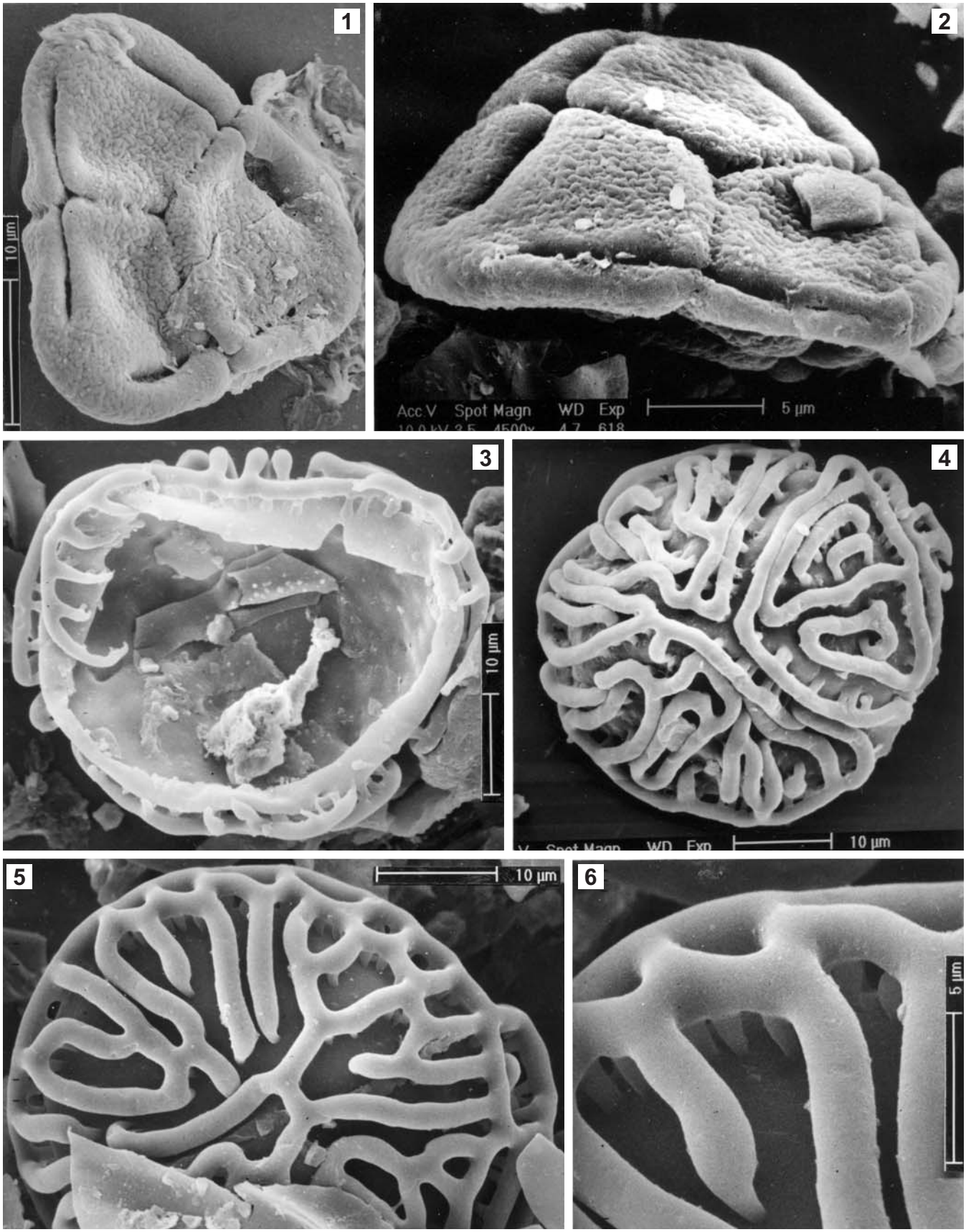


Plate 7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later completed by Gayó *et al.* (2005). The main difference with our material is the absence of Fungi in the latter.

7) The presence of pantropical elements (palmae types), associated with proteaceans, the absence of *Nothofagidites* and of the *Normapolles*-Group, as well as the scarcity of gymnosperms allow to compare these assemblages with the (earlier) Senonian Palmae Province of Africa and South America, described by Herngreen and Chlonova (1981).

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Plate. 7. 1–2, *Integritetradites* sp. 3–6, Angiosperm pollen with radiate, columellate muri, without defined aperture (indet.).

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Palynology and biostratigraphy of the Escucha Formation in the Early Cretaceous Oliete Sub-basin, Teruel, Spain

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Resumen

Se estudian un conjunto de asociaciones palinológicas obtenidas en materiales del Cretácico Inferior de la Subcuenca de Oliete, correspondientes a la Formación Escucha (Cordillera Ibérica, provincia de Teruel, España). La sucesión sedimentaria estudiada se depositó en un medio costero complejo en el cual se depositaron sedimentos ricos en materia orgánica. La medición y correlación detallada de secciones estratigráficas ha permitido establecer la localización estratigráfica detallada de las muestras con contenido palinológico. Las secciones estudiadas contienen asociaciones de miosporas abundantes y diversas, y únicamente el nivel más basal (M_1) muestra quistes de dinoflagelados. En total se han identificado más de 130 taxones entre los que se encuentran algunos significativos marcadores biostratigráficos. Por una parte, la presencia de ciertas esporas trilete como *Appendicisporites concentricus*, *Cicatricosisporites crassistriatus*, *C. mohrioides, C. patapscoensis*, *C. subrotundus* y *Phlebopterisporites globosus*, además de varios tipos de granos de polen de angiospermas primitivas (*Afropollis*, *Asteropollis*, *Clavatipollenites*, *Liliacidites*, *Brenneripollis-Pennipollis* y *Stellatopollis*, así como escasos granos tricolpados) permiten atribuir una edad Aptiense Superior a los materiales estudiados. Por otra, la identificación de las especies de dinoflagelados *Cyclonephelium compactum*, *Criboperidinium aceras*, *Apteodinium vectense* and *Surculosphaeridium? longifurcatum* señala una edad Aptiense Superior–Albiense Inferior para el nivel estudiado más basal. Estos nuevos datos bioestratigráficos asignan una edad más antigua a la última unidad sinrift (Fm. Escucha) de la Cuenca Ibérica.

Palabras clave: Palinología, Bioestratigrafía, Aptiense Superior, Albiense Inferior, Cretácico Inferior, Formación Escucha, Subcuenca de Oliete, Cordillera Ibérica, España

Abstract

Palynomorph assemblages of a Lower Cretaceous organic matter-rich sedimentary succession (Oliete Sub-basin, Iberian Ranges, Province of Teruel, Spain) from a complex coastal sedimentary environment are described. Detailed stratigraphic analyses were performed and correlations established in order to precisely record the stratigraphic location of the studied palynological samples. The studied sections contained abundant, well-diversified miospore assemblages. One level (M_1) contained an interesting assemblage of dinoflagellate cysts. More than 130 taxa were identified including biostratigraphically significant biomarkers. On the one hand, the presence of *Appendicisporites concentricus*, *Cicatricosisporites crassistriatus*, *C. mohrioides, C. patapscoensis*, *C. subrotundus* and *Phlebopterisporites globosus*, as well as several angiosperm pollen types (*Afropollis*, *Asteropollis*, *Clavatipollenites*, *Liliacidites*, *Brenneripollis-Pennipollis* and *Stellatopollis*, occurring with rare and poorly diversified tricolpate forms), suggests an Upper Aptian age for the studied material. On the other, the dinoflagellates *Cyclonephelium compactum*, *Criboperidinium aceras*, *Apteodinium vectense* and

Surculosphaeridium? longifurcatum indicate an Upper Aptian–Lower Albian age for the oldest level studied. These new biostratigraphic data assign an older age to the latest synrift unit (Escucha Formation) of the Iberian Basin.

Keywords: Palynology, Biostratigraphy, Upper Aptian, Lower Albian, Early Cretaceous, Escucha Formation, Oliete Sub-basin, Iberian Ranges, Spain

1. INTRODUCTION

From a palynological point of view, little information is available about the Lower Cretaceous rocks of the Iberian Peninsula. The first studies were undertaken in Portugal (Estremadura) in the 1960s (Groot and Groot, 1962). The first published palynological studies of the Lower Cretaceous of Spain were on the Aptian–Albian lignitiferous section of the Utrillas Basin (Province of Teruel) (Menéndez Amor and Esteras Martín, 1964), and on the lignitiferous Wealdian levels of Uña (Province of Cuenca) (Menéndez Amor, 1970). Limited studies have also been performed at Lower Cretaceous sites in the Spanish Pyrenees (Médus and Pons, 1967; Barale, 1991), the Basque-Cantabrian Basin (Fechner and Gruber, 1991; Alonso *et al*., 2000; Barrón *et al*., 2001; García-Blanco *et al*., 2004), the Betic Range (Busnardo and Taugourdeau, 1964; Leereveld *et al*., 1989), the Catalan Coastal Range (Médus, 1970; Solé de Porta, 1983), the southwestern Iberian Basin (Arias and Doubinger, 1980; Doubinger and Mas, 1981), and the Central Iberian and the Maestrat Basins (Boulouard and Canérot, 1970; Médus, 1970; Solé de Porta and García Conesa, 1987; Mohr, 1989; Querol and Solé de Porta, 1989; Diéguez *et al*., 1995a,b; Trincão and Diéguez, 1995; Gomez *et al*., 2000, 2001, 2002; Peyrot *et al*., 2005).

