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Portada: Ejemplares tipo de *Clavihedbergella subcretacea* (Tappan, 1943) (Foraminiferida, Globigerinina), de la Formación Duck Creek (Albiense superior) de Love County, Oklahoma (USA). Micrografías de M.D. Georgescu.

Cover: Type specimens of Clavihedbergella subcretacea (Tappan, 1943) *(Foraminiferida, Globigerinina) from the upper Albian Duck Creek Formation of Love County, Oklahoma (USA). Micrographs by M.D. Georgescu.*

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Palynofloras of the Chigua (Devonian) and Malimán (Mississippian) formations from the Precordillera Argentina: Age, correlation and discussion of the D/C boundary

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Resumen

Se presenta el análisis cualitativo y cuantitativo de las asociaciones palinológicas obtenidas de las formaciones Chigua (Devónico) y Malimán (Mississippiano), aflorantes en la Cuenca Río Blanco, Precordillera Argentina. La relación estratigráfica entre ambas unidades es mediante una discordancia angular. Una detallada correlación de ambas palinofloras con otras coetáneas permite su datación precisa. La palinoflora de la Formación Chigua es correlacionable con la Zona *G. lemurata-C. magnificus* del Givetiano temprano de Euramerica. El alcance estratigráfico de las especies autóctonas halladas en la Formación Malimán sustentan una edad viséana temprana, aunque la presencia de algunas especies del Tournaisiano tardío sugieren que esta edad podría estar representada en la parte inferior de la formación. Esta palinoflora es correlacionada con 1) la Zona *Endoculeospora larga* del Viséano de Australia, 2) las zonas CM y Pu del Tournaisiano tardío – Viséano temprano de Euramerica y 3) la palinoflora de la Formación Itacua atribuida al Viséano temprano presente en el extremo sur de Bolivia. El hiato estratigráfico entre ambas formaciones está avalado por las distintas edades de las palinofloras encontradas y por el rango estratigráfico de los palinomorfos retrabajados registrados en la Formación Malimán. Así, se documentan dos períodos de acumulación de sedimentos durante el Frasniano y probablemente durante el Tournaisiano temprano. La ausencia de formas retrabajadas del Devónico más tardío (Famenniano tardío o "Struniano") sugiere que no habría depositación durante este intervalo. Otros palinomorfos retrabajados del Silúrico Tardío y Devónico Temprano se encuentran en la Formación Malimán. La mezcla de palinomorfos del Silúrico al Tournaisiano temprano se vincula con la erosión penecontemporánea de áreas levantadas que habrían conformado la Protoprecordillera, por una combinación de procesos tectónicos y glacio-eustáticos durante el Frasniano tardío, Fameniano y Tournaisiano temprano.

Palabras clave: Palinoestratigrafía, Givetiano temprano, Viséano temprano, Retrabajo, Hiato, Argentina.

Abstract

A qualitative and quantitative analysis is presented of palynological assemblages recovered from outcrops of the Chigua (Devonian) and Malimán (Mississippian) formations, in the Río Blanco Basin, Precordillera of Argentina. An angular unconformity separates these two formations. Both units are dated precisely in comparison with palynofloras elsewhere. The Chigua Formation is correlatable with the early Givetian *G. lemurata-C. magnificus* Zone of Euramerica. The stratigraphic ranges of the non-reworked taxa in the Malimán Formation support an early Viséan age. However, the presence of some late Tournaisian species suggests that the lower part of the formation correspond to this age. The palynoflora of the Malimán Formation suggests correlation with 1) the Viséan *Endoculeospora larga* Assemblage of Australia, 2) the late Tournaisian – early Viséan CM and Pu zones of Euramerica, and 3) the early Viséan assemblage of the Itacua Formation of southernmost Bolivia. A hiatus comprising Frasnian to early Tournaisian is confirmed on the basis of the different ages of the two assemblages and the stratigraphic ranges of reworked palynomorphs found in the Malimán Formation. These, attest to sedimentation and subsequent erosion of Frasnian and probably also Tournaisian strata. The absence of reworked forms of the latest Devonian (late Famennian or "Strunian") suggests a corresponding period of non-deposition. The Malimán Formation also contains reworked palynomorphs of Late Silurian and Early Devonian ages. The reworking of palynomorphs documents the penecontemporaneous erosion of uplifted areas that would have conformed the Protoprecordillera, due to late Frasnian, Famennian and early Tournaisian tectonic and glacio-eustatic processes affecting the area involved.

***Key words*:** Palynostratigraphy, Early Givetian, Early Viséan, Reworking, Hiatus, Argentina.

1. INTRODUCTION

Several contributions have improved the knowledge of the Mississippian palynofloras of South America. Earlier studies are related to the Retama Formation of the Madre de Dios Basin of Bolivia (Azcuy and Ottone, 1987) and the Zorritas Formation of Arizaro Basin of Chile (Rubinstein *et al.*, 1996).

In recent years the palynological investigations of Mississippian South American deposits have increased in number, dealing with the following: Parnaíba and Amazonas basins, Brazil (Melo and Loboziak, 2000, 2003); Ambo Formation, Peru (Azcuy and di Pasquo, 2005, 2006); Llanos Orientales Basin, Colombia (Dueñas and Césari, 2006); and the Kaka and Itacua formations of the Madre de Dios and Tarija basins respectively, Bolivia (Figure 1) (Fasolo *et al.*, 2006; di Pasquo, 2005, 2007a, b). Palynological work on the Mississippian deposits of Argentina is scarcer, Mississippian rocks with palynomorphs occur in the Precordillera of San Juan Province (Río Blanco and Calingasta-Uspallata basins), comprising the Malimán, Cortaderas and El Ratón formations (Figures 1, 2). Previous palynological studies consist only partly of publications with illustrations (Sessarego and Césari, 1989; Césari and Limarino, 1992, 1995; Césari and Gutiérrez, 2001); another papers does not include figures of palynomorphs, only lists (Limarino *et al.*, 1996). The most recent contributions are those by Rodríguez Amenábar *et al.* (2003), Pérez Loinaze and Césari (2003), Rodríguez Amenábar and di Pasquo (2004), Pérez Loinaze (2007), Pazos *et al.* (2005a, b), Amenábar (2006) and Amenábar *et al.* (2006, 2007). An exhaustive palynological investigation of the Chigua, Malimán and El Ratón formations was carried out by the first author for her Doctoral degree (Amenábar, 2007a).

With reference to the Devonian, rich palynological assemblages of different South American basins are known, e.g. the Amazonas, Paraná and Solimões basins, Brazil (Dino, 1999; Quadros, 1999; Melo and Loboziak, 2003; Rubinstein *et al.*, 2005; Grahn, 2005); Madre de Dios Basin, Bolivia (Vavrdová *et al.*, 1993, 1996; Ottone and Rossello, 1996; Vavrdová and Isaacson, 1997, 2000); and Tarija Basin of southern Bolivia and northern Argentina (Blieck *et al.*, 1996; Ottone, 1996; Limachi *et al.*, 1996; Grahn and Gutiérrez, 2001; Grahn, 2002; di Pasquo, 2005, 2007a, b, c; Noetinger and di Pasquo, 2007). In contrast, despite some palynological papers of these strata are known (Le Hérissé *et al.,* 1997; Rubinstein, 1999, 2000; Rubinstein and Steemans, 2007; Amenábar, 2007b, 2009), materials from the Precordillera of Argentina have retrieved poor palynofloras (Figure 1).

Studies on reworked palynomorphs are still required for a better knowledge of the Devonian and Mississippian palynofloras, as well as can be used to refine the D/C boundary definition in South America, and to improve the understanding of palaeogeographic and palaeoclimatic changes which influenced microfloral evolution in Western Gondwana (di Pasquo and Azcuy, 1997; Vavrdová and Isaacson, 2000; di Pasquo, 2007a, b, c). The present paper completes two previous contributions (Amenábar *et al.*, 2006, 2007) on the Chigua (Devonian) and Malimán (Mississippian) formations cropping out in the Precordillera of Argentina. Whilst the two first papers deal with the taxonomic description of the microplankton and spores in these units, the present contribution focuses on a comparison with palynofloras of similar ages in different parts of South America and elsewhere. This includes an assessment of the age and correlation of both assemblages. Additionally, a discussion is presented on the importance of the recognition of some Late Silurian and Early Devonian reworked palynomorphs in the Chigua Formation and also some Devonian and possibly Tournaisian reworked taxa recorded in the Malimán Formation (not previously mentioned by Amenábar, 2006). The palynological data also allow an estimation and characterisation of the stratigraphic gap between both formations (Figure 2B-C).

2. GEOLOGICAL SETTING

Palaeozoic deposits crop out in the northwestern part of the Precordillera Range in San Juan Province, at about 30° S and 69° W (Figure 2), represented by fossiliferous marine Devonian and marine/terrestrial Mississippian strata. The outcrops extend to east of the Río Blanco, on the western slope of the Punilla and Volcán ranges. The Devonian Pircas Negras and Chigua formations constitute the Chinguillos Group (Baldis and Sarudiansky, 1975). The succeeding

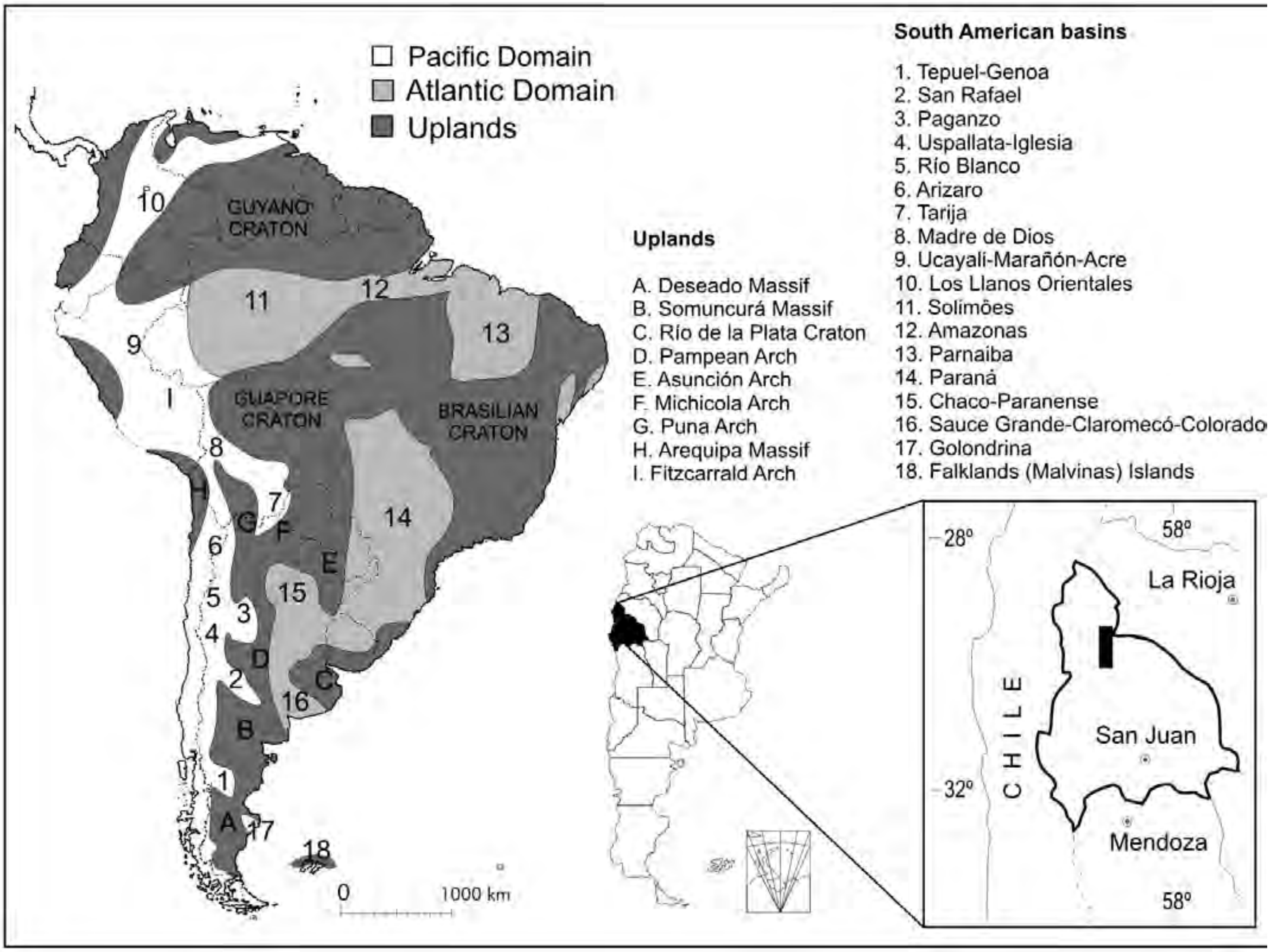


Figure 1. Main Carboniferous basins of South America (after Azcuy *et al.*, 2007).

Mississippian Malimán and Cortaderas formations form part of the Angualasto Group (Limarino and Césari, 1993; Figure 2).

The Chigua Formation (700 m thick) is in tectonic contact with the Pircas Negras Formation; it underlies the Malimán Formation with angular unconformity (Figure 2). The Chigua Formation is subdivided into two members (Figure 2), viz. the lower Chavela (marine) and the upper Ramadita (marine/terrestrial). The Chigua lithology, with green-brown colours, consists mainly of shales with limestone nodules and lenses, and subordinate sandstone beds. Fossiliferous layers have yielded marine invertebrates including the trilobites *Punillaspis argentina* Baldis, *Phacops chavelai* Baldis and Longobucco and *Acanthopyge balliviani* Kozlowski, also the cephalopods *Tornoceras baldisii* Leanza and *Orthoceras* sp., the cnidarian *Conularia* sp., as well as Gastropoda and Pelecypoda indet. (Baldis and Sarudiansky, 1975; Baldis and Longobucco, 1977). Herbaceous lycopsids "*Haplostigma*" *furquei* Frenguelli, "*H.*" *baldisii* Gutiérrez and ?*Cyclostigma* sp. are recorded (Baldis and Sarudiansky, 1975; Gutiérrez, 1996) from the Chavela Member, whist the Ramadita Member contains mainly "*Haplostigma*" *furquei* and less frequent *Phacops* sp. and Gastropoda indet.

Homoclinal strata of the Malimán Formation (1300 m thick) are followed conformably by contact with the Cortaderas Formation at La Cortadera Valley (Figures 2A, 3). The Malimán Formation begins with thick-bedded paraconglomerates with a few intercalated fine-grained sandstones and shales with abundant herbaceous lycopsids

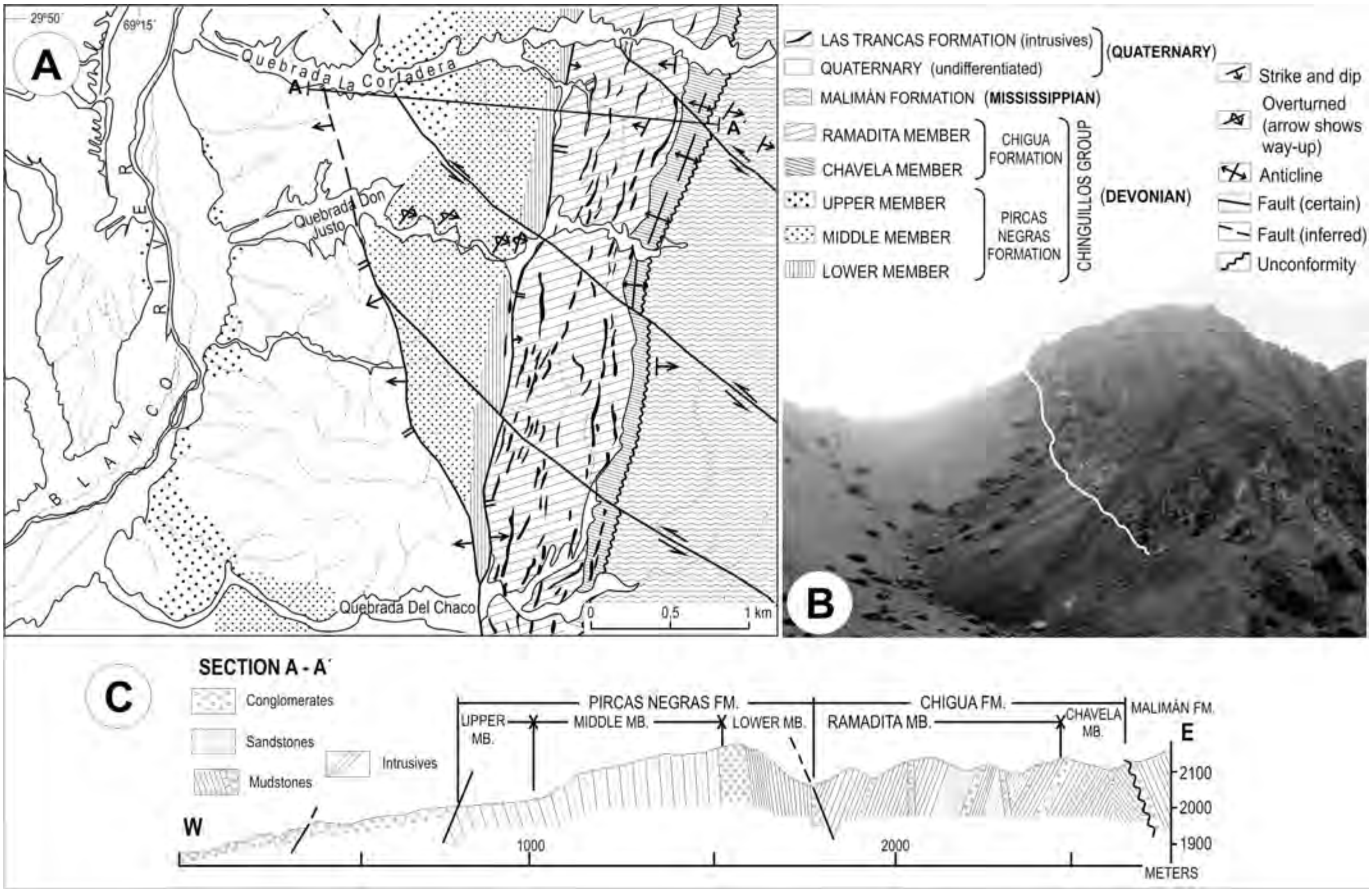


Figure 2. A, Geological map and geographic location of the Quebrada La Cortadera in San Juan Province, Argentina (modified from Baldis and Sarudiansky, 1975). B, Photograph illustrating the unconformity between the Chigua Formation (to the left of the white line) and the conglomerates of the basal Malimán Formation. C, Structural cross-section of the Chinguillos Group and Malimán Formation (modified from Baldis and Sarudiansky, 1975). Bar scale: 50 m.

and pteridosperms (Figure 3); species identified include *Frenguellia eximia* (Frenguelli) Arrondo, Césari and Gutiérrez, "*Eusphenopteris*" *devonica* (Frenguelli) Sessarego and Césari and *Diplothmema bodenbenderi* (Kurtz) Césari (Azcuy *et al*., 2000). Coarse to medium-grained sandstones overlie the conglomerates and contain similar megaflora remains. They are followed in turn by thick sandstone beds containing thin conglomerate lenses with massive organic-rich mudstone intercalations. The latter contain a marine fauna belonging to the *Protocanites scalabrini - Azurduya (=Paurorhyncha) chavelensis* Zone (Sabattini *et al.,* 2001) and comprising ammonoids, brachiopods, bivalves, gastropods, conulariids and crinoid stems (e.g., González, 1994; Sabattini *et al*., 2001). The stratigraphic section continues upwards with alternating sandstones and siltstones, with subordinate fine-grained diamictites. This sandy and muddy section contains the same plant species present in the basal conglomerate unit, together with some pteridosperms (e.g., "*Rhodea*" sp., "*Hyenia*" sp. and an *incertae sedis* form named *Paulophyton* sp.), which are characteristic of the *Frenguellia–Paulophyton* Phytozone (Carrizo and Azcuy, 1997). The upper part of the stratigraphic succession is dominated by thick beds of sandstone and orthoconglomerate (Figure 3). The Malimán Formation represents mixed deposits with alternating transgressive-regressive cycles (Limarino and Césari, 1993). New studies carried out by Pazos *et al.* (2005b) in different localities, allowed the definition of various sections with different palaeontological and sedimentological features, thus improving the previous information. Pazos *et al.* (2005b) determinated that the transgressive-regressive cycles in the Malimán Formation are due to glacio-eustatic/climatic influences. The unpublished (more detailed) stratigraphic section is presented in Figure 3.

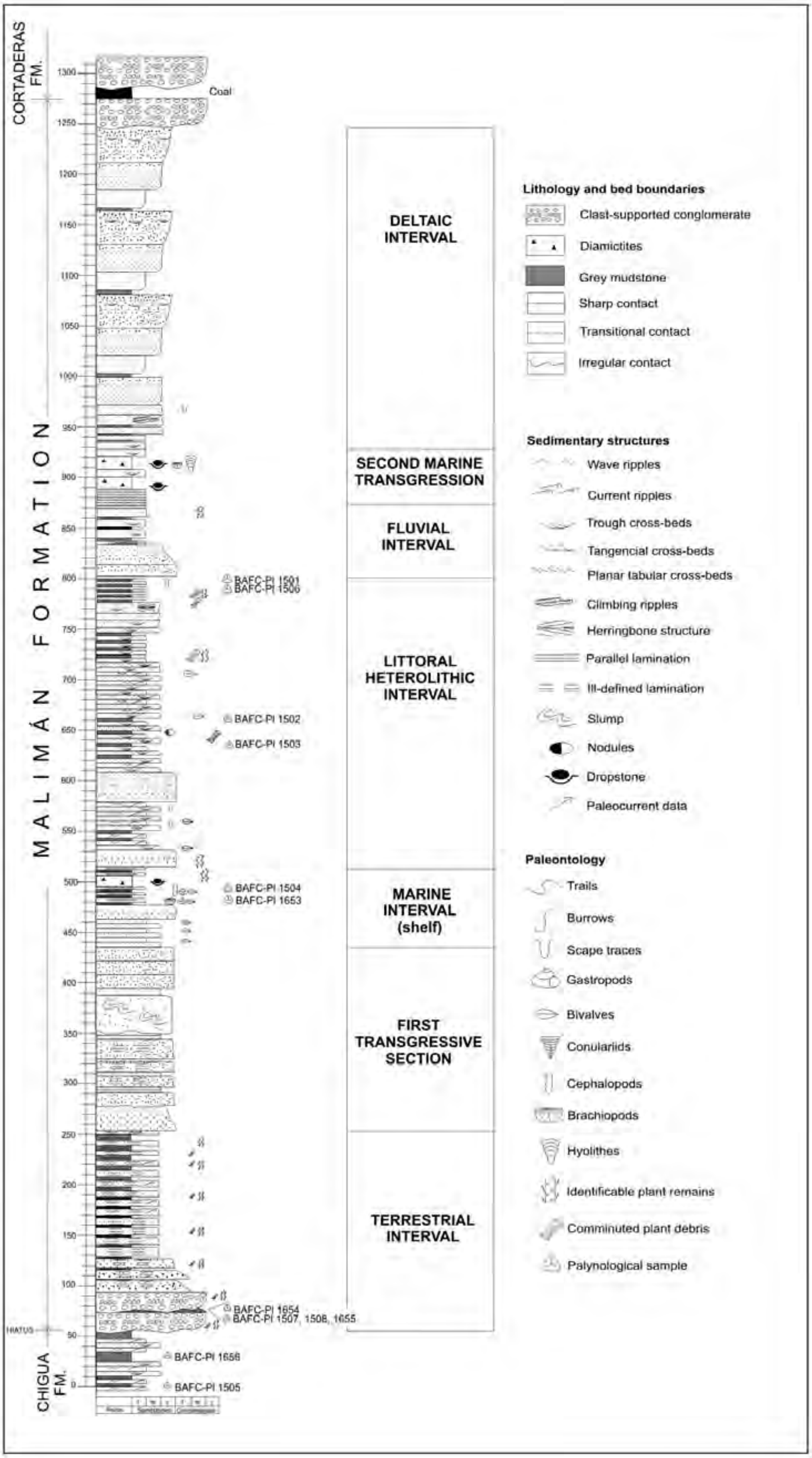


Figure 3. Stratigraphic section of the Chigua and Malimán formations at La Cortadera showing the location of palynological samples. Palaeoenvironmental interpretation after Pazos *et al*. (2005 a, b).

3. COMPOSITION, AGE AND CORRELATION OF THE PALYNOLOGICAL ASSEMBLAGES

3.1. Chigua Formation

The palynoflora of the Chigua Formation (Chavela Member) was obtained from two shales located at 50 m (BAFC-Pl 1505) and 30 m (BAFC-Pl 1656) below the base of the Malimán Formation at Quebrada La Cortadera (type locality, Figure 3). Amenábar *et al*. (2006, 2007) presented the identification and the geographic and stratigraphic distribution of the species found in this unit. Additionally, a worldwide geographic and stratigraphic ditribution of the species recorded through the Eifelian to the Frasnian in South America has been recently presented by di Pasquo et al. (2009). The palynomorphs are abundant and moderately diverse; some are fragmented and corroded but they are generally well preserved with diagnostic characters; their thermal maturity (TAI) varies between 2 and 3 according to the scale of Utting *et al*. (in Utting and Wielens, 1992). Both levels present quite similar proportions of major groups of palynomorphs, with the spores dominating slightly over the microplankton (Figure 4). The assemblage also includes some possibly reworked species (Amenábar *et al.,* 2006) that will be discussed subsequently in this paper. Spores belonging to the genus *Grandispora* in both levels are most abundant (e.g., *G. pseudoreticulata*) (Figure 4). The species recorded are listed in Figure 4 and some are illustrated on Plate 1.

An analysis of the stratigraphic ranges of the species recognised in the Chigua Formation allows the assignment of an early Givetian age (Figure 5). The species *Dictyotidium venulosum, Crucidia camirense, Polygonium barredae, Cymatiosphaera perimembrana, Geminospora lemurata*, appear from basal Givetian upwards. Their occurrence together with species appearing slightly later,

Figure 4. Quantitative analysis of the assemblage of palynomorphs in the Chigua Formation. The species are organized by first appearance according to two major groups: spores and microplankton, and in alphabetical order within groups. Symbols refer to relative abundance (calculated from counts of ca. 200 specimens per sample): □ (empty square): <2.5%; ■ (black square): 2.5-6.4 %; ▲ (triangles): >6.4%. The species cited and/or illustrated for the first time in Middle Devonian sediments of South America are marked with a single asterisk (*); whilst species cited for the first time in the Middle Devonian of Argentina with two asterisks (**).

SPECIES RECORDED IN THE CHIGUA FORMATION			samples (BAFC-PI)	
			1505	1656
MICROPLANKTON	*	*Botryococcus* sp.	□	
	*	*Dictyotidium granulatum* Playford in Playford and Dring	□	
	*	*Dictyotidium venulosum* (Playford in Playford and Dring) Colbath	□	
		Estiastra rythidoa Wicander and Wood	■	
		Maranhites sp.	□	
	*	*Polyedryxium leptum* Turner	□	
	*	*Pulvinosphaeridium trifidum* Kiryanov	□	
		Quadrisporites granulatus (Cramer) Strother	■	
		Stellinium micropolygonale (Stockmans and Willière) Playford	□	
SPORES		*Anapiculatisporites* sp. A	□	
	**	*Apiculatisporis grandis* Menéndez and Pöthe de Baldis	□	
		Apiculatisporis sp. A	□	
	*	*Apiculiretusispora laxa* Amenàbar, di Pasquo, Carrizo and Azcuy	□	
		Apiculiretusispora plicata (Allen) Streel	□	
		Cymbosporites catillus Allen	□	
	*	*Geminospora* sp. cf. *G. tuberculata* var. *tuberculata* McGregor	□	
	*	*Leiotriletes trivialis* Naumova	□	
		Leiotriletes sp. B	□	
	*	*Punctatisporites glaber* (Naumova) Playford	■	
	*	*Punctatisporites planus* Hacquebard	□	
		Retusotriletes spp.	□	
		Verrucosisporites tumulentus Clayton and Graham	□	
		Verrucosisporites sp.	□	
MICROPLANKTON		*Cymatiosphaera canadensis* Deunff	□	□
	*	*Cymatiosphaera* sp. cf. *C. subtrita* Playford in Playford and Dring	□	□
		Dictyotidium munificum (Wicander and Wood) Amenábar, di Pasquo, Carrizo and Azcuy	■	□
		Duvernaysphaera angelae Deunff	□	□
		Exochoderma arca Wicander and Wood	□	□
		Hemiruptia legaultii Ottone	□	□
		Leiosphaeridia spp.	■	■
		Navifusa bacilla (Deunff) Playford	□	▲
		Polyedryxium decorum Deunff	□	□
		Polygonium barredae Ottone	□	□
		Pterospermella sp. cf. *P. capitana* Wicander	□	□
		Quadrisporites variabilis (Cramer) Ottone and Rosello	■	□
		Veryhachium spp.	□	□
SPORES	**	*Acinosporites acanthomammillatus* Richardson	□	□
	**	*Apiculatasporites microconus* (Richardson) McGregor and Camfield	■	□
	**	*Archaeozonotriletes chulus* var. *chulus* (Cramer) Richardson and Lister	□	□
	**	*Cymbosporites cyathus* Allen	□	□
	**	*Dibolisporites* sp. cf. *D. eifeliensis* (Lanninger) McGregor	□	▲
	**	*Dibolisporites* sp. cf. *D. quebecensis* McGregor	□	□
	**	*Dictyotriletes emsiensis* Morphon Rubinstein, Melo and Steemans	□	□
		Emphanisporites rotatus McGregor emend. McGregor	▲	■
		Geminospora lemurata Balme emend. Playford	□	□
		Grandispora pseudoreticulata (Menéndez and Pöthe de Baldis) Ottone	▲	■
		Grandispora spp.	■	■
	**	*Leiotriletes balapucensis* di Pasquo (= *Leiotriletes* sp. A in Amenábar, di Pasquo, Carrizo and Azcuy)	■	□
		Punctatisporites sp.	■	■
		Verrucosisporites scurrus (Naumova) McGregor and Camfield	□	□
	**	*Verrucosisporites* sp. cf. *V. polygonalis* Lanninger, 1968	□	□
MICROPLANKTON		*Arkonites bilixus* Legault		□
		Belonechitina sp.		□
		Crucidia camirense (Lobo Boneta) emend. Ottone		□
		Cymatiosphaera perimembrana Staplin		□
	*	*Micrhystridium* sp. cf. *M. pentagonale* Stockmans and Willière		□
		Micrhystridium sp. A		□
	**	*Onondagaella asymmetrica* (Deunff) Playford		■
	*	*Orygmahapsis pachyderma* Colbath		□
		Polyedryxium pharaonis Deunff *ex* Deunff		□
		Polyedryxium sp.		□
		Stellinium octoaster (Staplin) Jardiné, Combaz, Magloire, Peniguel and Vachey		□
		Tunisphaeridium caudatum Deunff and Evitt		□
		Veryhachium polyaster Staplin		□
SPORES		*Acinosporites lindlarensis* Riegel		□
	*	*Dibolisporites varius* Tiwari and Schaarschmidt		■
		Emphanisporites annulatus McGregor		□
	*	*Granulatisporites muninensis* Allen		□
		Verruciretusispora sp.		□

e.g. *Orygmahapsis pachyderma, Pterospermella capitana* and *Geminospora tuberculata* var. *tuberculata* suggest a level within the lower Givetian. The presence of putative Frasnian elements such as *Micrhystridium pentagonale, Cymatiosphaera subtrita, Dictyotidium granulatum* and *Polyedryxium leptum* is not regarded as determinative, since the two former species are only identified with doubts, whilst the latter two corresponds to first records for Argentina (Figure 4; Amenábar *et al*., 2006) and, therefore, not well constrained stratigraphically. A downward extension of their ranges to early Givetian is regarded as quite likely, but uncertain. On the other hand, the range of *O. asymmetrica*, which is currently known from the Silurian of Argentina (e.g., Rubinstein, 1997; Rubinstein and Brussa, 1999; Rubinstein and Toro, 2006) must be extended upwards to the early Givetian in the Precordillera (Figure 5). The large size of a majority of the spores (80 µm on average) in the Chigua Formation agrees with that found in other Middle Devonian palynofloras as determinated by Loboziak (1999). Besides, younger Devonian species such as *Samarisporites triangulatus, Verrucosisporites bulliferus, Samarisporites* spp., *Pseudolunulidia imperatrizensis, Maranhites* spp., *Umbellasphaeridium deflandrei* present as reworked elements in the Malimán Formation due to the recycling of Frasnian deposits (Amenábar, 2006), are absent in the Chigua palynoflora, thus reinforcing its attribution to an age not later than Middle Devonian.

Figure 5. Stratigraphic ranges of species recorded in the Chigua Formation, after selected literature cited in Amenábar *et al*. (2006, 2007). The grey area corresponds to the time interval proposed for the assemblage. Dashed lines indicate doubtful records. Species marked with an asterisk are doubtfully indentified ("cf.").

A comparison with selected Devonian palynofloras throrought the world but mainly from South America is presented in Figure 6. Ottone (1996) described a similar assemblage from the late Givetian – early Frasnian of the Tarija Basin in northern Argentina, whilst di Pasquo (2007a) documented two assemblages from the same basin in southern Bolivia; i.e. a late Eifelian and a middle to late Givetian one identified on the basis of key taxa and relative stratigraphic position. Despite several taxa in common (especially *Grandispora pseudoreticulata* along with other species of the same genus as well as many microplankton forms), there are compositional differences which support an early Givetian age for the assemblage from the Chigua Formation and prevent the exact correlation with either of the assemblages reported from the Tarija Basin. On the other hand, the Chigua assemblage may be correlated to the early Givetian *Verrucosisporites premnus/V. scurrus* Zone from Bolivia (Limachi *et al*., 1996) due to the common presence of *Verrucosisporites scurrus, Cymatiosphaera canadensis* and *Arkonites bilixus*, and the scarcity of *Maranhites*, which is more frequent in the subsequent *Samarisporites/Maranhites brasiliensis* Zone of late Givetian to Frasnian age (Figure 6).

The Punta Negra Formation, of the Precordillera in San Juan Province, Argentina, has yielded two assemblages, i.e. A1 of the Middle Devonian (Eifelian-Givetian) and A2 straddling the Givetian/Frasnian boundary (Rubinstein, 1999, 2000). It is difficult to compare these assemblages with the palynoflora of the Chigua Formation because they only share non-age-diagnostic species.

The late Eifelian-early Givetian Association 5 from the Ponta Grossa Formation in the Paraná Basin (Dino, 1999) and the early Givetian *Geminospora lemurata-Chelinospora* ex gr. *ligurata* (LLi) Zone of Melo and Loboziak (2003) from the Amazonas Basin are also comparable. The first appearance of *Geminospora lemurata* accompanied by patinate spores with a prominent verrucate-baculate sculpture (*Cymbosporites catillus, C. cyathus, Chelinospora* ex gr. *ligurata* complex) and *Verrucosisporites scurrus* in all those assemblages support their correlation (Figure 6).

According to the miospore zonation established for the Old Red Sandstone Continent of Euramerica (McGregor, 1979; Richardson and McGregor, 1986; Streel *et al.*, 1987; Braman and Hills, 1992) and that of Eastern Europe (Avchimovitch *et al.*, 1993; Turnau, 1996), the Chigua Formation contains an assemblage correlatable with the early Givetian *G. lemurata-C. magnificus* and *Geminospora extensa* (EX) zones (Figure 6). Shared characters with the Euramerican palynofloras are the presence of *Geminospora lemurata* in conjunction with spores characterised by highly irregular warts or bacula (*Verrucosisporites* spp. and *Dibolisporites* spp.) as well as diverse patinate spores (*Archaeozonotriletes* spp., *Cymbosporites* spp.). The only species with a more restricted range in common with the Eastern Europe assemblages is *Geminospora tuberculata*; the other shared elements are long-ranging (Figure 5).

The Middle Devonian assemblages of the Rhadamés and Ghadamis basins in Libya (Moreau-Benoit, 1989; Loboziak and Streel, 1989) and the early Givetian palynoflora of Saudi Arabia (Breuer *et al.*, 2007) share only cosmopolitan species with the Chigua Formation (e.g., *Acinosporites acanthomammillatus, Verrucosisporites scurrus, V. premnus, Geminospora lemurata, Cymbosporites catillus* and *C. cyathus*). Hashemi and Playford (2005) described three assemblages (I, II, III) from the Adavale Basin (Australia), of Emsian to early Frasnian ages, whilst Balme (1988) and Playford and Dring (1981) documented Frasnian palynofloras from the Gneudna Formation in the Carnarvon Basin (Australia). These papers showed that only a few cosmopolitan species of stratigraphic importance extend across the Gondwana area (Figures 5 and 6).

In summary, the Argentinian assemblage of Givetian age is composed of many cosmopolitan species (e.g., *Dibolisporites varius, Geminospora lemurata, Apiculiretusispora plicata, Cymbosporites catillus, Acinosporites acanthomammillatus, Verrucosisporites scurrus*) occurring together with endemic elements, such as *Grandispora pseudoreticulata, Leiotriletes balapucensis, Apiculatisporis grandis* and *Polygonium barredae*. Di Pasquo *et al.* (2007,

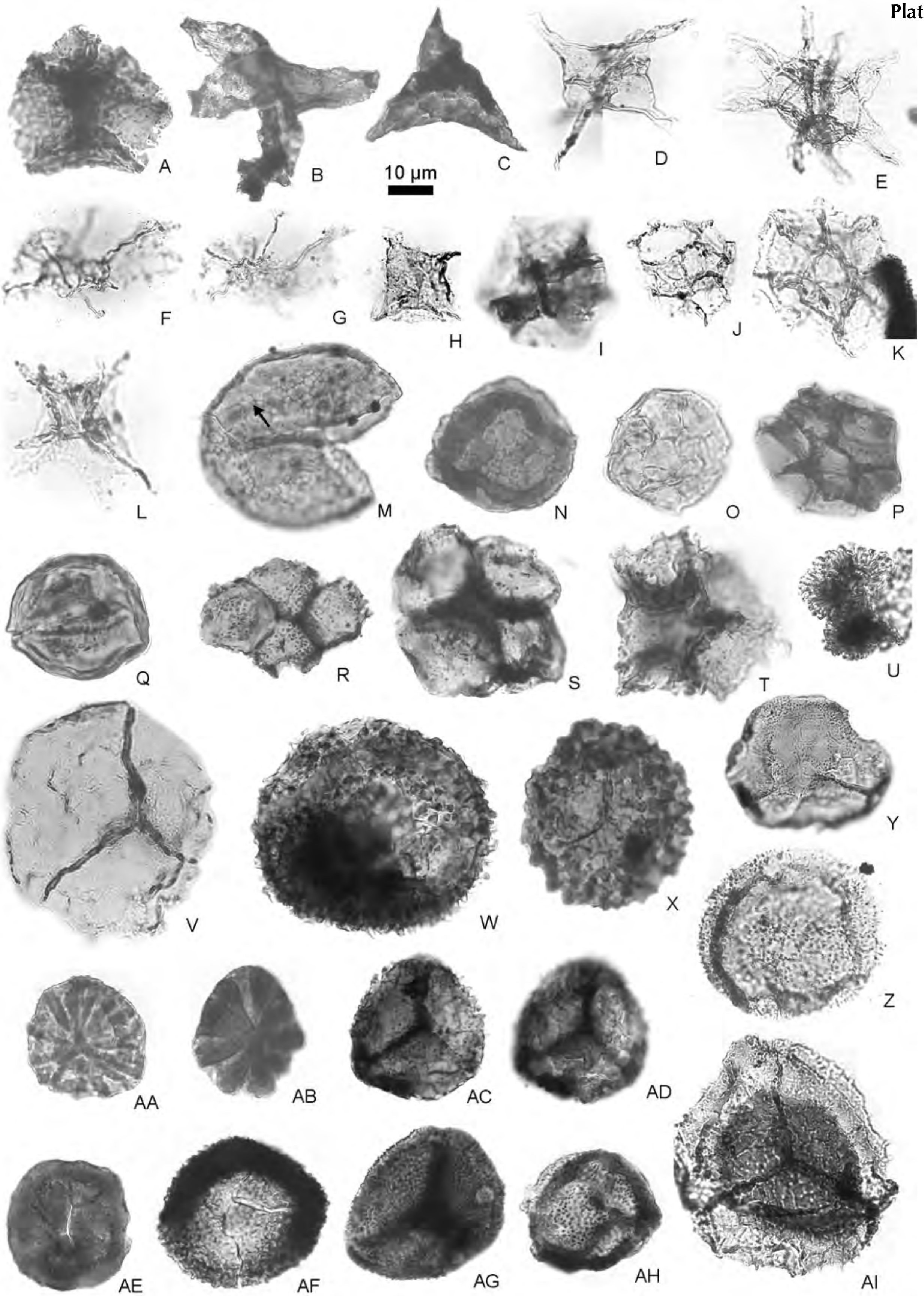
Plate 1. Microplankton and spores from the Chigua Formation. Coordinates after EF (England Finder) graticule. Coordinates of the selected illustrated specimens are prefixed BAFC-Pl referring to the repository of slides in the Palynostratigraphy and Paleobotany Laboratory, Department of Geology, University of Buenos Aires. Prefix is followed by the slide number and the reference. Scale bar: B, C, F, G, V, AF, AI =20 μm (x 500), the remainder =15 μm (x 750).