Most of the palynological studies performed on Lower Cretaceous materials from the Central Iberian and Maestrat Basin focused in lignitiferous beds from the Escucha Formation, defined by Aguilar *et al*. (1971). This formation is a heterolithic unit with coal-bearing deposits in its lowermost part (Cervera *et al*., 1976; Pardo, 1979; Querol, 1990). Although this unit has traditionally been described as reflecting deltaic-estuarine sedimentary environments (Pardo, 1979; Querol, 1990), more transgressive sedimentary systems have been recognized such as barrier island systems with backbarrier marshes and flood-tidal deltas (Rodríguez-López *et al*., 2005).

The Escucha Formation shows a great variety of synrift features, such as sharp lateral facies and thickness variations, synsedimentary listric faults, wedge-shaped sedimentary units, angular unconformities and palaeoseismites (Rodríguez-López *et al*., 2004, 2006, 2007). The first palynological studies of this formation were performed by Boulouard and Canerot (1970) in lignitiferous beds in the Traiguera area (northern flank of the Valdancha Synclinal, Province of Tarragona). These authors reported an assemblage with few miospore species which they attributed to the Upper Albian due to the presence of foraminifera, bivalves, echinoids, solitary corals and ammonoids in neighbouring beds. The palynological studies of the above lignite beds were continued by Cabanes and Solé de Porta (1986), Solé de Porta and García Conesa (1987) and Solé de Porta *et al*. (1994), who reported a rich assemblage containing more than fifty taxa, characterised by an abundance of psilate trilete spores and the presence of the tricolpate pollen grains of primitive angiosperms. This assemblage was attributed to the Lower–Middle Albian based on stratigraphic correlation with other sectors in which the ammonite *Douvilleiceras monile* (Sowerby 1836) appears. In their study of an ensemble of samples from the Calanda and Castellote sub-basins (Province of Teruel), Querol and Solé de Porta (1989) observed less diverse assemblages than that at Traiguera, characterised by *Cyathidites*, *Concavissimisporites*, *Classopollis* and bisaccate pollen grains. Comparison with the Traiguera assemblage, led to their being assigned a Lower–Middle Albian age.

The palynological study of the Lower Cretaceous of the Oliete Sub-basin began with the analysis of lignite samples collected at Estercuel, Ariño, Alloza and Barrabasa (Solé de Porta *et al*., 1994). Dinoflagellate cysts and *Classopollis* appeared abundantly in levels attributed to lower deltaic facies, whereas pteridophytic spores, bisaccate pollen and *Classopollis* characterised the upper deltaic plain facies, in which dinoflagellate cysts were scarce or

absent. These authors which did not studied the dinoflagellate cysts, compared again these assemblages with those of Traiguera and attributed them a Lower–Middle Albian age.

Recently, palynological assemblages from the Arroyo de la Pascueta outcrop (Rubielos de Mora, Province of Teruel) have been reported as showing a great abundance of coniferous inaperturate pollen grains, *Classopollis* and spores of Cyatheaceae. They were dated as Lower–Middle Albian due to the presence of the foraminifera *Mesorbitolina* gr. *subconcava* (Leymerie) (Gomez *et al*., 2000). Studies in the Oliete Sub-basin were continued by Peyrot *et al*. (2005), who have described several assemblages from the Mina Z, Gargallo and Barranco del Colocho sites. These assemblages show very large amounts of Cyatheaceae and Schizaeaceae spores, as well as pollen grains related to Peltaspermales, conifers and primitive angiosperms.

The aim of the present work was to establish the age of the Lower Cretaceous Escucha Formation of the Oliete Sub-basin using palynology and stratigraphic record. The assemblages obtained from the sampled levels were compared with others from Lower/mid-Cretaceous palaeogeographic sectors for dating.

2. GEOLOGICAL SETTING

The study area is located in the link zone between the Iberian and the Catalan Coastal Ranges (Fig. 1a, 1b). The Escucha Formation represents the last synrift unit deposited during the Late Jurassic–Early Cretaceous rift stage that affected the Iberian Basin (Fig. 1c) (Salas and Casas, 1993). The crust thinning associated with this rift stage is the response to the northwards propagation of the Central Atlantic rift system and the opening of the North Atlantic oceanic basin (Salas and Casas, 1993; Martín-Chivelet *et al*., 2002). This rift stage faulted the broad Jurassic carbonate platforms, generating several extensional sub-basins (Fig. 1d) (Salas and Guimerà, 1996; Soria, 1997; Soria *et al*., 2000; Salas *et al*., 2001).

The studied outcrops belong to the Escucha Formation in the Oliete extensional Sub-basin (1 in Fig. 1d). This Sub-basin was controlled by NW-SE and NE-SW striking basement faults (Álvaro *et al*., 1979), which define several blocks with different subsiding patterns activated by listric faults (Salas, 1987).

The synrift sedimentation of the Oliete sub-basin began in the Lower Barremian with the deposition of the Blesa Formation (Soria, 1997; Soria *et al*., 1997; Meléndez *et al*., 2000), and continued from the late Barremian to the late Aptian with the development of the Urgonian platforms (Alacón, Forcall and Oliete Formations) (Fig. 1c) (Soria *et al*., 1994). The Escucha Formation deposited over these carbonate platforms in more continental and coastal environments.

3. MATERIAL AND METHODS

Four detailed stratigraphic sections (with an accumulated thickness of more than 260 m) were studied in order to establish the stratigraphic location of organic levels for palynological study. The stratigraphic panel of Fig. 2 shows the correlations of the studied sections and the locations of the sampled levels. Correlation analysis allowed the Escucha Formation has been divided by Rodríguez-López *et al*. (2007) into three different lithological units: E_1, E_2 and E_3, based on lithological differences and the occurrence of angular unconformities (Fig. 2). The vertical facies stacking pattern of sampled intervals is shown in Fig. 3. Levels indicated with the letter M (Fig. 2) belong to unit E_1 (Rodríguez-López *et al*., 2007). It is characterized by coal levels with millimetre- to centimetre-sized amber fragments, carbonate marine levels with foraminifera and glauconite, and by the presence of sandy-silty transgressive sedimentary systems such as barrier islands with a great variety of sedimentary sub-environments (e.g., flood-tidal deltas and backbarrier marshes [Rodríguez-López *et al*., 2005, 2007]).

Five sampled levels (M_1-M_5) from unit E_1 provided palynomorphs (Fig. 3a). The remainder (M_6, M_{10} and M_{11}) contained large amounts of carbonaceous fragments but no organic matter-walled microfossils. The samples from M_1 and M_2 were obtained from black mudstones containing plant fragments, gypsum, mica, ostracods and foraminifera suggesting marine influence. The sample