A, *Arkonites bilixus* Legault. BAFC-Pl 1656 (1): N32/1. **B,** *Crucidia camirense* (Lobo Boneta) emend. Ottone. BAFC-Pl 1656 (2): B27. **C,** *Estiastra rhytidoa* Wicander and Wood. BAFC-Pl 1505 (2): O47/1.

D, *Exochoderma arca* Wicander and Wood. BAFC-Pl 1656 (1): S24/1-3. **E,** *Polyedryxium pharaonis* Deunff *ex* Deunff. BAFC-Pl 1656 (2): K23/1. **F-G,** *Tunisphaeridium caudatum* Deunff and Evitt. BAFC-Pl 1656 (2): U36. **H,** *Duvernaysphaera angelae* Deunff. BAFC-Pl 1505 (2): W39/3. **I,** *Polyedryxium leptum* Turner. BAFC-Pl 1505 (3): H48/4. **J,** *Cymatiosphaera perimembrana* Staplin. BAFC-Pl 1656 (1): J26/3. **K,** *Cymatiosphaera canadensis* Deunff. BAFC-Pl 1656 (1): Z32/4. **L,** *Stellinium octoaster* (Staplin) Jardiné, Combaz, Magloire, Peniguel and Vachey. BAFC-Pl 1656(2): T42/2. **M,** *Orygmahapsis pachyderma* Colbath. BAFC-Pl 1656 (1): M49/4. Arrow shows fields bearing an internal pore.

N, *Dictyotidium venulosum* (Playford) Colbath. BAFC-Pl 1505 (3): D22. **O,** *Dictyotidium granulatum* Playford in Playford and Dring. BAFC-Pl 1505 (1): R38/1. **P,** *Dictyotidium munificum* (Wicander and Wood) Amenábar, di Pasquo, Carrizo and Azcuy. BAFC-Pl 1505(5): Z24/2. **Q,** *Hemiruptia legaultii* Ottone. BAFC-Pl 1656 (1): D35. **R,** *Quadrisporites variabilis* (Cramer) Ottone and Rosello. BAFC-Pl 1656 (2): L45. **S,** *Quadrisporites granulatus* (Cramer) Strother. BAFC-Pl 1505 (3): R43/2. **T,** *Polyedryxium decorum* Deunff. BAFC-Pl 1656 (2): D31/3. **U,** *Botryococcus* sp. BAFC-Pl 1505 (1): W50/1. **V,** *Leiotriletes balapucensis* di Pasquo BAFC-Pl 1505 (2): B37. **W,** *Apiculatisporis grandis* Menéndez and Pöthe de Baldis. BAFC-Pl 1505 (1): R52/1. **X,** *Verrucosisporites scurrus* (Naumova) McGregor and Camfield. BAFC-Pl 1505 (5): 47/1. **Y,** *Apiculatasporites microconus* (Richardson) McGregor and Camfield. BAFC-Pl 1505 (3): H29/3. **Z,** *Dibolisporites varius* Tiwari and Schaarschmidt. BAFC-Pl 1656 (1): J29/3. **AA,** *Emphanisporites annulatus* McGregor. BAFC-Pl 1656 (1): Z24. **AB,** *Emphanisporites rotatus* McGregor emend. McGregor. BAFC-Pl 1656 (1): V27. **AC-AD,** *Acinosporites acanthomammillatus* Richardson. BAFC-Pl 1656 (1): R35, **AC**, proximal face showing a labiate trilete mark; **AD**, distal face showing the rugulae pattern. **AE,** *Cymbosporites catillus* Allen. BAFC-Pl 1505 (2): G38/2. **AF,** *Cymbosporites cyathus* Allen. BAFC-Pl 1505 (3): C37/3. **AG** *Geminospora lemurata* Balme 1962 emend. Playford. BAFC-Pl 1505 (5): D28/2. **AH,** *Geminospora* sp. cf. *G. tuberculata* var. *tuberculata* McGregor. BAFC-Pl 1505 (2): P52/4. **AI,** *Grandispora pseudoreticulata* (Menéndez and Pöthe de Baldis) Ottone. BAFC-Pl 1656 (1): F24/1.

Plate 1



2009) suggest that such endemisms among Middle Devonian palynofloras of South American and elsewhere justifies the definition of an Afro-South American Subrealm, due most likely, to palaeolatitude/paleoclimate as well as the palaeogeographical configuration (i.e. distribution of land and sea areas).

3.2. Malimán Formation

The palynoflora of the Malimán Formation was obtained from ten claystone and siltstone samples and one from fine-grained sandstone, collected from the lower and middle portions of the stratigraphic section in Quebrada La

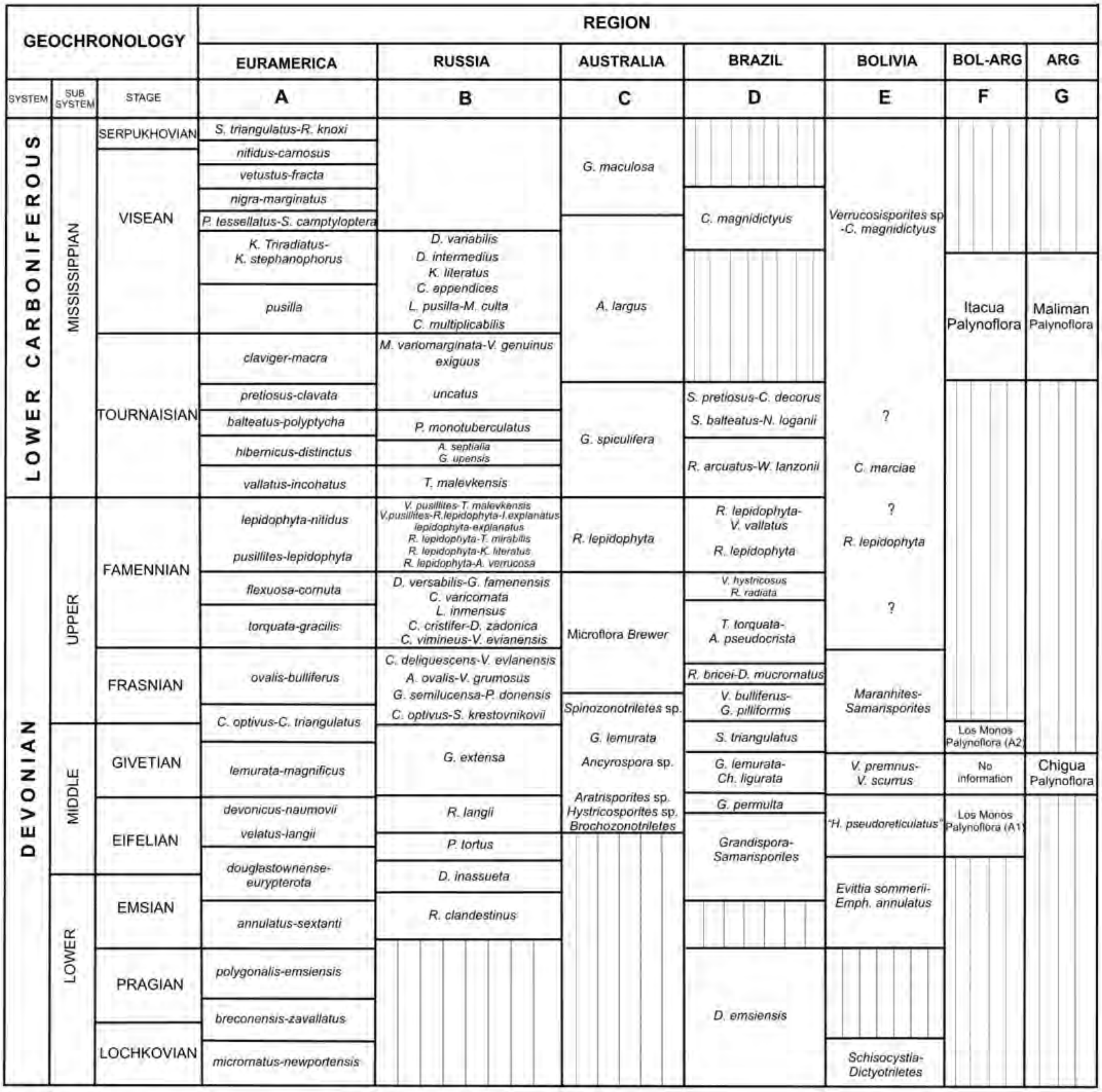


Figure 6. Correlation chart of the assemblages studied (G) and other biozones or assemblages of the Devonian and Mississippian. Literature references given after geography: (A) Western Europe and North America, (B) Eastern Europe, (C) Australia, (D) Brazil, (E) Bolivia, (F) Bolivia-Argentina. A: Richardson and McGregor (1986), Higgs *et al.* (1988); B: Avchimovitch *et al.* (1988, 1993), Byvsheva (1997); C: Playford (1985, 1991); Young (1996); D: Melo and Loboziak (2003); E: Suárez Soruco and Lobo Boneta (1983); Limachi *et al.* (1996); F: di Pasquo (2007a, b).

Cortadera. The upper part of the section is predominantly coarse-grained (sandstones and conglomerates), and therefore, is likely to be barren of palynomorphs (Figure 3). The taxonomic analysis and distribution of the species registered in the sampled unit were presented by Amenábar *et al.* (2006, 2007). Recovered palynomorphs are of moderate diversity and quality of preservation; their thermal maturity (TAI) varies between 2 and 4 on the scale of Utting *et al.* (in Utting and Wielens, 1992). Due to their dark colour, some specimens could not be identified specifically. Two different groups of palynomorphs may be distinguished on the basis of their quantitative distribution along the outcrop section, taphonomical characteristics, and their stratigraphic range. One comprises 79 spore species (acavate, cavate, pseudosaccate and cingulizonate forms) and 10 microplankton taxa (Amenábar *et al.*, 2006, 2007), all considered to be autochthonous elements (Figure 7A-B). The other group consists of evidently reworked spores, acritarchs and prasinophytes (Amenábar, 2006; Amenábar *et al.*, 2007). A likely provenance for most of the reworked palynomorphs originating from Upper Silurian through Mid-Devonian units in the Precordillera was discussed by Amenábar (2006). The significance of certain species known to characterise late Famennian ("Strunian") to Tournaisian is considered in the present paper. Average percentages of spores and microplankton are shown in Figure 7A-B, and selected specimens are illustrated on Plate 2. Selected biozones or palynofloras of the Mississippian in South America and elsewhere are compared to the assemblage of the Malimán Formation, while the correlation age of the assemblage shown in Figure 6, are briefly discussed as follows.

Remarkable similarities exist between the Malimán assemblage and recently described palynofloras from the late Tournaisian-early Viséan in Colombia (Dueñas and Césari, 2006) and the Itacua Formation in southernmost Bolivia (di Pasquo, 2005, 2007b) (Figure 6). Moreover, the cosmopolitan index *Schopfites claviger* is shared also with the middle Tournaisian *Spelaeotriletes pretiosus-Colatisporites decorus* (PD) Interval Zone of Melo and Loboziak (2003) in the Amazonas Basin, Brazil (Figure 6). However, these authors have recognised a hiatus between the latter and the late Viséan *C. magnidictyus* (Mag) Zone that could explain the presence of certain Viséan taxa in the Malimán Formation not found in the Brazilian assemblages mentioned (Figure 8).

Several species are also shared with Western European assemblages (e.g., Clayton *et al.*, 1977; Higgs *et al.,* 1988). The age of the Mississippian miospore zonation in Ireland is calibrated with the aid of conodonts (see Higgs *et al.*, 1988). Turnau *et al.* (1997) and Utting and Giles (2004) discussed the correlation between the Tournaisian-Viséan biozones of Western Europe and Atlantic Canada, where the base of the Viséan is marked by the incoming of the genus *Lycospora* found throughout Europe. This is linked to the first occurrence of *Densosporites columbaris* and *Vallatisporites ciliaris* in Canada. None of these species regarded as determinative are present in the Malimán assemblage. On the other hand, although *Colatisporites decorus, Raistrickia clavata* and *Crassispora trychera* of the late Tournaisian PC Zone, and *Schopfites claviger* and *Anapiculatisporites hystricosus* of the CM Zone (Higgs *et al.,* 1988), are all present in the Malimán Formation, they persist into later assemblages of Viséan age (Pu Zone; Figures 4 and 6).

The palynoflora of the Malimán Formation shows a certain affinity with Mississippian assemblages from Australia, with which it has a number of common species (Figure 6). The latter do not contain reworked specimens (Dino and Playford, 2002). It is particularly close to the Viséan *Endoculeospora larga* Assemblage (*E. larga* (Playford) di Pasquo, 2007b) of Australia (Kemp *et al.,* 1977), showing the presence of *Schopfites claviger* together with earlier species such as *Apiculiretusispora semisenta, Grandispora spiculifera, Velamisporites perinatus, Dibolisporites medaensis, Crassispora invicta* and *C. scrupulosa* (Playford, 1985, 1991). Jones and Truswell (1992) suggested later that the *E. larga* Assemblage would extend from the Tournaisian-Viséan boundary into the Serpukhovian in the Bonaparte, Canning and Drummond basins. They based their opinion on a comparison between Australian palynofloras and the British ones and a calibration provided by faunal remains in the Australian basins (Playford, 1971).

In view of the above considerations, some qualitative differences may be noted among these palynofloras and others elsewhere. In agreement with Dino and Playford (2002), such differences may be attributed to various factors, like the scarcity of palynological studies, the effects of floral distribution through migration patterns, local or regional palaeoenvironmental variations, and taxonomical imprecision and/or incorrect dating of palynomorph assemblages. An accurate correlation between the early Viséan Euramerican and Argentinean assemblages is impeded due to the absence of *Lycospora* in Argentina and Australia (Playford, 1991) and throughout most of South America (abstraction made of some patchy occurrences could be found in the Amazonas Basin after Melo and Loboziak, 2003). *Schopfites claviger* is used as a marker for the base of the Viséan in the Australian palynozonation and for the late Tournaisian in Euramerican assemblages (Higgs *et al.,* 1988). Hence, even though a late Tournaisian age is possible for the lower part of the Malimán Formation, an early Viséan age is most likely for most of this unit due to the occurrence of many species known to appear in the early Viséan (Figures 4 and 6). The compositional differences (i.e., index species) between the assemblages of the late Viséan Cortaderas (Pérez Loinaze, 2007) and Malimán formations from the same basin (Figure 2A) support a late Tournaisian to early Viséan age for the Malimán Formation (Figures 1D and 4). Besides, the presence of *Cordylosporites magnidictyus* (Playford and Helby) Melo and Loboziak and *Schopfipollenites ellipsoides* (Ibrahim) Potonié and Kremp which characterises the Mag Zone of Melo and Loboziak (2003) in Brazil and Perú (Azcuy and di Pasquo, 2005), prevents the correlation with the Malimán Formation.

Finally, an abundance of specimens of *Cristatisporites*, some of which are identified at specific level (Figure 7A-B), is recorded in the Malimán Formation (Amenábar *et al.,* 2007). Several index taxa along with species of *Cristatisporites* are shared with the assemblage obtained from the Lower Member of the El Ratón Formation (cropping out next to Calingasta, Km 114-117), supporting the correlation of these two units (Amenábar, 2007a; Amenábar and di Pasquo, 2009). Also, *Cristatisporites matthewsii*, which was defined in the late Tournaisian of Ireland (CM Zone, Figure 6, Plate 2), is well-preserved and recorded frequently in the assemblage of the Malimán Formation (Figure 7A-B; Amenábar *et al*., 2007). In the Tournaisian-early Viséan of Scotland a very similar spore was illustrated as *Acanthotriletes* cf. *macrogaleatus* Phillips and Clayton by Stephenson *et al*. (2004 in figure 9A-L). This is regarded as part of *C. matthewsii* since there is intergradation between these two taxa (Stephenson *et al*., 2004). Therefore, an extension of its stratigraphic range into the early Viséan is proposed here.

4. ANALYSIS OF REWORKED SPECIES

Reworked palynomorphs were mainly interpreted on the recognition of species that are known to be recorded in older chronostratigraphic intervals than the age of the host unit. Other features such as frequency, preservation and taphonomy (e.g. thermal maturity, fragmentation, corrosion) and palaeoecology (e.g. marine or continental origin) of palynomorphs are also taken into consideration. The recognition of reworked palynomorphs may be applied to solve or improve chronological, diastrophic and palaeoenvironmental questions and to prevent an unwarranted extension of stratigraphic ranges. It is especially useful when the contact between stratigraphic units is a paraconformity, condensed section, or generally different to appreciate on field evidence (di Pasquo and Azcuy, 1997). The chronological meaning of such reworked species recorded in the Chigua and Malimán formations is discussed below.

4.1. Reworking in the Chigua Formation

The acritarch *Pulvinosphaeridium trifidum*, registered in the Chigua Formation, is well-known from the Late Silurian-Early Devonian deposits of Ukraine (Kiryanov, 1978). This species, which is rarely mentioned in the literature, was recorded in an early Serpukhovian palynoflora from northern Bolivia (Fasolo *et al*., 2006), illustrated as *Pulvinosphaeridium* sp. in Azcuy and Ottone (1987, p. 249, plate III, fig. 6). It was regarded as derived from Devonian rocks together with some other species (e.g., *Retispora lepydophyta*). The spore *Verrucosisporites polygonalis* characterises the *V. polygonalis-D. emsiensis* Zone of the Pragian-Emsian in Europe (Richardson and McGregor, 1986). *Archaeozonotriletes chulus* var. *chulus* has been recorded from the Lochkovian to basal Eifelian in the Old Red Sandstone (e.g. Richardson and McGre-

Figure 7. Quantitative analysis of the autochthonous palynomorphs found in the Malimán Formation. Spore species organised in order of first appearance. Symbols refer to relative abundance, based on counts of ca. 300 specimens per sample: □ (empty square): <1%; ■ (black square): 1-5.6 %; ▲ (triangles): >5.6%. Species cited and/or illustrated for the first time in Mississippian sediments of South America are marked with single asterisk (*); species cited for the first time in the Mississippian of Argentina are marked with two asterisks (**).

	SPECIES REGISTERED IN THE MALIMAN FORMATION	samples (BAFC-PI)									
		1507	1508	1655	1654	1653	1504	1503	1502	1506	1501
SPORES	** *Cristatisporites indignabundus* (Loose) Potonié and Kremp emend. Staplin and Jansonius	■								■	
	* *Velamisporites perinatus* (Hughes and Playford) Playford	■								■	□
	Crassispora sp.	■	□	□			■		■	■	□
	Apiculiretusispora semisenta (Playford) Massa, Coquel, Loboziak and Taugordeau-Lantz		■	□				□		□	□
	Densosporites spinifer Hoffmeister, Staplin and Malloy		□	□				□		□	
	** *Spelaeotriletes arenaceous* Neves and Owens		□	□							
	** *Convolutispora insulosa* Playford		□	□							
	Cyclogranisporites sp.		□								
	Retusotriletes sp.		□								
	Granasporites medius (Dybová and Jachowicz) Ravn, Butterworth, Phillips and Peppers		□								
	* *Crassispora invicta* Playford		□								
	** *Crassispora trychera* Neves and Ioannides		□								
	Grandispora debilis Playford		■								
	** *Grandispora facilis* (Kedo) Avkhimovitch in Avchimovitch, Byvscheva, Higgs, Streel and Umnova (=*Grandispora notensis* Playford)		□								
	Grandispora spiculifera Playford		■								
	** *Emphanisporites hibernicus* Clayton, Higgs and Keegan		□								
	Bellispores sp.		□								
	* *Convolutispora* sp. cf. *C. usitata* Playford		□								
	* *Raistrickia gemmifera* Playford and Satterwaith		□								
	Waltzispora polita (Hoffmeister, Staplin and Malloy) Smith and Butterworth		□								
	* *Lophozonotriletes dentatus* Hughes and Playford		□								
	* *Dibolisporites* sp. cf. *D. setigerus* Playford and Satterthwait		□								
	** *Auroraspora macra* Sullivan		□				□				
	** *Pustulatisporites dolbii* Higgs, Clayton and Keegan		□					□			
	Crassispora scrupulosa Playford emend. Playford and Satterthwait		□							□	
	* *Raistrickia intonsa* (Playford) Playford and Satterthwait		□								□
	* *Verrucosisporites microtuberosus* (Loose) Smith and Butterworth		□								□
	Dibolisporites microspicatus Playford		□	▲	▲	■	■	▲	▲	■	▲
	* *Anapiculatisporites hystricosus* Playford			■	▲	■	■	■	▲	■	▲
	** *Convolutispora varicosa* Butterworth and Williams			□							
	* *Pustulatisporites papillosus* (Knox) Potonié and Kremp			□							
	* *Granulatisporites triconvexus* Staplin			□							
	* *Anapiculatisporites ampullaceus* (Hacquebard) Playford			□				□		□	
	* *Densosporites* sp. cf. *D. triangularis* Kosanke			■				□		■	□
	* *Densosporites asperus* Braman and Hills			▲				□	□		
	Leiotriletes ornatus Ishchenko			■					□	□	□
	** *Densosporites anulatus* (Loose) Schopf, Wilson and Bentall			■						□	□
	* *Densosporites gracilis* Smith and Butterworth			□						■	
	** *Auroraspora solisorta* Hoffmeister, Staplin and Malloy			□							□
	* *Pustulatisporites malimanensis* Amenábar, di Pasquo, Carrizo and Azcuy			■							□
	* *Densosporites secundus* Playford and Satterthwait			□		■				■	
	** *Vallatisporites pusillites* (Kedo) Dolby and Neves			■		■	□				
	Anapiculatisporites amplus Playford and Powis			■			□			□	■
	** *Densosporites regalis* (Bharadwaj and Venkatachala) Smith and Butterworth			■			□	□		□	
	Schopfites claviger (Sullivan) emend. Higgs, Clayton and Keegan										
	* *Convolutispora tuberculata* (Waltz) Hoffmeister, Staplin and Malloy					■	□				

gor, 1986), whilst *Dictyotriletes emsiensis* Morphon (Rubinstein *et al*., 2005) ranges from Lochkovian to early Emsian (Nβ to AB zones of Steemans, 1989). These three spores are also known from the Early Devonian of Bolivia (McGregor, 1984; Limachi *et al*., 1996) and Brazil (Dino, 1999; Melo and Loboziak, 2003; Rubinstein *et al*., 2005; see also Figure 7A-B). A comparison between the assemblage of the Chigua Formation and Early Devonian palynofloras from the Precordillera of Argentina is fraught with difficulty because of the scarcity of productive assemblages in this region. The palynoflora of the Talacasto Formation, which is attributed to early Lochkovian-Emsian, has yielded only few palynomorphs (Le Hérissé *et al*., 1997). Among these, the only common species is *Archaeozonotriletes chulus* (Figure 5). A recently documented palynoflora from the Villavicencio Formation in Mendoza Province is dated as late Pragian to early Emsian (Rubinstein and Steemans, 2007). It only has *Apiculiretusispora plicata* in common with the Chigua Formation (Figure 5). Therefore, the stratigraphic information on *Verrucosisporites polygonalis, Dictyotriletes emsiensis, Archaeozonotriletes chulus* and *Pulvinosphaeridium trifidum* suggests that these are reworked elements from the eroded Lower Devonian, a conclusion which is supported by their low frequency (Figure 4). The presence of these Early Devonian reworked forms in the Chigua Formation suggests an imput of fine sediment from a nearby source area composed of Upper Silurian and Lower Devonian strata. The evidence of uplift is in agreement with Astini's (1996) proposal regarding a compressional interval, called the Precordilleran Orogeny, occurring during Early to Mid Devonian times. However, it is also possible to assume that regressive-transgressive cycles within the Devonian might have contributed to a partial reworking of palynomorphs as suggested by Bustos and Astini (1997).

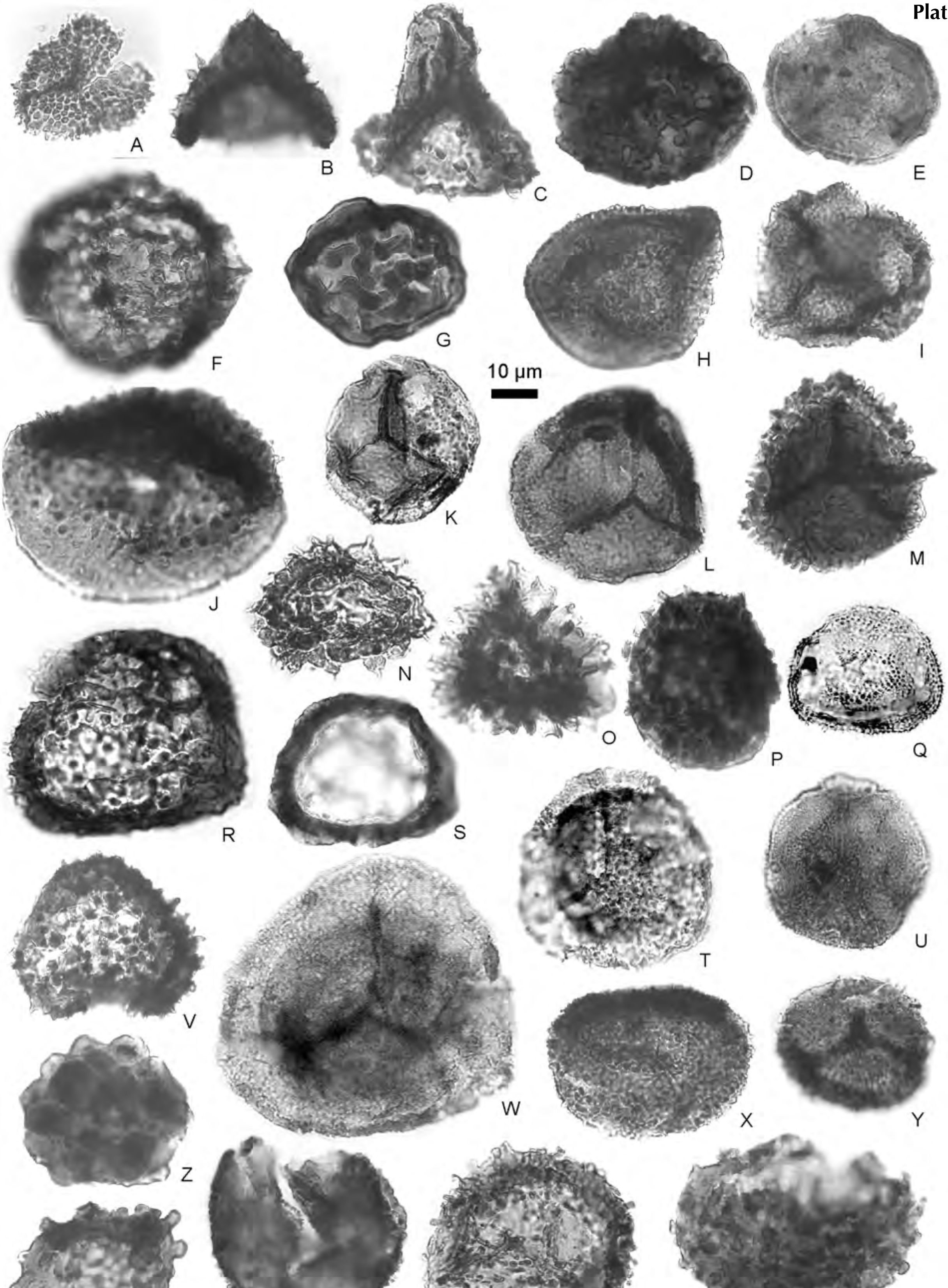
4.2. Reworking in the Malimán Formation

Amenábar (2006) presented a preliminary list of reworked taxa in the Malimán Formation and discussed their provenance on the basis of their stratigraphic range and frequency of occurrence in the Carboniferous samples. She recognized two groups representing Early Devonian (Emsian) and Middle-Late Devonian (Givetian-early Famennian), respectively. A third group comprised scarce forms of a probable Late Silurian age. Based on a comparison with Silurian and Devonian palynofloras of Argentina and taking into account the palaeogeographic reconstructions of the Mississippian in South America, the Precordillera was interpreted as the main source area. Additional reworked palynomorphs as identified by Amenábar *et al*. (2007) include the Givetian-Frasnian spore species *Hystricosporites* sp. cf. *H. gravis* Balme, *Hystricosporites* sp. cf. *H. porrectus* (Balme and Hassell) Allen and *Corystisporites* sp., as well as the Early Devonian acritarch *Estiastra improcera* Loeblich and the Givetian acritarch *Petalosphaeridium ancorum* (Wicander and Loeblich) Sarjeant and Vavrdová.

Long-ranging spore species (Late Devonian to Viséan) recorded in the Malimán Formation (Figure 8) include *Auroraspora macra, A. solisorta, Bascaudaspora submar-*

Plate 2**.** Autochthonous spores from the Malimán Formation. Scale bar: All 15 µm (x 750). **A,** *Anapiculatisporites hystricosus* Playford. BAFC-Pl 1654 (2): A28/3. **B,** *Anapiculatisporites ampullaceus* (Hacquebard) Playford. BAFC-Pl 1655 (2): S32/2. **C,** *Anapiculatisporites amplus* Playford and Powis. BAFC-Pl 1655 (2): Y50. **D,** *Bascaudaspora submarginata* (Playford) Higgs, Clayton and Keegan. BAFC-Pl 1506 (4): A39/2. **E,** *Colatisporites decorus* (Bharadwaj and Venkatachala) Williams in Neves, Gueinn, Clayton, Ioannides, Neville and Kruszewska. BAFC-Pl 1501 (1): R38/3. **F,** *Convolutispora varicosa* Butterworth and Williams. BAFC-Pl 1655 (2): R31/2. **G,** *Convolutispora insulosa* Playford. BAFC-Pl 1508 (1): V22. **H,** *Convolutispora tuberculata* (Waltz) Hoffmeister, Staplin and Malloy. BAFC-Pl 1504 (2): Q39/2. **I,** *Convolutispora* sp. cf. C. clavata (Ischenko) Hughes and Playford. BAFC-Pl 1506 (1): Q35. **J,** *Crassispora invicta* Playford. BAFC-Pl 1508 (1): W36. **K,** *Crassispora trychera* Neves and Ioannides. BAFC-Pl 1508(2): F49/4. **L,** *Crassispora scrupulosa* Playford emend. Playford and Satterthwait. BAFC-Pl 1508(4): F23/2-4. **M,** *Cristatisporites indolatus* Playford and Satterthwait. BAFC-Pl 1506(5): D50/1. **N,** *Cristatisporites matthewsii* Higgs, Clayton and Keegan. BAFC-Pl 1655 (2): B40/1. **O,** *Cristatisporites indignabundus* (Loose) Potonié and Kremp emend. Staplin and Jansonius. BAFC-Pl 1506 (2): K24/4. **P,** *Dibolisporites medaensis* (Playford) Playford. BAFC-Pl 1506 (1): R25/2. **Q,** *Dibolisporites microspicatus* Playford. BAFC-Pl 1655 (2): R31/2. **R,** *Cristatisporites peruvianus* Azcuy and di Pasquo. BAFC-Pl 1506(4): Z50. **S,** *Densosporites anulatus* (Loose) Schopf, Wilson and Bentall. BAFC-Pl 1506 (3): Y48. **T,** *Grandispora notensis* Playford. BAFC-Pl 1508 (4): Z51/1. **U,** *Grandispora spiculifera* Playford. BAFC-Pl 1508 (1): Z27/3. **V,** *Lophotriletes severus* Playford and Satterthwait. BAFC-Pl 1504 (3): A53/1. **W,** *Grandispora debilis* Playford. BAFC-Pl 1508 (3): K28/1. **X,** *Verrucosisporites microtuberosus* (Loose) Smith and Butterworth, BAFC-Pl 1508 (1): U30/1. **Y,** *Apiculatisporis castanea* (Butterworth and Williams) Amenábar, di Pasquo, Carrizo and Azcuy. BAFC-Pl 1503 (2): J27/1. **Z,** *Pustulatisporites gibberosus* (Hacquebard) emend. Playford. BAFC-Pl 1503 (1): V25/2. **AA,** *Raistickia clavata* Hacquebard emend. Playford. BAFC-Pl 1501 (1): P27. **AB,** *Schopfites claviger* (Sullivan) emend. Higgs, Clayton and Keegan. BAFC-Pl 1504 (2): D33/2. **AC,** *Raistrickia gemmifera* Playford and Satterthwait. BAFC-Pl 1508 (4): Y42/4. **AD,** *Verrucosisporites morulatus* (Knox) Smith and Butterworth. BAFC-Pl 1502 (2): P42.

Plate 2



ginata, Pustulatisporites gibberosus, Crassispora scrupulosa, Cordylosporites marciae, C. spathulatus, Raistrickia clavata, Vallatisporites pusillites, Spelaeotriletes obtusus, Grandispora facilis (= G. notensis) and *Grandispora spiculifera*. Although these taxa are widespread, being recognised in Brazil (Melo and Loboziak, 2003), Chile (Rubinstein *et al*., 1996), northern Bolivia (Vavrdová *et al*., 1996) and Australia (Playford, 1976), they are useless biostratigraphically. In the assemblage from the Malimán Formation, they may be indistinctly reworked or autochthonous. In this respect the present writers agree with di Pasquo (2007b, c) who proposed a re-evaluation of certain latest Devonian assemblages, mainly from Bolivia, so as to verify their ages, in this case because the Devonian/Carboniferous boundary strata in the Tarija Basin proved to contain quite important mixtures of autochthonous and reworked palynomorphs as result of tectonic and glacial processes which affected the western region of Gondwana (see also di Pasquo and Azcuy, 1997; Streel *et al*., 2000).

Species recorded with a very low frequency in the Malimán Formation, i.e. *Cordylosporites marciae, Emphanisporites hibernicus, Raistrickia* sp. cf. *R. condylosa, C. spathulatus, Dictyotriletes trivialis, Spelaeotriletes obtusus, Vallatisporites pusillites, Pustulatisporites dolbii* and *Gorgonispora* sp. cf. *G. crassa* (Figures 7A-B and 8; Amenábar et *al.,* 2006, 2007), may have been derived from the reworking of upper Famennian and/or part of the Tournaisian strata although the physical evidence of strata of these ages seems absent from the Precordillera of Argentina. Hence, there is no incontrovertable proof as yet.

Practically all the microplankton species registered in the Malimán Formation are known to occur in Devonian strata. It is noted that they are found together with Devonian spores (e.g., *Archaeozonotriletes chulus, Emphanisporites rotatus, Grandispora pseudoreticulata, Verrucosisporites scurrus*) in the Chigua Formation (Figures 5 and 7A-B). Therefore, the proposal of Césari and Limarino (1992, 1995) of considering acritarchs, prasinophytes and chitinozoans as autochthonous in the Malimán and Cortaderas formations, is ruled out here. A remarkable fact supporting the idea that most of the microplankton registered in the Malimán Formation is recycled, is the massive extinction noted in the marine realm near the Devonian/Carboniferous boundary, where a phytoplankton collapse occurred (e.g., Algeo *et al.,* 1995; Streel *et al*., 2000; Filipiak, 2005). The expansion of a dense terrestrial vegetation coverage during the Late Devonian when the first leafy forests developed, may have caused the progressive retention of carbon, nitrogen and phosphorous in terrestrial environments. These elements constituting important nutrients in marine ecosystems were largely sequestered in the terrestrial environments, thus not being available for phytoplankton and producing a great planktonic crisis (Tappan, 1986). So, low planktonic diversity and scarce primary productivity, the so-called "phytoplanktonic blackout" (Riegel, 1996) characterised latest Famennian/Tournaisian times, during which only few opportunistic acritarchs and prasinophytes managed to survive. Thus, the autochthonous phytoplankton assemblages of Mississippian times throughout the world, were poor diversified, with species of the opportunistic genera *Veryhachium* and *Micrhystridium* being most dominant (e.g., Wicander, 1974; Streel, 1999). An example of this strong decrease in the diversity and abundance of microplankton was documented for Late Devonian and Mississippian assemblages of central Poland by Filipiak (2005). Only a few species from the long-ranging genera *Cymatiosphaera, Hemiruptia, Leiosphaeridia, Tasmanites, Dictyotidium, Micrhystridium* and *Veryhachium* are present in the upper Viséan. A careful analysis of the microplankton found in the Malimán Formation has shown the presence of well-preserved species identified as *Veryhachium* sp. cf. *V. trispinosum, Dictyotidium torosum,* and specifically unidentificable forms of *Dictyotidium, Cymatiosphaera, Micrhystridium* and *Tasmanites* (Figure 7A-B). These were described and illustrated by Amenábar *et al*. (2007). They were obtained from marine and littoral strata (Figure 3) where they occurred together with several species of *Quadrisporites*, and could well represent autochthonous microplankton linked to a generalised Mississippian transgression. Instead, some other taxa (e.g., *Synsphaeridium* sp., scolecodonts indet.) are regarded of doubtful origin. It is clear that the use of acritarchs for palaeoenvironmental interpretations or biostratigraphy is valid only when their autochthonous nature is beyond doubt.

5. DISCONFORMITY AND HIATUS BETWEEN THE CHIGUA AND MALIMÁN FORMATIONS

The Devonian/Carboniferous boundary in the Late Palaeozoic basins of Argentina is characterised locally by an angular unconformity, which involved a different time-span depending on the location. The actual contact is often covered and paraconformable relationships exist in some areas (Azcuy *et al*., 2007). An angular unconformity contact is recognised between the Devonian Chigua and the Mississippian Malimán formations in the area studied (Figure 2B-C). A stratigraphic gap between these two formations became apparent after the faunal and floral remains were studied from the Chigua Formation (see item 1), and also the sparce flora and scarce palynomorphs from the Malimán Formation (see items 1 and 4.2). An analysis of the stratigraphic ranges of the authochtonous palynomorphs (Figures 5 and 8) registered by Amenábar *et al*. (2006, 2007) in both formations, allowed changing the length of the time gap which proved to extend form the Frasnian to the early Tournaisian. The analysis of the reworked species recorded from the Malimán Formation, allowed further precision with regard to the geological history of the area during this time gap.

Different opinions about the nature of this unconformity still exist. Traditionally, the Devonian/Carboniferous unconformity was attributed to the Chanic Orogeny, which was described as a strongly compressional tectonic phase that caused the most important deformation of the Devonian deposits (see Azcuy *et al*., 2000). Ramos (1988) related this tectonic phase to the collision of an allochthonous terrane ("Chilenia") in the western part of the Gondwanaland that would have happened towards the end of the Devonian. The accretion of a "Chilenia" terrane would have been the main cause of uplift of a Protoprecordillera composed of Devonian and older rocks. This would have created a discontinuous mountainous chain, which separated different depocentres in the Carboniferous times (e.g., Azcuy *et al*., 2000, 2007; Figure 1).

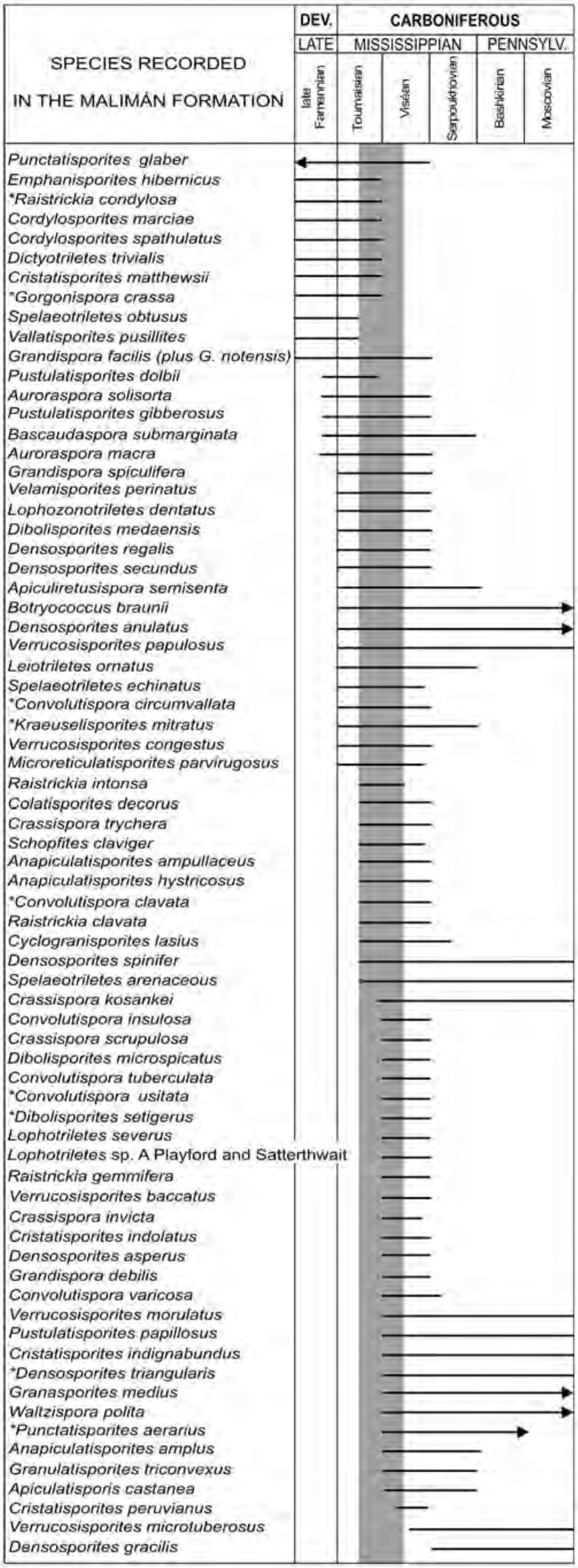


Figure 8. Stratigraphic ranges of species recovered from the Malimán Formation, after selected literature cited in Amenábar *et al.* (2006, 2007). Species marked with an asterisk are asterisk are doubtful indentifications ("cf."). The grey area corresponds to the time interval proposed for the assemblage.