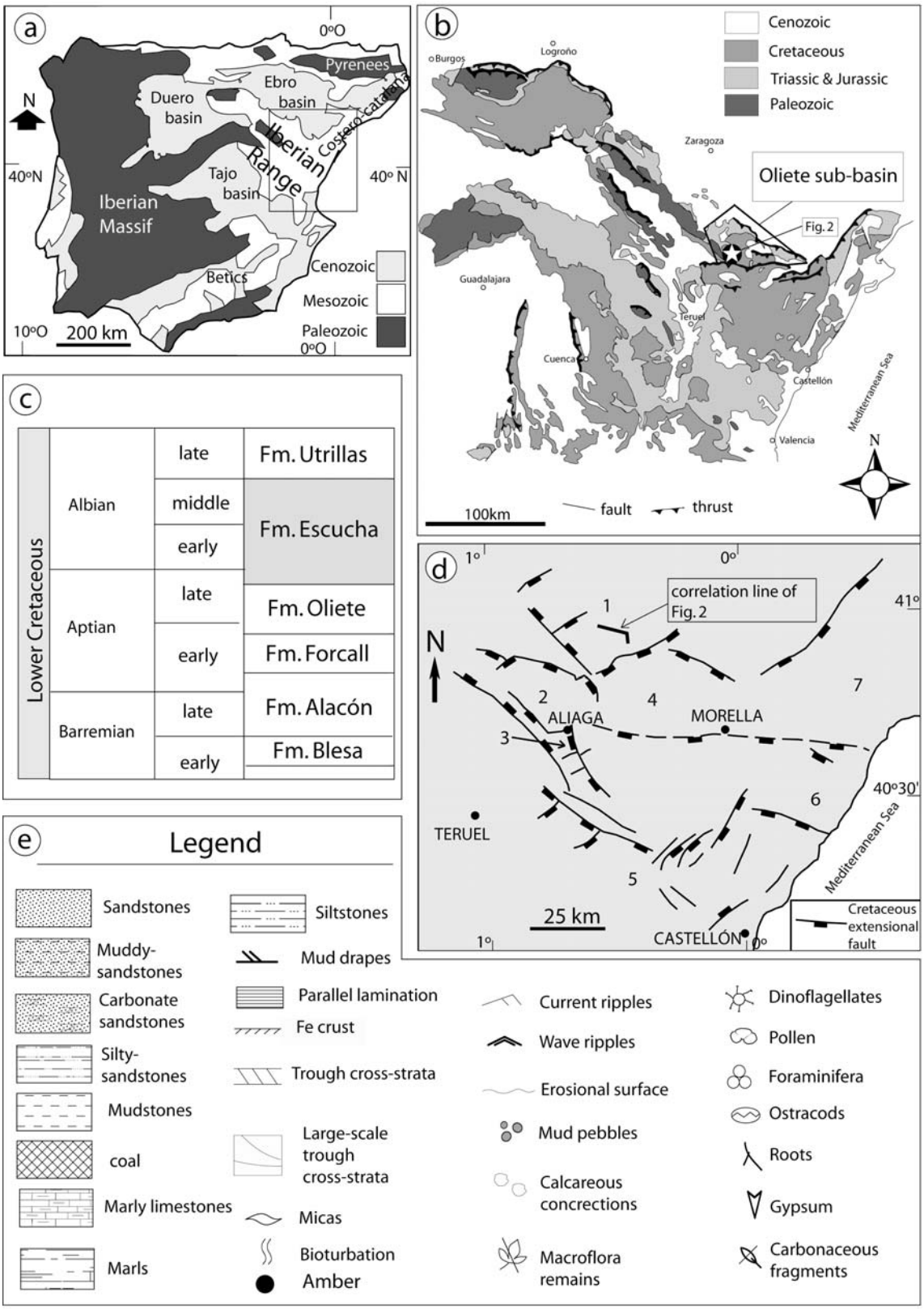


Figure 1. a) Geological map of the Iberian Peninsula; b) Geological map of the Iberian Range showing the location of the study area (modified after Capote *et al.*, 2002); c) Proposed Lower Cretaceous chronostratigraphic chart of the Oliete sub-basin; d) Extensional sub-basins of the Iberian Basin during the second rift stage late Jurassic-early Cretaceous: 1. Oliete, 2. Las Parras, 3. Galve, 4. Morella, 5. Penyagolosa, 6. Salzedella, 7. El Perelló (Modified after Liesa *et al.*, 2004); e) Legend of stratigraphic sections.

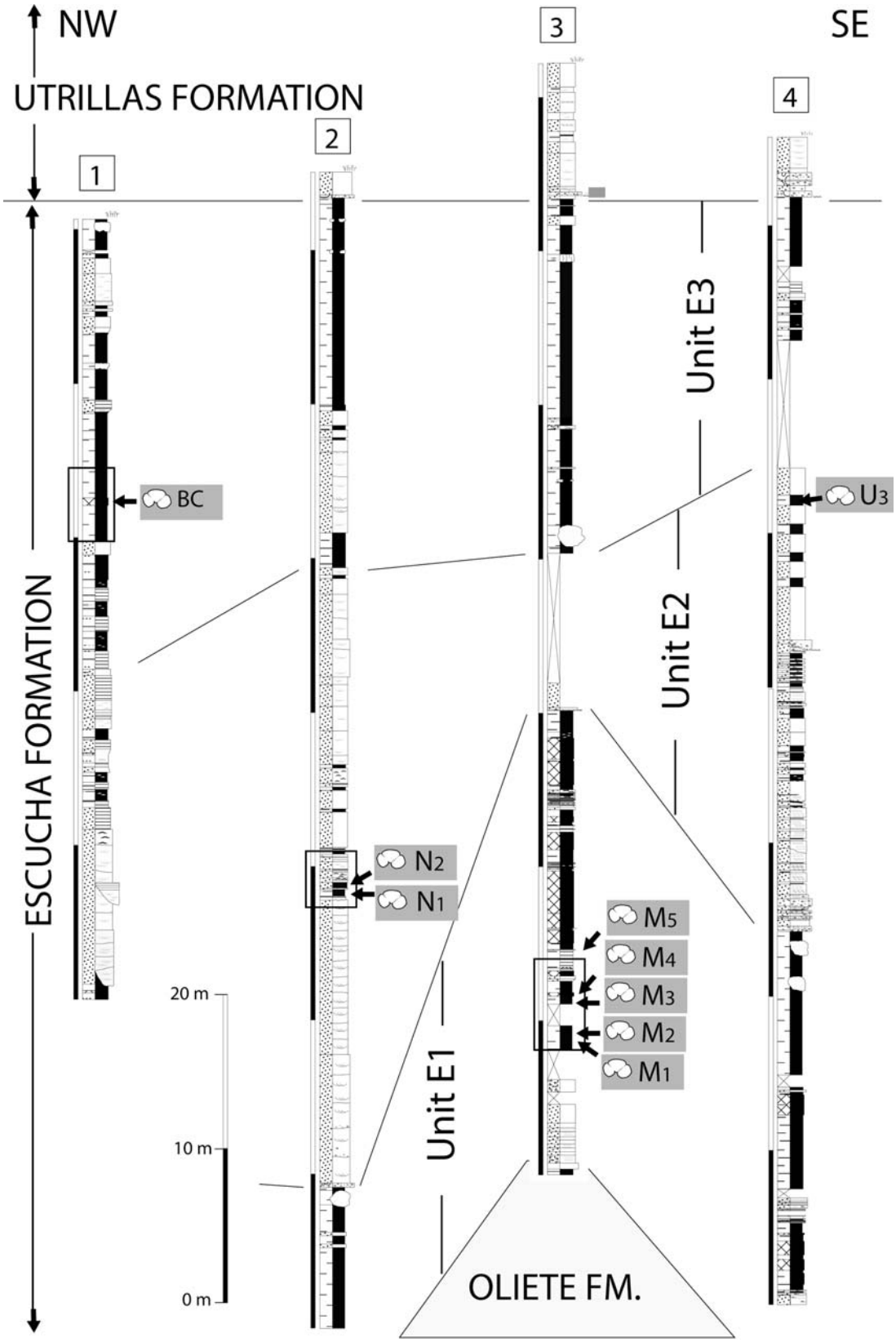


Figure 2. Stratigraphic correlation of studied sections. Samples location is indicated. 1. Barranco del Colocho section, 2. Barranco del Tubo section, 3. Mina Z section, 4. Gargallo section.

from M_3 came from a level of black mudstones with roots and carbonaceous plant fragments (Fig. 3.1).

Four samples have been sampled from unit E_2 (Rodríguez-López *et al*., 2007)(see panel of Fig. 2). Samples N_1 to N_3 (Fig. 3.2) and U_3 (Fig. 3.3) were collected from organic matter-rich, silty levels deposited in a still-water environment. N_1 and N_2 provided palynological remains, while N_3 was barren. Sample U_3 was collected from sandy siltstones deposited in a shallow marine environment with clear tidal influence (Rodríguez-López *et al*., 2006, 2007).

Finally, sample BC was obtained from unit E_3 (Fig. 2) at the top of the Escucha Formation (Rodríguez-López *et al*., 2007). This sample was recovered from carbonaceous mudstones with high sulfur content (Fig. 3.4). This level has been interpreted as a marsh deposit interbedded with palaeosols developed on an arid coastal plain (Rodríguez-López and Meléndez, 2004; Rodríguez-López *et al*., 2007).

Samples were prepared at the Department of Stratigraphy, Complutense University of Madrid, following the standard palynological technique (Batten, 1999) based on acid treatment (HCl, HF, HNO_3) at high temperature. Slides were mounted in glycerine jelly and studied with a Leitz Laborlux D microscope and an Olympus BX51 wide field light microscope. The latter incorporated a Color View IIIu Camera.