On the other hand, Astini (1996) suggested that this collision would have occurred earlier, i.e. in Middle Devonian times. He adduced structural, palaeontological as well as stratigraphic evidence. Astini's interpretation finds support in the presence of reworked Late Silurian-Early Devonian palynomorphs in the Chigua Formation discussed in the present paper. Astini (1996) stated that the uplift taking place in Late Devonian times would probably be linked to extension, an interpretation which is different from that of Ramos (1984, 2004), who suggested a strongly compressional phase near the end of the Devonian (Chanic Orogeny) as a result of the accretion of "Chilenia", as mentioned before. According to González Bonorino (1990) and Astini (1996), the unconformity has a strong erosional component related to glaciation affecting the western margin of Gondwanaland during the Late Devonian/Carboniferous. Scotese *et al*. (1999) referred to a Late Devonian (Famennian)-Early Permian Ice House divided into two Ice House intervals, separated by a warmer one. The first interval was assigned to the Tournaisian. However, the ice cap of Tournaisian times would be only of limited extent. Althought they mentioned that this inference is based mainly on the occurrence of glendonite in shales from western Alberta, the hypothesis is in agreement with the record of glacial deposits in South America (Bolivia and Brazil) and Niger during the latest Famennian ("Strunian"); this are supposed to be related to palaeoequatorial cyclothems in North America and Europe (e.g., Isaacson *et al.,* 1999; Streel *et al*., 2000; Isbell *et al*., 2003). Hence, the contemporaneous shallow and marginal marine deposits in Gondwana such as the Precordillera of Argentina would have been affected.

The geological history of the Precordillera is obviously quite complex. Data presented in this paper strongly suggest that sediments accumulated during the Frasnian and probably also during the early Tournaisian. Indeed the stratigraphic ranges of some reworked species recorded in the Malimán Formation (Figures 6 and 8) point in this direction. The uppermost Devonian (late Famennian or "Strunian") may have been a time of non-deposition since cosmopolitan taxa restricted to this time are notably absent (e.g. *Retispora lepidophyta* and *Umbellasphaeridium saharicum*, see Vavrdová and Isaacson, 1999), whilst other reworked species corresponding to those times also occur in the Tournaisian assemblages elsewhere (Figure 8). Hence, the presence of late Famennian species among the reworked taxa cannot be confirmed for the palynoflora of the Malimán Formation. The absence of Famennian deposits may be due to a combination of tectonics and glaciation, but this is conjectural. The tectonic effect might be due to the accrection of a "Chilenia" terrane in Late Devonian times, while glaciation refers to a lowering of sea level as the result of an ice cap covering an area located around 60º S lat. (after Scotese, 2003). However, a general lack of information of this time span in the Precordillera (Azcuy *et al*., 2000, 2007) prevents an exact assessment.

In summary, the mixture of reworked palynomorphs with different stratigraphic ranges (Late Silurian to early Tournaisian), occurring together in the same assemblage with late Tournaisian-early Viséan authochtonous miospores, shows that older areas of uplift were being eroded (e.g., Protoprecordillera). This helps to complete part of the complex D/C geological history of erosion and sedimentation in the Rio Blanco Basin.

6. CONCLUSIONS

The palynological data analysed in this paper provide a more accurate dating and correlation of Devonian and Mississippian strata of the Precordillera in Western Argentina.

An early Givetian age is postulated here for the Chigua Formation (Chavela Member) at Quebrada La Cortadera, based on the stratigraphic ranges of several species. The Malimán Formation is assigned a late Tournaisian to early Viséan age on the basis of the stratigraphic ranges of 72 autochthonous spore species. A comparison with other assemblages in the world confirmes that South American, Australian and Euramerican affinities exist. The absence of a few key taxa such as *Lycospora,* and the appearance of others (e.g., *Schopfites claviger*) suggest a late Tournaisian age for the lower part of the Malimán Formation. This palynoflora is here correlated to the *Endoculeospora larga* Assemblage defined in Australia, and recently found in the Itacua Formation of southernmost Bolivia, and also with the CM and Pu Zones of Euramerica.

The palynological analysis presented here confirmes the conclusion published by Amenábar (2006) about the extention of the hiatus between the two formations analysed, and which ranges from Frasnian to early Tournaisian. The detailed analysis of stratigraphic ranges of taxa recongnised as reworked elements has prevented an erroneous assumption of extended ranges for certain key-species and of unnecessary palaeoenvironmental interpretations. Some microplankton taxa with a restricted position in the Malimán Formation are recognised as autochthonous in the present paper, and this has allowed distinguishing a Mississippian microplankton assemblage which was still poorly known worldwide. The stratigraphic analysis of recycled palynomorphs in the Malimán Formation allowed the recognition of two intervals of sediment accumulation during the Frasnian and probably also during the early Tournaisian. No index species of uppermost Devonian (late Famennian or "Strunian") have been detected, thus suggesting a corresponding interval of non-deposition. The presence of reworked palynomorphs in both the Chigua and Malimán formations suggests that erosion of older uplifts areas took place (e.g., Protoprecordillera). Transgressive-regressive events during the Middle Devonian in this region may have been at least partially responsible for the reworking, but extensional tectonic processes may have been involved as well. Alternatively, reworking during late Tournaisian to early Viséan times might be due to a combination of both tectonics processes and glaciation.

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The Mississippian miospore *Neoraistrickia loganensis* (Winslow, 1962) Coleman & Clayton, 1987: morphological variation and stratigraphic and palaeogeographic distribution

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Resumen

Desde su descripción original, la especie *Neoraistrickia loganensis* (Winslow, 1962) Coleman & Clayton, 1987 ha sido registrada en niveles Misisipienses (Carbonífero Inferior) de varias regiones de Euroamérica y Gondwana. Los numerosos ejemplares descritos e ilustrados en este trabajo confirman, tanto la variabilidad morfológica de esta especie de miospora trilete acavada y apiculada, como su registro vertical. Éste queda restringido a dos biozonas sucesivas de miosporas del Misisipiense Inferior previamente establecidas en la Formación Oriximiná de la Cuenca de Amazonas [Zonas de intervalo *Spelaeotriletes balteatus–Neoraistrickia loganensis* (BL) y *Spelaeotriletes pretiosus–Colatisporites decorus* (PD)]. La edad de estas biozonas, y por tanto la amplitud temporal de *Neoraistrickia loganensi*, abarca el intervalo Tournaisiense medio temprano – Tournaisiense medio tardío a tardío inicial. Este rango de edad coincide con registros conocidos en otras regiones, especialmente de América del Norte, Irlanda y Norte de África. En consecuencia, *Neoraistrickia loganensis* puede ser considerada como una especie guía, efectiva y fácilmente reconocible, de amplia representación local, regional y hasta cierto punto global.

Palabras clave*:* Miosporas, Cuenca del Amazonas, Sistemática, Bioestratigrafía, Paleogeografía, Misisipiense.

Abstract

Since its initial description, *Neoraistrickia loganensis* (Winslow, 1962) Coleman & Clayton, 1987 has been reported from Mississippian (Lower Carboniferous) strata of various Euramerican and Gondwanan regions. Numerous specimens of this species, described and illustrated herein from the Amazonas Basin (northern Brazil), affirm the morphological variability of this acavate, apiculate, trilete miospore and its vertical restriction to two Lower Mississippian miospore biozones – viz., the *Spelaeotriletes balteatus–Neoraistrickia loganensis* [BL] Interval Zone and the succeeding *Spelaeotriletes pretiosus–Colatisporites decorus* [PD] Interval Zone – previously established within the basin's Oriximiná Formation. Dating of those biozones, and hence the species' temporal range, as early middle Tournaisian and late middle to early late Tournaisian, respectively, accords with prior reports from elsewhere, notably North America, Ireland, and northern Africa. Consequently, *Neoraistrickia loganensis* can be regarded as an effective and readily recognizable palynostratigraphic index, locally, regionally, and, to an appreciable extent, globally.

Key words: Miospores, Amazonas Basin, Systematics, Biostratigraphy, Palaeogeography, Mississippian.

1. INTRODUCTION

Palynostratigraphic studies of Mississippian (Lower Carboniferous) strata of northern Brazilian sedimentary basins, in particular the Amazonas Basin (Figure 1), disclose the persistent presence of an acavate, apiculate, trilete miospore that has previously been reported as, inter alia, *Granulatisporites logani* Winslow, 1962 and *Neoraistrickia logani(i)* (Winslow, 1962) emend. Coleman &

Figure 1. Map showing the major Palaeozoic sedimentary basins of Brazil; Amazonas Basin stippled.

Clayton, 1987. Originally described from the Mississippian of Ohio, U.S.A., this species has subsequently been recorded widely and coevally, not only from elsewhere in Euramerica, but also from various localities in Northern and Western Gondwana.

The availability of numerous specimens assignable to this species (the epithet of which is orthographically corrected herein to *loganensis*), from Tournaisian subsurface sections of the Amazonas Basin's Oriximiná Formation, provides an ample opportunity to examine its considerable – and continuous – morphological variability. Accordingly, the purpose of this paper is to illustrate and describe in detail the morphological variation of the species and to assess its biostratigraphic and palaeogeographic significance.

2. MATERIAL AND METHODS

All core samples that yielded the spore specimens described and illustrated herein were obtained from four wells drilled by Petróleo Brasileiro S.A. (Petrobras) in the course of extensive petroleum exploration in the Amazonas Basin. These wells (Figure 2) are as follows: 1-CM-1-PA and adjacent 1-CM-2-PA, in the basin’s North Platform; 2-LF-1-AM, in the area transitional between the North Platform and the Central Basin; and 1-RX-3-AM, in the Central Basin. A comprehensive account of the stratigraphy and miospore biozonation of the Devonian and Carboniferous succession of the Amazonas Basin, including that cored in the aforementioned wells, has been furnished by Melo & Loboziak (2003) and literature cited therein.

The Oriximiná Formation, from which the study samples were obtained, is widely developed in the Amazonas Basin subsurface, consisting of up to 420 m of sandstone, siltstone, and shale, occasionally with diamictite intervals in its lower part (Caputo *et al.*, 1972; Grahn, 1992; Melo & Loboziak, 2003). The formation reportedly accumulated in fresh to brackish water and in restricted or transitional marine environments. Miospores provide the sole means of precise dating, other fossils being uncommon. Accordingly, on palynological grounds, Melo & Loboziak (2003) demonstrated an immediately post-Devonian (Tournaisian) age for the entire Oriximiná Formation, or at least the bulk of it in the relatively few wells where the formation’s lowermost part is attributable to the end-Devonian, i.e., latest Famennian a.k.a. “Strunian” (Melo & Loboziak, 2003, p. 151; Text-figs. 13A, B, 15).

The samples comprise mainly carbonaceous and abundantly palyniferous siltstones. They are variously representative of two of the three successive miospore biozones – viz., the *Spelaeotriletes balteatus–Neoraistrickia loganensis* [BL] Interval Zone and the immediately overlying *Spelaeotriletes pretiosus–Colatisporites decorus* [PD] Interval Zone – defined by Melo & Loboziak (2003, pp. 190-192) from within Lower Mississippian (Tournaisian) strata of the Oriximiná Formation. Sampling details are as follows:

- 1-CM-1-PA, core 2 (3/5) at 242-243 m, core 3 (3/4) at 247.4 m and 247-248 m [BL Zone]. See Melo & Loboziak (2003, p. 191; Fig. 13B).
- 1-CM-2-PA, core 12 (2/5) at 265.47 m, core 13 (7/7) at 274.95 m [PD Zone]. See Melo & Loboziak (2003, p. 192; Figs. 8, 13B).

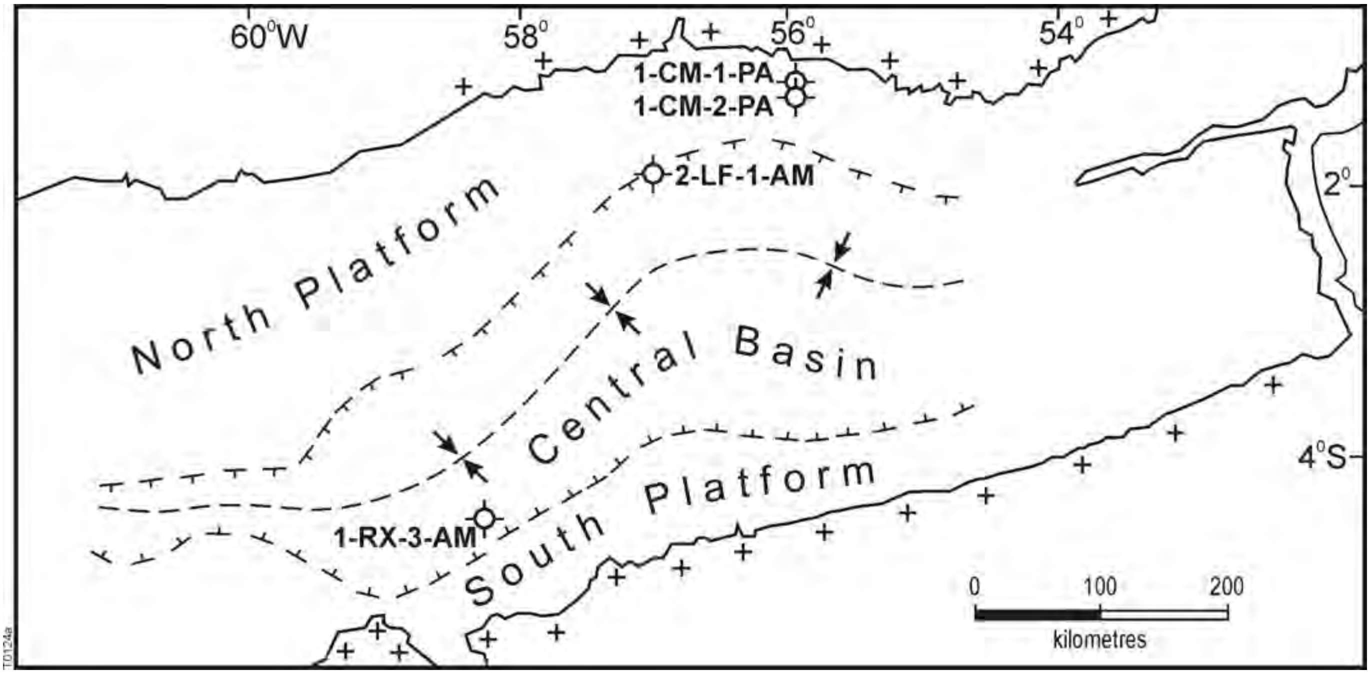

Figure 2. Map of Amazonas Basin, northern Brazil (adapted from Melo & Loboziak, 2003, Fig. 1), showing positions of Petrobras wells, whence core samples that yielded the miospores described herein were obtained. Geographic coordinates are as follows: 1-CM-1-PA, Lat. 1º19’10.037”S, Long. 55º55’14.863”W; 1-CM-2-PA, Lat. 1º19’15.036”S, Long. 55º56’7.865”W; 2-LF-1-AM, Lat 1°57’20.053’’S, Long. 56°58’16.999’’W; and 1-RX-3-AM, Lat. 4º22’45.825”S, Long. 58º15’29.527”W.

- 2-LF-1-AM, core 35 (1/1) at 2197.82 m, core 51 (1/2) at 2253.20 m, core 51 (2/2) at 2254.24 m, core 52 (1/3) at 2255.00 m, 2255.33 m, and 2255.50 m, core 52 (2/3) at 2255.83 m [PD Zone]; present study (re core 35), Melo & Loboziak (2003, p. 192; Fig. 13B; re cores 51, 52).

- 1-RX-3-AM, core 26 (1/2) at 2212.70 m, core 28 (2/2) at 2223.42 m [BL Zone]; present study, cf. Melo & Loboziak (2003, p. 191; Fig. 13B).

The samples were prepared in the Petrobras/Cenpes laboratories, where conventional physico-chemical methods (e.g., Playford & Dino, 2000, pp. 10, 12) were employed for the extraction and concentration of the palynological microfossils. Quality of palynomorph preservation ranged from good to fair, and, as noted above, the yields proved consistently high. Transmitted light microscopy of strew slides was conducted at Petrobras/Cenpes by means of a Zeiss Axioplan binocular microscope equipped with Zeiss AxioCam MRc/Axiovision 4.6.3 for digital photomicrography; and, at The University of Queensland, School of Earth Sciences, using an Olympus BH2 binocular microscope with attached Leica DFC320 digital camera and complementary image-acquisition computer software (Leica IM50). Scanning electron microscopy of selected specimens, picked and mounted as per Playford & Martin (1984, pp. 189-190), was undertaken with a Zeiss Evo 40 instrument of Petrobras/Cenpes.

3. SYSTEMATIC PALAEONTOLOGY

Figured specimens (Plate 1, Figs.1-12; Plate 2, Figs. 1-6) are housed at the Biostratigraphy and Paleoecology Management of Petrobras Research Center (Petrobras/ Cenpes/Pdexp/Bpa), Ilha do Fundão, Rio de Janeiro, RJ, Brazil. Curatorial data are incorporated in the plate explanations.

Anteturma PROXIMEGERMINANTES R. Potonié, 1970
Turma TRILETES Reinsch, 1881 emend. Dettmann, 1963
Suprasubturma ACAVATITRILETES Dettmann, 1963
Subturma AZONOTRILETES Luber, 1935 emend. Dettmann, 1963
Infraturma APICULATI Bennie & Kidston, 1886 emend. R. Potonié, 1956
Subinfraturma BACULATI Dybová & Jachowicz, 1957

Genus *Neoraistrickia* R. Potonié, 1956

1956 *Neoraistrickia* R. Potonié, p. 34.

Type species.- *Neoraistrickia truncata* (Cookson, 1953) R. Potonié, 1956; by original designation

Discussion.- Potonié (1956, p. 34) established *Neoraistrickia* to incorporate trilete miospores characterized essentially by a subtriangular amb, long laesurae, and exinal sculpture consisting of generally scattered, ± uniformly developed bacula. Bharadwaj & Kumar's (1972, p. 214) proposal that the genus be restricted to forms bearing exclusively distal bacula is negated by the sculptural character of its type species (see Dettmann, 1963, p. 36; Pl. V, Figs. 4, 5; Fig. 4m). Most authors distinguish *Neoraistrickia* from the similarly sculptured *Raistrickia* Schopf, Wilson & Bentall, 1944 emend. R. Potonié & Kremp, 1954 (pp. 133-134) simply on the grounds of its amb triangularity compared to the essentially circular-subcircular amb exhibited by the latter genus, which is typified by *R. grovensis* Schopf, Wilson & Bentall, 1944. In an extensive commentary, Rigby & Hekel (1977, p. 13) questioned the putative distinctions among the trio of *Raistrickia*, *Neoraistrickia*, and *Horriditriletes* Bharadwaj & Salujha, 1964 (type species, *H. curvibaculosus* Bharadwaj & Salujha, 1964). Foster (1979, p. 38) reasoned that these genera could be maintained separately, while de Jersey & Raine (1990, pp. 30-31) regarded *Horriditriletes* as a junior synonym of *Neoraistrickia*. We incline towards Foster's (1979) viewpoint, but concede that the morphological variations linking the three genera make taxonomic discrimination somewhat less than satisfactory.

Conbaculatisporites Klaus, 1960 (p. 125) resembles *Neoraistrickia* in featuring a subtriangular amb, but, as exemplified by the type species *C. mesozoicus* Klaus, 1960, it differs in being sculptured with finer bacula that, moreover, tend to be rather more prominent and closer spaced in the three apical (equatorial-radial) regions. Schulz's (1967, p. 563) contention that *Cepulina* Maljavkina, 1949

(p. 73) warrants senior-synonymic status over *Neoraistrickia* is untenable, given the invalidity of Maljavkina's genus (Jansonius & Hills, 1976, card 439) and its illustrative defectiveness (Ravn, 1991, p. 72).

Neoraistrickia loganensis **(Winslow, 1962) emend. Coleman & Clayton, 1987**

Plate 1, Figs. 1-12; Plate 2, Figs.1-10; Figure 3

1962 *Granulatisporites logani* Winslow, p. 62; Pl. 22, Figs. 10, 11.
1969 *Triquitrites* sp. no. 2836 of Lanzoni & Magloire, Pl. V, Fig. 8. [no description]
1973 Spore-1 of Warg & Traverse, Pl. 1, Fig. 9. [no description]
1974 *Acanthotriletes* sp. 2528 of Daemon, p. 559; Pl. VIII, Fig. 4.
1986 *Umbonatisporites baculatus* Coquel & Moreau-Benoit, p. 34; Pl. 3, Figs. 5, 14, 20.
1987 *Neoraistrickia logani* (Winslow) emend. Coleman & Clayton, pp. 83-84; Pl. 2, Figs. 5-9; Fig. 5.
1997 *Umbonatisporites baculatus* Coquel & Moreau-Benoit; Abdesselan-Rouighi & Coquel, Pl. II, Fig. 9. [no description]
2003 *Mooreisporites* sp. of Atta-Peters & Anan-Yorke, p. 17; Text-fig. 2, 7.
2003 *Mooreisporites* sp. of Melo & Loboziak, Pl. V, 9. [no description]
? 2007 *Neoraistrickia loganii* (Winslow) Coleman & Clayton; di Pasquo, Pl. 4, Fig. U [no description]

Original diagnosis (Winslow, 1962, p. 62).- "Spores trilete, subtriangular in outline, generally proximodistally compressed; ranging from 49μ to 76μ in diameter, commonly over 60μ. Inter-radial margins slightly concave to slightly convex; margins at radial extremities broadly rounded.

"Trilete suture distinct at apical pole, poorly defined towards spore margin, generally extending to within 4μ or 5μ of margin in proximodistal compression; suture margins simple. Proximal pole enclosed by a small, circular, and vaguely defined contact zone with a more granulose surface, darker, but not thicker than remainder of spore coat (pl. 22, figs. 10, 11).

"Proximal surface smooth; distal surface sparsely ornamented with blunt to pointed tubercular processes, 1.2-5μ in diameter and 1.5-8μ in length. Tubercles smaller and some more closely set, adjacent to radial extremities. Spore coat ranging in thickness on different specimens from 1μ-3μ, thickest distally (pl. 22, fig. 11); deep yellow by transmitted light."

Locus typicus and stratum.- Ohio, U.S.A., Appalachian Basin; locality 7 of Winslow (1962, pp. 17-19; Fig. 2); R.J. Dalier No. 3 well, cuttings, 452-460 feet (137.8-140.2 m); Black Hand and Cuyahoga formations (undifferentiated), Lower Mississippian, Kinderhookian-?lower Osagean (Matchen & Kammer, 2006).

Emended diagnosis/description (Coleman & Clayton, 1987, p. 84).- "Trilete acamerate miospores. Amb triangular with rounded apices and more or less straight sides. Trilete mark simple; suturae straight, extend almost to the equator. Proximal surface relatively flat; distal surface inflated. Equator, distal surface and proximal surface of apices sparsely ornamented by rounded coni and bacula which are often surmounted by single, small coni or spinae forming biform elements.

"Specimens exhibit considerable variation in ornament (Fig. 5). Some specimens are ornamented by simple, blunt bacula; others bear biform elements consisting of bacula 1.5-6μm high and 2.5-4μm wide surmounted by single coni or spinae 0.5-1μm high and 0.5-1μm wide. Exine otherwise laevigate, 1-2μm thick. Lateral and oblique compressions are common.

"Dimensions: Equatorial diameter inclusive of ornamentation, 50 (75) 95μm; 20 specimens."

Description of Amazonas Basin specimens.- Spores radial, trilete, acavate. Amb subtriangular with convex, ± straight, or slightly concave sides and typically obtusely rounded apices. Distal surface convex, commonly strongly so; proximal surface ± planar. Laesurae distinct or indistinct, length usually exceeding two-thirds of spore radius; simple or with low, generally inconspicuous lips extending 2-5 μm on either side of suturae. Apiculate/tuberculate

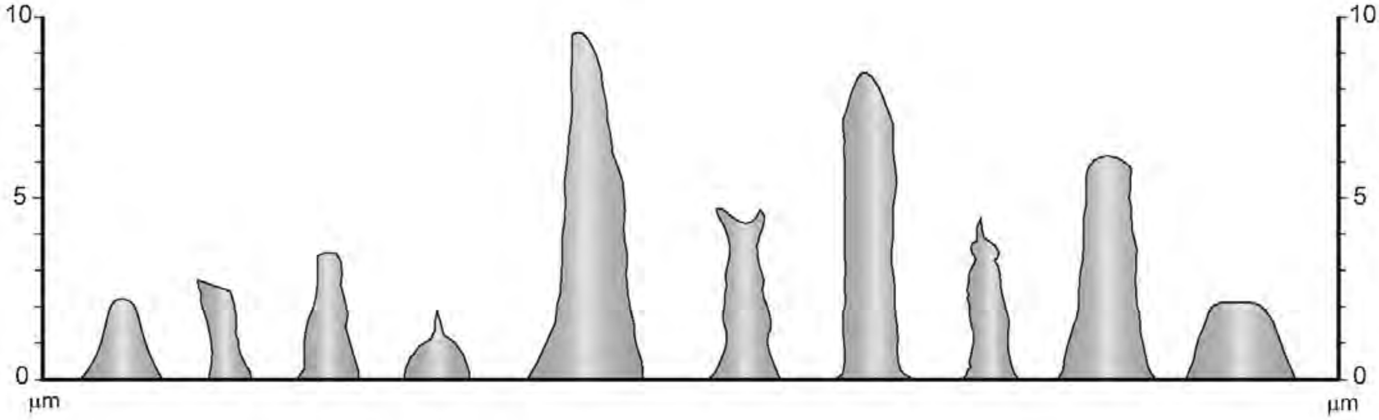

Figure 3. Sculptural elements of *Neoraistrickia loganensis* (Winslow, 1962) emend. Coleman & Clayton, 1987; lateral views.

sculptural elements robust and highly variable in form and distribution on distal surface and equatorially, consisting of bacula, simple or torulose spinae and coni, and verrucae in varying proportions; distal termini of elements commonly rounded or truncate, with or (more commonly) without diminutive spinae (hence some elements galeate/biform) or showing inconspicuous bifurcation. Sculptural elements normally discrete and irregularly distributed (sparse to crowded), up to at least 12 µm apart on distal surface and equator, more closely spaced or basally confluent in apical (radial) regions of some specimens; height of elements commonly in range of 2-7 µm, exceptionally up to 20 µm, basal diameter 1-8 µm. Proximal surface laevigate or with minor and sparse sculpture, mostly around amb apices. Unsculptured exine ca. 1-2.5 µm thick; proximal exine usually slightly thinner than distal, apart from uncommon development of polumbra extending ca. one-quarter to one-third of distance to equator.

Dimensions of Amazonas Basin specimens.- Equatorial diameter, sculptural projections excluded, 39 (69) 103 µm; based on 100 specimens.

Specific epithet.- Winslow's (1962) naming of this species was non-patronymic, being derived primarily from one of its hosting lithostratigraphic units (i.e., Logan Formation of Ohio, U.S.A.). Hence, in compliance with Article 60 of the International Code of Botanical Nomenclature (McNeill *et al.*, 2006), the epithet *loganensis*, cited above, is a necessary orthographic correction of the original *logani(i)*.

Remarks and comparision.- The present cohort of specimens signifies a broader size range for *Neoraistrickia loganensis*, and exhibits a greater diversity in terms of size and form of sculptural elements, than has previously been reported on the basis of lesser numbers of specimens. The very appreciable morphological variation of the sculptural elements (Figure 3), both among specimens and on individual specimens, clearly renders generic assignment within the infraturma Apiculati somewhat equivocal. As Coleman & Clayton (1987, p. 84) contended, the original attribution to *Granulatisporites* Ibrahim, 1933 emend. R. Potonié & Kremp, 1954 is clearly untenable, and their choice of *Neoraistrickia* as generic repository is followed here. Specimens bearing very closely spaced or fused sculptural projections in the equatorial-subequatorial radial regions approach a *Mooreisporites*-like appearance

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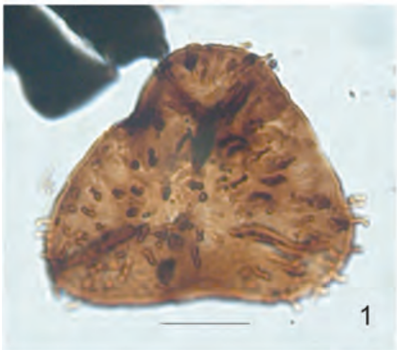
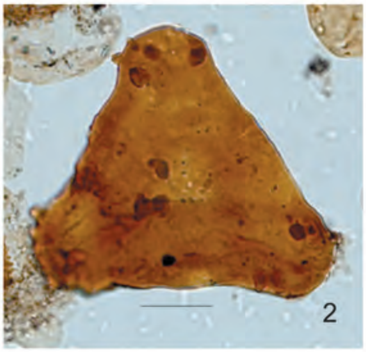
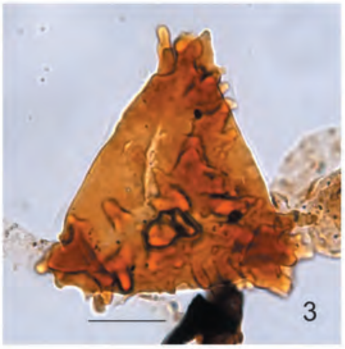
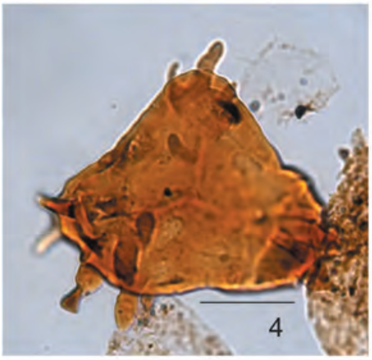
Plate 1. Optical photomicrographs of *Neoraistrickia loganensis* (Winslow, 1962) emend. Coleman & Clayton, 1987, from Tournaisian strata of the Oriximiná Formation, Amazonas Basin. Scale bars represent 20 µm. *1*, median focus, slide 9705932, EF (England Finder coordinates) B49/3; well 2-LF-1-AM, core 51 (1/2), 2253.20 m. *2*, median focus, slide 13.594-2, EF Y46; well 1-CM-2-PA, core 13 (7/7), 274.95 m. *3*, median-proximal focus, slide 9305306, EF S37/1; well 1-CM-1-PA, core 2 (3/5), 242-243 m. *4*, median-distal focus, slide 9305311, EF V46; well 1-CM-1-PA, core 3 (3/4), 247-248 m. *5*, median focus, slide 9705938, EF O38/3; well 2-LF-1-AM, core 52 (1/3), 2255.50 m. *6*, proximal focus, slide 96.0569, EF W56; well 1-RX-3-AM, core 28 (2/2), 2223.42 m. *7*, median focus, slide 9705935, EF Z45/1; well 2-LF-1-AM, core 51 (2/2), 2254.24 m. *8*, distal focus, slide 9305311, EF S43; well 1-CM-1-PA, core 3 (3/4), 247-248 m. *9*, proximal focus, slide 9305311, EF W28/1; well 1-CM-1-PA, core 3 (3/4), 247-248 m. *10*, median focus, slide 9305311, EF N46/1; well 1-CM-1-PA, core 3 (3/4), 247-248 m. *11*, proximal focus, slide 20070520, EF H54/3; well 2-LF-1-AM, core 35 (1/1), 2197.82 m. *12*, distal focus, slide 9705938, EF F39/1; well 2-LF-1-AM, core 52 (1/3), 2255.50 m.

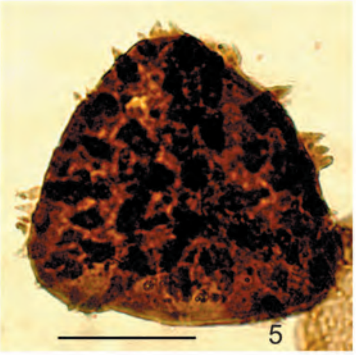
Plate 1

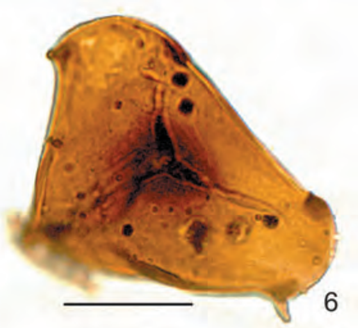


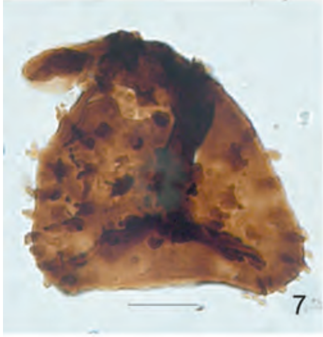


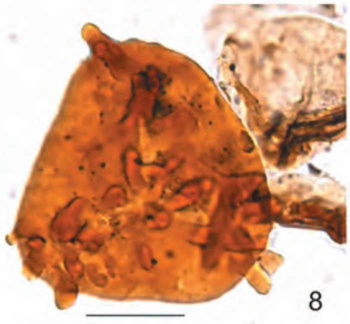


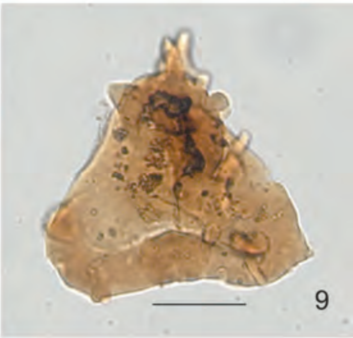


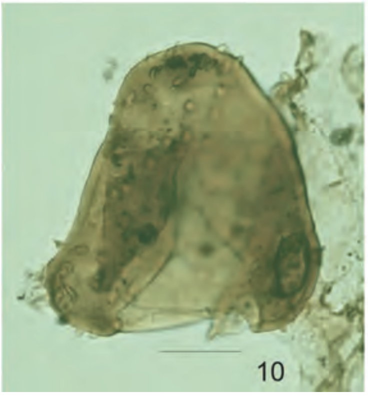


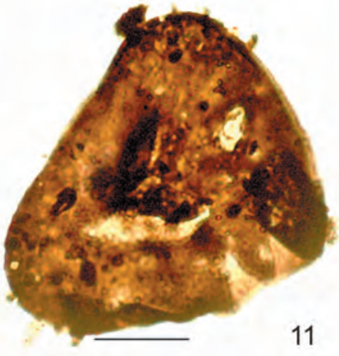


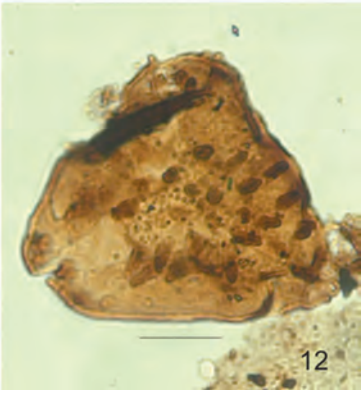












(e.g., Atta-Peters & Anan-Yorke, 2003, Text-fig. 2, 7; Melo & Loboziak, 2003, pl. V, 9; and Plate 1, Figs. 3, 9 and Pl. 2, Fig. 9 herein). However, the sculptural projections, where basally confluent, do not tend to form a distinct bar- or pad-like structure about the amb apices, as was specified in the diagnosis of *Mooreisporites* (see Neves, 1958, p. 7). Sculptural elements of less well preserved specimens are commonly incomplete, their apical portions in particular having been lost or otherwise modified through abrasion (e.g., Plate 1, Figs. 9, 11; Plate 2, Figs. 7-9).

In the absence of a description and clearer illustration, a specimen labelled *Neoraistrickia loganii* from the Mississippian (allegedly lower Visean) of Bolivia (di Pasquo, 2007, Pl. 4, Fig. U) cannot currently be endorsed as a bona fide representative of the species.

Waltzispora lanzonii Daemon, 1974 (p. 561; Pl. VII, Figs. 2, 3) – an associate of *Neoraistrickia loganensis* in the Tournaisian BL and PD Interval Zones of the Amazonas Basin's Oriximiná Formation – is distinguishable from the latter species mainly on account of its shoulder-like amb apices and its much less prominent exinal sculpture (Playford & Melo, in press).

4. STRATIGRAPHIC AND PALAEOGEOGRAPHIC SIGNIFICANCE

The discussion that follows is a survey of presently known occurrences of *Neoraistrickia loganensis* (including its synonyms listed above), in both stratigraphic and palaeogeographic contexts, based on current data from the Amazonas Basin and from globally elsewhere.

4.1. Stratigraphic distribution

Following its initial description from Lower Mississippian – i.e., Kinderhookian through lower Osagean – strata of Ohio, U.S.A. (Winslow, 1962; subsequently recorded there by Clayton *et al.*, 1998), *Neoraistrickia loganensis* has been reported from within that stratigraphic interval elsewhere in eastern U.S.A.; viz., Michigan (Richardson, 2006), Pennsylvania (Warg & Traverse, 1973), Indiana (Richardson & Ausich, 2004), and Kentucky (Coleman & Clayton, 1987; Richardson & Ausich, 2004). Farther north, in eastern Canada, Utting *et al.* (1989) noted its presence in the lower Horton Bluff Formation (mid Tournaisian) of Nova Scotia.

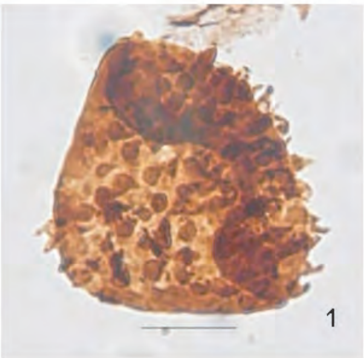
In the Tournaisian succession of Ireland, *Neoraistrickia loganensis* is a component of the upper middle to lower upper Tournaisian PC Miospore Zone (Higgs *et al.*, 1988). However the species is as yet unreported from either the United Kingdom or from continental Western Europe (e.g., Clayton *et al.*, 1977).

Published African occurrences of *Neoraistrickia loganensis* are relatively numerous. North African (Central Sahara Platform) records include those of: (i) Lanzoni & Magloire (1969) and Coquel & Abdesselam-Rouighi (2000) from Sub-zone M3 and equivalent strata of Algerian Sahara (Grand Erg Occidental), dated as mid to early late Tournaisian by Loboziak, Melo & Streel (2000, Fig. 3); (ii) Coquel & Moreau-Benoit (1986) from the basal M'rar Formation, specifically Palynozone XII, of the Ghadamis Basin (western Libya), dated as mid Tournaisian by Loboziak, Melo & Streel (2000, Fig. 3); (iii) Belhaj (2000, p. 134) from an unspecified level or interval within the M'rar Formation (the latter purportedly spanning the Tournaisian through upper Serpukhovian interval); and (iv) Abdesselam-Rouighi & Coquel (1997) from Palynozone III of Algerian Sahara (Illizi Basin), dated as mid Tournaisian by Loboziak, Melo & Streel (2000, Fig. 3). From coastal Ghana, Atta-Peters & Anan-Yorke (2003) observed the species in what they regarded as the lower Tournaisian portion of the Takoradi Shale Formation.