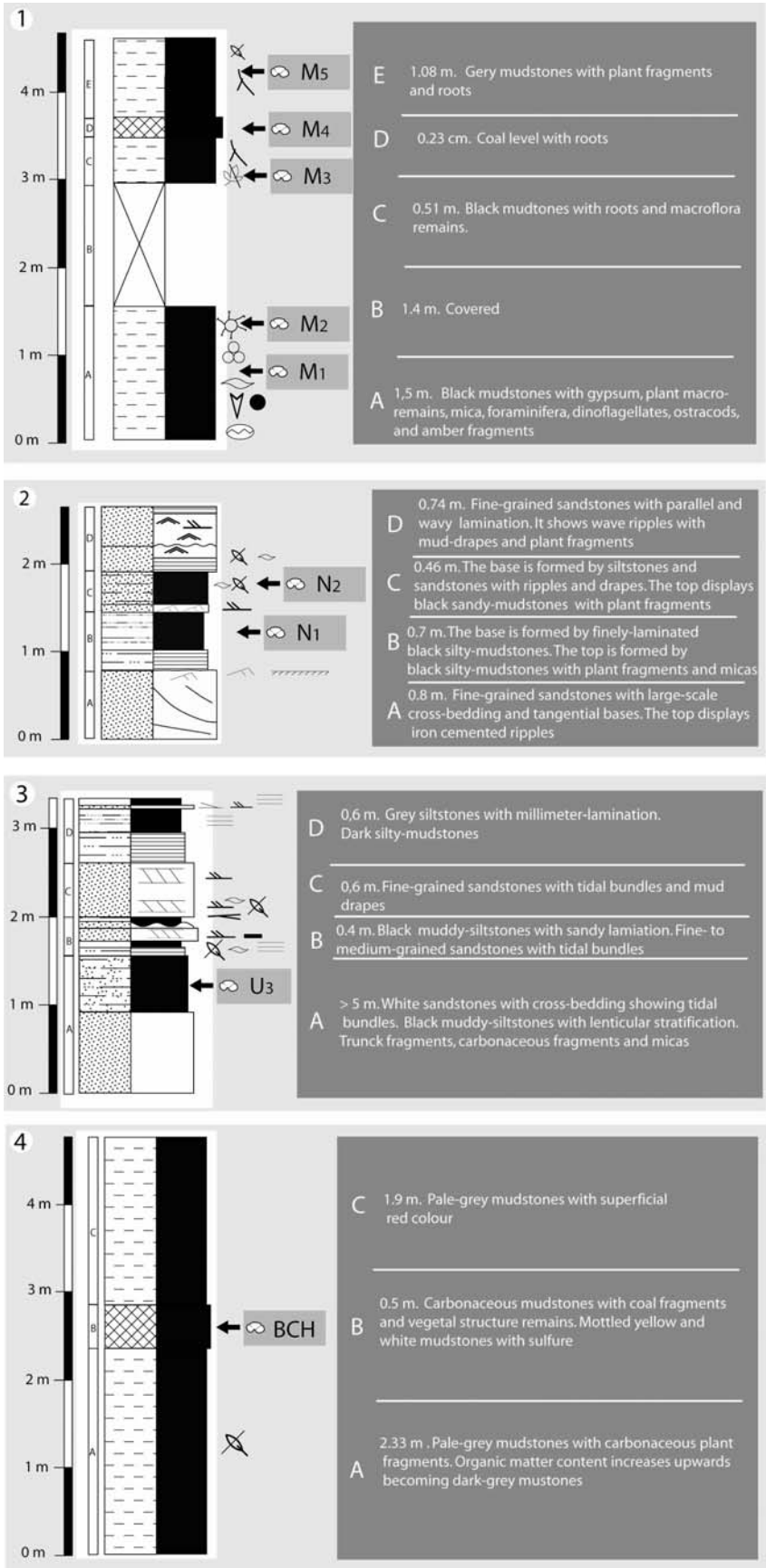


Figure 3. Detailed stratigraphic section of sampled levels. 1. Mina Z section, 2. Barranco del Tubo section, 3. Gargallo section, 4. Barranco del Colocho section.

4. PALYNOLOGICAL STUDY

Palynological analysis yielded assemblages with a high diversity of species. Eighty three spores, forty four pollen grains (33 from gymnosperms and 11 from angiosperms), thirteen dinoflagellate cysts, one phycome of Prasinophyte, one acritarch, one algal taxon, and several types of linings of foraminifera were identified (Table 1). The spores showed possible relationships to mosses and liverworts (*Cingutriletes*, *Staplinisporites*, *Stereosporites*, *Triporoletes*), clubmosses and spikemosses (*Camarozonosporites*, *Densoisporites*, *Foveotriletes*, *Kraeuselisporites*, *Leptolepidites* [Pl. 1, Fig. 3], *Lycopodiumsporites*, *Neoraistrickia*, *Patellasporites*, *Retitriletes*, *Uvaesporites*) and ferns (the rest). The spores of schizaeaceaous ferns representing six genera (*Appendicisporites*, *Cicatricosisporites*, *Cicatricososporites*, *Costatoperforosporites* [Pl. 2, Fig. 3], *Ischyosporites* [Pl. 2, Fig. 1], *Nodosisporites*) and 33 species were significant owing to their abundance and diversity. These spores appeared in large numbers in all the studied levels except for BC, although psilate spores related to the families Cyatheaceae, Dicksoniaceae and Dipteridaceae were the dominant forms. In all the studied levels the last three families showed a number of genera similar to that shown by the Schizaeaceae (*Biretisporites*, *Cibotiumspora*, *Concavissimisporites* [Pl. 1, Fig. 5], *Converrucosisporites*, *Deltoidospora*, *Dictyophyllidites*, *Kuylisporites*), but only 11 species compared to 33.

Conifer pollen grains attributed to the genera *Inaperturopollenites* and *Classopollis* numerically dominated all the analysed samples except that of level BC (Table 1). *Inaperturopollenites* were attributed to the families Cuppressaceae and Taxodiaceae, and *Classopollis* (Pl. 1, Fig. 11) to the extinct family Cheirolepidiaceae. *Araucariacites* was well represented in all the studied samples, and abundantly appeared in the level M_1.

Pollen attributed to the genus *Alisporites*, produced by seed ferns of the order Peltaspermales, were the most conspicuous bisaccate pollen in the studied levels except for BC (Table 1). Small numbers of pollen grains attributed to Cycadales, Ginkgoales and Bennettitales (*Bennettiteaepollenites*, *Cycadopites*, *Eucommiidites* [Pl. 1, Fig. 10], *Exesipollenites*, *Monosulcites* and verrucate monosulcate pollen of uncertain taxonomic status [Pl. 1, Fig. 6]) were observed throughout all sections. Genera of doubtful botanical affinities - *Cerebropollenites* (Pl. 1, Fig. 7) and *Spheripollenites* - were scarce except at level M_1. Gnetales (*Equisetosporites*) were found in levels M_5, N_1, U_3 and BC.

Pollen grains of primitive angiosperms were found in all the studied levels (Table 1). Columellate-tectate monosulcate pollen attributed to the genus *Clavatipollenites* (Pl. 1, Figs. 8, 12) were the most common angiosperm representatives. This genus was especially abundant in M_4. In contrast, the monosulcate pollen grains showed a reticulum of varying thickness and were attributed to the genus *Liliacidites*; coarsely reticulate-acolumellate forms of possible alismatalean affinity, here included in the *Brenneripollis-Pennipollis* complex (Doyle, 1999; Friis *et al*., 2000, 2006), were recorded in smaller amounts (Pl. 1, Fig. 9). Tricolpate forms attributed to the genus *Tricolpites* (Pl. 1, Fig. 13) were found in M_3, N_1, N_2 and BC, but the number of grains was always very small. The pollen grains of the genera *Afropollis*, *Asteropollis* and *Stellatopollis* were relatively uncommon (Table 1).

Foraminifera linings (Pl. 2, Fig. 12) and chorate and proximate dinoflagellate cysts (Pl. 2, Figs. 4–12) were found only in M_1, indicating a clear marine influence at this level. Among the dinoflagellate cyst *Circulodinium distinctum* (Deflandre & Cookson 1955) Jansonius 1986 (Pl. 2, Fig. 7), *Tenua hystrix* Eisenack 1958 emend. Sarjeant 1985 (Pl. 2, Fig. 5), *Oligosphaeridium complex* (White 1842) Davey & Williams 1966 (Pl. 2, Fig. 4), *Cribroperidinium orthoceras* (Eisenack 1958) Davey 1969 (Pl. 2, Fig. 6), *C. aceras* Eisenack 1958 emend. Sarjeant 1985 (Pl. 2, Figs. 10-11), *Kiokansum unituberculatum* (Tasch 1964) Stover & Evitt 1978 (Pl. 2, Fig. 8), *Subtilisphaera perlucida* (Alberti 1959) Jain & Millepied 1973, *Muderongia staurota* Sarjeant 1966, *Aptea polymorpha* Eisenack 1958 emend. Dörhöfer & Davis 1980, *Cyclonephelium compactum* Deflandre & Cookson 1955 (Pl. 2, Fig 9), *Apteodinium granulatum* Eisenack 1958 emend. Sarjeant 1985, *A. vectense* (Duxbury 1983) Lucas-Clark 1987, *Surculosphaeridium*? *longifurcatum* (Firtion 1952) Davey *et al*. 1966 were identified. Colonies of *Botryococcus* were recorded in N_1 and N_2, indicating fresh or brackish water influxes during the deposition of these sediments.