In an investigation of Upper Devonian-Mississippian palynofloras of the Border Folds region of southeastern Turkey, Higgs *et al.* (2002) listed the presence of *Neo-*

Plate 2. Optical photomicrographs (Figs. 1-6) and scanning electron micrographs (Figs. 7-10) of *Neoraistrickia loganensis* (Winslow, 1962) emend. Coleman & Clayton, 1987, from Tournaisian strata of the Oriximiná Formation, Amazonas Basin. Scale bars (Figs. 1-6) represent 20 µm. *1*, distal focus, slide 9305937, EF T57; well 2-LF-1-AM, core 52 (1/3), 2255.33 m. *2*, distal focus, slide 9705939, EF ~C65/4; well 2-LF-1-AM, core 52 (2/3), 2255.83 m. *3*, distal focus, slide 9705937, EF E55/2; well 2-LF-1-AM, core 52 (1/3), 2255.33 m. *4*, equatorial view, slide 9705936, EF J66/1; well 2-LF-1-AM, core 52 (1/3), 2255.00 m. *5*, equatorial view, slide 9705935, EF J50/4; well 2-LF-1-AM, core 51 (2/2), 2254.24 m. 6, equatorial view, slide 96.0565, EF X54; well 1-RX-3-AM, core 26 (1/2), 2212.7 m. *7*, proximal surface, x870; well 1-CM-1-PA, core 3 (3/4), 247.4 m. *8*, equatorial aspect, x600; well 1-CM-2-PA, core 12 (2/5), 265.47 m. *9*, proximal-equatorial aspect, x900; well 1-CM-1-PA, core 3 (3/4), 247.4 m. *10*, distal surface, x750; well 1-CM-2-PA, core 12 (2/5), 265.47 m.

Plate 2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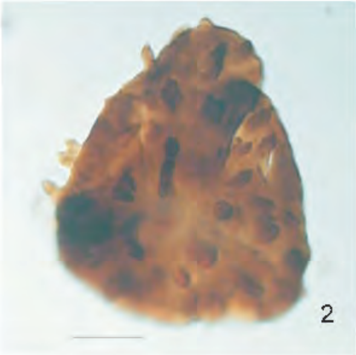
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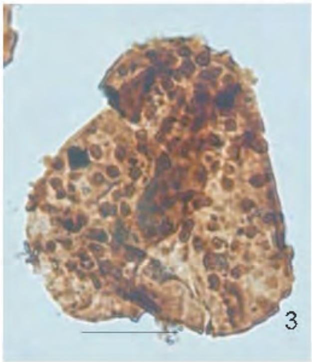
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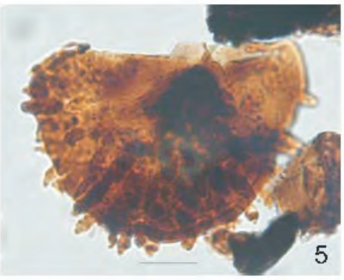
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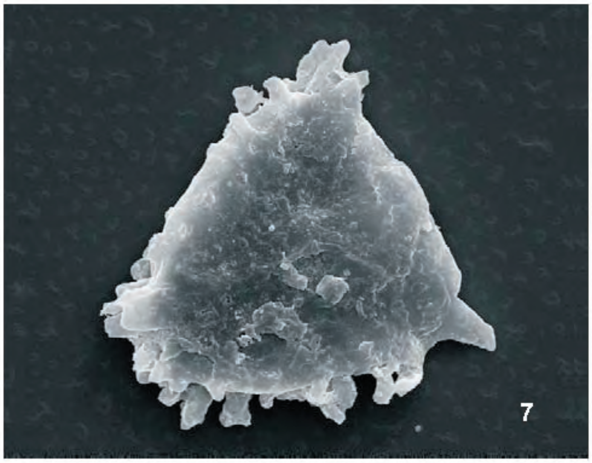
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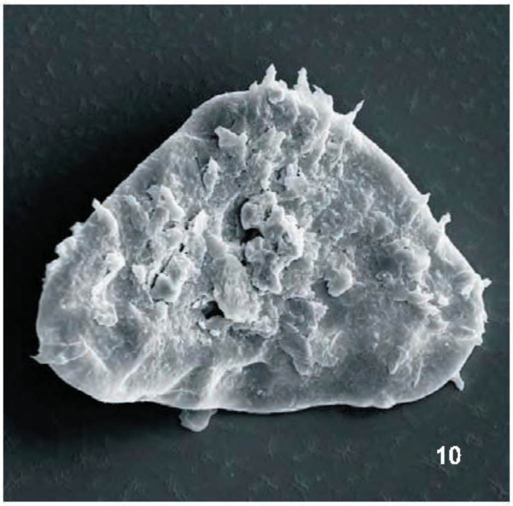
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raistrickia loganensis in an assemblage from the middle, shaly part (Unit 2) of the Köprülü Formation. Their correlation of this assemblage with the Western European PC Miospore Zone accords with the Tournaisian dating of an abundant ostracode and brachiopod fauna hosted by the Köprülü shales (Janvier *et al.*, 1984).

Known occurrences of *Neoraistrickia loganensis* in the southern hemisphere are confined to South America, principally – and perhaps exclusively so far as authentic or demonstrably in situ occurrences are concerned – to the northern Brazilian basins of Solimões, Amazonas, and Parnaíba. In an unpublished 1994 Petrobras report, Loboziak and coauthors (cited by Melo & Loboziak, 2003, pp. 191, 200, as Loboziak *et al.*, 1994b) illustrated bona fide, albeit highly carbonized specimens of *N. loganensis* from the Tournaisian part of the Jandiatuba Formation, Solimões Basin (Juruá Sub-basin). In the Amazonas Basin, the species is represented within the major (post-Devonian; i.e., Tournaisian) section of the Oriximiná Formation (Melo & Loboziak, 2003; present study) and, according to Daemon (1974), it occurs also in the Faro Formation [excepting its younger (late Visean) portion]. Parnaíba Basin occurrences are allegedly in the Poti Formation (Daemon, 1974) or most likely the Longá Formation (Loboziak, Caputo & Melo, 2000; Melo & Loboziak, 2003, footnote to p. 191). The species is a key component of the miospore biozonation of the Amazonas Basin (Melo & Loboziak, 2003, pp. 155, 191-192; Figs. 8-11, 14B). Thus, within the Oriximiná Formation, its stratigraphic introduction marks the base of the *Spelaeotriletes balteatus–Neoraistrickia loganensis* [BL] Interval Zone and its exit marks the top of the succeeding *Spelaeotriletes pretiosus–Colatisporites decorus* [PD] Interval Zone. Melo & Loboziak (2003) dated their BL Zone as early middle Tournaisian, correlating it with the BP zone of Western Europe; and their PD zone as late middle to early late Tournaisian, with inferred equivalence to the Western European PC zone. There are no reports of *Neoraistrickia loganensis* thus far from northern South America. For instance, the species was not among the numerous spore taxa identified by Dueñas & Césari (2005, 2006) in Mississippian (Tournaisian-?Visean) assemblages of Colombia's Llanos Orientales Basin; however, it is possible or even likely that their sampled succession postdates the species' upper stratigraphic limit.

From the foregoing data, *Neoraistrickia loganensis* can be regarded as a taxon of considerable stratigraphic import, locally, regionally, and to some degree internationally, its temporal range bracketed consistently within the confines of the Early Mississippian; i.e., from early or middle Tournaisian (early Kinderhookian) through early late Tournaisian (early Osagean). In quantitative terms, it should be noted that *Neoraistrickia loganensis* is normally a fairly minor palynofloral constituent. However, its morphological distinctiveness and durability conduce to favour its confident recognition even when it occurs only sparingly.

The species is one of an appreciable number of miospore taxa (as discussed, for instance, by Playford, 1991, 1993; Clayton, 1996; Dino & Playford, 2002; Playford & Melo, in press) that combine well-defined stratigraphic ranges (i.e., first- and/or last-appearance biohorizons) in Mississippian stratal sections with extensive geographic distributions, thus enhancing their long-distance biostratigraphic and palaeogeographic applicability.

4.2. Palaeogeographic distribution

From a palaeogeographic perspective, the known occurrences of *Neoraistrickia loganensis* present a somewhat disjunct distributional pattern within both Euramerica and Gondwana (Figure 4).

Most Euramerican occurrences of the species are located in a cluster of eastern states of the U.S.A., west of the Appalachian Mountains. It has been recorded from Nova Scotia (Canadian Maritimes) and also Ireland, but not from elsewhere in Western Europe, nor from other regions, such as Svalbard, European Russia (Russian Platform), and northwestern North America, whence Sullivan (1967) characterized his Lower Mississippian "*Lophozonotriletes* Suite".

Neoraistrickia loganensis is known from several regions of Northern and Western Gondwana, but has not been identified in Eastern Gondwana. Its North African (Northern Gondwanan) occurrences are on or about the Central Sahara Platform; and the report from southeastern Turkey is from the Border Folds region of the Arabian Platform, situated on the northernmost fringe of Gondwana (Janvier *et al.*, 1984).

Figure 4. Occurrences (star symbols) of *Neoraistrickia loganensis* (Winslow, 1962) emend. Coleman & Clayton, 1987 located on Mississippian (Early Carboniferous) palaeogeographic map adapted from Torsvik & Cocks (2004, Fig. 8). Gondwana prescribed by bold dot-dashed line. Key to numbered locations (generalized) and respective sources of data: 1, eastern U.S.A. (Ohio and neighbouring states: Winslow, 1962; Warg & Traverse, 1973; Coleman & Clayton, 1987; Clayton *et al.*, 1998; Richardson & Ausich, 2004; Richardson, 2006); 2, Nova Scotia, eastern Canada (Utting *et al.*, 1989); 3, Ireland (Higgs *et al.*, 1988); 4, Grand Erg Occidental, Algerian Sahara (Lanzoni & Magloire, 1969; Coquel & Abdesselam-Rouighi, 2000); 5, Ghadamis Basin, western Libya (Coquel & Moreau-Benoit, 1986; Belhaj, 2000); 6, Illizi Basin, Algerian Sahara (Abdesselam-Rouighi & Coquel, 1997); 7, Ghana (Atta-Peters & Anan-Yorke, 2003); 8, southeastern Turkey (Higgs *et al.*, 2002); 9, Solimões Basin, northern Brazil (Loboziak and coauthors, 1994 unpublished report, vide Melo & Loboziak, 2003, pp. 191, 200); 10, Amazonas Basin, northern Brazil (Daemon, 1974; Melo & Loboziak, 2003; present study); 11, Parnaíba Basin, northern Brazil (Daemon, 1974; Loboziak, Caputo & Melo, 2000; Melo & Loboziak, 2003).

In Western Gondwana, published records of *Neoraistrickia loganensis* are from the northern Brazilian basins of Solimões, Amazonas, and Parnaíba, and from the palaeogeographically near-contiguous coastal region of Ghana, West Africa.

5. CONCLUSIONS

Neoraistrickia loganensis is a readily recognizable, albeit morphologically varied species of acavate, trilete spores characterized by an appreciable diversity of apiculate sculptural projections. Its confinement to a discrete part of the Mississippian – i.e., to the early or middle Tournaisian (early Kinderhookian) through early late Tournaisian (early Osagean) – underpins its importance as a biostratigraphic index in various regions of Euramerica and Northern and Western Gondwana.

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Upper Albian-lower Turonian non-schackoinid planktic foraminifera with elongate chambers: morphology reevaluation, taxonomy and evolutionary classification

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Resumen

La reevaluación taxonómica de los foraminíferos planctónicos no schackinioidos con cámaras alargadas del Albiense superior-Cenomaniense inferior, evidencia la existencia de cuatro linajes: *Clavihedbergella* Banner & Blow, 1959 (parte media del Albiense superior- Cenomaniense basal), *Claviticinella* Banner, 1982 (Albiense superior), *Pseudoclavihedbergella*-nov. (Albiense terminal-Turoniense inferior) and *Pessagnoina*-nov. (Cenomaniense superior-Turoniense basal). De esta forma se demuestra que el desarrollo de las cámaras alargadas radialmente fue un proceso repetitivo, coherente con el patrón evolutivo general de los foraminíferos planctónicos del Cretácico. En una clasificación evolutiva, a los cuatro linajes se les ha conferido un significado taxonómico en un nivel jerárquico inmediatamente superior al de especie.

Palabras clave: Foraminíferos planctónicos, Cretácico, Albiense superior-Turoniense inferior, clasificación evolutiva, nuevos linajes.

Abstract

Taxonomic reevaluation of the upper Albian-lower Cenomanian non-schackoinid planktic foraminifera with elongate chambers reveals four lineages: *Clavihedbergella* Banner & Blow, 1959 (upper middle Albian-lowermost Cenomanian), *Claviticinella* Banner, 1982 (upper Albian), *Pseudoclavihedbergella*-new (uppermost Albian-lower Turonian) and *Pessagnoina*-new (upper Cenomanian-lowermost Turonian). This demonstrates that the development of radially elongate chambers was an iterative process, consistent with the general evolutionary pattern in the Cretaceous planktic foraminifera. The four lineages are conferred taxonomic significance in an evolutionary classification at the hierarchical level immediately superior to that of species.

Key words: Planktic foraminifera, Cretaceous, upper Albian-lower Turonian, evolutionary classification, new lineages.

1. INTRODUCTION

Planktic foraminifera with radially elongate chambers are well-known in the Cretaceous (upper Albian-Santonian) sediments mostly in the western Tethys and Atlantic Ocean. Present-day classification of these tests at the genus level is based on the gross test architecture features, such as coiling mode (e.g., planispiral, trochospiral and trochospiral when juvenile and planispiral in the adult stage), morphology of the distal end of the elongate chambers (e.g., pointed or with bulbous projection), presence/absence of peripheral structures (e.g., simple periphery or with imperforate band) and main aperture position (e.g., extraumbilical-umbilical, extraumbilical-peripheral and equatorial) (Loeblich and Tappan, 1987). Other features, such as the number of chambers in the last whorl and rate of chamber increase in size, were considered significant at the species level. In contrast, the taxonomic significance of the high detailed morphological features, such as test ornamentation, test porosity, nature of the periapertural structures, etc. were only recently taken into consideration (Georgescu & Huber, 2008).

Morphologically, the upper Albian-Santonian tests with radially elongate chambers are very diverse and for this reason they were included in five genera: *Clavihedbergella* Banner & Blow, 1959 (Aptian-Coniacian), *Schackoina* Thalmann, 1932 (Albian-Maastrichtian), *Claviticinella* Banner, 1982 (upper Albian), *Eohastigerinella* Morozova, 1957 (Coniacian-Santonian) and *Hastigerinoides* Brönnimann, 1952 (Coniacian-Santonian). Stratigraphical ranges are those given by Loeblich & Tappan (1987). These genera are included in two superfamilies: Planomalinacea Bolli, Loeblich & Tappan, 1957 (*Eohastigerinella*, *Hastigerinoides* and *Schackoina*) and Rotaliporacea Sigal, 1958 (*Clavihedbergella* and *Claviticinella*), which are significant in typological classification and therefore have little likelihood to be included in a natural, evolutionary classification framework. As a result they were completely neglected in the phylogeny proposed by Caron (1983) and were rarely considered afterwards (Banner & Desai, 1988; Hart, 1999; Hart *et al.*, 2002).

A breakthrough in understanding the evolution and development of the radially elongate chambers of Cretaceous planktics happened when Georgescu & Huber (2008) demonstrated that the stellate species *Hastigerinoides alexanderi* (Cushman, 1931) evolved from the planispiral, globular-chambered *Globigerinelloides* Cushman & Ten Dam, 1948 in the Coniacian-Santonian lineage: *G. escheri* (Kaufmann in Heer, 1865)-*H. clavata* (Brönnimann, 1952)-*H. atlanticus* Georgescu & Huber, 2008-*H. alexanderi* (Cushman, 1931). This showed that the chamber shape, one of the most important features in typological classification, can highly variable along a lineage. This automatically raised the question of the origins of the other taxa with radially elongate chambers, as a major parameter in achieving a natural, evolutionary classification of this diverse, informal group.

The solution to this problem resides in the high resolution, Scanning Electron Microscope-based morphological study in correlation with biostratigraphic distribution. Two such studies carried out on the Upper Cretaceous (upper Turonian and lower Campanian) globular-chambered trochospiral tests of the Subfamily Hedbergellinae Loeblich & Tappan, 1961 (Georgescu 2008a, 2008b) showed not only the high potential of the method but also demonstrated unequivocally that the morphological diversity of the group is greater than previously thought. SEM-based studies revealed new structures, such as cancellate test wall, fully developed imperforate peripheral band, etc. in representatives of a group believed to retain primitive features throughout its evolution.

The diversity in morphology, test size and biostratigraphic distribution indicates that the radially elongate chambers might have separately evolved from different ancestral taxa during the upper Albian-Santonian stratigraphic interval. Several informal groups can be easily recognized by even using the stereomicroscope. A major separation that can be made is between the schackoinid (small-sized, dominantly planispiral in the adult stage) and non-schackoinid (large-sized, dominantly trochospiral) (Fig. 1). The schackoinid taxa, which are formalized as the genus *Schackoina* Thalmann, 1932, first occur in upper Albian sediments and the last are known from below the Cretaceous/Tertiary boundary. Non-schackoinid planktics with radially elongate chamber do not have continuous occurrences in the upper Albian-Santonian. Three intervals with such tests are now recognized: upper Albian-lower Turonian, upper Turonian and Coniacian-Santonian, which are separated by two intervals without such tests, namely middle Turonian and lower Coniacian.

The taxonomic revision of the upper Albian-Santonian tests with radially elongate chambers is subdivided into three parts, as follows: (1) non-schackoinid taxa of the upper Albian-lower Turonian, (2) non-schackoinid taxa of the upper Turonian-Santonian and (3) schackoinid taxa of the upper Albian-Santonian. In addition, a fourth and final part will present the schackoinid taxa of the Campanian-Maastrichtian. This article presents the first part in this succession, namely the non-schackoinid taxa of the upper Albian-lower Turonian. The high resolution morphological study of the tests with radially elongate chambers revealed the existence of four lineages, namely *Clavihedbergella* Banner & Blow, 1959 – emended, *Claviticinella* – Banner, 1982, *Pseudoclavihedbergella* – new and *Pessagnoina* – new. This demonstrates that the

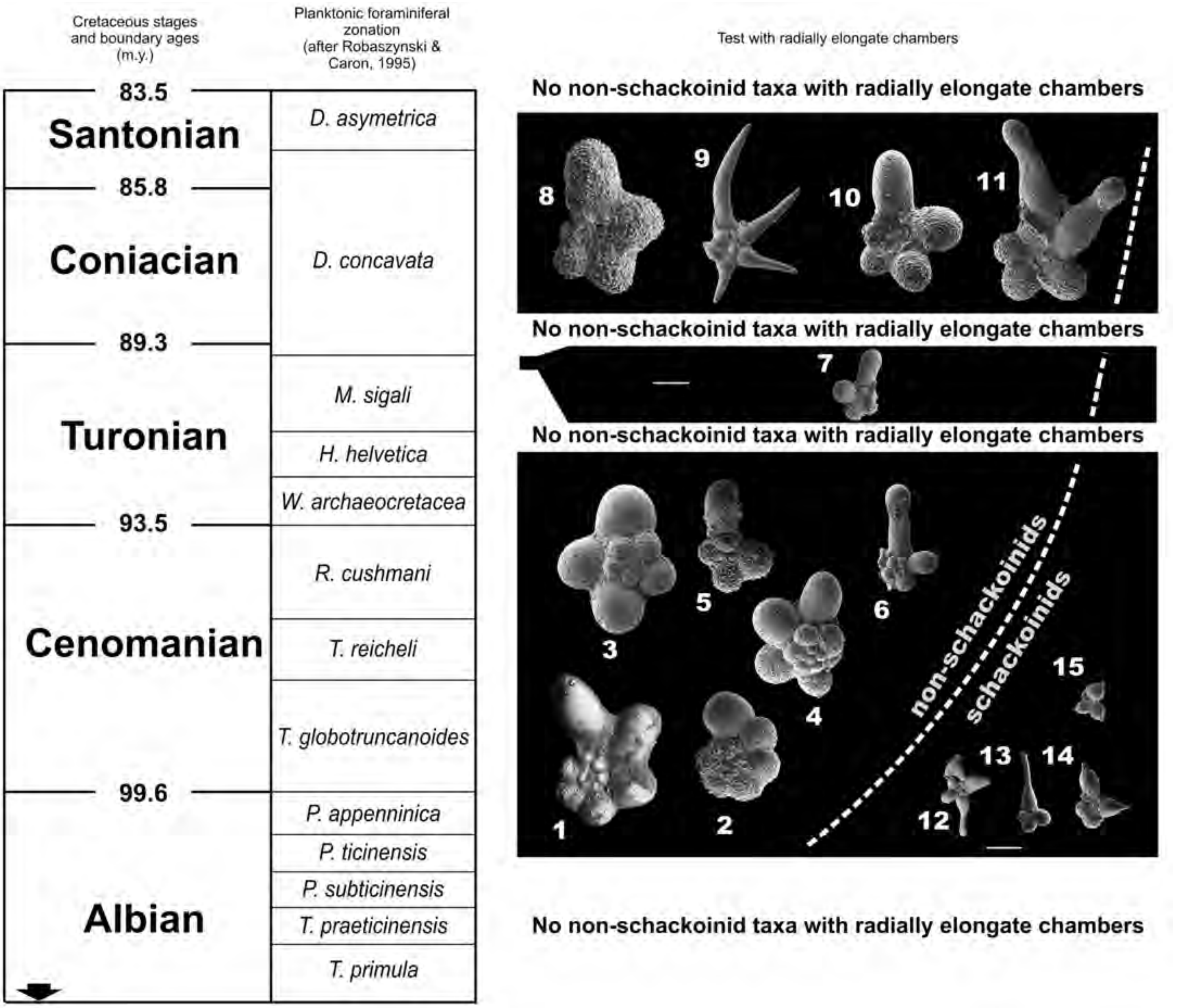


Figure 1. Schackoinid and non-schackoinid taxa with elongate chambers of the upper Albian-Santonian stratigraphical interval. Ages after Gradstein *et al.* (2004). Planktic foraminiferal zonation after Robaszynski & Caron (1995). 1-*Clavihedbergella subcretacea*, 2-*Claviticinella digitalis*, 3-*Pseudoclavihedbergella simplicissima*, 4-*P. amabilis*, 5-*Pessagnoina simplex*, 6-*P. moremani*, 7-*Hillsella* n. sp., 8-*Hastigerinoides clavata*, 9- *H. alexanderi*, 10-*Eohastigerinella subdigitata*, 11-*E. watersi*, 12-"*Schackoina*" sp. 1, 13-"*S.*" sp. 2, 14-"*S.*" sp. 3, 15-"*S.*" sp. 4. Scale bars for both schackoinid and non-schackoinid taxa represent 50 μm. Note that there is a gradual decrease in schackoinid diversity throughout the upper Albian-Santonian interval.

development of an evolutionary classification of the taxa with radially elongate chambers is possible and also desirable, as it results in the definition of natural units, based on ancestor-descendant relationships. It also shows that grouping species according to one or few features morphological resemblances, which describes with accuracy the present-day classification, results in the undesired definition of polyphyletic genera.

2. HISTORY OF CONCEPTS

First non-schackoinid species with radially elongate chambers from the upper Albian-lower Turonian were described from the Cenomanian sediments of Texas and Kansas (USA) and assigned to the genus *Hastigerinella* Cushman, 1927. Cushman (1931) described *H. moremani* from the Cenomanian sediments (Eagleford) of Texas and

H. alexanderi and *H. watersi* from the Austin Chalk (Santonian) of Texas. The use of chamber elongation as major taxonomic criterion in discriminating between species of *Hastigerinella* was generally accepted and a new species, namely *H. simplex*, was described by Morrow (1934) from the upper Cenomanian Greenhorn Formation (Hartland Shale Member) of Kansas. The oldest such species, *H. subcretacea,* was formally described by Tappan (1943) from the upper Albian Duck Creek Formation of Oklahoma (USA).

Brönnimann (1952) made the first attempt to clarify the taxonomy of the Cretaceous non-schackoinid tests with radially elongate chambers by grouping those with distally pointed chambers into a distinct genus: *Hastigerinoides*. Originally *Hastigerinoides* included species of upper Albian and Santonian age, namely *H. rohri* Brönnimann, 1952 and *H. alexanderi*; reexamination of the holotype showed that *H. rohri* belongs to the schackoinid group. A second genus was proposed by Morozova (1957), *Eohastigerinella*, to accommodate the Santonian species with bulbous distal projections on the last formed chambers of the final whorl. *Eohastigerinella* was considered monospecific, including only the type species, *E. watersi* (Cushman, 1931). A contrasting trend was initiated by Bolli *et al.* (1957) who considered *H. alexanderi* and *E. watersi* synonyms, therefore giving no taxonomical significance to the elongate chamber with either termination (pointed or bulbous projection).

Described initially as subgenus of *Praeglobotruncana* Bermúdez, 1952, *Clavihedbergella* Banner & Blow, 1959 consists of species with trochospiral coil and radially elongated last chambers and included: *C. subcretacea* (Tappan, 1940), *C. simplex* (Morrow, 1934) and *C. simplicissima* (Magné & Sigal, 1954), the first being designated the type species. *Hedbergella moremani* was assigned *Clavihedbergella* by Loeblich & Tappan (1961) and subsequently accepted by Pessagno (1967), Eicher & Worstell (1970) and Masters (1977). Loeblich & Tappan (1987) reviewed *Clavihedbergella* and included within it all the trochospiral species with clavate chambers of the Aptian-Coniacian interval. This point of view was contradicted by Banner & Desai (1988) who separated the species with pointed and clavate chambers of the Aptian as a distinct genus, *Lilliputianella* Banner & Desai, 1988, noting that there is an stratigraphic interval comprising most of the Albian stage, which is devoid of tests with radially elongate chambers. The separation between *Lilliputianella* and *Clavihedbergella* was subsequently accepted by Bou Dagher-Fadel *et al.* (1997). Banner & Desai (1988) specifically focused on Aptian tests with radially elongate chambers and were the first to consider test ultrastructure and porosity major taxonomical features.

The only genus with radially elongate chambers and accessory apertures on the umbilical side, *Claviticinella*, was described by Banner (1982). It was validated by Loeblich & Tappan (1987) but not widely accepted due to the status of the type species, *C. digitalis* (Sigal, 1966), which was often considered a junior synonym of *Ticinella raynaudi* Sigal, 1966. This study shows that both *Claviticinella* and its type species, *C. digitalis*, are valid.

3. MATERIAL AND METHODS

Tests with radially elongate chambers are difficult to study due to their relative scarceness in the stratigraphic record and restricted distribution. Additional difficulties are generated by the lack of knowledge on the test ultrastructure, ornamentation and porosity, with the exception to the *Hastigerinoides* lineage (Georgescu & Huber, 2008). For these reasons both collection and new material must be taken in consideration for the taxonomic revision of the group (Table 1).

In this regard, the holotypes and paratypes of four species were studied: *Clavihedbergella subcretacea*, *Pseudoclavihedbergella amabilis* (Loeblich & Tappan, 1961), *Pessagnoina simplex* and *P. moremani* (Cushman, 1931). All are deposited in the Cushman Collection at the National Museum of Natural History (NMNH), Washington, D.C. (USA). In addition, Dr A. Ando (University of Seoul) provided the ESEM micrographs of *Hedbergella trocoidea* (Gandolfi) subsp. *yezoana* Takayanagi & Iwamoto, 1962 from the Yezo Group of Japan and updated the information on the age of the type locality.

Significant numbers of specimens used in this study, came from the Loeblich and Tappan Topotype Collection from the NMNH, Washington, D.C. They were collected in

1. Primary types (holotypes and paratypes)

Clavihedbergella subcretacea (Tappan, 1943)	Holotype	USNM 64891	upper Albian, Duck Creek Fm., Love Co., Oklahoma, USA
Clavihedbergella subcretacea (Tappan, 1943)	Paratypes	USNM 370416	upper Albian, Duck Creek Fm., Love Co., Oklahoma, USA
Pseudoclavihedbergella amabilis(Loeblich & Tappan, 1961)	Holotype	USNM 479620	upper Cenomanian, Britton Clay, Dallas Co., Texas, USA
Pseudoclavihedbergella amabilis(Loeblich & Tappan, 1961)	Paratypes	USNM 479621 - USNM 479624	upper Cenomanian, Britton Clay, Dallas Co., Texas, USA
Pessagnoina simplex(Morrow, 1934)	Holotype	USNM 75376	upper Cenomanian, Greenhorn Fm., Hartland Shale Member, Hodgeman Co., Texas, USA
Psessagnoina moremani (Cushman, 1931)	Holotype	USNM 15746	upper Cenomanian, Texas, USA
Psessagnoina moremani (Cushman, 1931)	Paratypes	USNM 15747, USNM 15753	upper Cenomanian, Texas, USA

2. Secondary types (Loeblich and Tappan Topotype Collection)

Clavihedbergella yezoana(Takayanagi & Iwamoto, 1962)	Hypotypes	USNM 473266	Cenomanian, Blake Plateau, Western North Atlantic Ocean
Pseudoclavihedbergella simplicissima(Magné & Sigal, 1954)	Hypotypes	USNM 473237	upper Cenomanian, Greenhorn Fm., Hartland Shale Member, Hodgeman Co., Texas, USA
Pseudoclavihedbergella amabilis(Loeblich & Tappan, 1961)	Topotypes	USNM 472307	upper Cenomanian, Britton Clay, Dallas Co., Texas, USA
Psessagnoina moremani (Cushman, 1931)	Topotypes	USNM 472306	Cenomanian, Britton Clay, Midlothian, Ellis Co., Texas, USA

3. Secondary types (Alexander Collection, USNM, Washington, D.C.)

Psessagnoina moremani (Cushman, 1931)	Topotypes	not labeled	Cenomanian, Britton Clay, Midlothian, Ellis Co., Texas, USA; station 24102

4. Secondary types (Van Morkhoven Collection, USNM, Washington, D.C.)

Claviticinella digitalis(Sigal, 1966)	Hypotypes	Not labeled	upper Albian, Tunisia, northern Africa

5. Secondary types (Mc Gugan Collection, University of Calgary, AB, Canada)

Psessagnoina simplex(Morrow, 1934)	Hypotypes	WKB010045, WKB010046	lowermost Turonian, San Juan Island, Washington State, USA
Psessagnoina moremani (Cushman, 1931)	Hypotypes	WKB010047	lowermost Turonian, San Juan Island, Washington State, USA

Table 1. Synthetic presentation of the collection material used in this study.

Cenomanian sediments of Texas, USA, by Helen Tappan and Alfred R. Loeblich Jr. from the Britton Clay (Eagleford Group) and Hartland Shale Member (Greenhorn Formation). The specimens were identified by Loeblich and Tappan according to the shape of the radially elongate chambers. Those with bulbous projection were assigned to *Clavihedbergella moremani* and those without bulbous projection at the distal edge of the last formed chambers to *Hastigerinoides simplex*. Detailed study of these very well-preserved specimens, many of them illustrated herein, showed that they can be assigned to three species, namely *Pseudoclavihedbergella simplicissima*, *P. amabilis* and *Pessagnoina moremani*. The excellent state of preservation made these specimens suitable for high resolution observations on test ornamentation and ultrastructure. The Loeblich and Tappan Topotype Collection also yielded excellently preserved specimens of *C. yezoana* (Takayanagi & Iwamoto, 1962) from the Lamont Doherty Geological Observatory, namely Core 8167-25, drilled on the escarpment of the Blake Plateau, western North Atlantic Ocean (geographical coordinates: 28º 52′ N, 76º 47′ N; depth: 140-157 m). They were originally labeled as *Hedbergella trocoidea* (Gandolfi, 1942).

A couple of specimens of *P. moremani*, one photographed with the aid of the SEM and illustrated herein (Pl. 11, fig. 2), were found in an unlabeled slide in the Cushman Collection (NMNH). The two specimens were probably part of the original material offered to J. A. Cushman by C. I. Alexander (Texas Christian University, Fort Worth) and published by the former in his 1931 article on the Upper Cretaceous tests with radially elongate chambers of Texas. Although no specific assignment is mentioned on the slide, the precise provenance of the specimens is given with, as far as it could be ascertained, Cushman's handwriting.

Van Morkhoven Collection (NMNH) yielded some well-preserved specimens of *Claviticinella digitalis* (Sigal, 1966), six of them photographed with the SEM. The precise location of provenance for these specimens is not known. The slides are labeled only: "Upper Albian, Tunisia".

Well-preserved material was studied in the McGugan Collection at the University of Calgary, Alberta (Canada). This material was collected by Dr A. McGugan (University of Calgary) from upper Cenomanian-lowermost Turonian sediments of San Juan Island (Washington State, USA) during a field trip in 1973. The material is deposited in the Willi Karl Braun Micropaleontology Collection of the Museum of Natural History of the University of Calgary (Canada). Most of the specimens are in an excellent state of preservation and they belong to two species: *Pessagnoina simplex* and *P. moremani*.

Additional material was analyzed from lower-middle Cenomanian sediments of the Romanian Western Black Sea offshore. Only *Pseudoclavihedbergella amabilis* was reported from these sediments (Georgescu, 2000) and they are re-assigned to *P. simplicissima*. They are rare specimens and relatively poorly preserved.

New well-preserved material was studied from the upper Albian-Cenomanian sediments of the Ocean Drilling Program Leg 171B, Site 1050C situated in the Blake Plateau, western North Atlantic Ocean (geographical coordinates: 30º 05′ N, 76º 14′ W). Six species with significance for this study are recorded at this location, namely *Clavihedbergella yezoana*, *C. subcretacea*, *Claviticinella madecassiana*, *C. digitalis*, *Pseudoclavihedbergella simplicissima* and *Hedbergella delrioensis* (Carsey, 1926) (Table 2). Most of the specimens are in an excellent state of preservation, thus allowing excellent observations on the test ultrastructure, ornamentation and porosity.

4. TERMINOLOGY AND NEW MORPHOLOGICAL STRUCTURES

The systematic and detailed study of the upper Albian-Santonian foraminifera with radially elongated chambers revealed the complexity of the test architecture. It also shows that the features, which represent the primary dataset in taxonomy, should be studied separately for each lineage, in order to recognize the different evolution patterns followed. As a result, the descriptive terminology applied to this group needs refinement to accommodate the new observations. Three test features are presented in detail in this section: chamber shape, elongation mode and peripheral structures. They proved of paramount importance in recognizing four lineages in the upper Albian-lower Turonian foraminifera.

(1) Chamber shape significantly varied in the lineages that developed radially elongate chambers. This was demonstrated in the case of the *Hastigerinoides* lineage of the Coniacian-Santonian, where the globular-petaloid-clavate-strongly elongate, resembling tubulospines sequence of chamber elongation development was recognized (Georgescu & Huber, 2008). In addition to globular and subglobular types, six types of radially elongate chambers are herein recognized in the upper Albian-Santonian planktic foraminifera (Fig. 2): subcylindrical (e.g., *Clavihedbergella subcretacea*), petaloid (e.g., *Pseudoclavihedbergella amabilis*), with distal bulbous projection (e.g., *Pessagnoina moremani*), clavate [e.g., *Eohastigerinella*

subdigitata (Carman, 1929)], subtriangular (e.g., some species of *Schackoina*) and pointed, resembling tubulospines (e.g., *Hastigerinoides alexanderi*). Only the first three types are known in the non-schackoinids of the upper Albian-lower Turonian.

(2) Elongation mode refers to the angle made by the elongation axis of the elongate chambers and the previous whorl. Three kinds of elongation mode are recognized (Fig. 3). *Tangential elongation* (Fig. 3: A) is known only from the evolved species of the *Clavihedbergella* lineage and is characterized by a shift in the elongation axis (EA), with the first elongate chamber perpendicular or at a high angle (> 75°) to the previous whorl and in the subsequent ones the elongation axis is tangential or at a low angle (< 15°) with the previous whorl. When the elongation axis does not intersect the previous whorl, as in the evolved species of the *Claviticinella* lineage, it is referred to as *exterior* (Fig. 3: B). The elongation axis is perpendicular or at a high angle (> 75°) to the previous whorl in the case of *Pseudoclavihedbergella* and *Pessagnoina* species; this elongation mode is referred to as *perpendicular* (Fig. 3: C).

(3) The presence of an imperforate peripheral band was not included in the original description of *Clavihedbergella* (Banner & Blow, 1959, p. 18), who noted that the test wall is "… generally hispid, uniformly perforate, lacking imperforate peripheral bands, carinae or costellae". Masters (1977, p. 440) was the first to identify an imperforate peripheral band on the globular chambers of the final whorl in *Clavihedbergella* and this emendation was accepted by Loeblich and Tappan (1987, 466). Current observations on the test periphery are based on well-preserved tests, which show that a true imperforate peripheral band is not developed in any of the studied species. A new structure is described instead, namely the *peripheral band of low pore density and smaller pore size* (Fig. 4: A and B). Notewor-

Samples (core-section, interval in centimeters)	STAGES	Planktonic foraminiferal zonation	*Clavihedbergella yezoana*	*C. subcretacea*	*Claviticinella madecassiana*	*C. digitalis*	*Pseudoclavihedbergella simplicissima*	*Hedbergella delrioensis*
25-3 60-64	**lower Cenomanian**	***T. globotruncanoides***						C
25-3 142-146							R	F
25-4 16-20								F
26-1 7-9								C
26-1 53-56								R
26-1 139-141								
26-2 24-26							R	R
26-2 56-59								R
26-2 114-116								
26-2 115-117							R	C
26-3 33-36								C
26-3 73-76							R	F
26-3 120-122								R
26-4 34-37			R					R
26-4 83-86								C
26-4 140-142								C
26-5 28-30			R					R
26-5 83-86			R					C
26-CC, 9-10	**upper Albian**	***P. appenninica***					R	C
27-1 5-6			R					A
27-1 19-21			F		R		R	F
27-1 75-76			R		R		R	A
27-1 125-127			R		C			F
27-2 25-26			R		R		R	F
27-2 85-88			R		C			A
27-2 125-126							R	C
27-3 5-6			F		C		R	R
27-3 30-32			C		C		R	F
27-3 79-84			R		F		R	A
27-3 139-141			R		R			A
27-4 34-36			C		R			C
27-4 80-83			R		F			
27-4 134-136					C			R
27-5 32-34					F			C
27-5 90-94			R		R			F
27-5 123-125					R	R		F
27-6 29-31			R					C
27-6 74-78			R		C	R		F
27-7 20-22								C
27-CC			R		R	R		C
28-1 20-21			C		R	R		C
28-1 70-73			R					F
28-3 60-63		***P. ticinensis***	F		R			R
28-4 146-150			C		F	R		R
28-5 52-53			R					C
28-6 66-69			R	R		R		R
29-1 57-60			R		R	R		R
29-2 133-135								R
29-3 83-86								C
29-4 80-83			R		C			C
29-5 72-75					R			R
29-6 21-24			C		F			C
29-6 62-65			F	R	C			F
30-1 102-105			R		C			F
30-2 72-75			R		R			C
30-1 92-97					R			R
30-3 72-75					R			R
30-4 76-81			F	R	C			C
30-5 82-85			C	R	R			F
30-6 80-84					R			C
31-1 81-85			F		C			R
31-1 132-134			R		R			R
31-2 80-84					R			C
31-2 130-134			R		R			C
31-3 80-83			R	R	C			
31-4 22-27			R	R	R			C
31-4 87-90					R			C
31-5 81-84								R
31-6 79-83			R	R				C
31-6 88-91								R
31 CC			C	R				R

Table 2. Non-schackoinid species distribution and frequencies in the upper Albian-lower Cenomanian of the Blake Plateau (western North Atlantic Ocean), ODP Leg 171B, Hole 1050C. Frequency symbols: R-rare (1-5 specimens), C-common (6-10 specimens), F-frequent (11-25 specimens), A-abundant (over 25 specimens). Biostratigraphic zonation after Huber and others (1999), Petrizzo and Huber (2006) and Ando and Huber (2007).