	M_1	M_2	M_3	M_4	M_5	N_1	N_2	U_3	BC
Spores of vascular cryptogams									
Aequitriradites spinulosus (Cookson & Dettmann 1958) Cookson & Dettmann 1961	+		x		+	+			
Appendicisporites concentricus Kemp 1970						+			
Appendicisporites erdtmanii Pocock 1964						+	+		
Appendicisporites jansonii Pocock 1962			+	+			+		
Appendicisporites matesovae (Bolkhovitina 1961) Norris 1967		+							
Appendicisporites problematicus (Burger 1966) Singh 1971		+							
Appendicisporites robustus Kemp 1970							+		
Appendicisporites cf. *potomacensis* Brenner 1963			+	+	+				
Appendicisporites spp.			+		+	+	+	x	
Baculatisporites sp.	x	+		+	+	+	+	+	
Biretisporites sp.	+	+	+	x	x			●	x
Camarozonosporites sp.	+					+	+		
Cibotiumspora jurienensis (Balme 1957) Filatoff 1975				+	+		x		
Cicatricosisporites apicanalis Paden Phillips & Felix 1971			+		+		+	◇	
Cicatricosisporites cf. *apicanalis* Paden Phillips & Felix 1971			+						
Cicatricosisporites cf. *australiensis* Dettmann 1963		+	+						
Cicatricosisporites brevilaesuratus Couper 1958		+						+	
Cicatricosisporites crassiterminatus Hedlund 1966		+							
Cicatricosisporites crassistriatus Burger 1966		+							
Cicatricosisporites hallei Delcourt & Sprumont 1955		+	+	●	+	◇	+	+	
Cicatricosisporites hughesi Dettmann 1963	+	+	+			+	+		
Cicatricosisporites minutaestriatus (Bolkhovitina 1961) Pocock 1964						+	+		
Cicatricosisporites mohrioides (Delcourt & Sprumont 1955) Singh 1971	+			+				+	
Cicatricosisporites patapscoensis Brenner 1963		+	+	+				x	
Cicatricosisporites pseudotripartitus (Bolkhovitina 1961) Dettmann 1963	+	+		+	+			◇	
Cicatricosisporites recticicatricosus Döring 1965						+	+		
Cicatricosisporites sinuosus Hunt 1985						+			
Cicatricosisporites spiralis Singh 1971						+	+		
Cicatricosisporites subrotondus Brenner 1963			+					+	
Cicatricosisporites venustus Deák 1963	+	+	+	+	◇	+	+	◇	
Cicatricosisporites spp.	●	●	●	▲	▲	■	▲	▲	
Cicatricososporites auritus Singh 1971					+	+	+	+	
Cingutriletes sp.	+			+		x	+	◇	
Concavissimisporites verrucosus (Delcourt & Sprumont 1955) Delcourt, Dettmann & Hughes 1963	+	+		+	+	+			
Concavissimisporites punctatus (Delcout & Sprumont 1955) Brenner 1963		+	+						◇
Concavissimisporites sp.	+	+	+	x	+				◇
Contignisporites sp.					+		+	+	
Converrucosisporites sp.	+					+	+	+	
Costatoperforosporites foveolatus Deák 1962					+	x	◇	◇	
C. triangulatus Deák 1962						+			
Deltoidospora australis (Couper 1953) Srivastava 1975	●	●	◇	■		◇	x		■
Deltoidospora minor (Couper 1953) Pocock 1970	▲	●	◇	◇		◇	◇		▲
Deltoidospora sp.	x	+	●	x	●	◇	◇	●	●
Densoisporites velatus Weyland & Krieger 1953	+			+		x	+		
Dictyophyllidites harrisii Couper 1958	+	+	x	x	◇	+		◇	■
Echinatisporis sp.			+			+	+	+	
Foraminisporis asymmetricus Dettmann 1963		+							
Foveotriletes subtriangularis Brenner 1963	+								
Foveotriletes sp.			+		◇			◇	

Table 1. Semiquantitative study of the identified taxa. ■ > 100 specimens, very abundant; ▲100–50 specimens, abundant; ● 49–25 specimens, common; ◇ 24–10 specimens, frequent; x 9–5 specimens, rare; + 1–4 specimens, scarce.

	M_1	M_2	M_3	M_4	M_5	N_1	N_2	U_3	BC
Spores of vascular cryptogams (cont.)									
Gleicheniidites senonicus Ross 1949	x	+	+	+	◇	+	+	x	●
Impardecispora sp.					+				
Ischyosporites cf. *crateris* Balme 1957	+			+					
Ischyosporites cf. *pseudoreticulatus* (Couper 1958) Döring 1965		+				+	+		
Ischyosporites variegatus (Couper 1958) Schulz 1967	+							+	
Kraeuselisporites sp.						x	+		
Kuylisporites lunaris Cookson & Dettmann 1958		+							
Laevigatosporites sp.	+	◇	+	x	◇	x	+	●	+
Leptolepidites macroverrucosus Schulz 1967						+			
Leptolepidites spp.	+	+		+		x	+		
Lycopodiumsporites crassimacerius Hedlund 1966						+			
Matonisporites sp.								+	
Microreticulatisporites cf. *diatreus* Norris 1969							+		
Neoraistrickia sp.	+								
Nodosisporites sp.					+	+		+	
Patellasporites tavaredensis Groot & Groot 1962	+	+				◇	◇	◇	
Phlebopterisporites globosus (Kimyai 1966) Juhász 1979				+		+			
Punctatisporites sp.		+		+	x	+	+	x	
Retitriletes austroclavatidides (Cookson 1953) Döring, Krutzsch, Mai & Schulz in Krutzsch 1963		+							
Retitriletes sp.						+		+	
Rubinella sp.						+			
Staplinisporites caminus (Balme 1957) Pocock 1962					+	+			
Stereisporites cf. *aulosenensis* (Schulz 1966) Schulz 1967						+			
Stereisporites sp.				+		+			
Taurucosporites cf. *segmentatus* Stover 1962						+	+	+	
Trachysporites sp.		+		+		+	+		
Trilobosporites sp.	+	+			+	+	+	+	
Triporoletes reticulatus (Pocock 1962) Playford 1971			+						
Tuberositriletes sp.				+		+	+		
Todisporites major Couper 1958	+	+	+	+	◇	x	+	◇	
Undulatisporites sp.		+			+			x	
Uvaesporites sp.						+			
Verrucosisporites rotundus Singh 1964	+								
Verrucosisporites sp.		+				+	+		
Pollen grains (gymnosperms)									
Abietinaepollenites sp.			+			+	+		
Alisporites bilateralis Rouse 1959	x	◇	◇	●	▲	x	+	●	
Alisporites grandis (Cookson 1947) Dettmann 1963	x	◇	+	●	◇	x	+		
Alisporites spp.	■	x	x	●	■	▲	◇		
Araucariacites australis Cookson 1947	▲	●	●	x	●	◇	x	◇	
Bennettiteaepollenites sp.						+			
Cedripites sp.	◇	●	◇	x	●	+	+	+	
Cerebropollenites macroverrucosus (Thiergart 1949) Schulz 1967	◇		+	+		+	+	+	
Cerebropollenites sp.	x								
Classopollis classoides Pflug 1953 emend. Pocock & Jansonius 1961	■	■	■	■	◇	▲	▲		
Classopollis torosus (Reissinger 1950) Balme 1957	x			◇		●	+		
Classopollis cf. *caratinii* Reyre 1970	+			+					
Classopollis spp.	x	x	●	●	●	x	x	◇	
Cycadopites spp.	+	◇	x	x	▲	x	◇	◇	x

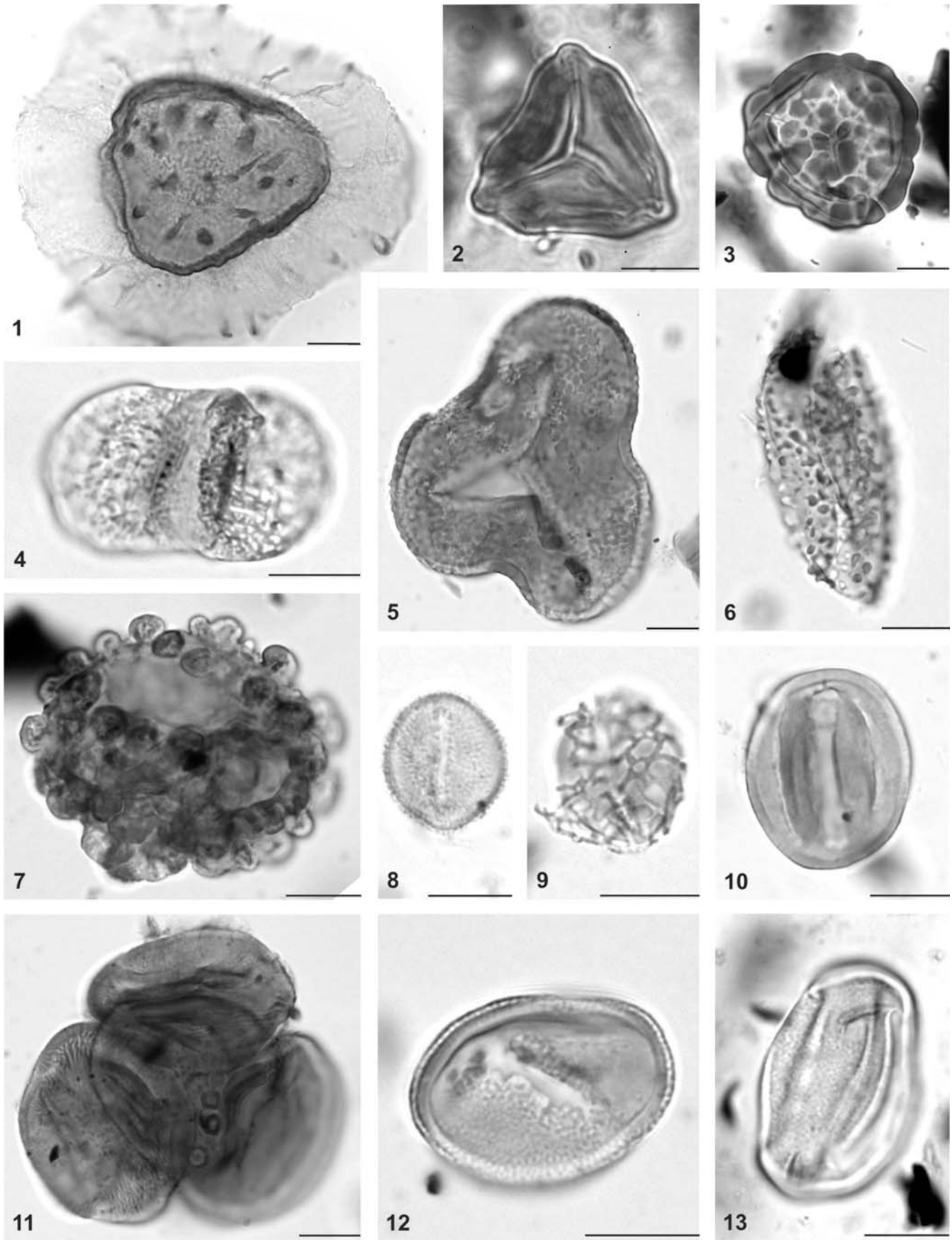
Table 1. (cont.) Semiquantitative study of the identified taxa. ■ > 100 specimens, very abundant; ▲100–50 specimens, abundant; ● 49–25 specimens, common; ◇ 24–10 specimens, frequent; x 9–5 specimens, rare; + 1–4 specimens, scarce.

	M_1	M_2	M_3	M_4	M_5	N_1	N_2	U_3	BC
Pollen grains (gymnosperms)									
Equisetosporites sp.					+	+		+	+
Eucommiidites troedsonii Erdtman 1948	+	+	+	+	●	+	+	+	
Eucommiidites minor Groot & Penny 1960	x		+	+	x	+			
Exesipollenites tumulus Balme 1957	+			+		●	◇		
Inaperturopollenites dubius (Potonié & Venitz 1932) Thompson & Pflug 1953	■	■	■	■	■	■	■	▲	
Inaperturopollenites hiatus Potonié 1958	◇								
Inaperturopollenites limbatus Balme 1957	+			+					
Inaperturopollenites spp.	+		x	●		◇	x		+
Monosulcites minimus Cookson 1947 ex. Couper 1953	+	◇	x	x	●	+	+	x	
Parvisaccites sp.	◇		+		◇	x			
Perinopollenites elatoides Couper 1958	x	+	+	+	+	+			
Pinuspollenites sp.	◇	+	◇	+	●	+			+
Phyllocladidites sp.	+	x			◇				
Podocarpidites sp.	+	+	+	+	x	+			
Rugubivesiculites sp.		+	+		◇				
Spheripollenites sp.	x			+	x	+	◇		
Undetermined bisaccate pollen grains	▲	●	●	●	■	▲	▲	▲	
Undetermined verrucate monosulcate pollen grains				+					
Vitreisporites pallidus (Reissinger 1950) Nilsson 1958	◇	+	+	+	◇	+	+		
Pollen grains (angiosperms)									
Afropollis sp.						+	+		
Asteropollis sp.			+						
Clavatipollenites hughesii Couper 1958	+		x	x		x	x		◇
Clavatipollenites tenellis Paden Phillips & Felix 1971	x								
Clavatipollenites minutus Brenner, 1963	+		+	+					
Clavatipollenites spp.	+	x	●	▲	+	●	●	◇	◇
Liliacidites spp.		+		●		+			
Pennipollis peroreticulatus (Brenner 1963) Friis, Pedersen & Crane 2000				+					
Brenneripollis-Pennipollis complex			x	x		+	+		
Stellatopollis dejaxii Ibrahim 2002						+			
Tricolpites sp.			+			+	+		+
Other palynomorphs									
Tasmanaceae	+								
Dinoflagellate cysts	◇								
Micrhystridium sp.	+								
Botryococcus				x		x			
Lining of foraminifera	x								

Table 1. (cont.) Semiquantitative study of the identified taxa. ■ > 100 specimens, very abundant; ▲100–50 specimens, abundant; ● 49–25 specimens, common; ◇ 24–10 specimens, frequent; x 9–5 specimens, rare; + 1–4 specimens, scarce.

Plate 1. Spore and pollen types of the Upper Aptian–Lower Albian Oliete Sub-basin. *1. Aequitriradites spinulosus* (Cookson & Dettmann 1958) Cookson & Dettmann 1961, level M_1 (Mina Z); *2. Gleicheniidites senonicus* Ross 1949, level N_1 (Barranco del Tubo); *3. Leptolepidites macroverrucosus* Schulz 1967, level N_1 (Barranco del Tubo); *4. Vitreisporites pallidus* (Reissinger 1950) Nilsson 1958, level M_1 (Mina Z); *5. Concavissimisporites verrucosus* (Delcourt & Sprumont 1955) Delcourt, Dettmann & Hughes 1963, level M_4 (Mina Z); *6.* Gymnospermous verrucate monosulcate pollen grain of uncertain taxonomic status, level M_4 (Mina Z); *7. Cerebropollenites macroverrucosus* (Thiergart 1949) Schulz 1967, level M_4 (Mina Z); *8. Clavatipollenites minutus* Brenner 1963, level M_4 (Mina Z); *9. Brenneripollis-Pennipollis* sp., level M_4 (Mina Z); *10. Eucommiidites troedsonii* Erdtman 1948, level M_4 (Mina Z); *11. Classopollis classoides* Pflug 1953 emend. Pocock & Jansonius 1961, level M_1 (Mina Z); *12. Clavatipollenites tenellis* Paden Phillips & Felix 1971, level M_4 (Mina Z); *13. Tricolpites* sp., level N_2 (Barranco del Tubo). Scale bar = 10 µm.

Plate 1



5. PALYNOMORPH-BASED BIOSTRATIGRAPHY

The palynological assemblages detected provided interesting biostratigraphic data. The presence of a high diversity of sculptured trilete spores (*Aequitriradites* [Pl. 1, Fig. 1], *Cicatricosisporites*, *Concavissimisporites* [Pl. 1, Fig. 5], *Pilosisporites*, *Taurucosporites* [Pl. 2, Fig. 2], *Trilobosporites*) and the abundance of gymnosperm pollen grains (*Pinuspollenites*, *Inaperturopollenites*, *Alisporites*, *Classopollis* [Pl. 1, Fig. 11]) reaffirm an affiliation with the North American-Eurasian Subprovince defined by Herngreen *et al*. (1996). However, several forms of Gondwanian affinities, such as the winteroid *Afropollis* and the possible magnoliid *Stellatopollis dejaxii*, must have reached the study area from further south (Gübeli *et al*. 1984; Penny, 1986, 1988, 1991; Schrank, 1992; Schrank and Ibrahim, 1995; Bettar and Méon, 2001; Ibrahim, 2002; Schrank and Mahmoud, 2002).

The biostratigraphically poorly constrained taxa included the trilete spores *Baculatisporites* sp., *Biretisporites* sp., *Cibotiumspora jurienensis*, *Baculatisporites* sp., *Cingutriletes* sp., *Converrucosisporites* spp., *Deltoidospora* spp., *Densoisporites velatus*, *Dictyophyllidites harrisii*, *Foveotriletes* spp., *Gleicheniidites senonicus* (Pl. 1, Fig. 2), *Ischyosporites* spp., *Leptolepidites macroverrucosus* (Pl. 1, Fig. 3), *Retitriletes austroclavatidites*, *Staplinisporites caminus*, *Stereosporites* cf. *aulosenensis*, *Todisporites major*, *Verrucosisporites* spp., and the pollen grains *Classopollis* spp. (Pl. 1, Fig. 11), *Alisporites* spp., *Araucariacites australis*, *Cerebropollenites* spp. (Pl. 1, Fig. 7), *Eucommiidites troedsonii* (Pl. 1, Fig. 10), *Exesipollenites tumulus*, *Inaperturopollenites* spp., *Monosulcites minimus*, *Parvisaccites* sp., *Perinopollenites elatoides*, *Phyllocladidites* sp., *Pinuspollenites* sp., *Podocarpidites* sp., *Vitreisporites pallidus* (Pl. 1, Fig. 4) and *Spheripollenites* sp. (Jansonius, 1962; Reyre, 1970; Guy-Olhson, 1986; Leereveld *et al*., 1989; Trincão, 1990; Batten and Koppelhus, 1996; Ravn, 1998). A Cretaceous age is indicated by species such as *Aequitriradites spinulosus* (Pl. 1, Fig. 1), *Eucommiidites minor*, *Patellasporites tavaredensis* and *Foveotriletes subtriangularis*, which have a long stratigraphic distribution in this system (Groot and Groot, 1962; Burger, 1966; Kemp, 1970; Médus, 1982; Leereveld *et al*., 1989; Ravn, 1998; Čech *et al*., 2005; Dejax *et al*, 2007), as do the taxa in Table 2. Almost all the taxa in this table have been recorded in the Aptian–Albian interval. The stratigraphic ranges of the trilete spores *Appendicisporites concentricus*, *Cicatricosisporites crassistriatus* and *C. mohrioides* extend to the Aptian, whereas the species *Appendicisporites matesovae*, *Cicatricosisporites patapscoensis*, *C. subrotundus*, *Costatoperforosporites triangulatus*, and *Phlebopteristisporites globosus* extend as far back as the Aptian in Laurasia (Juhász, 1979; Ravn, 1998; Table 2). The species *C. subrotundus* indicates an age not older than the Upper Aptian.