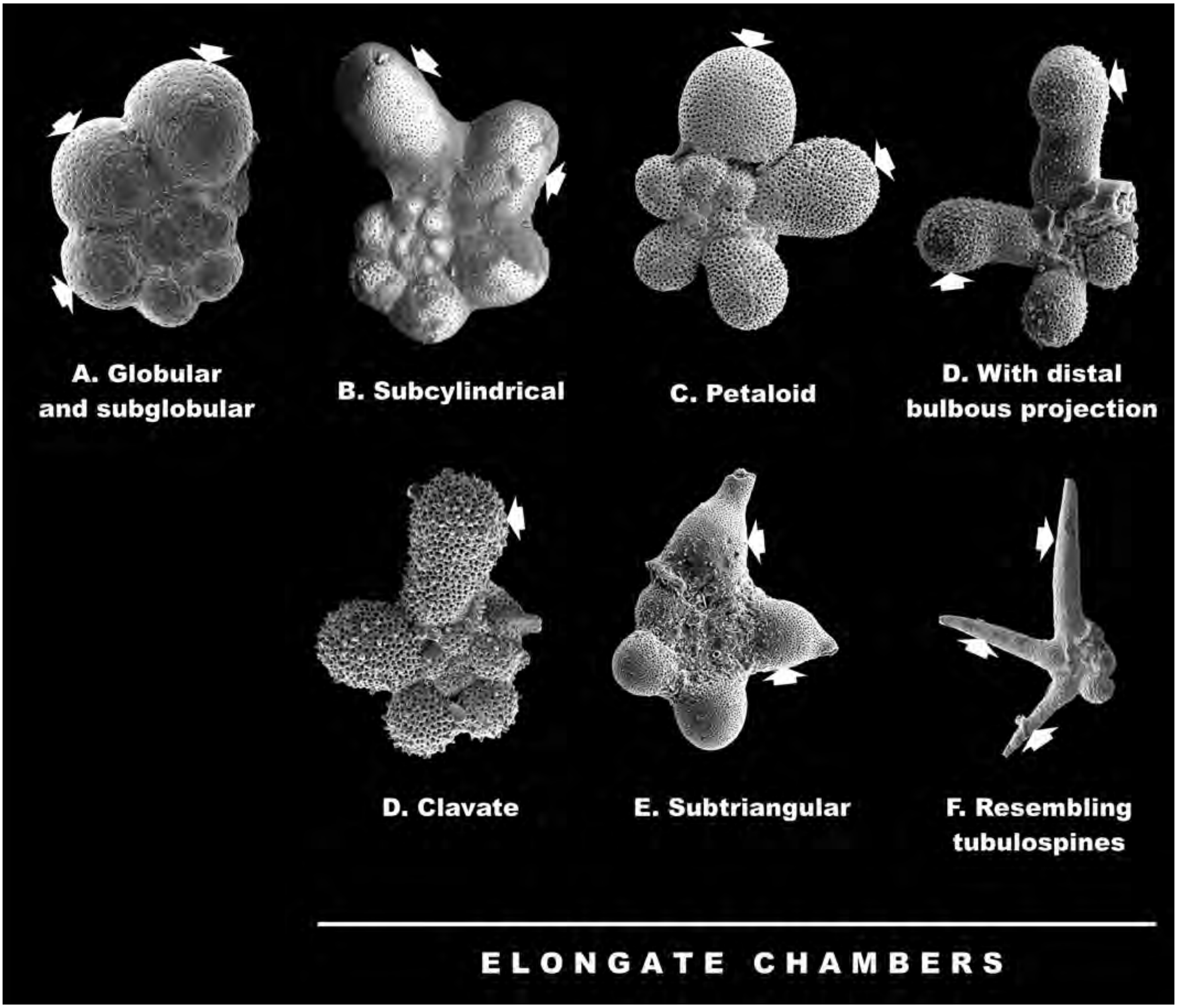


Figure 2. Chamber shape terminology in the upper Albian-Santonian planktic foraminifera. Only types A through D occur in the species analyzed in this study. Arrows point out to the chambers with the nominal shape.

thy, this structure can be smooth as in *Clavihedbergella subcretacea* or may bear scattered pustules as in *Pseudoclavihedbergella*.

5. GENUS OR LINEAGE?

Cretaceous planktic foraminiferal classification developed since the first decades of the XX^th^ century is a typological, Linnean one (Cushman, 1927, 1928; Loeblich & Tappan, 1964, 1984, 1987; Robaszynski & Caron, 1979; Robaszynski *et al.*, 1984; Nederbragt, 1991). According to its principles, species grouping into genera is entirely based on the morphological resemblances in certain, numerically limited, features. This grouping system inevitably results in an artificial classification scheme. For example, grouping all the species with a certain morphological feature rules out *a priori* the possibility of development of that peculiar feature in distinct lineages, as a result of convergent or iterative evolution. The possibility for these typological genera to represent natural units, based on ancestor-descendant relationship, as well as their potential to be included in a classification framework based on the ancestor-descendant relationship, is minimal.

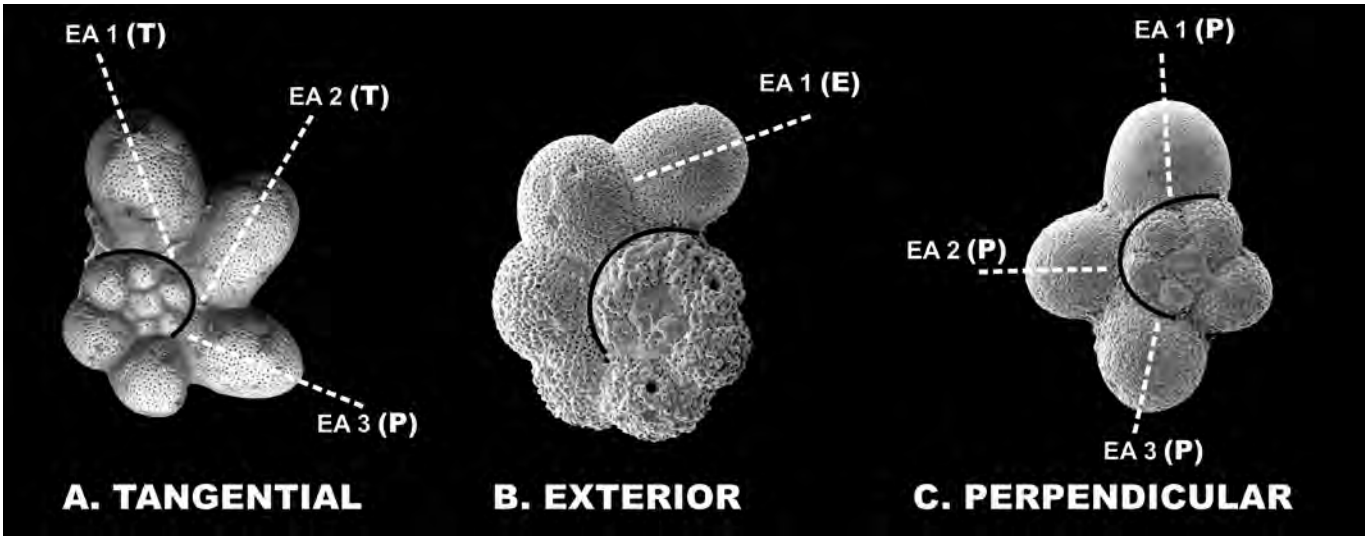


Figure 3. The three types of chamber elongation in the upper Albian-lower Turonian planktic foraminifera. Symbols: EA-chamber (elongation) axis, T-tangential, E-exterior, P-perpendicular. Note that chamber elongation can fluctuate in the case of the tangential type (A).

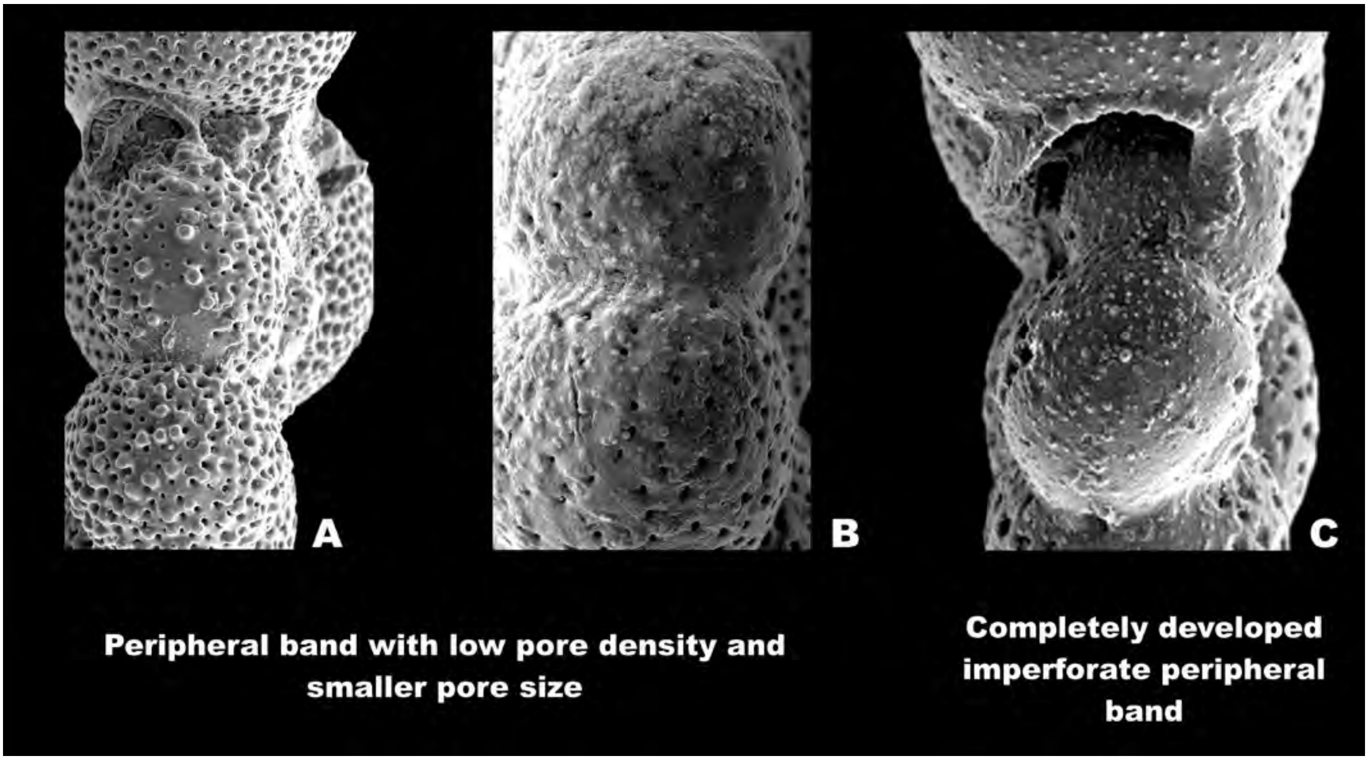


Figure 4. Peripheral structures in the upper Albian-lower Turonian taxa with elongate chambers: A-*Pseudoclavihedbergella amabilis*, B-*Clavihedbergella subcretacea*. Note the differences when compared to a hedbergellid taxon with completely developed imperforate peripheral band (C), namely *Liuella falklandica* Georgescu, 2008.

Species grouping in an evolutionary classification is based on the phylogenetic relationships between them. Phylogenetical relationships are ultimately defined as a combination of differences and resemblances between the ancestral and descendant species. Accordingly, two species can be included in the same supraspecific category if the phylogenetic relationship between them can be demonstrated morphologically and supported by biostratigraphic ranges (Georgescu & Huber, 2007). The changes in a lineage are of paramount importance and the evolutionary process generating them is what gives cohesion to the lineage as immediate supraspecific category. By grouping species into lineages, as opposed to grouping them into a genus, a taxonomist has a flexible system of classification, thereby avoiding a major disadvantage in the typological system, which is a "…rigid system imposed upon a non-rigid set of organisms" (Masters, 1977, p. 303).

A new hierarchical system, which is fundamentally different from the typological one, is used herein for the immediate supraspecific units. Species are included into lineages, which are natural groupings of species based on the phylogenetical relationships between them (Fig. 5). A formal definition of the lineage as a taxonomic unit is necessary. A ***lineage*** is a monophyletic taxonomic unit with significance in evolutionary classification, situated immediately above the species level, representing a grouping of species based on the phylogenetical relationships between them, having a distinct evolutionary history in space and time that can be reconstructed from the fossil and stratigraphic record and is separated by morphological gaps from other similar units. This definition shows clearly that a lineage cannot be equivalent to a genus as defined in the typological classification.

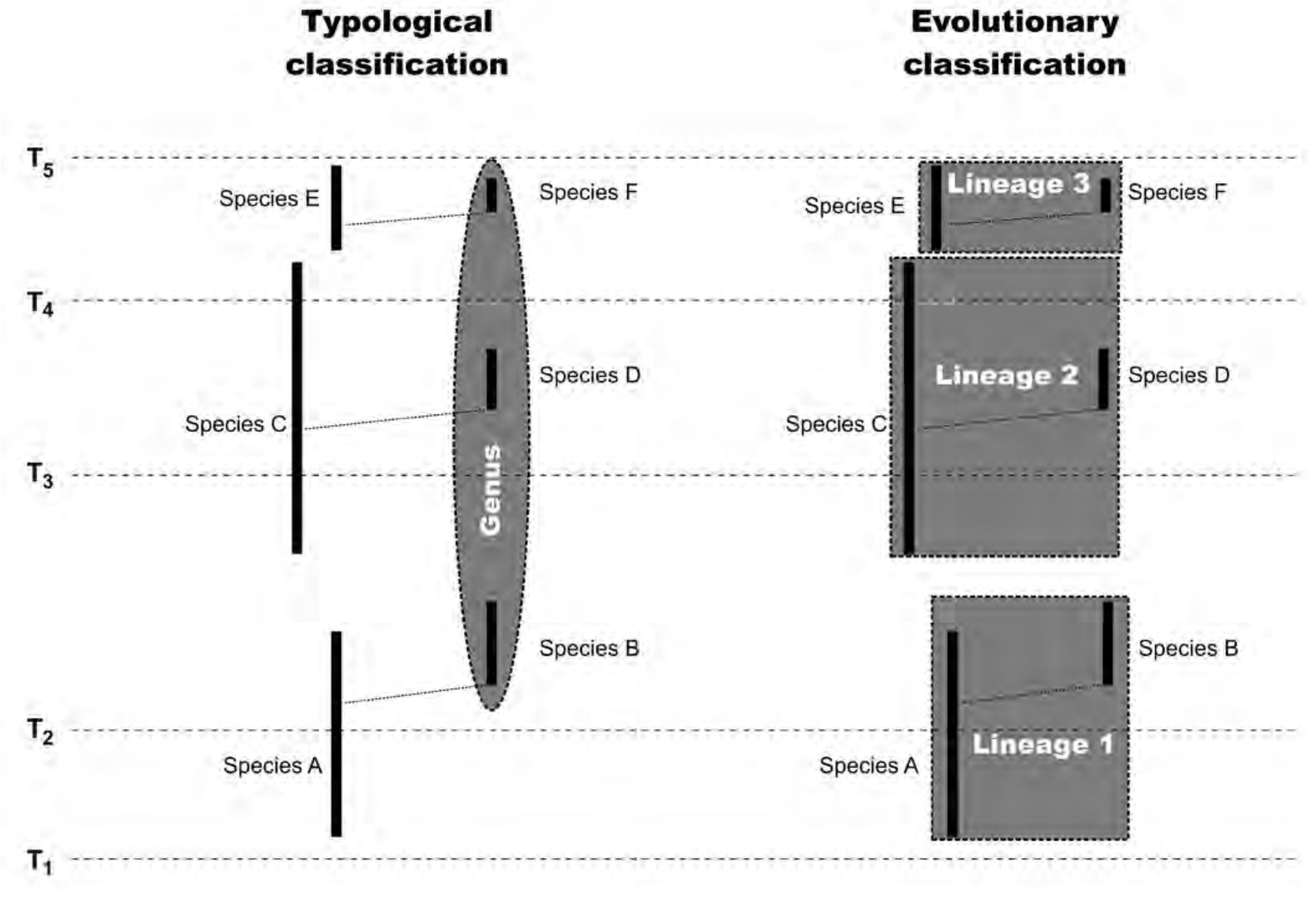


Figure 5. Diagram showing the differences in species grouping between the typological and evolutionary classification. This diagram illustrates a case in which a typological genus is defined for three species (B, D and F) that developed a peculiar feature or set of features through iterative evolution. Species are grouped according to the phylogenetical relationships between them (A with B, C with D, E with F) in evolutionary classification; the resulting three lineages confer taxonomic significance to the features resulted through iterative evolution. We can conclude that lineages are natural units, whereas the genus, as defined in this case, is an artificial unit.

6. SYSTEMATIC CLASSIFICATION

Suprageneric classification is after Loeblich & Tappan (1984, 1987). The classical typological units from the subfamily level and above are still used until a natural hierarchical framework based on the principles of evolutionary classification can be developed. Species are given in phylogenetic and stratigraphic order. Species concept used is that defined by Georgescu and Huber (2007).

Order FORAMINIFERIDA Eichwald, 1830
Suborder GLOBIGERININA Delage & Hérouard, 1896
Superfamily ROTALIPORACEA Sigal, 1958
Family HEDBERGELLIDAE Loeblich & Tappan, 1961
Subfamily HEDBERGELLINAE Loeblich & Tappan, 1961

Lineage *Clavihedbergella* Banner & Blow, 1959 – emended

Type species: *Hastigerinella subcretacea* Tappan, 1943 (original designation).

1959 *Clavihedbergella* Banner & Blow, p. 18.
1964 *Clavihedbergella* Banner & Blow, 1959 – Loeblich & Tappan, p. C659 (in part).
1977 *Clavihedbergella* Banner & Blow, 1959 – Masters, p. 440 (in part).
1987 *Clavihedbergella* Banner & Blow, 1959 – Loeblich & Tappan, p. 466 (in part).

Emended diagnosis.– Test trochospiral with globular chambers in the primitive species; evolved species with subcylindrical, tangentially elongate chambers in the last whorl; periphery occasionally with a band of low pore density and smaller pore size; test surface is generally smooth, rarely with small scattered pustules.

Emended description.– Test very low to low trochospiral, with globular to subglobular chambers in the early stage; last formed chambers subcylindrical, tangentially elongate in the evolved species. Test shape often slightly asymmetrical when seen in edge view. Periphery broadly rounded, occasionally with a band of low pore density and smaller pore size on the earlier chambers of the last whorl. Aperture is a low to medium high arch, umbilical-peripheral in position, bordered by a wide lip. Umbilicus is small to medium-sized, often with relict periapertural structures. Chamber surface is smooth, only occasionally with small pustules over the earlier chambers of the test. Test wall calcitic, hyaline and perforate.

Remarks.– *Clavihedbergella* is emended in the context of an evolutionary classification to accommodate a lineage of hedbergellid planktic foraminifera of the upper middle Albian-lowermost Cenomanian, which exhibits a gradual development of subcylindrical and tangentially elongate last formed chambers and discrete increase in umbilical diameter. This emendation of *Clavihedbergella* appears necessary in order to define a natural unit based on the ancestor-descendant relationship between component species, thereby avoiding groupings of species with various kinds of radially elongate chambers into a typological translineage unit. According to the original definition and subsequent revisions (Banner & Blow, 1959; Masters, 1977; Loeblich & Tappan, 1987), *Clavihedbergella* included only species with radially elongate chambers irrespective of the development of a bulbous projection at the distal end, thereby creating a translineage unit without phylogenetic significance. *Liuella* Georgescu, 2008 of the lower Campanian is the only Cretaceous hedbergellid foraminiferal genus with fully developed peripheral imperforate band (Georgescu, 2008a); *Clavihedbergella*-emended differs from *Liuella* by the subcylindrical and tangentially elongate last formed chambers in the evolved species and the peripheral structure, which consists of a low pore density and smaller pore size band on the earlier chambers of the last whorl rather than an imperforate peripheral band throughout the final whorl. *Clavihedbergella* differs from *Hastigerinoides* mostly by having trochospiral tests and the absence of the strongly elongate and distally tapering chambers in the final whorl.

Species included. – *Hedbergella trocoidea* (Gandolfi) subsp. *yezoana* – Takayanagi & Iwamoto, 1962, p. 191, pl. 29, figs. 1-2; *Hastigerinella subcretacea* – Tappan, 1943, p. 513, pl. 83, fig. 4.

Stratigraphical range.– Upper middle Albian – lowermost Cenomanian (from the upper part of *T. primula* Biozone throughout *T. globotruncanoides* Biozone).

Geographic distribution.– USA (Texas, Oklahoma), Asia (Japan), Europe (Germany, Spain), northern Africa (Libya), Asia (Japan) and western North Atlantic Ocean (Bermuda Rise, Blake Plateau).

Clavihedbergella yezoana **(Takayanagi & Iwamoto, 1962)**

(Pl. 1, Figs 1-3)

1959 *Praeglobotruncana gautierensis* (Brönnimann) – Bolli, p. 265, pl. 21, figs 4, 6.
1961 *Hedbergella trocoidea* (Gandolfi) – Loeblich & Tappan, p. 277, pl. 5, figs 1-2 (lower Cenomanian, Blake Plateau, western North Atlantic Ocean).
1962 *Hedbergella trocoidea* (Gandolfi) subsp. *yezoana* – Takayanagi & Iwamoto, p. 191, pl. 29, figs 1-2 (upper Albian, Yezo Group, Hokkaido, Japan).
1972 *Hedbergella delrioensis* (Carsey) – Barr, p. 13, pl. 2, fig. 1 (lower Cenomanian, Hilal Shale, Cyrenaica Province, Libya, northern Africa).
1973 *Hedbergella* (?) *punctata* Michael, p. 212, pl. 3, figs 1-3, pl. 7, figs 1-2 (upper Albian, Washita Group, Texas, USA).
1980 *Hedbergella yezoana* Takayanagi & Iwamoto – Miles & Orr, p. 799, pl. 4, figs 1-3 (upper Albian, Bermuda Rise, DSDP Holes 417, 417A, 417B, 417D, 418, 418A, 418B, western North Atlantic Ocean).
1984 *Hedbergella delrioensis* (Carsey) – Weidich, p. 81, pl. 3, figs 1-4 (lower Cenomanian, southern Germany).
2006 *Hedbergella* sp. – Petrizzo & Huber, pl. 7, fig. 6 (upper Albian, Blake Plateau, western North Atlantic Ocean).

Material.– Approximately 150 specimens.

Emended description.– Test very low trochospiral, with globular to subglobular, occasionally incipiently subcylindrical chambers arranged in 2 to 2 ½ whorls; 6-7 chambers, commonly 6-6 ½, in the last whorl. Chambers increase slowly to moderately in size and show reduced overlapping. Sutures are distinct, depressed and perpendicular to slightly oblique to the previous whorl. Test shape slightly asymmetrical in edge view; asymmetry can be further accentuated due to the axial elongation of the last formed chambers. Periphery broadly rounded, often simple or, ocassionally, with a band of low pore density and smaller pore size on the earlier one or, rarely, two chambers of the last whorl. Aperture is a low to medium high arch, umbilical-peripheral in position and bordered by a wide lip, which is often broken. Umbilicus small to medium-sized, approximately one third of the maximum test diameter; relict periapertural lips and apertures can occur in the umbilical area. Chamber surface generally smooth; small and rare pustules occasionally developed mostly in the periumbilical and/or periapertural areas. Test wall calcitic, hyaline and perforate; pore size is 1.2-2.8 µm over most of the test surface and 0.5-1.0 µm in the peripheral band region.

Remarks.– *Clavihedbergella yezoana* differs from *Hedbergella implicata* Michael, 1973 by having higher rate of chamber increase in size. The smooth test surface of *C. yezoana* (small pustules are only occasionally present) differentiates this species from *Hedbergella delrioensis* (Carsey, 1926) and *H. planispira* (Tappan, 1940), which are two species with chamber surface heavily ornamented with pustules. Incipient radially elongate chambers were figured by Takayanagi & Iwamoto (1962, pl. 28, figs 1a-b, 2a-b) and their existence is confirmed after the examination of the holotype ESEM micrographs.

Stratigraphical range.– Upper middle Albian to lower Cenomanian (from the upper part of *T. primula* Biozone to *T. globotruncanoides* Biozone).

Geographic distribution.– Asia (Japan), USA (Texas), Europe (Germany), northern Africa (Libya) and western North Atlantic Ocean (Bermuda Rise, Blake Plateau).

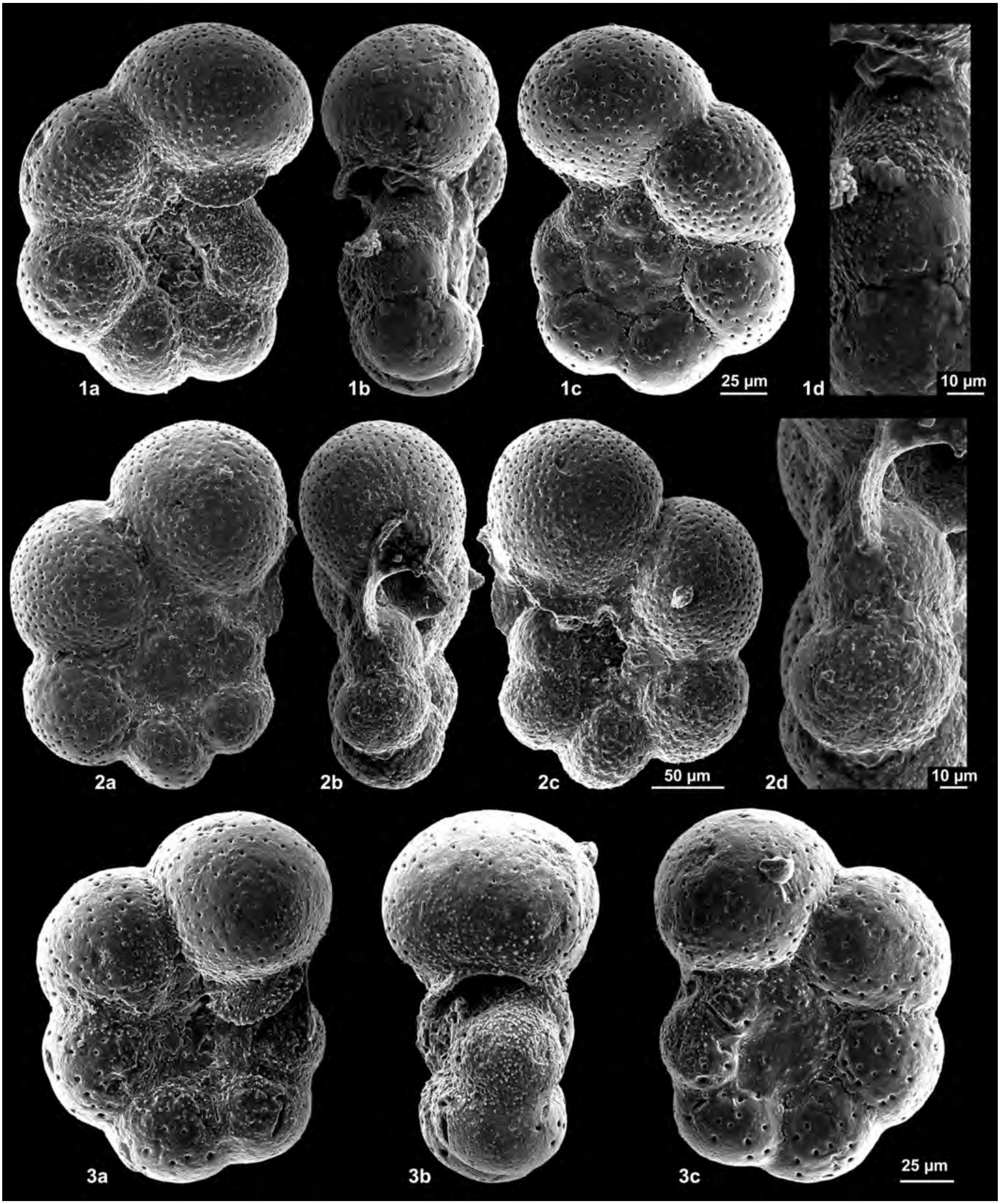
Clavihedbergella subcretacea **(Tappan, 1943) – emended**

(Pl. 2, Figs 1-3, Pl. 3, Figs 1-2)

1943 *Hastigerinella subcretacea* – Tappan, p. 513, pl. 83, fig. 4 (upper Albian, Love County, Oklahoma).
1971 *Clavihedbergella subcretacea* (Tappan) – Caron, fig. 6 (Albian, Subbetic Zone, Spain).
1973 *Clavihedbergella subcretacea* (Tappan) – Michael, p. 212, pl. 3, fig. 9 (lower Cenomanian, Texas, USA).

Plate 1. Three hypotypes of *Clavihedbergella yezoana* (Takayanagi & Iwamoto, 1962) from the upper Albian sediments (*P. ticinensis* Biozone) of the Blake Plateau, western North Atlantic Ocean (Sample 171B-1050C-31-1, 81-85 cm). The detail micrographs 1d and 2d show the peripheral band with lower pore density and smaller pore size.

Plate 1



Material.– Approximately 40 specimens.

Emended description.–Test low trochospiral, consisting of globular chambers in the early stage and the last one to three subcylindrical, tangentially elongate, resulting in a strongly lobate to stellate outline in the last portion of the test. Chambers show little overlapping and are arranged in 2-2 $^1/_2$ whorls; 5 $^1/_2$-7 chambers, commonly 5 $^1/_2$-6, in the final whorl. Chambers of the earlier portion of the test increase slowly in size, the elongate ones increase at higher rates. Sutures are distinct, depressed and perpendicular or slightly oblique to the previous whorl. Tests are slightly asymmetrical in edge view. Periphery broadly rounded and occasionally with a peripheral band of low pore density and smaller pore size on the first one or two chambers of the final whorl. Aperture is a medium to high arch, umbilical-peripheral in position and bordered by a wide lip. Umbilical diameter represents approximately one third to one half of the maximum test diameter; wider umbilici are developed in the tests with higher number of elongate chambers. Chamber surface is smooth. Test wall calcitic, hyaline and perforate; pore diameter over the test surface 1.5-3.2 μm, except for those in the peripheral band, where they are between 0.8-1.5 μm.

Remarks.– *Clavihedbergella subcretacea* differs from its ancestor, *C. yezoana*, by the last formed chambers, which are subcylindrical and tangentially elongate and as a result the larger tests lack the biumbilicate appearance; it also has larger pores, including those from the peripheral band region. It differs from the upper Albian-lower Cenomanian "schackoinids with bulbous chamber projection" by the subcylindrical, tangentially elongate chambers, which lack the distal bulbous projection and the aperture, which is umbilical-peripheral in position rather than peripheral.

Stratigraphical range.– Upper Albian (*P. ticinensis* Biozone).

Geographic distribution.– USA (Oklahoma, Texas), Europe (Spain) and western North Atlantic Ocean (Blake Plateau).

Lineage *Claviticinella* Banner, 1982 – emended

Type species: *Claviticinella digitalis* Banner, 1982 (original designation).

1982 *Claviticinella* Banner, p. 154.

1987 *Claviticinella* Banner, 1982 – Loeblich & Tappan, p. 466.

Emended diagnosis.–Test is low trochospiral; evolved species develop elongate chambers with elongation axis exterior to the previous whorls; supplementary apertures on the umbilical side.

Emended description.– Tests are low trochospiral, with globular chambers in the early stage; evolved species with elongate last formed chambers; elongation axis exterior to the previous whorls. Tests are asymmetrical in edge view. Periphery broadly rounded, occasionally with a band of lower pore density and smaller pore size on the earlier chambers on the final whorl in the primitive species. Aperture is a low to medium high arch, umbilical in position and bordered by an imperforate lip. Chamber surface is smooth. Test wall calcitic, hyaline, simple to reticulate and perforate.

Remarks.– *Claviticinella* differs from *Clavihedbergella*, from which it evolved, by having the elongate chambers in the evolved species with the elongation axis exterior to the previous whorls rather than tangentially elongate, accessory apertures around the umbilicus, lacking the peripheral band with lower pore density and smaller pore size on the earlier chambers on the final whorl in the evolved species and gradual development of a reticulate test wall, which contrasts to the simple test wall of the latter. *Claviticinella* lineage is characterized by the development of accessory apertures on the umbilical side, which tend to migrate towards the suture base, chamber elongation, which is unique among the Cretaceous planktic foraminifera, namely having the elongation axis exterior to the previous whorls and reticulate test wall, which is fully developed only in the evolved species.

Species included.– *Ticinella madecassiana* – Sigal, 1966, p. 197, pl. 3, figs 7-10; *Ticinella raynaudi* var. *digitalis* – Sigal, 1966, p. 202, pl. 6, figs 6-8.

Plate 2. Type specimens of *Clavihedbergella subcretacea* (Tappan, 1943) from the upper Albian Duck Creek Formation of Love County, Oklahoma (USA), deposited at NMNH, Washington, D.C. **1,** Holotype (USNM 64891). **2-3,** Paratypes (USNM 370416). The uncoated specimens were photographed using the Back Scatter Electron Detector.

Plate 2

Stratigraphical range.– Upper Albian (from the upper part of *P. ticinensis* Biozone to the *P. appenninica* Biozone).

Geographic distribution.– Africa (Madagascar, Tunisia), Europe (Spain), Middle East (Israel), North Atlantic Ocean (Blake Plateau, Mazagan Plateau), (?) Mexico.

Claviticinella madecassiana **(Sigal, 1966) – emended**
(Pl. 4, Figs 1-3, Pl. 5, Figs 1-3)

1966 *Ticinella madecassiana* – Sigal, p. 197, pl. 3, figs 7-10 (upper Albian, Madagascar, southern Africa).
1977 (?) *Ticinella albiana* Longoria & Gamper, p. 208, pl. 1, figs 4-6 (upper Albian, Sabinas Basin, northern Mexico).
1977 *Ticinella madecassiana* Sigal – Masters, p. 522 (taxonomic revision, no new material mentioned).
1984 *Ticinella madecassiana* Sigal – Leckie, p. 600, pl. 6, figs 7-12 (upper Albian, Mazagan Plateau, eastern North Atlantic Ocean).
1985 *Ticinella madecassiana* Sigal – Caron, p. 76, figs 36:4-5 (upper Albian, Spain).
2000 *Ticinella madecassiana* Sigal – Lipson-Benitah & Almogi-Labin, p. 12, pl. 1, figs 6-8 (upper Albian, Israel).
2006 *Ticinella madecassiana* Sigal – Petrizzo & Huber, pl. 2, fig. 1 (upper Albian, Blake Plateau, western North Atlantic Ocean).

Material.– Approximately 75 specimens.

Emended description.– Test low trochospiral consisting of globular chambers, overlapping at variable rate and arranged in 2 $^1/_2$ to, rarely, 3 whorls. Five to seven chambers, commonly six, in the final whorl. Test outline lobate in dorsal view. Sutures are distinct and depressed, perpendicular to or slightly oblique to the previous whorl. Test shape is asymmetrical in edge view; the last formed chamber is often dorso-ventrally elongate and tilted towards the umbilical side. Periphery broadly rounded, rare specimens present a band of low pore density on the earliest chamber of the final whorl. Aperture is a low arch, umbilical-peripheral in position and bordered by a lip. Umbilicus is small, approximately one eighth to one sixth of the maximum test diameter. One or two accessory apertures can occur in the umbilical area and they are small and adjacent to the last one or two sutures between the last formed chambers of the test. Tests without accessory apertures are the dominant ones. Test wall calcitic, hyaline and perforate (pore diameter 1.2-2.0 µm); it has a roughened appearance due to the gradual development of a reticulate network of ridges around the pores, which appear to be situated in the centre of depression areas.

Remarks.– *Claviticinella madecassiana* differs from *C. yezoana*, its ancestor, by having higher trochospire, occasionally incipiently reticulate test wall, narrower umbilicus and accessory apertures on the umbilical side. There is a gradual morphological transition between *C. yezoana*, as ancestor and *C. madecassiana*, as descendant. This study shows that, in contrast to what was previously considered, the accessory apertures do not occur in all the specimens assigned to this species. As a result, the initiation of the *Claviticinella* lineage is better documented by the development of the incipiently reticulate test wall and trochospire tightening as inferred from the narrower umbilici and higher trochospire. *Claviticinella madecassiana* differs from *C. subcretacea* mostly in the incipiently reticulate test wall and the absence of elongate chambers in the final part of the last whorl.

Stratigraphical range.– Upper Albian (from the upper part of the *P. ticinensis* Biozone to the *P. appenninica* Biozone).

Geographic distribution.– Africa (Madagascar, Tunisia), Europe (Spain), Middle East (Israel), North Atlantic Ocean (Blake Plateau, Mazagan Plateau), (?) Mexico.

Claviticinella digitalis **(Sigal, 1966) – emended**
(Pl. 6, Figs 1-3)

1966 *Ticinella raynaudi* var. *digitalis* – Sigal, p. 202, pl. 6, figs 6-8 (upper Albian, Madagascar, southern Africa).
1971 *Ticinella raynaudi digitalis* Sigal – Caron, figs 8, 21 (upper Albian, Spain).

Plate 3. Two hypotypes of *Clavihedbergella subcretacea* (Tappan, 1943) from the upper Albian sediments (*P. ticinensis* Biozone) of the Blake Plateau, western North Atlantic Ocean. **1,** Sample 171B-1050C-31, core catcher; **2,** Sample 171B-1050C-31-5, 81-84 cm. The detail micrographs show the smooth chamber surface (1d, 1f) and the peripheral band with lower pore density and smaller pore size (1e, 2d).

Plate 3

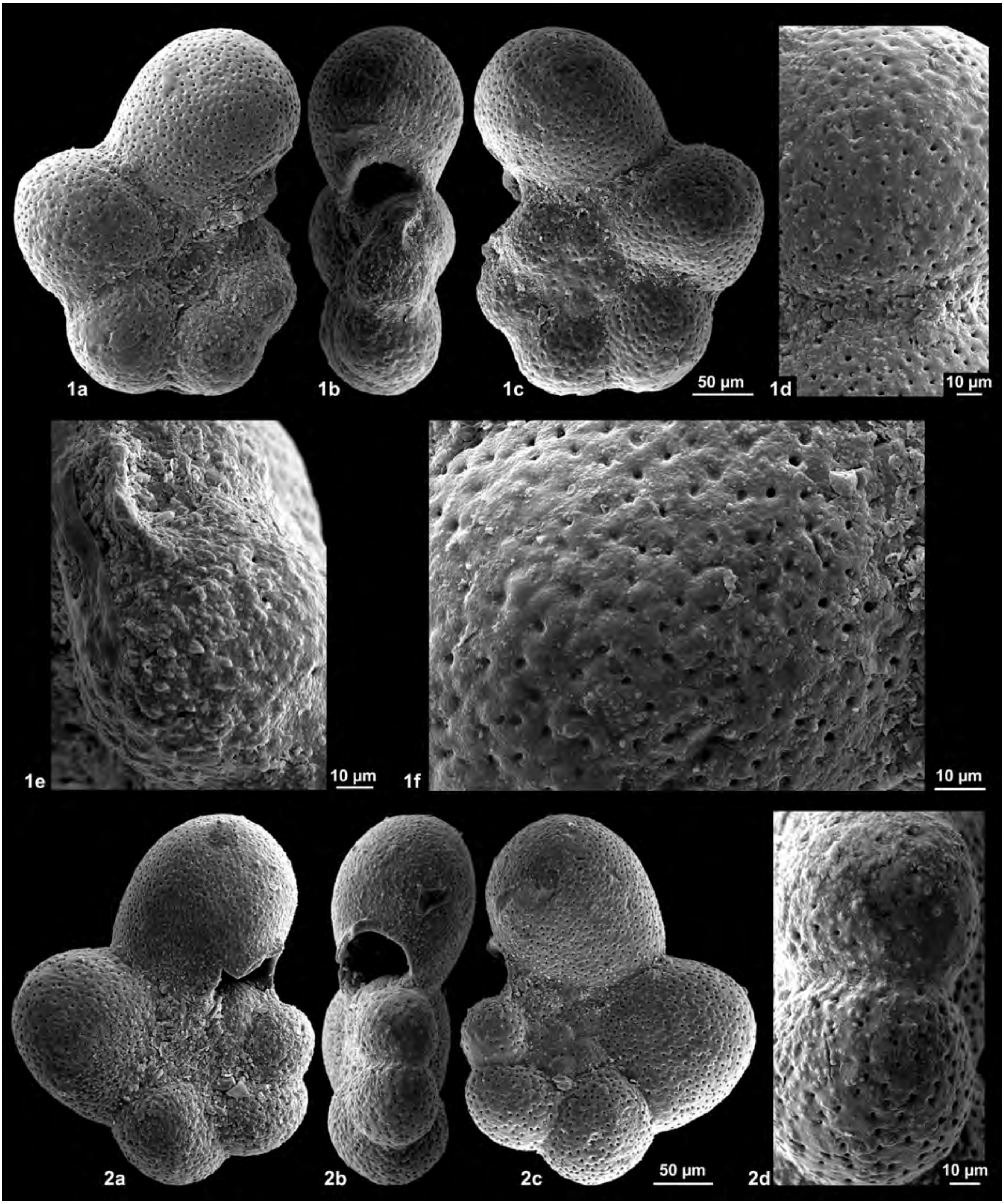


Plate 4

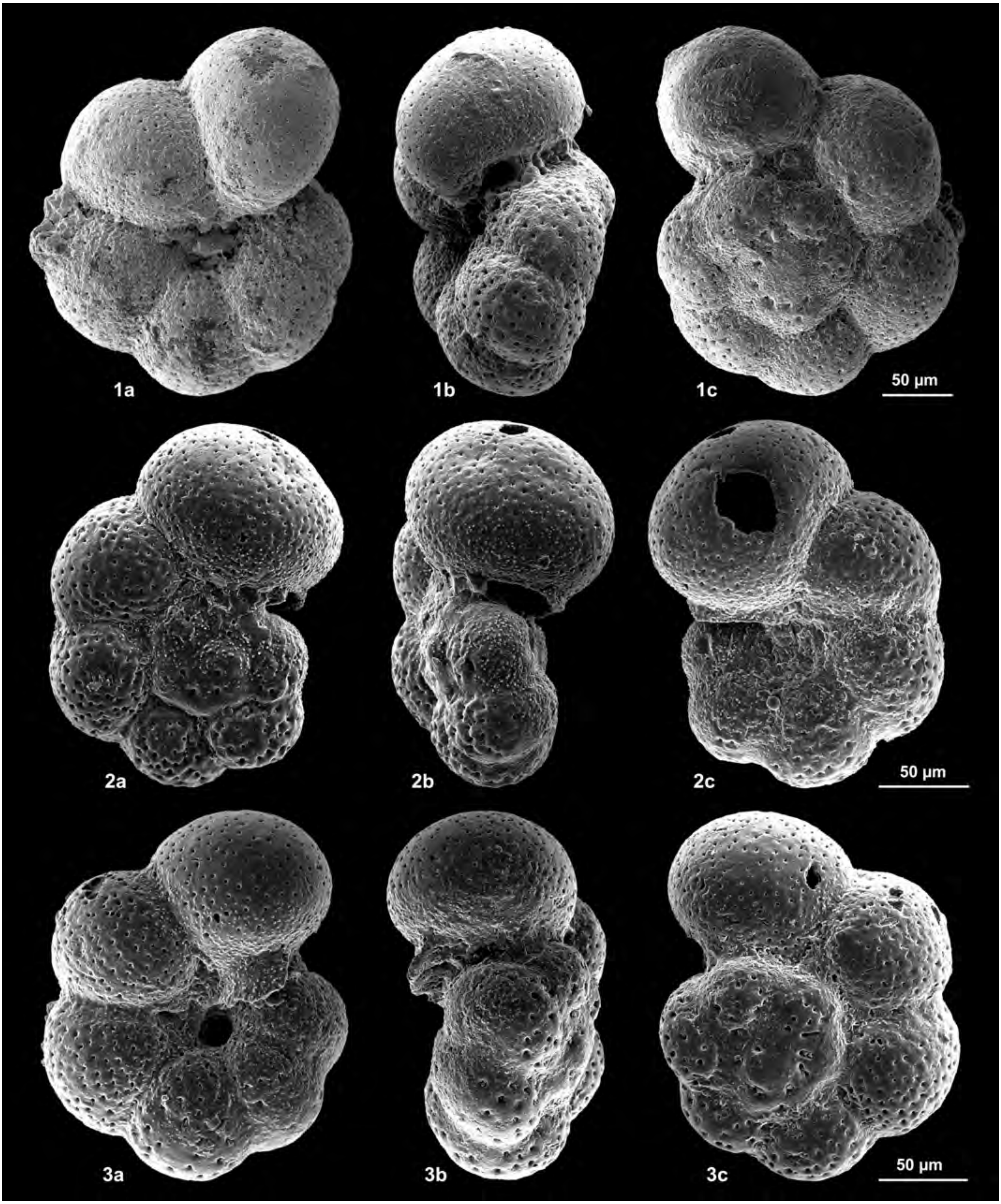


Plate 4. Hypotypes of *Claviticinella madecassiana* (Sigal, 1966) from the upper Albian sediments of the Blake Plateau, western North Atlantic. **1,** Specimen from Loeblich and Tappan Topotype Collection, USNM 473266. **2,** Specimen from the *P. appenninica* Biozone, Sample 171B-1050C-27-2, 85-88 cm. **3,** Specimen from the *P. appenninica* Biozone, Sample 171B-1050C-27-2, 85-88 cm.