The biostratigraphic evidence provided by the dinoflagellate cysts *Subtilisphaera perlucida*, *Cyclonephelium compactum*, *Muderongia staurota*, *Cribroperidinium aceras*, *Apteodinium vectense* observed in M_1 (Table 3) is more restrictive since the records of these species do not surpass the Lower Albian. Concretely, the presence of both *Apteodinium vectense* and *Surculosphaeridium? longifurcatum* indicates an Upper Aptian–Lower Albian age.

The information provided by the angiosperm pollen is essential for attributing a precise age to the recorded assemblages, since these plants from the Middle Hauterivian–Albian experienced an important phase of diversification resulting in a progressive increase of their presence in Cretaceous communities (Doyle, 1973, 1999; Lidgard and Crane, 1988; 1990; Lupia *et al*. 1999; Friis *et al*., 2006). One of the best studied palynological successions illustrating the evolution of primitive types of angiosperm pollen is that represented by the Potomac Group of the Atlantic Coastal Plain of the USA (Brenner, 1963; Doyle, 1969, 1992; Doyle and Robbins, 1977). The assemblages of angiosperm pollen from the Lower Cretaceous Oliete Sub-basin may be compared with those from the upper part of the Potomac Group Zone I (Aptian or Lower Albian), in which different types of *Clavatipollenites*, *Retimonocolpites*, *Stellatopollis*, *Asteropollis* and *Tricolpites* have been found. Nevertheless, despite successive re-evaluations (Doyle and Hickey, 1976; Doyle and Robbins, 1977; Doyle, 1992), the precise biostratigraphic position of the assemblages of the Atlantic Coastal Plain remains greatly dependent on comparisons with European and African successions (Doyle and Robbins, 1977; Doyle, 1992; Heimhofer *et al*., 2003). Hence, the angiosperm biomarkers observed in the palynoflora of the

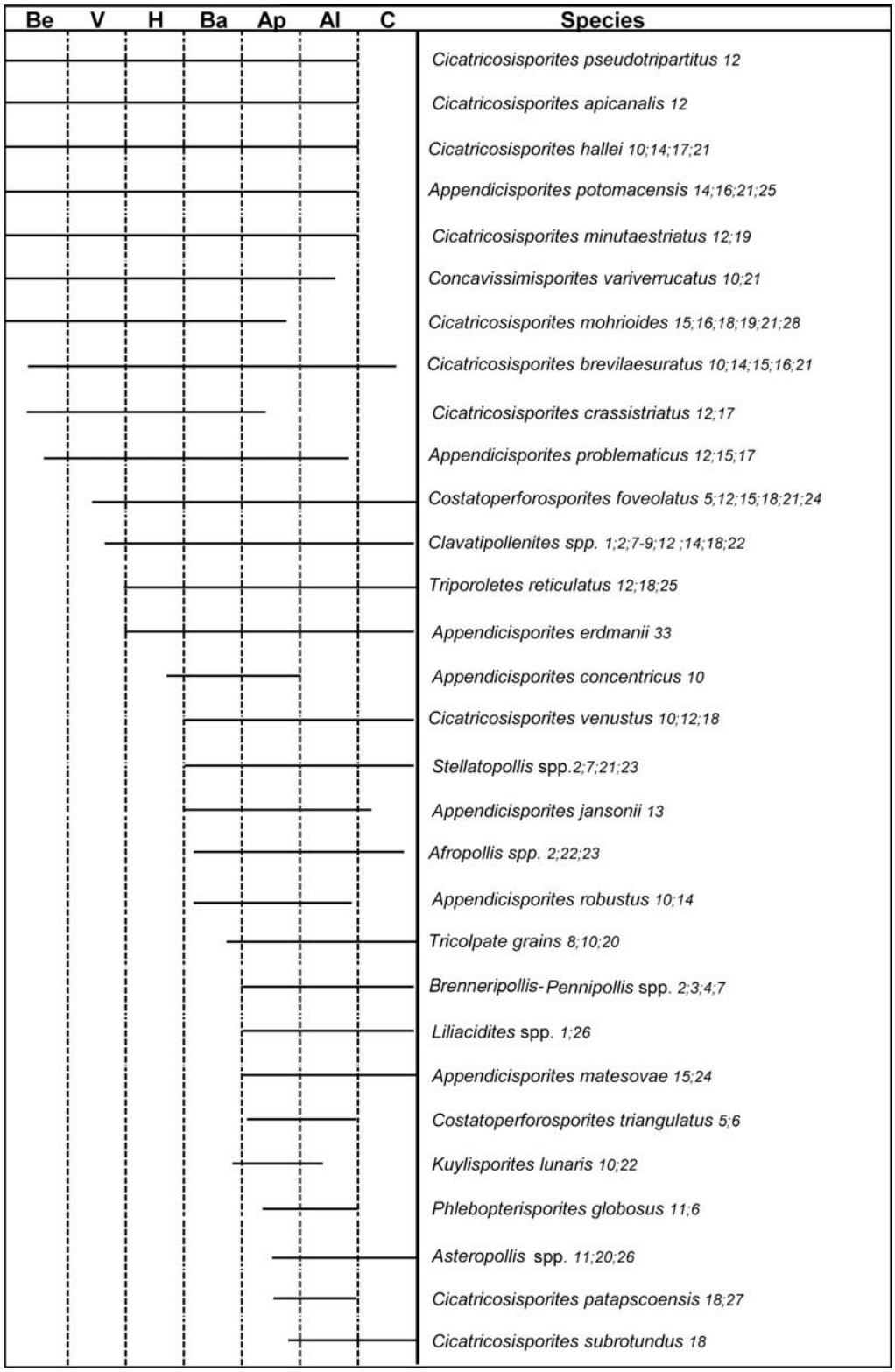


Table 2. Distribution throughout the Lower Cretaceous of the most relevant miospores from a biostratigraphic point of view. Consulted references: 1: Doyle, 1973; 2: Doyle *et al*. 1975; 3: Hughes *et al*., 1979; 4: Juhász & Góczán, 1985; 5: Deák, 1962; 6: Barrón *et al*., 2001; 7: Hughes, 1994; 8: Hughes & McDougall, 1994; 9: Kemp, 1968; 10: Kemp, 1970; 11: Groot & Groot, 1962; 12: Leereveld *et al*. 1989; 13: Vajda, 2001; 14: Batten, 1996; 15: Batten & Li, 1987; 16: Norris, 1969; 17: Burger, 1966; 18: Arias & Doubinger, 1980; 19: Dörhöfer, 1977; 20: Laing, 1975; 21: Dejax *et al*., 2007; 22: Médus, 1982; 23: Hochuli, 1981; 24: Azéma *et al*., 1990; 25: Doubinger & Mas, 1981; 26: Azéma *et al*., 1972; 27: Trincão, 1990. Be=Berriasian, V=Valanginian, H=Hauterivian, Ba=Barremian, Ap=Aptian, Al=Albian, C=Cenomanian.