Plate 5

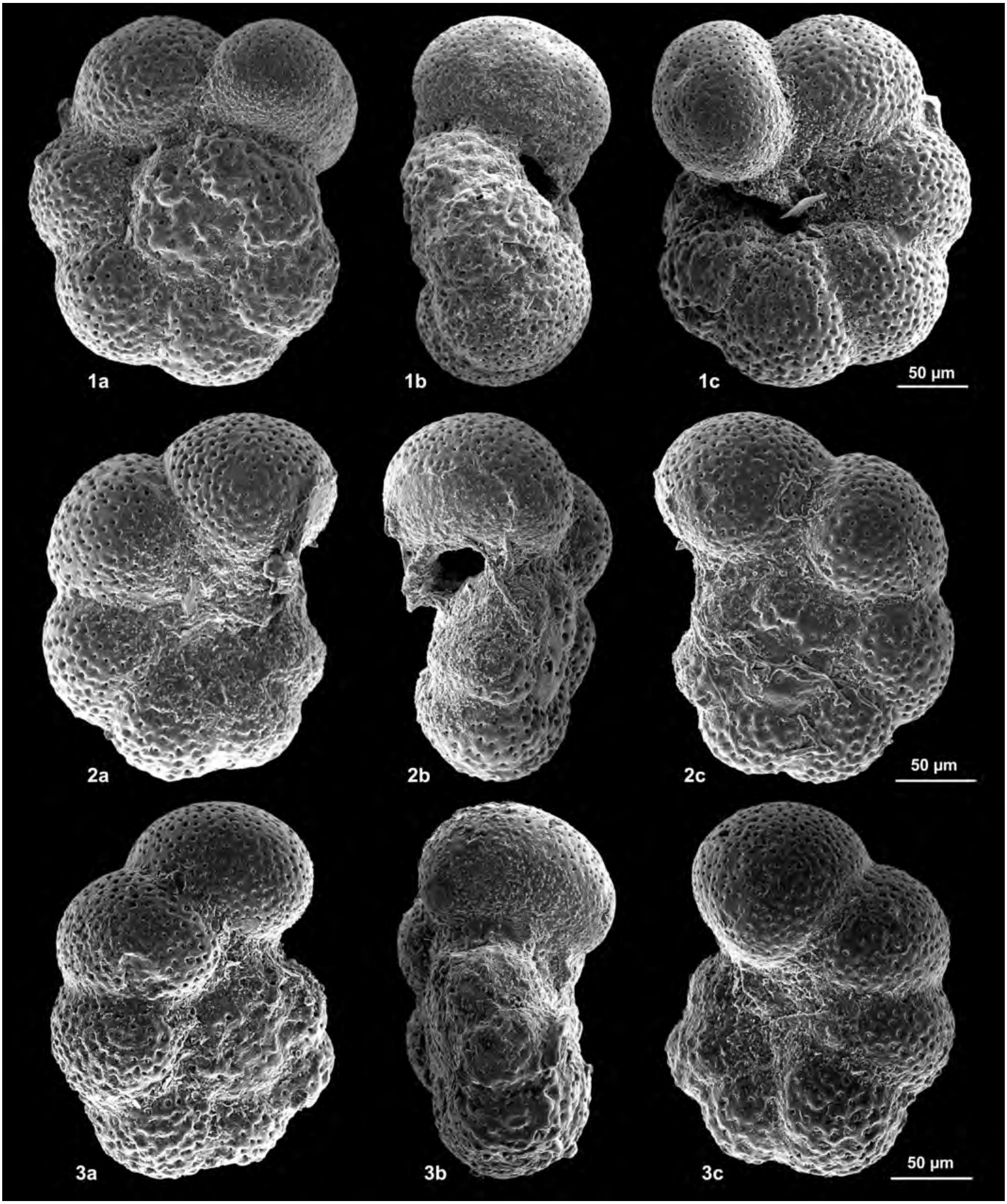


Plate 5. Three hypotypes of *Claviticinella madecassiana* (Sigal, 1966) from the upper Albian sediments of the Blake Plateau, western North Atlantic, ODP Leg 171B, Hole 1050C. **1,** Sample 171B-1050C-27-6, 74-78 cm (*P. appenninica* Biozone). **2,** Sample 171B-1050C-27-5, 32-34 cm (*P. appenninica* Biozone). **3,** Sample 171B-1050C-28-4, 146-150 cm (*P. ticinensis* Biozone).

1977 *Ticinella raynaudi digitalis* Sigal – Pflaumann & Krasheninnikov, p. 549, pl. 5, figs 3-4 (upper Albian-Cenomanian, DSDP Holes 367, 368, 368A and 370, eastern North Atlantic Ocean).
1984 *Ticinella raynaudi* Sigal – Leckie, p. 600, pl. 7, figs 2-3 (upper Albian, Mazagan Plateau, eastern North Atlantic Ocean).
2000 *Ticinella raynaudi digitalis* Sigal – Lipson-Benitah & Almogi-Labin, pl. 4, figs 1-3 (upper Albian, Israel).
2006 *Ticinella raynaudi* Sigal – Petrizzo & Huber, 2006, p. 181, pl. 2, figs 3-4 (upper Albian, Blake Plateau, western North Atlantic Ocean).

Material.– Approximately 25 specimens.

Emended description.– Test low trochospiral, with earlier chambers globular; the last formed chamber of the final whorl elongate, with the elongation axis exterior to the previous whorls. Chambers arranged in 2 $^1/_2$-3 whorls; 6 $^1/_2$ to 7 $^1/_2$, commonly 7 to 7 $^1/_2$ chambers in the final whorl. Test outline lobate to strongly lobate in dorsal view. Sutures are distinct and depressed, perpendicular to slightly oblique to the previous whorl. Test shape asymmetrical in edge view. Periphery broadly rounded, without peripheral structures. Aperture is a medium high arch, umbilical-peripheral in position and bordered by an imperforate lip. Umbilicus is small, one eighth to one sixth of the test maximum diameter. Small accessory apertures occur in the basal part of the sutures between the last four chambers; the bordering test wall is rimmed. Test wall calcitic, hyaline and perforate (1.9-2.8 µm) and with more or less developed reticulate appearance.

Remarks.– Claviticinella digitalis exhibits wide variability in the test wall ultrastructure; most of the specimens have well developed reticulate test wall and rarer specimens with incipient reticulation of the test wall are also known. It differs from *C. madecassiana* by having an elongate last chamber, more accessory apertures on the umbilical side, which are bordered by a rimmed wall prolongation and assume a sutural position between the last formed chambers, better developed reticulate test wall and larger pores. It differs from *C. subcretacea* by the presence of accessory apertures on the umbilical side, the elongate chamber having the elongation axis exterior to the previous whorls and reticulate rather than smooth test wall.

Stratigraphical range.– Upper Albian (from the upper part of the *P. ticinensis* Biozone to the lower part of *P. appenninica* Biozone).

Geographic distribution.– Africa (Madagascar, Tunisia), Europe (Spain), Middle East (Israel), North Atlantic Ocean (Blake Plateau, Mazagan Plateau).

Lineage *Pseudoclavihedbergella* – new

Type species: *Hedbergella amabilis* Loeblich & Tappan, 1961 (original designation).

Diagnosis.– Tests low trochospiral, with globular chambers in early stage and radially elongate, petaloid shaped chambers in adult stage; ornamentation consists of scattered pustules.

Description.– Tests are low trochospiral, with chambers that gradually increase in size. Chambers of the juvenile stage globular; the last formed ones are radially elongate and petaloid in shape, with the long axis perpendicular to or at a high angle (> 75º) to the previous whorl. Sutures are distinct and depressed, often limbated due to the lack of chamber overlapping. Periphery broadly rounded, simple or, rarely, with a peripheral band of low pore density and smaller pore size on the earlier chambers of the final whorl. Aperture is a low to medium high arch, umbilical-peripheral in position and bordered by an imperforate lip; relict periapertural structures and apertures can be present in the umbilicus. Chamber surface ornamented with dome-like scattered pustules, denser on the earlier chambers. Test wall calcitic, hyaline and perforate; pores show gradual increase in size along the lineage.

Remarks.– Pseudoclavihedbergella differs from *Clavihedbergella* by the pustulose chamber surface and radially elongate chambers that are petaloid in shape and with the elongation axis perpendicular to or at a high angle to the previous whorl, rather than subcylindrical and tangentially elongate. The simple test wall differentiates *Pseudoclavihedbergella* from the tests with radially elongate chambers of the upper Turonian, which were assigned to *Hillsella* Georgescu, 2008 and described as cancellate; however, a different terminology is needed for such tests (Georgescu, 2008b). *Eohastigerinella* lineage of the Santonian consists of *E. subdigitata* and *E. watersi* as ancestor

Plate 6

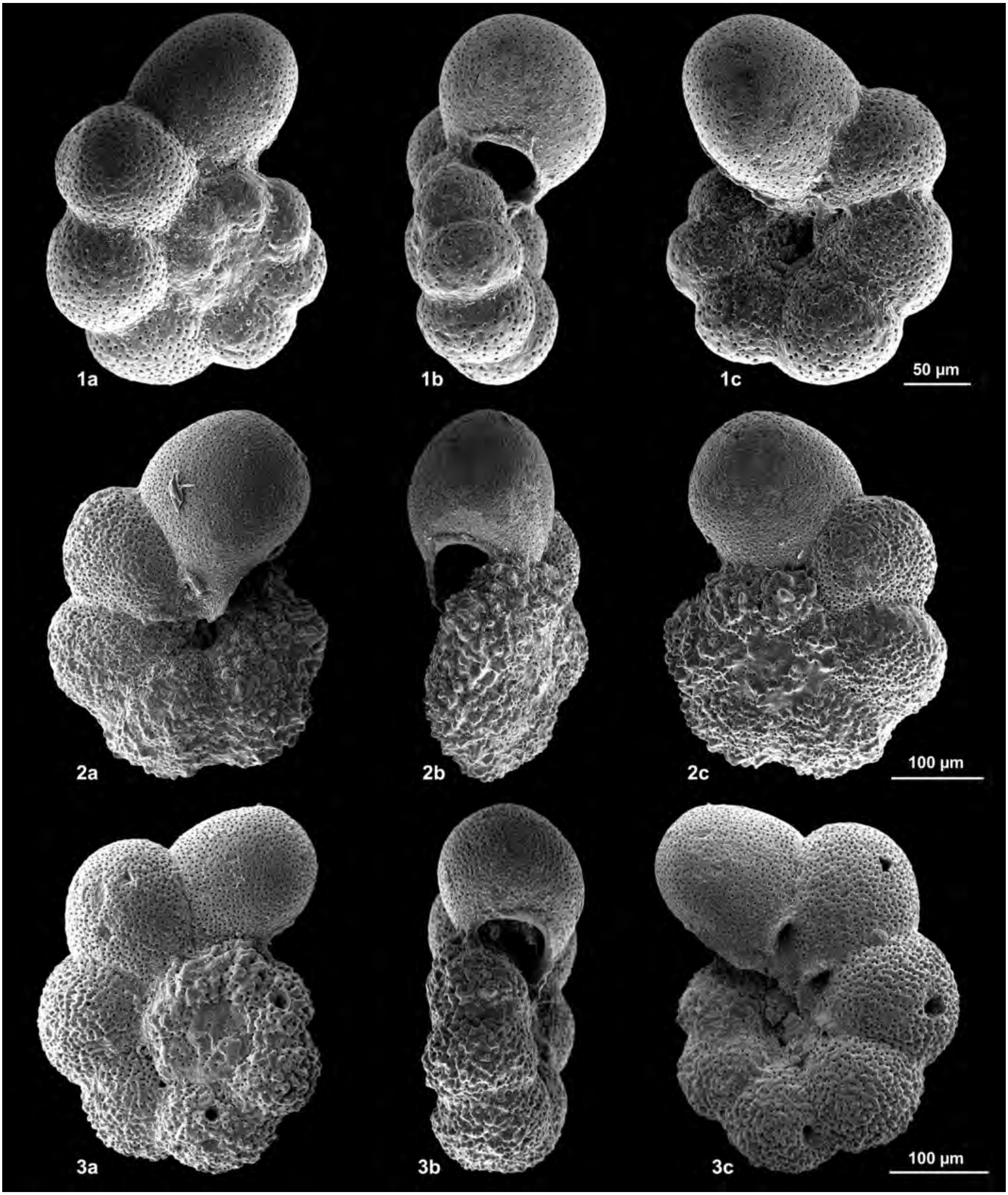


Plate 6. Three hypotypes of *Claviticinella digitalis* (Sigal, 1966) from the upper Albian sediments (*P. ticinensis* Biozone) of the ODP Leg 171B, Hole 1050C, Blake Plateau, western North Atlantic Ocean. **1,** Sample 171B-1050C-27-6, 74-78 cm (*P. appenninica* Biozone). **2,** Sample 171B-1050C-28-4, 148-150 cm (*P. ticinensis* Biozone). **3,** Sample 171B-1050C-27-6, 74-78 cm (*P. appenninica* Biozone). Note the narrow umbilici and roughened appearance of the test wall due to the development of the incipient reticulation (2-3). Specimen 1 belongs to a rare, almost smooth variety of the species.

and descendant respectively. The test wall of the *Eohastigerinella* species is simple, similar to those of *Pseudoclavihedbergella*, but the former lineage exhibits a well-developed trend toward planispiral tests.

Species included.– *Hastigerinella simplicissima* – Magné & Sigal, 1954, p. 487, pl. 14, fig. 11; *Hedbergella amabilis* – Loeblich & Tappan, 1961, p. 274, pl. 3, figs 1-10.

Etymology.– The Greek prefix "*Pseudo-*" (= false) is added to the preexisting genus name *Clavihedbergella*.

Stratigraphical range.– Upper Albian-lower Turonian (from the *P. appenninica* Biozone to *H. helvetica* Biozone).

Geographic distribution.– Cosmopolitan.

***Pseudoclavihedbergella simplicissima* (Magné & Sigal, 1954) – emended**

(Pl. 7, Figs 1-3, Pl. 8, Figs 1-2)

1948 *Hastigerinella* sp. – Cushman & Todd, p. 96, pl. 16, fig. 20 (Lower Cretaceous, California, USA).
1954 *Hastigerinella simplicissima* – Magné & Sigal in Cheylan *et al.*, p. 487, pl. 14, fig. 11 (lower-middle Cenomanian, Tunisia, northern Africa).
1961 *Clavihedbergella simplex* (Morrow) – Loeblich & Tappan, p. 279, pl. 3, fig. 13 (Cenomanian, Texas, USA).
1969 *Clavihedbergella simplicissima* (Magné & Sigal) – Neagu, p. 140, pl. 13, figs 1-6 (Cenomanian, southern Carpathians, Romania).
1970 *Clavihedbergella simplex* (Morrow) – Eicher & Worstell, p. 306, pl. 10, figs 6-7 (upper Cenomanian, Wyoming, USA).
1971 *Hedbergella simplicissima* (Magné & Sigal) – Caron, figs 3-4 (Albian, Subbetic Zone, Spain).
1977 *Globigerina simplicissima* (Magné & Sigal) – Masters, p. 473, pl. 24, figs 4, 6 (upper Cenomanian, Texas, USA).
1977 *Hedbergella simplicissima* (Magné & Sigal) – Pflaumann & Krasheninnikov, p. 547, pl. 2, figs 8-10 (upper Albian-Cenomanian, DSDP Holes 367, 368, 368A and 370, eastern North Atlantic Ocean).
1979 *Hedbergella simplex* (Morrow) – Robaszynski & Caron, p. 145, 150, pl. 29, figs 1-3, pl. 30, figs 1-2 (upper Cenomanian, Kansas, USA and Devon, UK).
1981 *Hedbergella simplex* (Morrow) – Magniez-Jannin, p. 93, pl. 1, fig. 7 (upper Albian, Kent, UK).
1984 *Hedbergella simplicissima* (Magné & Sigal) – Leckie, p. 599, pl. 8, figs 5-6 (upper Albian-Cenomanian, DSDP Sites 545 and 547A, Mazagan Plateau, eastern Atlantic Ocean).
2000 *Hedbergella amabilis* Loeblich & Tappan – Georgescu, p. 163, pl. 1, figs 3-4 (lower-middle Cenomanian, Romanian Western Black Sea offshore).
2005 *Hedbergella simplicissima* (Magné & Sigal) – Neagu, p. 317, pl. 2, fig. 24 (upper Albian, Moesian platform, Romania).
2006 *Hedbergella simplex* (Morrow) – Petrizzo & Huber, pl. 4, fig. 1 (upper Albian, Blake Plateau, ODP Holes 1050C, 1052E, western North Atlantic Ocean).

Material.– Approximately 50 specimens.

Emended description.– Test is low trochospiral, consisting of chambers that increase gradually in size. Earlier chambers globular and those of the last whorl with incipient radial elongation [the elongation axis of the chambers is perpendicular or at a high angle (> 75°) to the previous whorl]. Chambers arranged in 2-2 $^{1}/_{2}$ whorls. Four to six chambers, commonly 4 $^{1}/_{2}$-5, in the last whorl. Sutures are distinct and depressed, radial and often limbate between the chambers of the last whorl. Test shape is asymmetrical in edge view, convex-concave. Periphery broadly rounded, rarely with a peripheral band of low pore density and smaller pore size, which is developed on the earliest chamber of the last whorl. Aperture is a medium high arch, umbilical-peripheral in position and bordered by a narrow lip. Umbilicus shallow, one fourth to one third of the maximum test diameter; relict periapertural structures and apertures rarely occur in the umbilicus. Test ornamented with scattered dome-like pustules (diameter 3.6-7.0 µm), which are denser on the earlier chambers of the test. Test wall calcitic, hyaline and perforate; pore diameter over the chamber surface between 0.9 and 2.2 µm (commonly 1.6-2.1 µm); pores from the peripheral band are smaller (0.9-1.3 µm).

Remarks.– Test architecture of *P. simplicissima* generally resembles that of its ancestor, *H. delrioensis*, except for the incipiently radially elongate last chambers of the final whorl and wider umbilicus. Significant differences be-

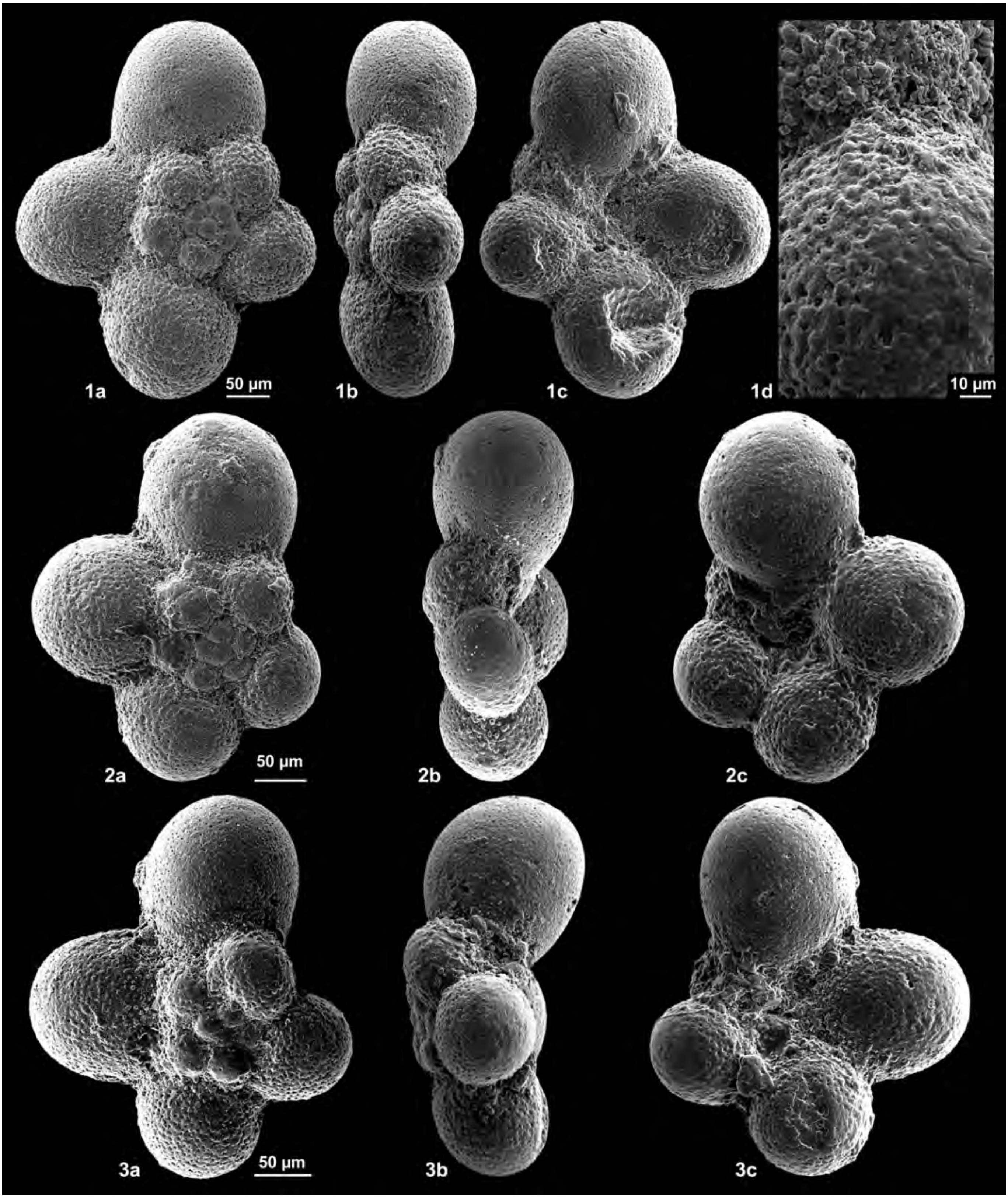


Plate 7. **1-3**, Three hypotypes of *Pseudoclavihedbergella simplicissima* (Magné & Sigal, 1954) from the type locality of *Pessagnoina simplex* namely upper Cenomanian Greenhorn Formation, Hartland Shale Member (Hodgeman County, Kansas, USA). Specimens from the Loeblich and Tappan Topotype Collection, NMNH, Washington, D.C. (USNM 473237). Note the peripheral band with lower pore density and smaller pore size shown in the detail micrograph (1d).

tween the two species exist mostly in the test ultrastructure and ornamentation (e.g., development of a peripheral band with lower pore density and size, smaller pustule size and larger pore diameter in the former). *P. simplicissima* differs from *C. subcretacea* by having pustulose ornamentation and perpendicular elongation mode rather than tangentially elongate as in the latter.

Stratigraphical range.– Upper Albian-Cenomanian (from the *P. appenninica* Biozone to *R. cushmani* Biozone).

Geographic distribution.– USA (California, Texas), Europe (UK, Spain, Romania), northern Africa (Tunisia) and western North Atlantic Ocean (Blake Plateau).

Pseudoclavihedbergella amabilis **(Loeblich & Tappan, 1961) – emended**

(Pl. 9, Figs 1-3, Pl. 10, Figs 1-2)

1961 *Hedbergella amabilis* – Loeblich & Tappan, p. 274, pl. 3, figs 1-10 (Cenomanian, Georgia and Texas, USA and Blake Plateau, western North Atlantic Ocean).

1961 *Clavihedbergella simplex* (Morrow) – Loeblich & Tappan, p. 279, pl. 3, fig. 11 (upper Cenomanian, Kansas, USA).

1967 *Hedbergella amabilis* Loeblich & Tappan – Pessagno, p. 281, pl. 52, figs 6-8 (Cenomanian-Coniacian of Mexico, Cenomanian of Texas, USA).

1970 *Hedbergella amabilis* Loeblich & Tappan – Eicher and Worstell, p. 300, pl. 9, figs 6-7, 9 (upper Cenomanian-lower Turonian, Colorado, Kansas, South Dakota and Wyoming, USA).

1972 (?) *Hedbergella amabilis* Loeblich & Tappan – Barr, p. 13, pl. 2, fig. 3 (Cenomanian-lower Coniacian, Cyrenaica Province, Libya, northern Africa).

1975 *Hedbergella amabilis* Loeblich and Tappan – Playford *et al.*, fig. 3: 7-9 (Cenomanian, Great Artesian Basin, Australia).

1977 *Clavihedbergella simplex* (Morrow) – Masters, p. 443, pl. 19, figs 1-2 (upper Cenomanian, Texas, USA).

1984 *Clavihedbergella simplex* (Morrow) – Leckie, p. 600, pl. 8, figs 7-8 (Cenomanian, DSDP Hole 547A, Mazagan Plateau, eastern North Atlantic Ocean).

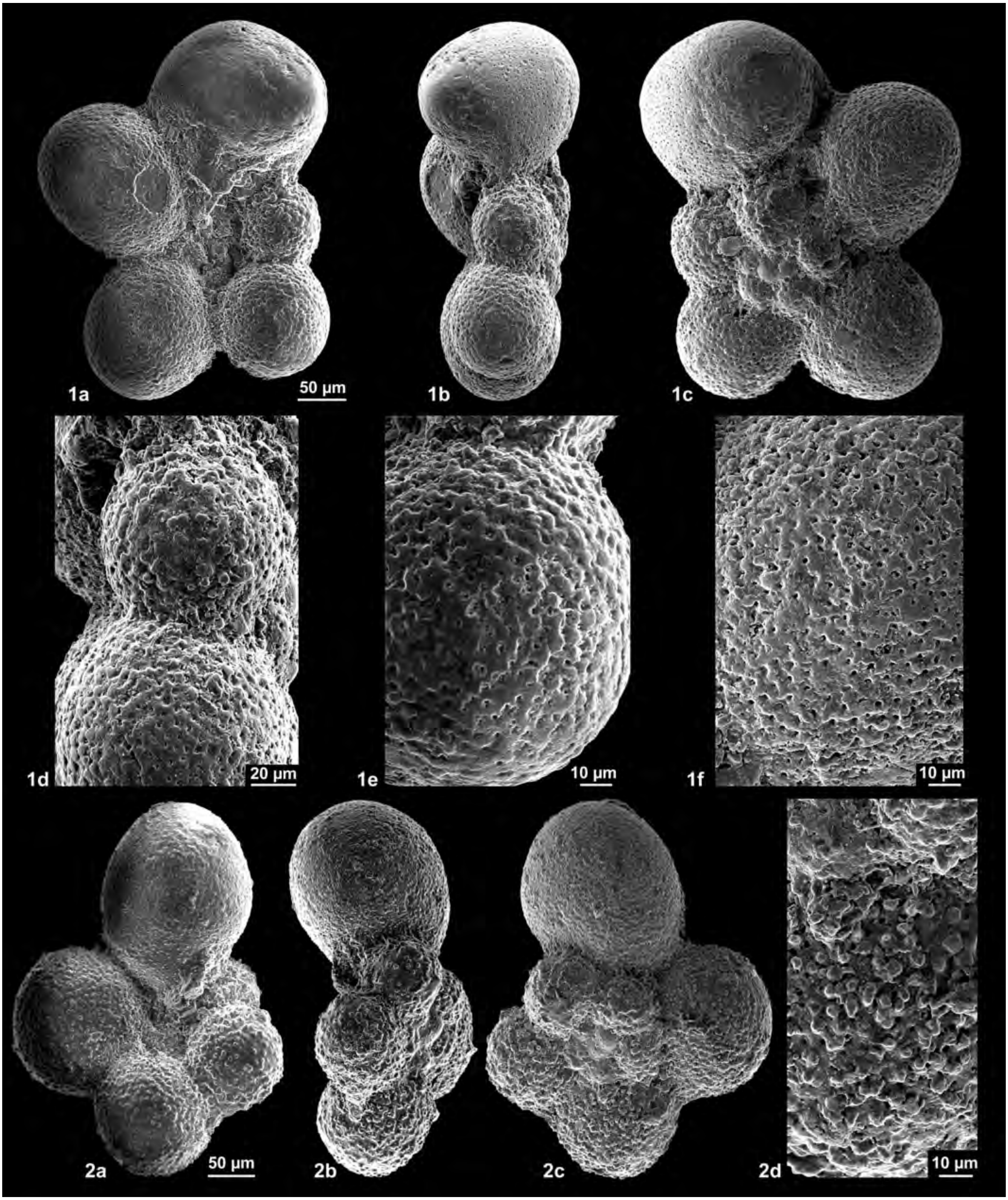
Material.– Approximately 100 specimens.

Emended description.– Test is low trochospiral, consisting of chambers that gradually increase in size. Earlier chambers globular; the last one or two chambers of the final whorl slightly radially elongate, petaloid in shape and with the elongation axis perpendicular or slightly oblique to the previous whorl. Chambers show little or no overlapping, which results in a strongly lobate outline in dorsal/umbilical view. Chambers arranged in 2 $^1/_2$-3 whorls; 4 $^1/_2$-6 chambers, commonly 5-5 $^1/_2$, in the final whorl. Sutures are depressed, straight and radial. Test shape convex-concave, asymmetrical. Periphery broadly rounded and occasionally with a peripheral band with lower pore density and smaller pore size developed on the first chamber of the final whorl. Aperture is a low to medium high arch, umbilical-peripheral in position and bordered by an imperforate lip. Umbilicus medium-sized and shallow, approximately one third to nearly a half of the maximum test diameter; relict periapertural structures and apertures can occur in the umbilical area. Chamber surface with scattered dome-like pustules, which are denser on the earlier chambers; pustule diameter is 4.5-8.0 µm. Test wall calcitic, hyaline and perforate; pores can be simple or in the middle of a depression. Pore size over most of the test surface is 1.8-5.0 µm, those of the peripheral band are smaller (1.0-2.1 µm). Test wall is simple, sometimes with quasi-cancellate appearance due to the high density of the large pores.

Remarks.– *Pseudoclavihedbergella amabilis* exhibits significant morphologic variability in the presence/absence of the peripheral band with lower pore density and smaller pore size and pore size and density over the other chambers of the test. Some authors regarded *P. amabilis* as a junior synonym of *P. simplicissima* (Masters, 1977; Leckie, 1984); this study shows that *P. amabilis* differs from *P. simplicissima* by having more chambers in the last whorl, larger pores over the test surface and peripheral band and more elongate last formed chambers. *Clavihed-*

Plate 8. **1-2**, Two hypotypes of *Pseudoclavihedbergella simplicissima* (Magné & Sigal, 1954) from the type locality of *M. simplex* namely upper Cenomanian Greenhorn Formation, Hartland Shale Member (Hodgeman County, Kansas, USA); slide originally labeled '*Hastigerinoides simplex*'. Specimens from the Loeblich and Tappan Topotype Collection, NMNH, Washington, D.C. (USNM 473237). Note the peripheral band with lower pore density and smaller pore size (1d) and pustulose chamber surface (1e, 1f, 2d).

Plate 8



bergella subcretacea differs from *P. amabilis* by the smooth test surface and subcylindrical, tangentially elongate chambers; the latter species has the test surface ornamented with scattered domical pustules and radially elongate, petaloid last chambers with the longer axis perpendicular to or at a high angle to the previous whorl.

Stratigraphical range.– Cenomanian-lower Turonian (from the *T. globotruncanoides* Biozone to *H. helvetica* Biozone).

Geographic distribution.– USA (Colorado, Georgia, Kansas, South Dakota, Texas, Wyoming), Mexico, Europe (Romania), (?) northern Africa (Libya), Australia (Great Artesian Basin), Atlantic Ocean (Blake Plateau, Mazagan Plateau).

Lineage *Pessagnoina* – new

Type species: *Hastigerinella moremani* Cushman, 1931(original designation).

Diagnosis.– Tests low trochospiral, with radially elongate chambers in the adult; elongation axis is perpendicular, rarely backwards tilted; last formed chambers in the evolved species with a bulbous projection at the distal end; earlier species have pustulose test surface, evolved ones can be smooth.

Description.– Tests low trochospiral, with chambers that increase gradually in size. Chambers of the juvenile stage globular; last formed ones radially elongated, subcylindrical or dorso-ventrally compressed in edge view and with the elongation axis perpendicular or at a high angle (> 85°) to the previous whorl. Sutures are distinct and depressed, often limbate due to the lack of chamber overlapping. Periphery is rounded and simple. Aperture is a low to medium high arch, umbilical-peripheral in position and bordered by an imperforate lip; relict periapertural structures and apertures can occur in the umbilicus. Chamber surface of the earlier species ornamented with dome-like scattered pustules, denser on the earlier chambers; evolved species are mostly smooth. Test wall calcitic, hyaline and perforate; pores show gradual increase in size along the lineage.

Remarks.– *Pessagnoina* differs from *Clavihedbergella* by the pustulose chamber surface in the primitive species and radially elongate last formed chambers with bulbous distal projections in the evolved ones. It differs from *Pseudoclavihedbergella* by the more elongate chambers, which have a bulbous distal projection in the evolved species and the absence of the peripheral band with lower pore density and smaller pores that occasionally occurs in the latter. The test wall is simple, contrasting to the cancellate wall of the upper Turonian tests with radially elongate chambers. *Eohastigerinella* lineage of the Santonian is a homeomorph of *Pessagnoina*; the two lineages document the iterative pattern in developing radially elongate chambers with bulbous projections in the upper Cenomanian (i.e., *Pessagnoina*) and Santonian (i.e., *Eohastigerinella*). *Pessagnoina* differs from *Eohastigerinella* by being trochospiral, in contrast to the latter that has a clear trend to develop planispiral tests in the evolved species.

Species included.– *Hastigerinella simplex* – Morrow, 1934, p. 198, pl. 30, fig. 6; *Hastigerinella moremani* – Cushman, 1931, p. 86, pl. 11, figs 1-3.

Etymology.– Genus named in honor of Dr Emile A. Pessagno Jr. (University of Texas) for his studies on the Cretaceous planktic foraminifera of USA, Mexico and Puerto Rico.

Stratigraphical range.– Upper Cenomanian-lowermost Turonian (from the *R. cushmani* Biozone to *W. archaeocretacea* Biozone).

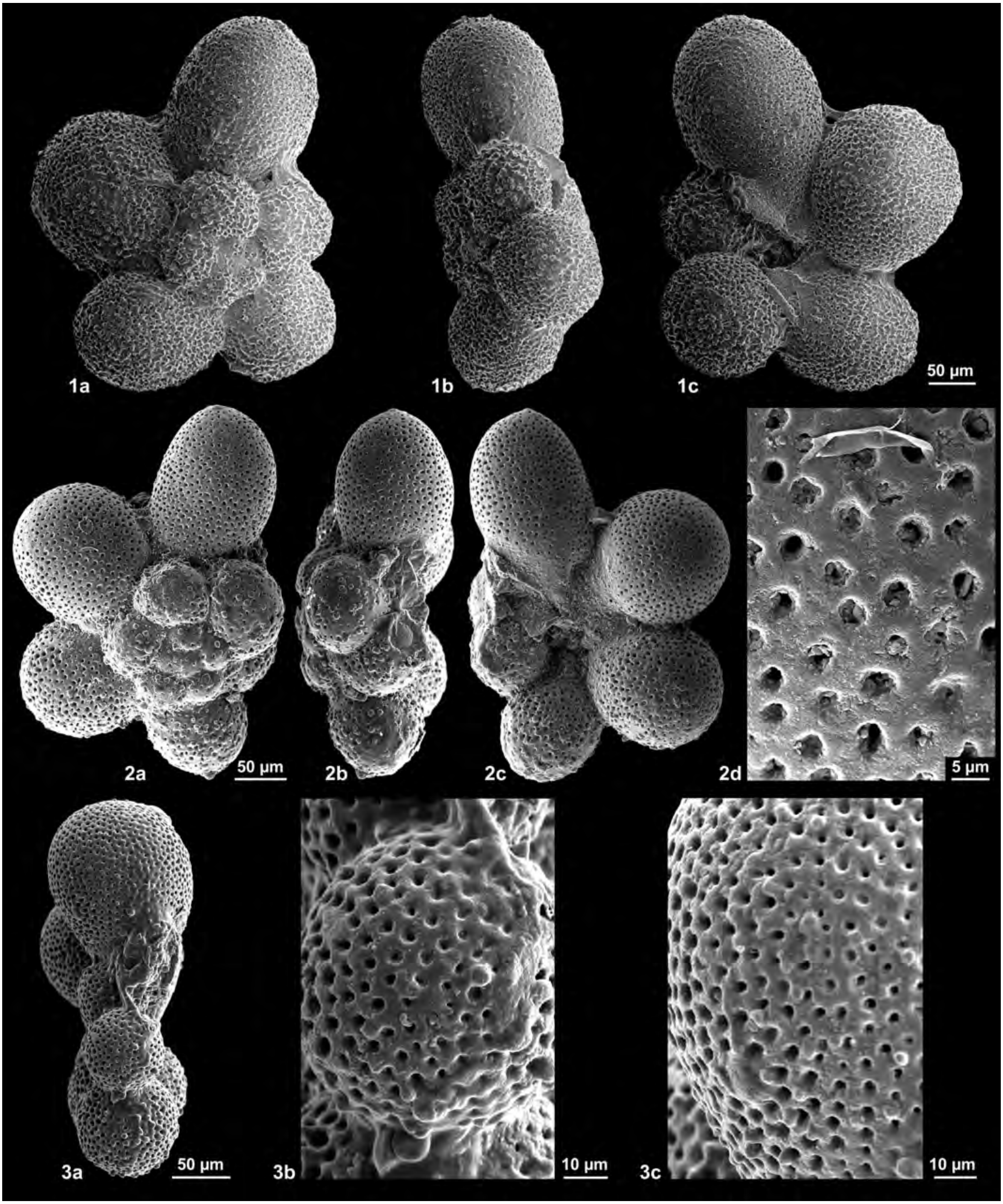
Geographic distribution.– USA (Georgia, Kansas, Texas, Washington State, Wyoming), Canada (Manitoba and southern Saskatchewan) and northern Africa (Egypt).

Pessagnoina simplex (Morrow, 1934) – emended

(Pl. 11, Figs 1-3, Pl. 12, Fig. 1)

Plate 9. Holotype and two hypotypes of *Pseudoclavihedbergella amabilis* (Loeblich & Tappan, 1961). **1,** Holotype (USNM 479620) from the upper Cenomanian Britton Clay, Eagle Ford Group at Midlothian (Ellis County, Texas, USA) originally figured by Loeblich and Tappan (1961, pl. 3, fig. 1) as *Hedbergella amabilis*; specimen originally figured in the online Mesozoic Planktonic Foraminiferal Taxonomic Dictionary (www.chronos.org). **2-3,** Hypotypes from the upper Cenomanian Britton Clay (Ellis County, Texas, USA) deposited in the Loeblich and Tappan Collection, NMNH, Washington, D.C. (USNM 472304); slides are labeled *Clavihedbergella simplex* (Morrow). The detail micrographs show the large pores (1d), periphery without band with lower pore density and smaller pore size (3b) and rare scattered pustules over the test surface (3c).

Plate 9



1934 *Hastigerinella simplex* – Morrow, p. 198, pl. 30, fig. 6 (upper Cenomanian, Kansas, USA).
1961 *Clavihedbergella simplex* (Morrow) – Loeblich & Tappan, p. 279, pl. 3, figs 12, 14 (upper Cenomanian, Kansas and Texas, USA).
1970 *Clavihedbergella simplex* (Morrow) – Eicher & Worstell, p. 306, pl. 10, fig. 4 (upper Cenomanian, Wyoming, USA).
1977 *Clavihedbergella simplex* (Morrow) – Masters, p. 443, pl. 19, fig. 3 (upper Cenomanian, Texas, USA).
1981 *Clavihedbergella simplex* (Morrow) – McNeil & Caldwell, p. 257, pl. 21, figs 4-5 (upper Cenomanian-lower Turonian, Manitoba and eastern Saskatchewan, Canada).
1981 *Clavihedbergella subcretacea* (Tappan) – McNeil & Caldwell, p. 260, fig. 3 (Turonian, Manitoba and eastern Saskatchewan, Canada).
2009 *Hedbergella simplex* (Morrow) – Samuel *et al.*, fig. 6:o (upper Cenomanian, Egypt).

Material.– Approximately 40 specimens.

Emended description.– Test low trochospiral, consisting of chambers that gradually increase in size and show little overlapping in the last whorl. Earlier chambers globular, the last one to three are radially elongate, with the elongation axis perpendicular or slightly oblique to the previous whorl and occasionally backward oriented; most of the radially elongate chambers are subcylindrical in shape. Chambers arranged in 2 -2 ½ whorls and there are 4-4 ½ chambers, commonly 4, in the last whorl. Sutures are distinct, depressed and radial on both sides of the test, often limbate between the last chambers due to the lack of chamber overlapping. Test convex-concave, slightly asymmetrical when seen in edge view. Aperture is a low to medium high arch, umbilical-peripheral in position and bordered by an imperforate lip. Umbilicus shallow, with the diameter between one third and a half of the maximum test diameter; no relict periapertural structures and/or apertures can be observed in the umbilical region. Chamber surface ornamented with rare and scattered dome-like pustules; pustule diameter between 2.6-4.8 µm. Test wall calcitic, hyaline and perforate; pore diameter over most of the test surface 1.5-4.0 µm, except for the peripheral band, where pores are as small as 1.1 µm in diameter.

Remarks.– *Pessagnoina simplex* differs from *P. simplicissima* by having more elongate last chambers, less developed peripheral band and larger pores. It differs from *C. subcretacea* by the elongation axis perpendicular or at a high angle to the previous whorl, pustulose chamber surface and denser pores.

Stratigraphical range.– Upper Cenomanian-lowermost Turonian (from the *R. cushmani* Biozone to *W. archaeocretacea* Biozone, possibly the lower part of *H. helvetica* Biozone).

Geographic distribution.– USA (Kansas, Texas, Washington State, Wyoming), Canada (Manitoba and southern Saskatchewan) and northern Africa (Egypt).

Pessagnoina moremani **(Cushman, 1931) – emended**

(Pl. 12, Fig. 2, Pl. 13, Figs 1-3, Pl. 14, Figs 1-2)

1931 *Hastigerinella moremani* – Cushman, p. 86, pl. 11, figs 1-3 (upper Cenomanian, Texas, USA).
1946 *Hastigerinella moremani* Cushman – Cushman, p. 147, pl. 61, figs 1-3 (upper Cenomanian, Texas, USA).
1961 *Clavihedbergella moremani* (Cushman) – Loeblich & Tappan, p. 279, pl. 5, figs 12-16 (upper Cenomanian, Georgia and Texas, USA).
1967 *Clavihedbergella moremani* (Cushman) – Pessagno, p. 285, pl. 53, fig. 5, pl. 55, figs 1-2 (upper Cenomanian-Turonian, Texas, USA).
1970 *Clavihedbergella moremani* (Cushman) – Eicher & Worstell, p. 304, pl. 10, fig. 5 (upper Cenomanian-lower Turonian, Kansas and South Dakota, USA).
1977 *Clavihedbergella moremani* (Cushman) – Masters, p. 442, pl. 18, figs 1-4 (upper Cenomanian, Texas, USA).

Material.– Twenty five specimens.

Emended diagnosis.– Test low trochospiral, composed of chambers that gradually increase in size. Earlier chambers

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Plate 10. **1-2**, Two hypotypes of *Pseudoclavihedbergella amabilis* (Loeblich & Tappan, 1961) from the Loeblich and Tappan Collection, NMNH, Washington, D.C. (USNM 472304); slides are labeled *Clavihedbergella simplex* (Morrow). The detail micrographs show the chamber surface ornamented with scattered pustules (1c), peripheral band with lower pore density and smaller pore size (2d) and dense large pores and simple, non-cancellate test wall (2e, 2f).

Plate 10

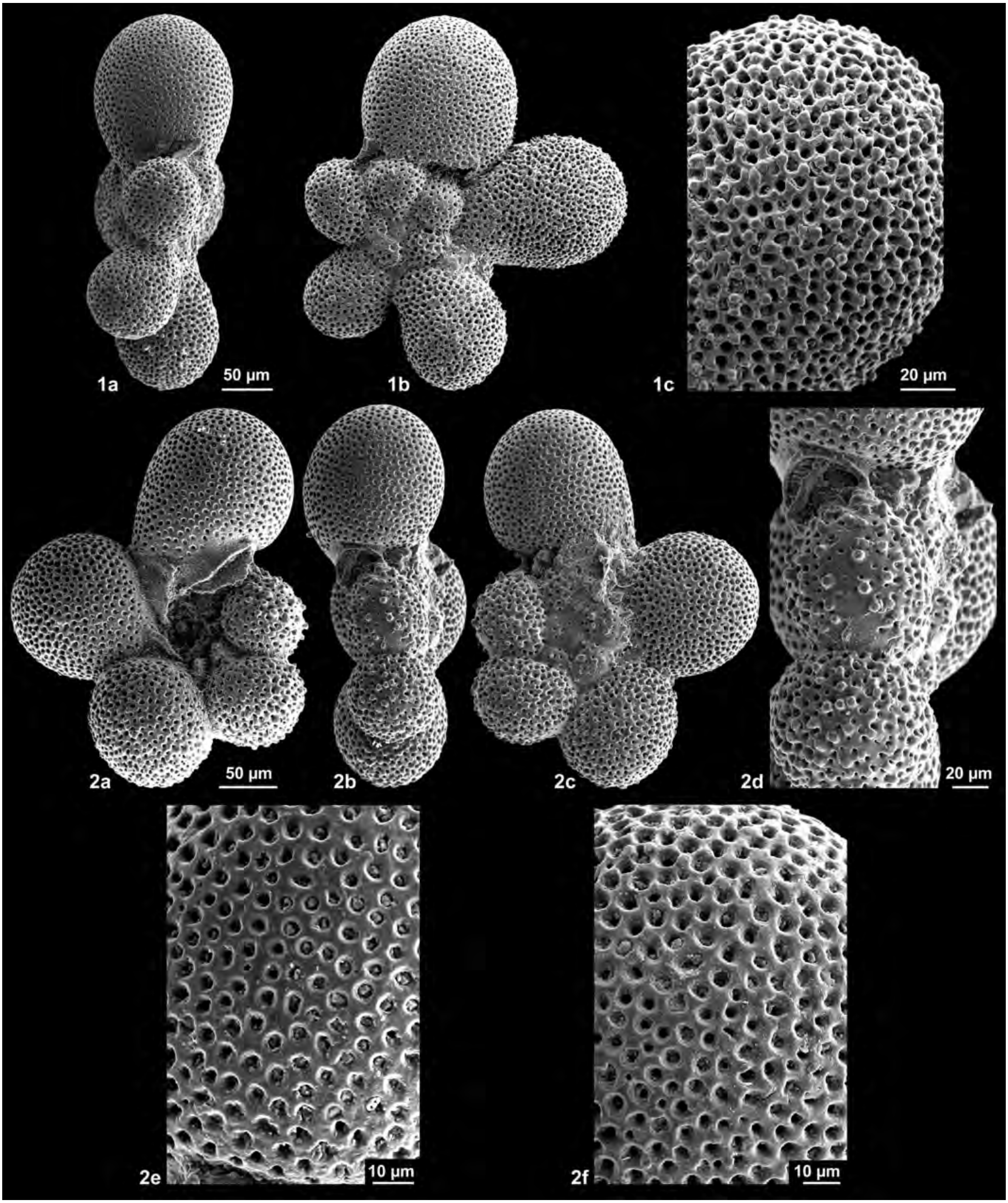

Plate 11

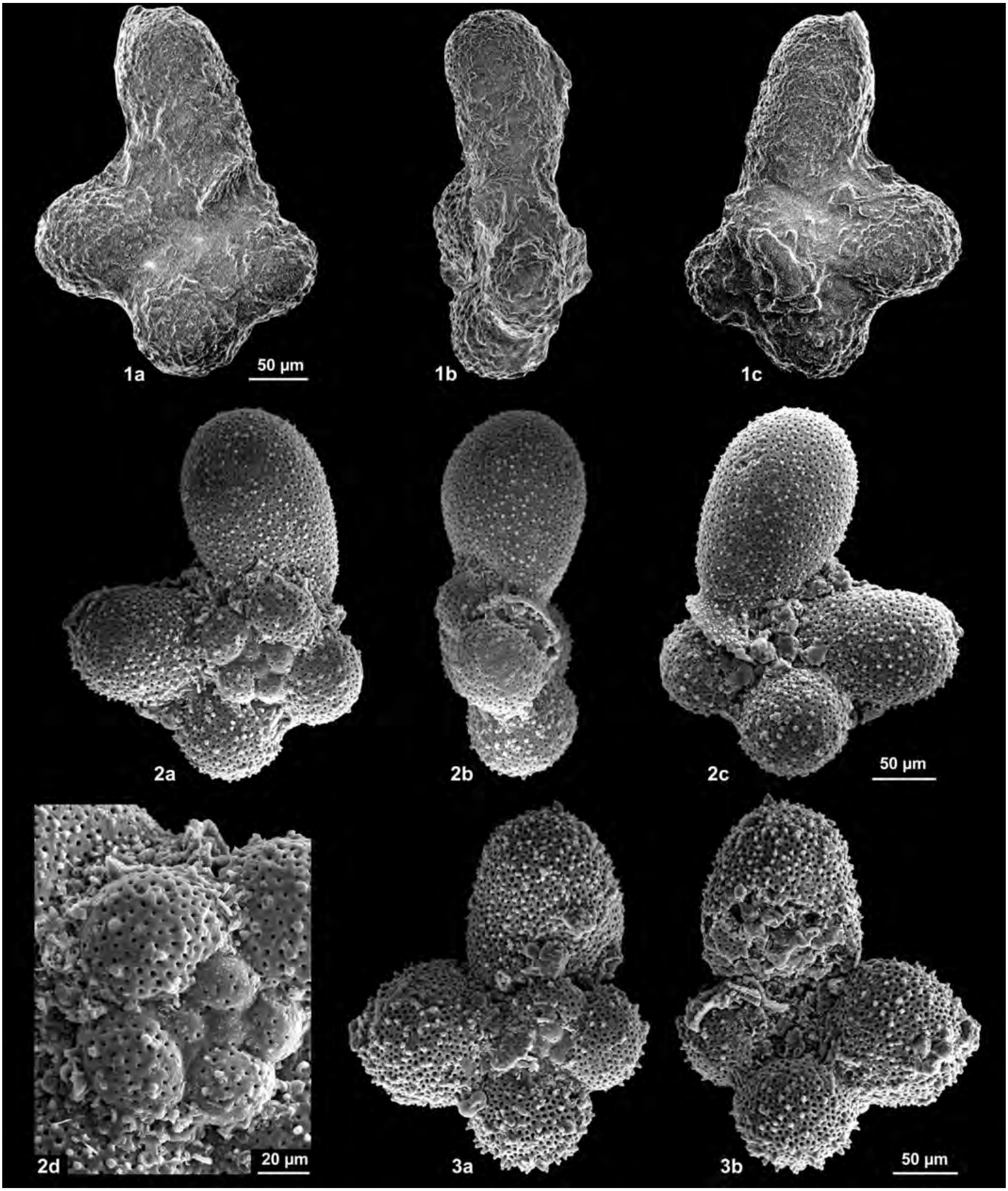

Plate 11. Holotype and two hypotypes of *Pessagnoina simplex* (Morrow, 1934). **1,** Holotype deposited in the Cushman Collection (USNM 75376) from the upper Cenomanian Greenhorn Formation, Hartland Shale Member (Hodgeman County, Kansas, USA), originally figured by Morrow (1934, pl. 30, fig. 6); specimen originally figured in the online Mesozoic Planktonic Foraminiferal Taxonomic Dictionary (www.chronos.org). **2-3,** Hypotypes from the lowermost Turonian of San Juan Island (Washington State, USA); specimens deposited in the McGugan Collection of the University of Calgary (Calgary, Alberta, Canada).

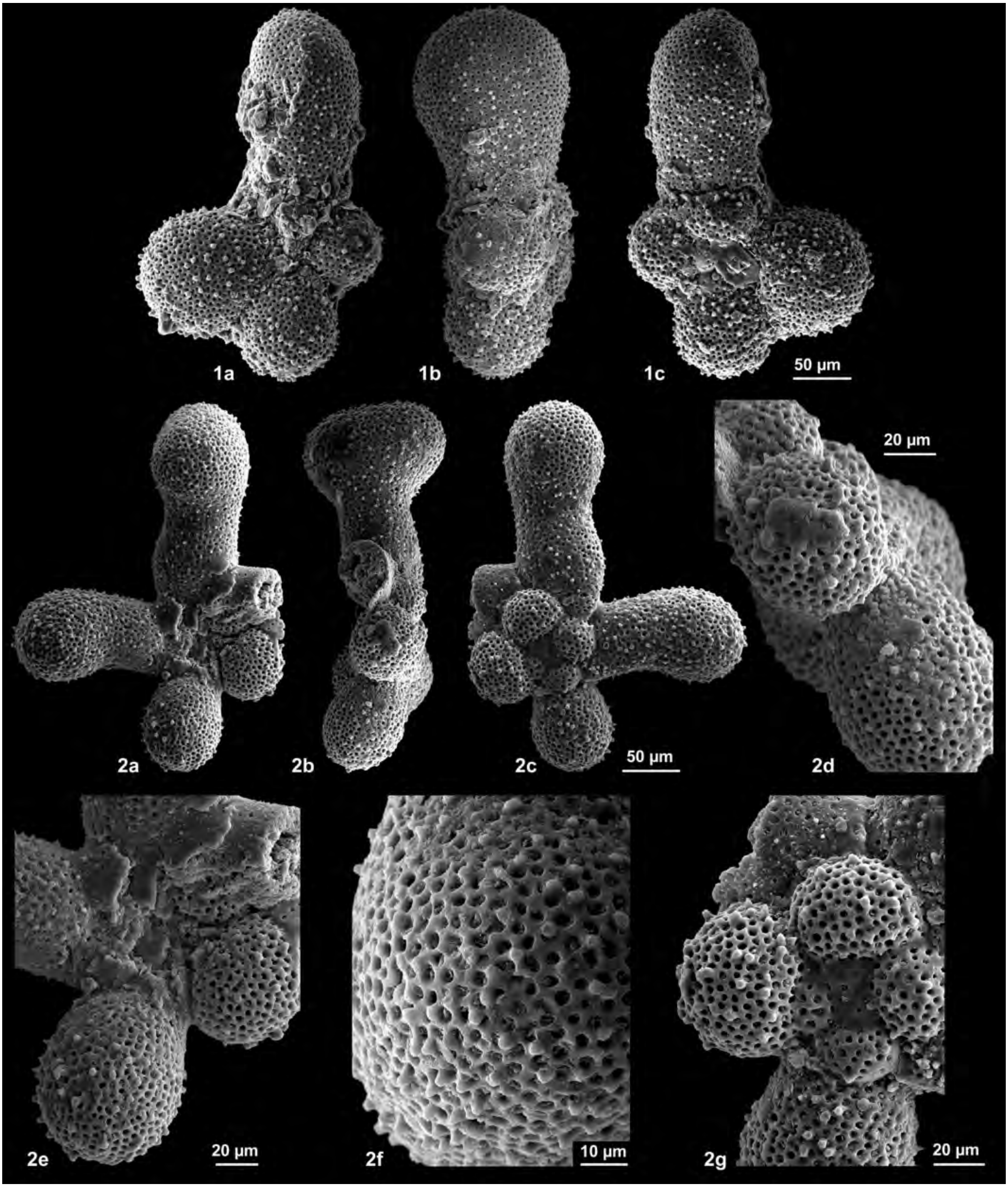

Plate 12. Hypotypes of *Pessagnoina simplex* (Morrow, 1934) and *P. moremani* (Cushman, 1931). **1,** Hypotype of *M. simplex* from the lowermost Turonian of San Juan Island (Washington State, USA); specimen deposited in the McGugan Collection of the University of Calgary (Calgary, Alberta, Canada). **2,** Hypotype of *P. moremani* from the lowermost Turonian of San Juan Island (Washington State, USA); specimen deposited in the McGugan Collection of the University of Calgary (Calgary, Alberta, Canada). Detail micrographs show the lack of peripheral band (2d), umbilical area with relict periapertural structures (3e), and scattered domical pustules over the chamber surface (2f, 2g).

Plate 13

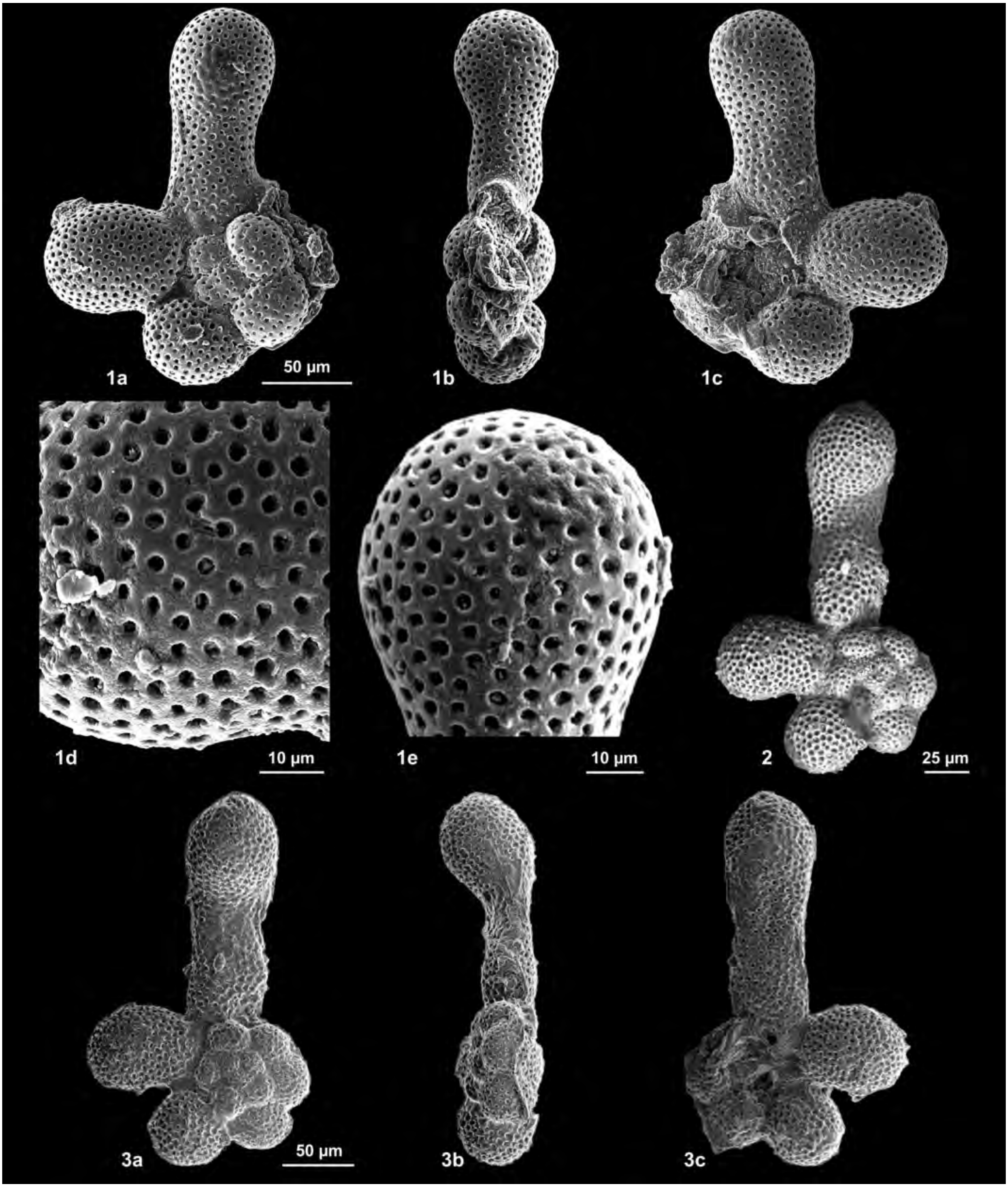

Plate 13. A hypotype and the holotype of *Pessagnoina moremani* (Cushman), 1931. **1,** Hypotype of *P. moremani* from the upper Cenomanian Britton Clay, Eagle Ford Group at Midlothian (Ellis County, Texas, USA); specimen deposited in the Loeblich and Tappan Topotype Collection (USNM 472306). Note the large pores and lack of pustules on the chamber surface (1d, 1e). **2-3,** Holotype of *P. moremani* (USNM 15746) from upper Cenomanian of Texas (USA), originally figured by Cushman (1931, pl. 11, fig. 1); 2-spiral side photographed using the Back Scatter Electron Detector; 3-complete illustration of the specimen using the ESEM.

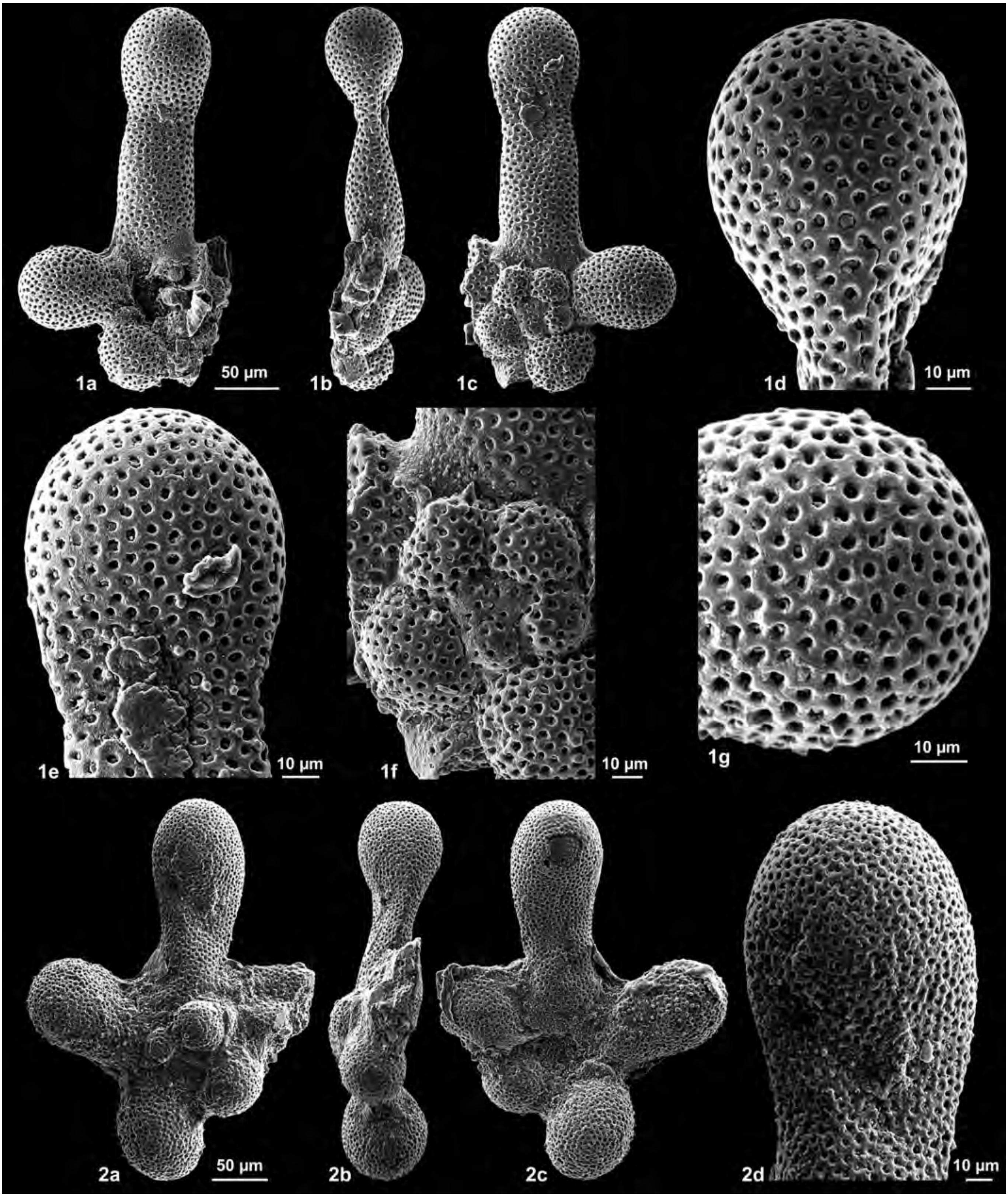

Plate 14. Two hypotypes of *Pessagnoina moremani* (Cushman, 1931). **1,** Hypotype of *P. moremani* from the upper Cenomanian Britton Clay, Eagle Ford Group at Midlothian (Ellis County, Texas, USA); specimen deposited in the Loeblich and Tappan Topotype Collection (USNM 472306). **2,** Hypotype of *P. moremani* from the Eagle Ford Group (Station 24102) from the Alexander Collection (NoF-2467.1); specimen deposited in the Micropaleontology Collection of the University of Calgary (Calgary, Alberta, Canada).

globular, those of the last whorl radially elongate subcylindrical or distinctly dorso-ventrally compressed and with the elongation axis perpendicular or at a high angle to the previous whorl. The last formed one or two chambers have a bulbous projection at the distal end, which occasionally can be dorso-ventrally elongate. Chambers arranged in 2-2 1/2 whorls; 4-6 chambers, commonly 4 1/2-5, in the final whorl. Sutures are deeply incised, limbate due to lack of chamber overlapping, straight and radial. Test shape convex-concave, slightly asymmetrical in edge view. Periphery is broadly rounded and simple, without peripheral band. Aperture is a low to medium high arc, umbilical-peripheral in position and bordered by a wide imperforate lip. Umbilicus medium-sized, approximately one fourth to one third of the maximum test diameter; relict periapertural structures and apertures can occur in the umbilical region. Chamber surface mostly smooth and only occasionally with scattered, dome-like pustules; pustule diameter 2.0-3.0 µm. Test wall calcitic, hyaline and perforate; pore diameter 2.7-4.1 µm.

Remarks.– *Pessagnoina moremani* differs from *P. simplex* by the well developed bulbous projections at the distal end of the last formed one to three chambers, generally smooth test surface, with the domical pustules only occasionally developed. *Eohastigerinella watersi* (Cushman, 1931) is a species of the Santonian, which is very low trochospiral to, mostly, planispiral and with scattered pustules over the test surface. The development of chambers with bulbous projections at the distal end in *P. moremani* and *E. watersi* is apparently the result of iterative evolution processes.

Stratigraphical range.– Upper Cenomanian (*R. cushmani* Biozone).

Geographic distribution.– USA (Texas, Georgia, Kansas, South Dakota, Washington State).

7. DISCUSSION AND CONCLUSIONS

Taxonomic reevaluation of the upper Albian-lower Turonian planktic foraminifera with radially elongate chambers in the context of evolutionary classification reveals the existence of four lineages in which the chamber elongation was achieved independently (Fig. 6). Each lineage has not only its own morphological characteristics but also dis-

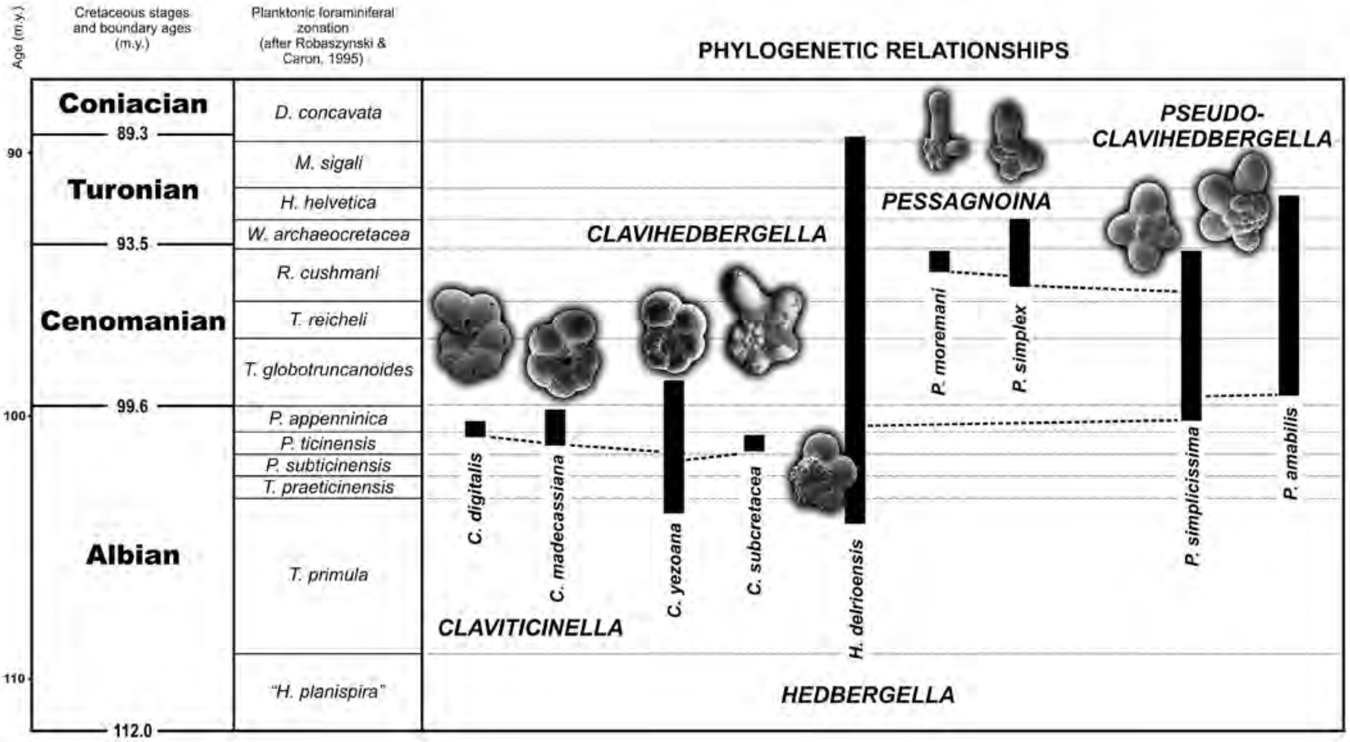

Figure 6. Inferred phylogenetic relationships showing the four non-schackoinid planktic foraminiferal lineages, which led to the development of tests with elongate chambers in the upper Albian-lower Turonian stratigraphical interval. Ages after Gradstein *et al.* (2004).

	***Clavihedbergella* Banner & Blow, 1959**		***Claviticinella* Banner, 1982**	
	C. yezoana (Takayanagi & Iwamoto), 1962	***C. subcretacea*** (Tappan), 1943	***C. madecassiana*** (Sigal), 1966	***C. digitalis*** (Sigal), 1966
SELECTED FEATURES				
Shape of the radially elongate chambers	Occasionally incipiently subcylindrical	Subcylindrical, tangentially elongate	Absent	Subcylindrical, with the elongation axis exterior to the previous whorls
Peripheral band with low pore density and smaller pore size	Occasionally present (Ø = 0.5-1.0 μm)	Occasionally present (Ø = 0.8-1.5 μm)	Occasionally present	Absent
Accessory apertures	Absent	Absent	One or two, sometimes absent	One to three, mostly two to three
Ornamentation	Occasionally with dome-like scattered pustules	Absent	Absent	Absent
Test wall ultrastructure	Simple	Simple	Incipiently reticulate	Well-developed reticulation in most of the specimens
Porosity (pore diameter)	Ø = 1.2-2.8 μm	Ø = 1.5-3.2 μm	Ø = 1.2-2.0 μm	Ø = 1.9-2.8 μm

Figure 7. Synthetic presentation of key morphological feature variability in the *Clavihedbergella*-*Claviticinella* lineage of the upper Albian-lowermost Cenomanian.

tinct evolutionary trends. Species are grouped into lineages by using a combination of morphological resemblances and inferred changes. Lineages are defined as taxonomic units of rank immediate above the species.

Clavihedbergella Banner & Blow, 1959 (upper middle Albian-lowermost Cenomanian) includes two species: *C. yezoana* (Takayanagi & Iwamoto, 1962) and *C. subcretacea* (Tappan, 1943). The two species have simple test wall, smooth chamber surface, rarely with scattered small-sized pustules and a peripheral band with lower pore density and smaller pore size on the first one or two chambers of the final whorl. Tangentially elongate, subcylindrical chambers are developed only in *C. subcretacea* (Fig. 7).

Clavihedbergella yezoana is the ancestral species for the *Claviticinella* Banner, 1982 lineage (upper Albian). *Claviticinella* consists of two species, *C. madecassiana* (Sigal, 1966) and *C. digitalis* (Sigal, 1966). The lineage shows gradual development of the reticulate ultrastructure of the test wall, development of elongate chambers in the final part of the last whorl, having the elongation axis exterior to the previous whorls and reticulate test wall. A peripheral band with lower pore density occasionally occurs only in *C. madecassiana*, an atavism from its ancestor, *C. yezoana*. There is a gradual development of accessory apertures on the umbilical side in the *Claviticinella* lineage. However, these structures can be absent in some specimens of *C. madecassiana*, demonstrating its origins among the simple *Hedbergella*-like species.

Another lineage began in the late Albian and resulted in the development of tests with petaloid chambers (Fig. 8). This lineage is formalized herein as the *Pseudoclavihed-*

	***Pseudoclavihedbergella* new lineage**		***Pessagnoina* new lineage**	
	P. simplicissima (Magné & Sigal), 1954	***P. amabilis*** (Loeblich & Tappan), 1961	***P. simplex*** (Morrow), 1934	***P. moremani*** (Cushman), 1931
SELECTED FEATURES				
Shape of the radially elongate chambers	Petaloid	Petaloid	Petaloid, then subcylindrical and without bulbous projection	Petaloid, then subcylindrical with distal bulbous projection
Peripheral band with low pore density and smaller pore size	Occasionally present (Ø = 0.9-1.3 µm)	Occasionally present (Ø = 1.0-2.1 µm)	Absent	Absent
Ornamentation (pustule diameter)	Dome-like pustules, denser on the earlier part of the test (Ø = 3.6-7.0 µm)	Dome like pustules, denser on the earlier part of the test (Ø = 4.5-8.0 µm)	Dome-like pustules, denser on the earlier part of the test (Ø = 2.6-4.8 µm)	Smooth, occasionally with scattered dome-like pustules (Ø = 2.0-3.0 µm)
Porosity (pore diameter)	Ø = 0.9-2.2 µm	Ø = 1.8-5.0 µm	Ø = 1.5-4.0 µm	Ø = 2.7-4.1 µm

Figure 8. Synthetic presentation of key morphological feature variability in the *Pseudoclavihedbergella-Pessagnoina* lineage of the upper Albian-lowermost Cenomanian.

bergella lineage-new and apparently it evolved from the pustulose species *Hedbergella delrioensis*. Its stratigraphical range is upper Albian-lower Turonian and it includes two species: *P. simplicissima* (Magné & Sigal, 1954) and *P. amabilis* (Loeblich & Tappan, 1961). Both species have dome-like scattered pustules on the chamber surface. The last formed chambers of the test are petaloid and have the elongation axis perpendicular or nearly perpendicular to the previous whorl. A peripheral band with low pore density and smaller pore size is known occasionally in both species of *Pseudoclavihedbergella*.

A distinct lineage initiated in the late Cenomanian from the specimens of *Pseudoclavihedbergella simplicissima* with simple periphery through elongation of chambers (Masters, 1977, p. 445). *Pessagnoina*-new consists of two species: *P. simplex* (Morrow, 1934) and *P. moremani* (Cushman, 1931). It spans from the upper Cenomanian to the lowermost Turonian (*Whiteinella archaeocretacea* Biozone), possibly in the lower part of the *Helvetoglobotruncana helvetica* Biozone. The end member of this lineage, *P. moremani*, is the only species of the upper Albian-lower Turonian with a bulbous projection at the distal end of the radially elongate chambers.

8. ACKNOWLEDGMENTS

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2006 stay. Dr A. Ando (University of Pusan, South Korea) is thanked for the SEM micrographs of *Clavihedbergella yezoana* (Takayanagi and Iwamoto, 1962) and information regarding the age at the type locality in Japan. Drs L.V. Hills and R. Mayer (University of Calgary) critical comments and improvements in the presubmittal phase of the manuscript are greatly appreciated. Drs M. Schoel (Microscope Imaging Facility, University of Calgary) and S. Whittaker (NMNH) enthusiastic and professional help during the SEM operations are greatly acknowledged.

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Recent marine Ostracoda from the Solomon Islands. Part 7: Cytheroidea: Loxoconchidae

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Resumen

Se registraron nueve especies de la familia Loxoconchidae en las Islas Salomón pertenecientes a tres géneros. De ellas, seis son nuevas: *Loxoconcha grammani, L. athersuchi, L. shortlandensis, Loxocorniculum labyrinthos, Sagmatocythere eridmatos* y ?*S. microreticulata* ssp. nov. Una última especie de *Loxoconcha* se deja en nomenclatura abierta debido a la escasez del material, y tres especies: *Loxoconcha pumicosa* Brady, *L. tumulosum* Hu y *Loxocorniculum insulaecapricornensis* Hartmann ya fueron descritas previamente. Las especies de Loxoconchidae constituyen un pequeño porcentaje (6.25%) del número de especies totales (160) de la fauna de podocópidos encontrados en las Islas Salomón. Sin embargo, conforman un componente muy significativo y reconocible de la fauna. Ninguna de las nueve especies está muy extendida y su distribución es endémica, local o regional; ninguna ocurre fuera del Pacifico occidental ni del área Indonésica/Australásica.

Palabras clave: Islas Salomón, ostrácodos marinos, Loxoconchidae, Recientes.

Abstract

Nine species of the family Loxoconchidae are recorded from the Solomon Islands. They belong to three genera and 6 species are new: *Loxoconcha grammani, L. athersuchi, L. shortlandensis, Loxocorniculum labyrinthos, Sagmatocythere eridmatos* and ?*S. microreticulata* ssp. nov. Another species of *Loxoconcha* is left in open nomenclature due to paucity of material and three species *Loxoconcha pumicosa* Brady, *L. tumulosum* Hu and *Loxocorniculum insulaecapricornensis* Hartmann have been previously described. The Loxoconchidae, by species, make up a relatively small percentage (6.25%) of the total number of podocopid ostracod species (160) encountered in the Solomon Island. However, they form a significant and readily recognisable component of the fauna. None of the 9 species is very widespread in its distribution and most are endemic, local or regional; none occur outside the West Pacific/Indonesian/Australasian general area.

Key words: Solomon Islands, marine Ostracoda, Loxoconchidae, Recent.

1. INTRODUCTION

A list of the most important papers published recently on Indo-Pacific ostracod faunas is given in the introduction of recent papers by the present authors (Titterton & Whatley, 2005, 2006 a & b) and Warne *et al.,* 2006. This contribution is the 7th and final paper of a series on the taxonomy of the Recent marine Ostracoda of the Solomon Islands. Nine species of the family Loxoconchidae belonging to 3 genera are described; six of the species are new, one is left in open nomenclature and three have been described previously from elsewhere in the Pacific and Australasia. By number of species the Loxoconchidae make up some 6.25% of the total ostracod fauna of the Solomon Islands which comprised some 160 species belonging to 56 genera. The overwhelmingly dominant group are the Cytheroidea (63%) the remainder are cyprids (15%), bairdiids (8%) and platycopids/cladocopids (13%).