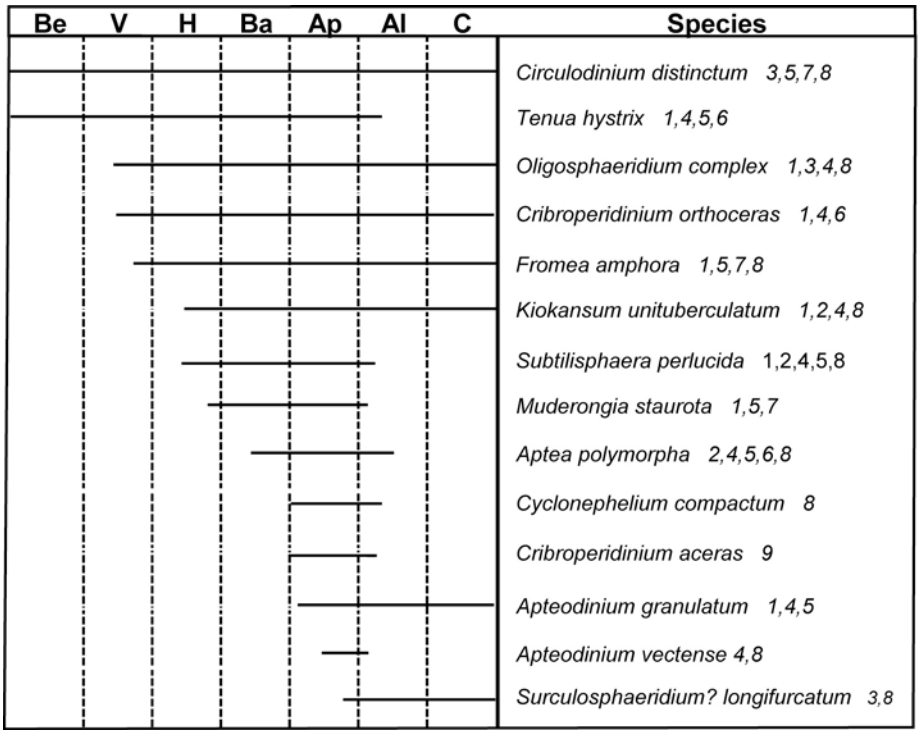
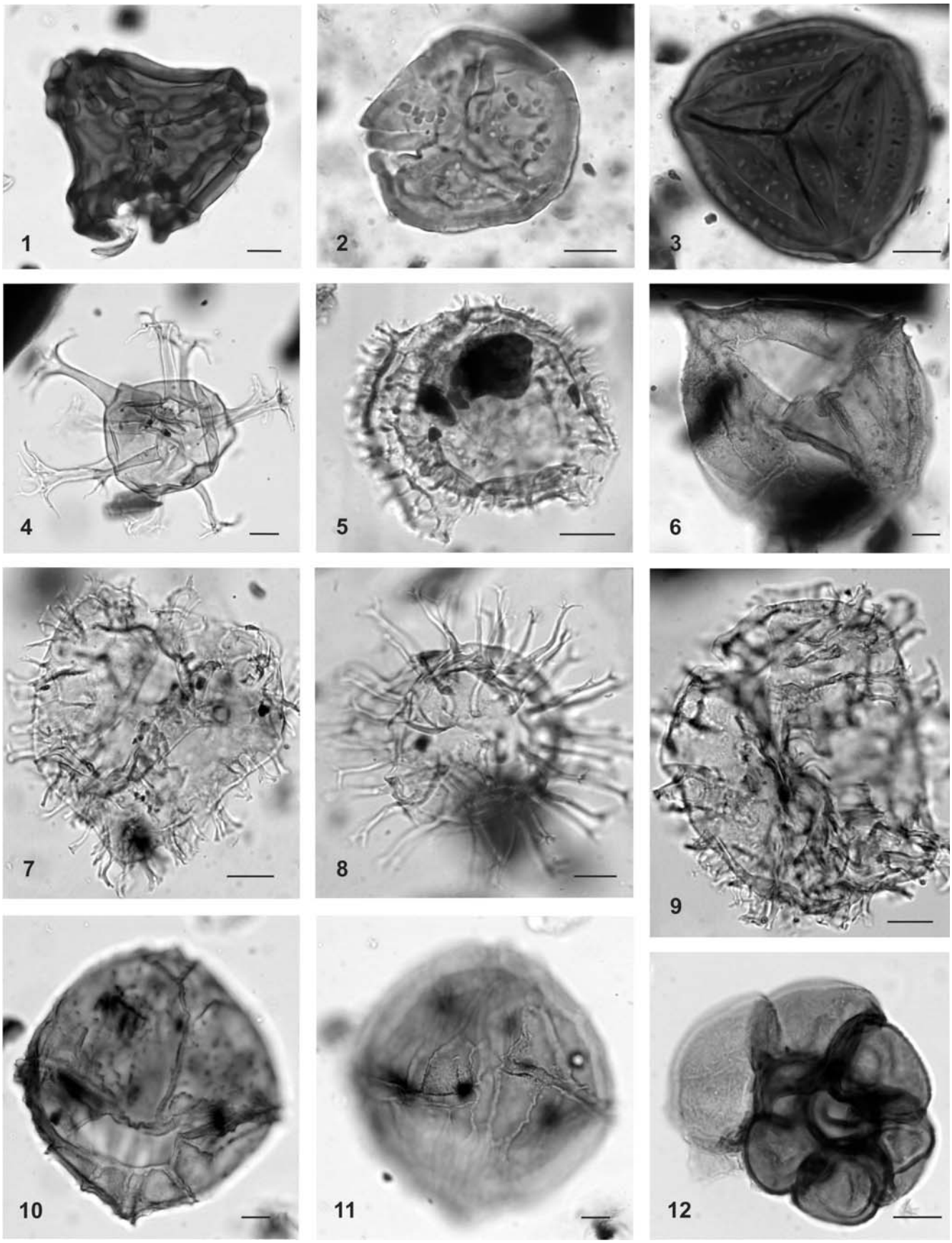


Table 3. Age distribution of the most relevant dinoflagellate cysts and acritarchs identified in level M_1. Consulted references: 1: Costa & Davey, 1992; 2: Williams & Bujak, 1985; 3: Williams *et al*. ,1993; 4: Lister & Batten, 1988; 5: Below, 1981; 6: Below, 1984; 7: Duxbury, 1977; 8: Duxbury, 1983; 9: Sarjeant, 1985. Be=Berriasian, V=Valanginian, H=Hauterivian, Ba=Barremian, Ap=Aptian, Al=Albian, C=Cenomanian.

Oliete Sub-basin were compared with their European and African counterparts.

In the Oliete succession, the columellate-tectate monosulcate genus *Clavatipollenites* (Table 1; Pl. 1, Figs. 8, 12) is a well-represented angiosperm group. This genus seems to have been the first widespread angiosperm taxon and is a useful biostratigraphic index species. It has been recorded from the Valanginian of Portugal (Trincão, 1990), the Late Hauterivian of Israel (Brenner and Bickoff, 1992; Brenner, 1996) and the Early Hauterivian (possibly Late Valanginian) of Morocco (Gübeli *et al*., 1984) and England (here described as non-Linnean biorecords by Hughes and McDougall [1987, 1994], Hughes *et al*. [1991] and Hughes [1994]). The other angiosperm pollen grains observed in the Oliete sub-basin have only been seen in younger rocks in Europe (Table 2). The winteroid forms associated with the genus *Afropollis* observed in N_1 and N_2, plus the tricolpate pollen grains (i.e., *Tricolpites* sp.) of M_3, N_1, N_2 and BC (Table 1; Pl. 1, Fig. 13) are important indicators since they range as far back as the Late Barremian in southern Laurasia (Kemp, 1970; Laing, 1975, 1976; Doyle and Robbins, 1977; Hickey and Doyle, 1977; Doyle *et al*., 1982; Penny, 1989; Hughes and McDougall, 1990; Doyle, 1992; Hughes, 1994). Further, the presence of representatives of the *Brenneripollis-Pennipollis* complex in several studied levels (Table 1; Pl. 1, Fig. 9) is particularly important since these forms are generally considered to appear in the European record only from the Aptian onwards (Hughes *et al*., 1979; Juhász and Góczán 1985; Hughes and McDougall, 1990; Trincão,

Plate 2. Spore types, dinoflagellate cysts and organic linings of the Upper Aptian–Lower Albian Oliete Sub-basin. *1*. *Ischyosporites* cf. *crateris* Balme 1957, level M_1 (Mina Z); *2*. *Taurucosporites* cf. *segmentatus* Stover 1962, level U_3 (Gargallo); *3*. *Costatoperforosporites foveolatus* Deák 1962, level N_2 (Barranco del Tubo); *4*. *Oligosphaeridium complex* (White 1842) Davey & Williams 1966, level M_1, (Mina Z); *5*. *Tenua hystrix* Eisenack 1958 emend. Sarjeant 1985, level M_1, (Mina Z); *6*. *Cribroperidinium orthoceras* (Eisenack 1958) Davey 1969, level M_1, (Mina Z); *7*. *Circulodinium distinctum* (Deflandre & Cookson 1955) Jansonius 1986, level M_1, (Mina Z); *8*. *Kiokansum unituberculatum* (Tasch 1964) Stover & Evitt 1978, level M_1, (Mina Z); *9*. *Cyclonephelium compactum* Deflandre & Cookson 1955, level M_1, (Mina Z); *10-11*. *Cribroperidinium aceras* Eisenack 1958 emend. Sarjeant 1985, proximate cyst in different focus, level M_1, (Mina Z); *12*. Organic lining, level M_1, (Mina Z). Scale bar = 10 µm.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1990; Hughes, 1994; Doyle; 1999; Heimhofer *et al*., 2003).

As a result, the very low representation of poorly diversified tricolpate forms compared to other palynofloras of southern Laurasia and northern Gondwana dated Lower to Middle Albian (Médus and Berthou, 1980; Bettar and Méon, 2001) also support an Upper Aptian-Lower Albian.

6. CONCLUSIONS

The palynological succession of the Lower Cretaceous Oliete sub-basin provides new biostratigraphic data. The study of miospores indicates an upper Aptian age. However, the presence of various well stratigraphically-constrained dinoflagellate cysts such as *Subtilisphaera perlucida*, *Muderongia staurota*, *Aptea polymorpha*, *Cyclonephelium compactum*, *Criboperidinium aceras*, *Apteodinium granulatum*, *A. vectense* and *Surculosphaeridium? longifurcatum* in the lowermost studied level (M_1) supports an Upper Aptian–Lower Albian age, what is corroborated by the study of the angiospermous pollen grains. So, the representation of *Clavatipollenites*, *Brenneripollis-Pennipollis*, *Afropollis*, *Stellatopollis*, *Asteropollis*, *Liliacidites* as well as rare tricolpate forms allow us by comparison with other European Early Cretaceous records, confirm the mentioned Upper Aptian–Lower Albian age. This age is of special interest because is older than that proposed by Solé de Porta *et al*. (1994) and could correlate with the inferred in ambarigenous rocks from the Escucha Formation of the Basque-Cantabrian Basin (Barrón *et al*., 2001).

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