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

2. SYSTEMATIC DESCRIPTIONS

All the material is housed in the collections of the Natural History Museum, London, catalogue numbers are prefixed RT/SIR and refer to the Aberystwyth collections. 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, IM=inner margin, OM=outer margin. All new taxa are fully described.

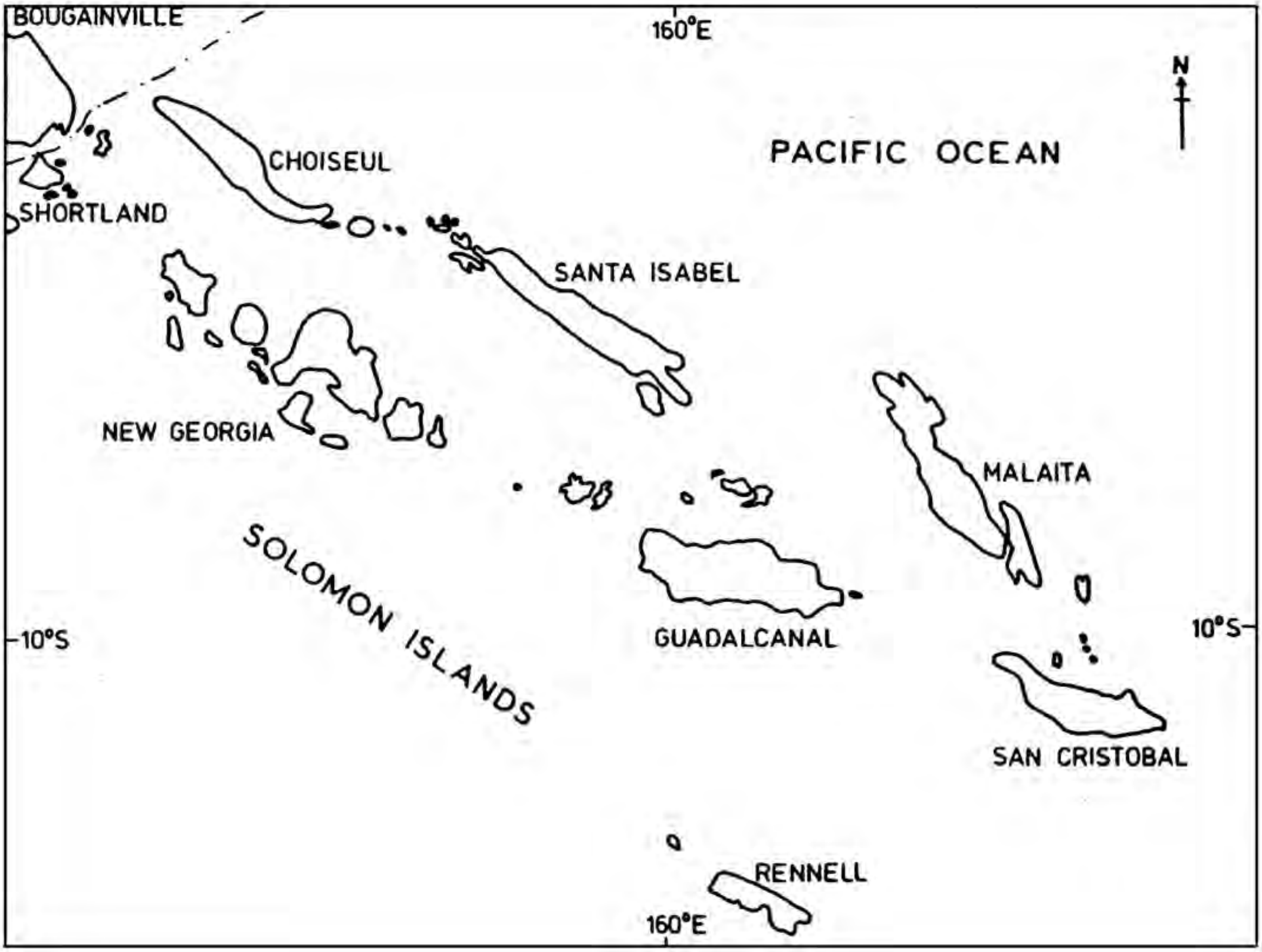


Figure 1.The Solomon Islands.

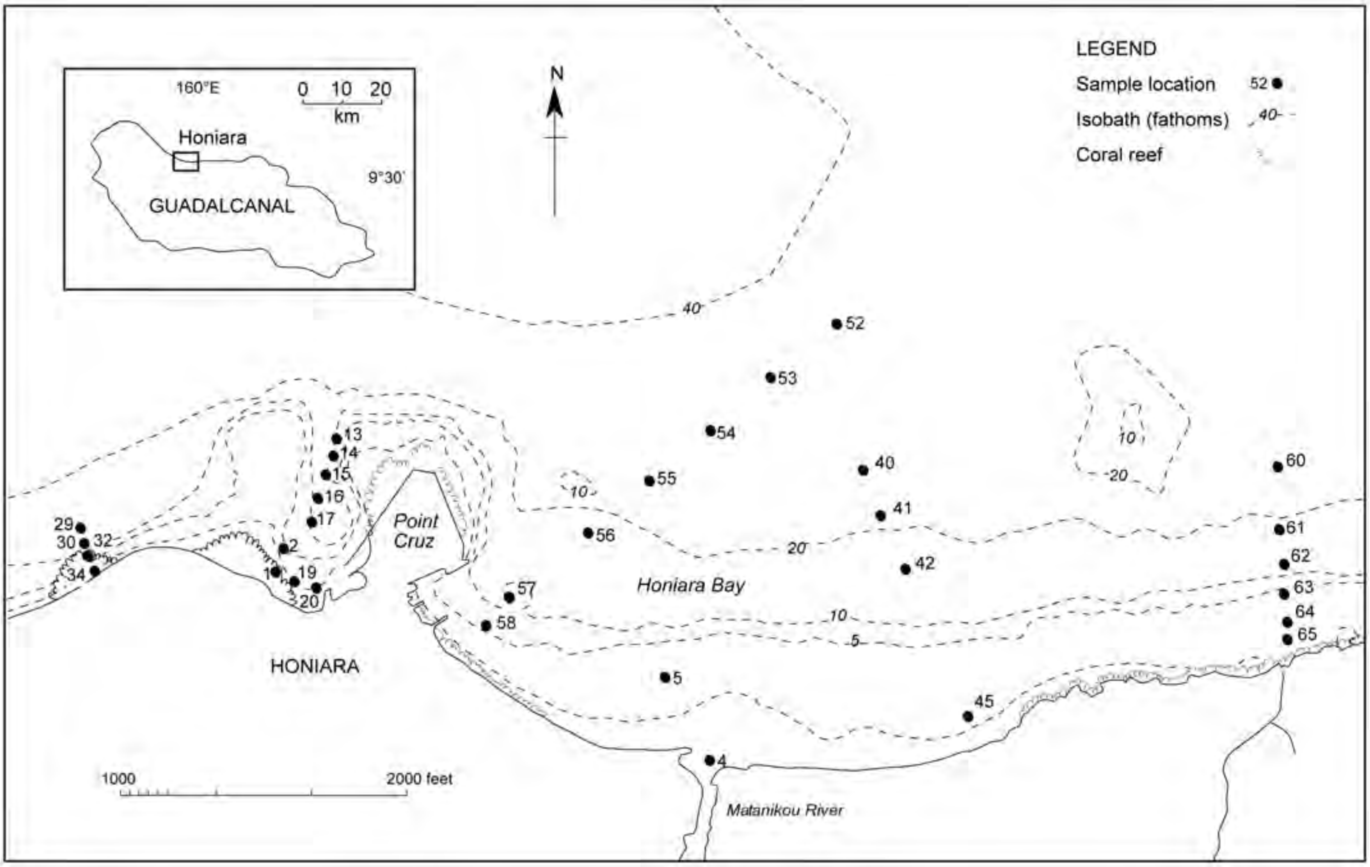


Figure 2. Location of sample stations, Honiara Bay, N. Guadalcanal, Solomon Islands.

Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily CYTHEROIDEA Baird, 1850
Family LOXOCONCHIDAE Sars, 1925
Subfamily LOXOCONCHINAE Sars, 1925

Genus *Loxoconcha* Sars, 1866

Type species.- *Cythere rhomboidea* Fischer, 1855 (subsequent designation by Brady & Norman, 1889).

Remarks.- The species of *Loxoconcha* encountered in the present material are placed in a morphological series, based primarily on surface ornament and are described below in the order they occur in this series. The trend of the series is an increase in strength of development of the ornament with an associated reduction and loss of the posterodorsal tubercle. The series begins with *L. gramanni* sp. nov. which is ornamented with deep puncta, concentrically arranged about mid-point. The puncta are ovate sub-centrally, becoming slightly more quadrate peripherally. A strong, posterodorsal tubercle is developed just below the posterior cardinal angle. The next in the series, *L. athersuchi* sp. nov., differs from *L. gramanni* principally in that the posterodorsal swelling is conspicuously less well developed. *Loxoconcha shortlandensis* sp. nov. is placed third in the series because the posterodorsal tubercle is absent. Although this latter species possesses a similar punctate ornament, the puncta are more strongly developed, are larger and denser subcentrally and the muri are concentric with the margins, particularly ventrally. The forth species, *L. pumicosa* Brady, 1880 is slightly smaller and more inflated ventrally than *L. shortlandensis* and the dorsal margin is almost straight to gently biconvex. The last species in the series, *L. tumulosa* Hu 1979, closely resembles *L. pumicosa* but the ornament is more reticulate, irregular and somewhat randomly arranged and shows some affinity to the species of *Loxocorniculum* encountered. It possesses a more subrectangular shape with almost straight dorsal and ventral margins and has a slight alar development that is more typical of *Loxocorniculum*

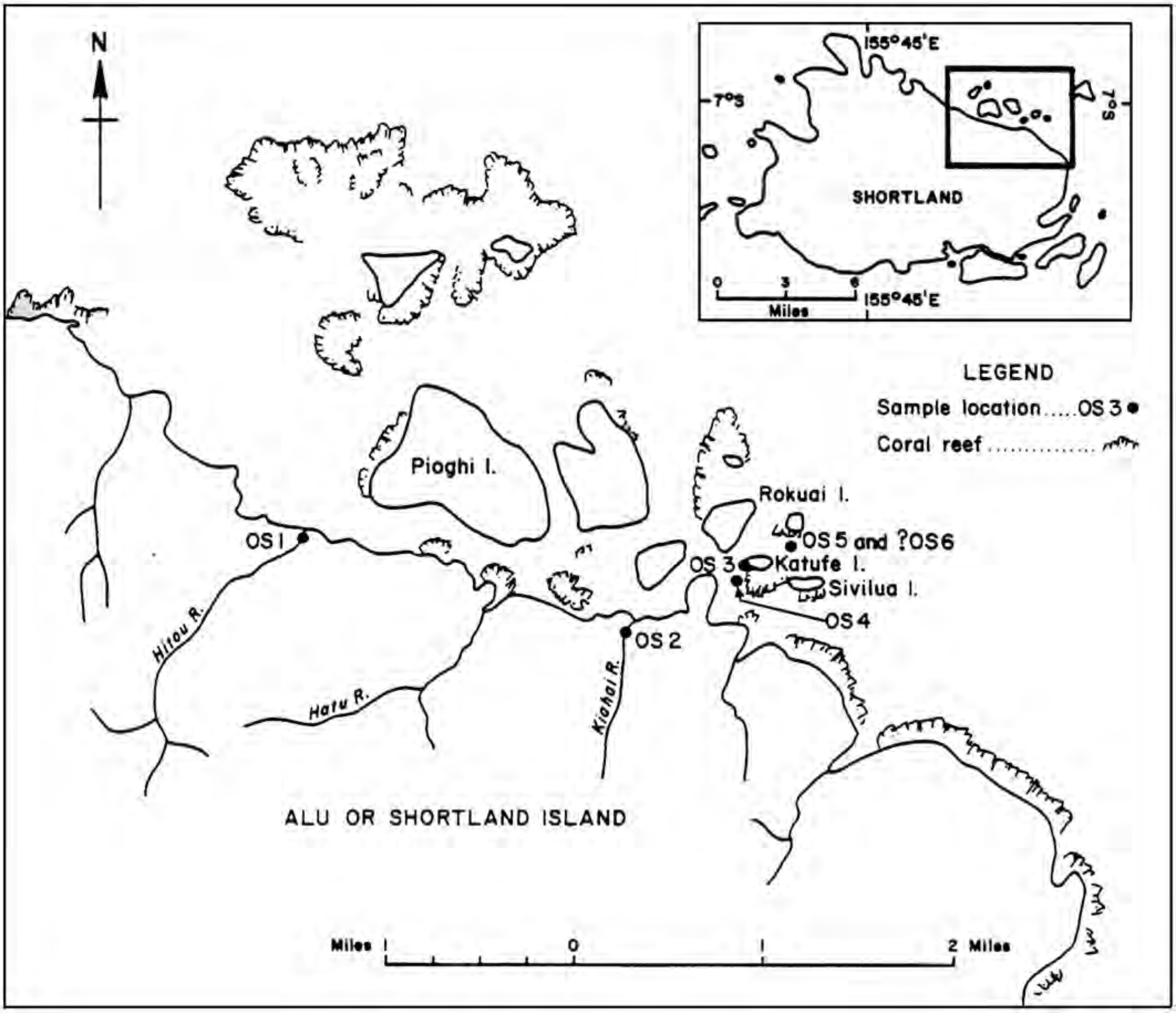


Figure 3. Location of sample stations, Shortland Island, Solomon Islands.

but it does not possess lateral ribs. *Loxoconcha* sp. A, represented by a single valve, could not be placed in this morphological series, being very delicately ornamented by discrete, small puncta but the posterodorsal tubercle is absent.

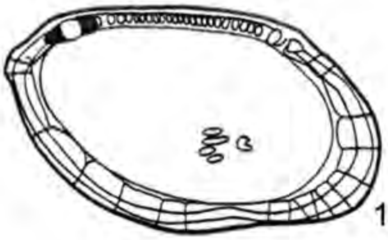
Loxoconcha gramanni **sp. nov.**

(Fig. 4, Nos 1, 2, 4, 5; Pl. 1, Figs 3-11)

? 1954 *Loxoconcha lilljeborchi* Brady; Keij: 358 pl. 3 fig. 4.

1975 *Loxoconcha* sp. cf. *Loxoconcha lilljeborchi* Brady, 1868; Gramann: 29; pl. 5, figs 6-8.

Figure 4. Internal lateral views. *1, 2, 4, 5, Loxoconcha gramanni* sp. nov. *1,* Male left valve RT/SIR/429 x 92.3, *2,* Female left valve RT/SIR/428 x 95.9, *4,* Male right valve RT/SIR/427 x 96.0, *5,* Female right valve RT/SIR/426 x 93.8. *3, 6, Loxoconcha athersuchi* sp. nov. *3,* Male left valve RT/SIR/439 x 100.0, *6,* Female right valve RT/SIR/440 x 94.0. *7, 10, Loxoconcha pumicosa* (Brady, 1880) *7,* Male left valve RT/SIR/457 x 86.8, *10,* Female left valve RT/SIR/459 x 94.1. *8, 11, Loxoconcha shortlandensis* sp. nov. *8,* Male left valve RT/SIR/449 x 73.0, *11,* Female right valve RT/SIR/450 x 83.6. *9, 12, Loxoconcha tumulosa* Hu, 1979 *9,* Male left valve RT/SIR/467 x 81.0, *12,* Female right valve RT/SIR/468 x 90.0. *13, 16, Loxocorniculum insulaecapricornensis* (Hartmann) 1981 *13,* Male left valve RT/SIR/481 x 74.2, *16,* Female right valve RT/SIR/480 x 88.7. *14, 17, Sagmatocythere eridmatos* sp. nov. *14,* Paratype male left valve RT/SIR/490 x 82.1, *17,* Female right valve RT/SIR/491 x 86.5. *15, 18, Loxocorniculum labyrinthos* sp. nov. *15,* Paratype left valve RT/SIR/497 x 100.0, *18,* Right valve RT/SIR/496 x 97.4. *19-20, ?Sagmatocythyere microreticulata* sp. nov. *19,* Paratype left valve RT/SIR/503 x 105.0, *20,* Right valve RT/SIR/502 x 115.4.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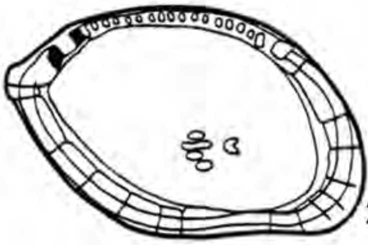
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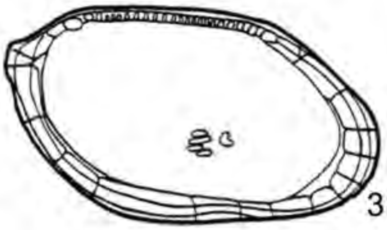
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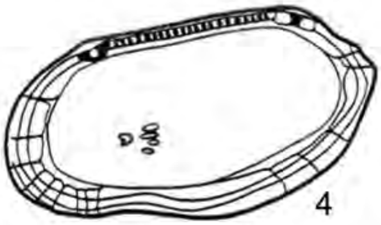
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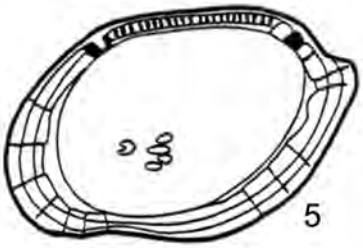
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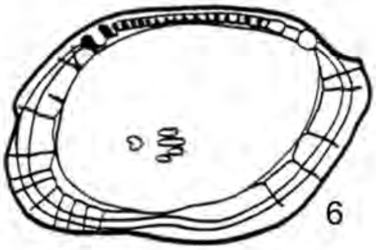
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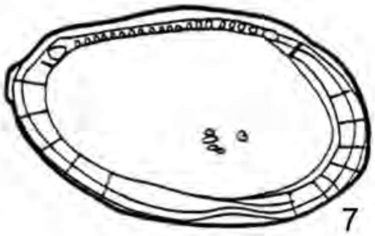
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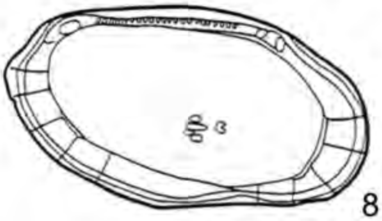
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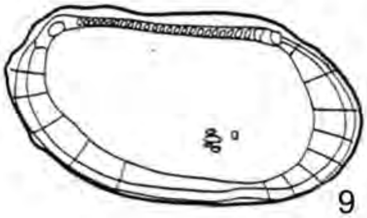
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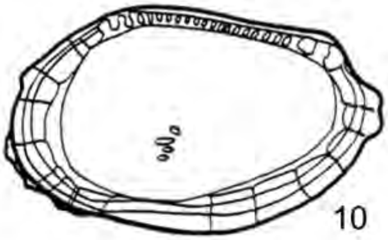
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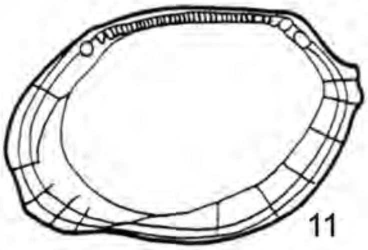
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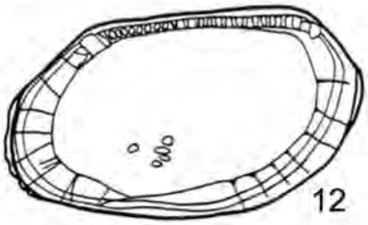
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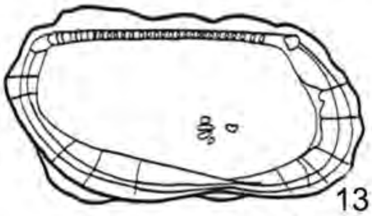
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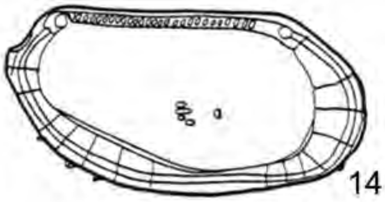
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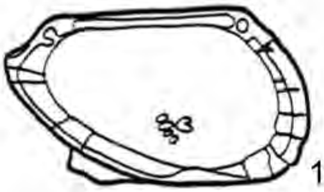
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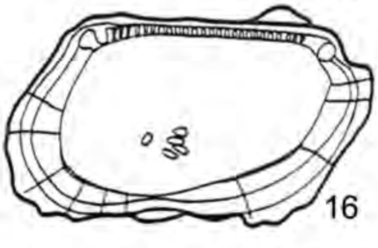
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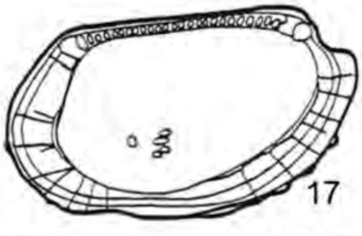
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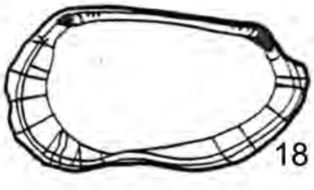
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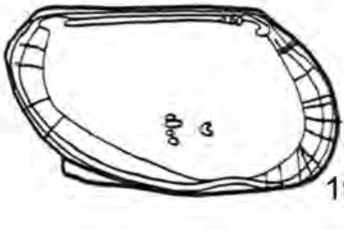
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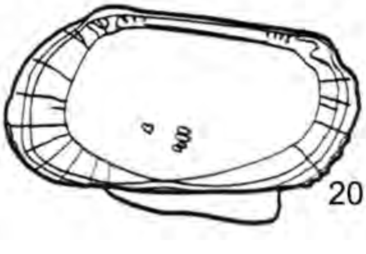
20

1986 *Loxoconcha lilljeborgii* Brady; Zhao, Wang & Zhang: pl. 2, figs 14, 15.
1992 *Loxoconcha lilljeborgii* Brady; Mostafawi: 151, pl. 5, fig. 102.
non 1868 *Loxoconcha lilljeborgii* Brady: 183, pl. 8, figs 11-14.

Derivatio nominis.- L. In honour of Dr. F. Gramann who first illustrated this species.

Holotype.- Female LV, RT/SIR/421. Plate 1, Fig. 3.

Type locality and horizon.- Sample 13, 1,800 feet offshore, west of Point Cruz, Honiara Bay, Guadalcanal. 11 fathoms. Unconsolidated, medium-grained, coral sand. Recent.

Material.- 492 valves and carapaces, A-4 to adult. Samples:1, 2, 5,13-15, 17, 20, 29, 30, 32, 40-42, 55-58, 60-62, OS5, OS6, Guadalcanal and Shortland islands.

Diagnosis.- A subrhomboidal species of *Loxoconcha* distinguished by ornament of discrete, deep, subcircular puncta concentric about mid-point with a degree of longitudinal orientation and by the prominent crescentic tubercle just below the posterodorsal angle.

Description.- Small to medium. Thick-shelled. Translucent. Male more elongate and less tumid than female. Subrhomboidal in lateral view: elliptical in dorsal view. Anterior margin well rounded anteroventrally, oblique anterodorsally; extremity well below mid-height in LV, at about mid-height in RV. Posterior margin with small upturned caudal process well above mid-height with a long, gently convex posteroventral slope and short concave posterodorsal slope. Dorsal margin very gently arched, anterior cardinal angle rounded; posterior obtuse. Ventral margin gently biconvex with distinct oral concavity not overhung by valve tumidity. Greatest length below mid-height; greatest height at posterior third of length; greatest width median. LV slightly larger than RV with small overlap at dorsal cardinal angle and orally. Eye-spot conspicuous, large, round, low, glassy. Small but distinct, crescentic tubercle just below posterior cardinal angle. Surface of valves strongly punctate; puncta circular, deep, concentric about mid-point but with a degree of longitudinal orientation: marginal rim smooth and with weak, crescentic riblets being developed antero and postero-laterally. NPCs recessed, large, sieve-type, circular except around dorsal marginal rim where they are elongate and narrow, aligned parallel to dorsal margin. Inner lamella wide with very narrow crescentic anterior and slightly wider posterior vestibula. LOC and IM subparallel to OM, coincident orally, 10 anterior and 7 posterior rpcs; simple, straight, well spaced with 2 distinct canals at posterior caudal process. Strong selvage, particularly posteroventrally, subperipheral. Hinge gongylodont, robust, gently arched: in the LV the denticules of the median element are oval and discrete; in the RV they are arched. Central muscle scars: 4 small subovate adductor scars in a gently curved vertical row, dorsomedian scar more elongate; small v-shaped frontal scar.

Dimensions.-

	Length	Height	Width
Holotype Female LV, RT/SIR/421	0.45	0.30	
Paratype Male C, RT/SIR/416	0.49	0.32	0.25
Paratype Female C, RT/SIR/417	0.46	0.31	0.26
Paratype Male RV, RT/SIR/419	0.47	0.31	
Female LV, RT/SIR/423	0.49	0.33	
Female RV, RT/SIR/424	0.46	0.31	
Male RV, RT/SIR/425	0.49	0.30	
Female RV, RT/SIR/426	0.48	0.31	
Male RV, RT/SIR/427	0.50	0.31	
Female LV, RT/SIR/428	0.49	0.32	
Male LV, RT/SIR/429	0.52	0.31	

Mean Dimensions. –

	Length	Height	Width
20 Female LV	0.45(0.41-0.47)	0.31(0.29-0.32)	
20 Male LV	0.50(0.48-0.52)	0.32(0.31-0.33)	
5 A-1 C	0.39(0.38-0.41)	0.25(0.24-0.25)	0.21(0.20-0.21)
13 A-2	0.32(0.30-0.34)	0.20(0.18-0.21)	
1 A-3	0.26	0.15	
1 A-4	0.21	0.13	

Distribution.- Recorded from Burma, the South Sea, Malaysia and the Java Sea (Watson, 1988). Gramann (1975) noted in his text that the species occurs on the Tenasserim coast, Ngapali, Burma, but in the plate explanations the material was said to be from a rocky tidal pool on the Arakan coast.

Remarks.-The present material is identical with the Recent species illustrated by Gramann (1975) which he remarked closely resembled *L. lilljeborgii* Brady 1868. Brady's original illustration of *L. lilljeborgii* (Recent, off Mauritius), is not detailed enough for comparison, but he describes it as possessing oblong pits. In contrast the "pits" of the present species are circular mid-laterally. The original material is a considerable larger species and is similar in size to that recorded by Whatley & Zhao, 1987, all as juveniles, from the Malacca Straits. All records placed in the synonymy above are of material conforming to the dimensions of the present type collection. The present authors believe that Gramann's species and the present material represent a new species very closely related to *L. lilljeborgii* and that many authors have previously confounded the two. *Loxoconcha lilljeborgii* Brady, of Whatley & Keeler (1989) (Recent, Réunion Island) is of similar size to *L. grammani*, but differs in its horizontal ribs that are particularly well developed at the end margins.

Hartmann (1978) described *L. broomensis* and *L. georgei* ssp. nov (Recent eulittoral, Western Australia). The line drawings of the internal characters and soft parts and the SEM photographs of the externals of the males show them to be distinct species. The ornament of the male of *L. broomensis* is dominated anteriorly by two branched lateral ribs formed by the stronger development of the muri and a short rib extends dorsolaterally from the prominent posterodorsal tubercle. The female of *L. broomensis*, however, lacks the anterior ribs and the posterodorsal tubercle is not as strongly developed. Conversely, the male of *L. georgei* lacks the anterior branched ribs and the posterodorsal tubercle is less well developed. The female of *L. georgei* possesses the 2 anterior branched ribs and a well-developed posterodorsal tubercle. As these two species were found in the same localities, except at Port Samson, where *L. broomensis* was absent, it is conceivable that the sexes have been confused. The female of *L. broomensis* should be placed with the male of *L. georgei* and *vice versa*. Consequently, only the males are compared to the present material. The male of *L. broomensis* is very similar in size, shape and ornament and particularly in the degree of development of the posterodorsal tubercle. However, the two anterior lateral ribs of *L. broomensis* are absent in *L. gramanni* and there are also differences in the detail of the pitted ornament. The male of *L. georgei*, although similar to the present species, differs in that the posterodorsal tubercle is less well developed and the posterior tooth of the left valve is illustrated as being bifid, while in the present species it is simple.

***Loxoconcha athersuchi* sp. nov.**

(Fig. 4, Nos 3, 6; Pl. 1, Figs 12-19)

Derivatio nominis.- L. For Dr. John Athersuch in recognition of his important contribution to our knowledge of Recent British and Mediterranean Ostracoda.

Holotype.- Female LV, RT/SIR/433. Plate 1, Fig. 12.

Type locality and horizon.- Sample 54, 3,600 feet offshore, east of Point Cruz, Honiara Bay, Guadalcanal. 24 fathoms. Unconsolidated, very fine-grained sand. Recent.

Material.- 56 valves and carapaces, A-2 to adult. Samples: 1, 2, 5, 14, 15, 17, 40, 41 53-58, 60-62, Guadalcanal.

Diagnosis.- A species of *Loxoconcha* with small, deep, discrete circular puncta sub-centrally, becoming more elongate anteriorly and posteriorly; concentric about mid-point with a degree of longitudinal orientation. A weakly developed tubercle just below posterior cardinal angle. Eye-spot small, low, inconspicuous.

Description.- Small to medium. Thick-shelled. Translucent in well preserved specimens, otherwise opaque. Subrhomboidal in shape in lateral view: elliptical in dorsal view. Male longer, less tumid than female. Anterior margin well rounded anteroventrally, oblique anterodorsally: extremity above mid-height. Posterior margin with small, distinct, subdorsal caudal process with a long, gently convex posteroventral slope and a short, concave posterodorsal slope. Dorsal margin almost straight, very gently arched in female LV; anterior cardinal angle rounded; posterior obtuse. Ventral margin biconvex with distinct oral concavity. Greatest length at about mid-height; greatest height at posterior third, greatest width median. LV slightly overlaps RV at dorsal cardinal angles and orally. Eye-spot inconspicuous, small, round, glassy. Very small tubercle just below posterior cardinal angle. Surface of valves strongly and deeply punctate; puncta circular subcentrally becoming more quadrate peripherally, concentric about mid-point; dorsal and posterior marginal rims smooth. Npc's large, circular, slightly recessed, sieve-plate toward exterior, pore open internally, moderately numerous, evenly distributed on edge of puncta or on muri. Dorsally pores become elongate and narrow, aligned parallel to margin. Inner lamella wide, very narrow crescentic anterior and posterior vestibulae. LOC and IM subparallel to OM, coincident orally. Mpc's few; 9 anterior and 6 posterior canals: 2 distinct canals at caudal process, simple, straight, well spaced. Very strong, distinct, subperipheral selvage. Hinge gongylodont, delicate for the genus: median element straight in LV with subquadrate denticles; in RV narrow, elongate denticles. Central muscle scars: 4 subovate adductors, dorsomedian scar more elongate and a kidney-shaped frontal scar open anteriorly.

Dimensions.-

	Length	Height	Width
Holotype Female LV, RT/SIR/433	0.50	0.33	
Paratype Female C, RT/SIR/431	0.48	0.32	0.26
Paratype Male C, RT/SIR/432	0.48	0.30	0.24
Male LV, RT/SIR/434	0.52	0.32	
Female RV, RT/SIR/435 0.	49	0.34	
Male RV, RT/SIR/437	0.51	0.30	
Male LV, RT/SIR/439	0.48	0.30	
Female RV, RT/SIR/440	0.50	0.32	

Mean Dimensions.-

	Length	Height	Width
17 Female C	0.42(0.40-0.48)	0.29(0.28-0.33)	0.23(0.21-0.27)
19 Male C	0.49(0.43-0.55)	0.29(0.25-0.35)	0.25(0.22-0.29)
11 A-1 LV	0.36(0.32-0.40)	0.23(0.20-0.25)	
2 A-2	0.27, 0.28	0.17, 0.18	

Distribution.- Williams (1980, MS) found this to be the dominant species in Quaternary sediments from the Indespensible reefs and Guadalcanal.

Remarks.- Loxoconcha athersuchi is similar in shape, size and punctate ornament to the male of *L. georgei* Hartmann, 1978 (Recent euttittoral, Western Australia), but differs in detail of the ornament subcentrally and ventrally. *Loxoconcha georgei* appears to be morphologically intermediate between *L. gramanni* sp. nov. and the present species in the development of the posterodorsal tubercle. *Loxoconcha mandiviensis* Jain, 1978, (Recent , Western India) differs in that it does not possess a posterodorsal tubercle and in the detail of the ornament. The relationship of *L. athersuchi* sp. nov. to *L. minyaustralis* McKenzie in Howe & McKenzie, 1989 is difficult to determine, as the latter is inadequately illustrated by a single figure and lacks a description. It is also small (L= 0.46) but there are a number of shape and ornament differences and its caudal process is much less "upturned".

***Loxoconcha shortlandensis* sp. nov.**

(Fig. 4, Nos 8, 11; Pl. 1, Figs 20-27)

Derivatio nominis.- L**.** Named for the type locality, Shortland Island.

Holotype. -Female LV, RT/SIR/443. Plate 1, Fig. 22.

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.- 102 valves and carapaces, A-2 to adult. Samples: 1, 2, 13-15, 17, 50, 55-58, OS5, OS6, Guadalcanal and Shortland islands.

Diagnosis.- A medium species of *Loxoconcha* strongly and evenly inflated mediolaterally with ventral margin not overhung by valve tumidity and rotund-elliptical in dorsal view. Surface with deep, closely spaced, circular puncta

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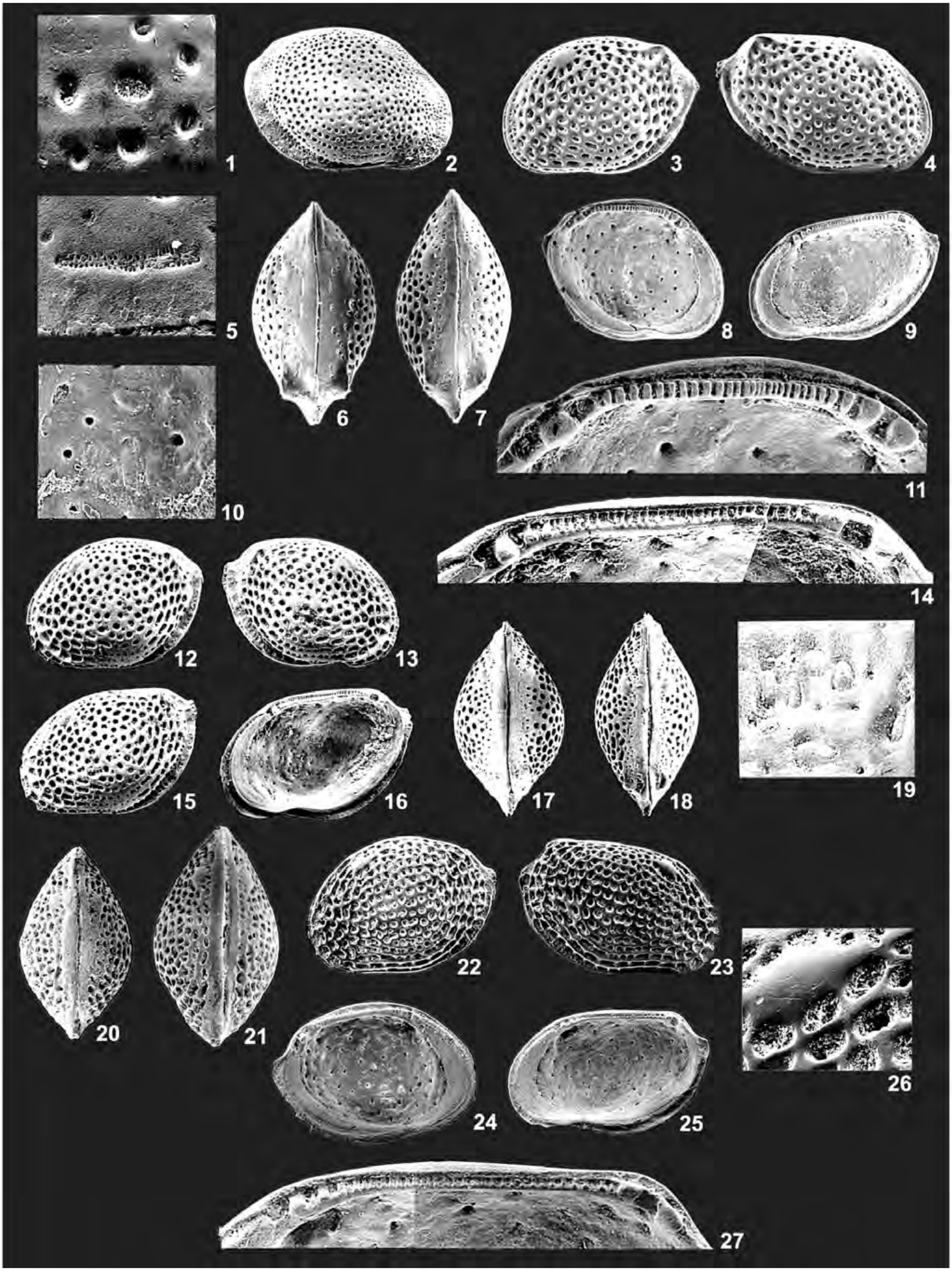
Plate 1. *1-2 Loxoconcha* sp. A *1, 2, R*ight valve RT/SIR/430 *1,* detail of normal pore canal x 367.6, *2,* external lateral view x 58.7. *3-11, Loxoconcha pumicosa* (Brady, 1880) *3,* Holotype female left valve RT/SIR/421 external lateral view x 77.8. *4,* Paratype male right valve RT/SIR/419 external lateral view x 80.9. *5, 7,* Paratype male carapace RT/SIR/416 *5,* detail of normal pore canal x 629.5, *7,* dorsal view x 83.7. *6,* Paratype female carapace RT/SIR/417 dorsal view x 84.8. *8, 11,* Female left valve RT/SIR/423 *8,* internal view x 65.3, *11,* detail of hinge x 245.4. *9,* Male right valve RT/SIR/425 internal view x 69.4. *10,* Female right valve RT/SIR/424 central muscle scars x 275.8. *12-19, Loxoconcha athersuchi* sp. nov. *12,* Holotype female left valve RT/SIR/433 external lateral view x 62.0. *13,* Female right valve RT/SIR/435, external lateral view x 63.3. *14, 16, 19,* Male right valve RT/SIR/437 *14,* detail of hinge x 249.9, *16,* internal view x 64.7, *19,* central muscle scars x 453.8. *15,* Male left valve RT/SIR/434 external lateral view x 59.6. *17,* Paratype female carapace RT/SIR/431 dorsal view x 70.8. *18,* Paratype male carapace RT/SIR/432 dorsal view x 72.9. *20-27, Loxoconcha shortlandensis* sp. nov. *20,* Paratype female carapace RT/SIR/448, dorsal view x 63.0. *21,* Paratype male carapace RT/SIR/441, dorsal view x 67.2. *22,* Holotype female left valve RT/SIR/443 external lateral view x 59.3. *23,* Paratype male right valve RT/SIR/445 external lateral view x 55.6. *24,* Female left valve RT/SIR/447 internal view x 66.7. *25, 27,* Male right valve RT/SIR/446 *25,* internal view x 60.0, *27,* detail of hinge x 207.0. *26,* Male left valve RT/SIR/442, detail of eye-spot x 308.2.

Plate 1



subcentrally, becoming reticulate peripherally; ornament concentric about mid-point with strong alignment of muri ventro-laterally and ventrally. Anterior marginal rim with larger quadrate reticulae. Eye-spot large, low, conspicuous.

Description.- Medium. Thick-shelled. Opaque. Sub-rhomboidal in lateral view; rotund-elliptical in dorsal view. Dimorphic, male longer and less tumid than female. Anterior margin well rounded anteroventrally, becoming oblique anterodorsally; extremity at mid-height. Posterior margin with small, distinct caudal process well above mid-height with a gently convex, oblique posteroventral slope and short, concave -posterodorsal slope. Posterior more rounded in male. Dorsal margin almost straight, more gently arched in female LV. Anterior cardinal angle rounded; posterior obtuse. Ventral margin biconvex; oral concavity more pronounced in male, not overhung by valve tumidity. Greatest length below mid-height; greatest height at posterior third; greatest width medianly. LV a little larger than RV with slight overlap at dorsal cardinal angles and orally. Eye-spot large, low, conspicuous, round, glassy. Surface of valves strongly and deeply punctate; puncta circular subcentrally becoming: more quadrate peripherally, arranged concentrically about mid-point with a strong alignment of lateral muri ventro-laterally and ventrally. Anterior marginal rim with larger quadrate reticulae. Npcs large, circular, sieve-type, evenly distributed usually to one edge of puncta, moderately numerous, sieve-plate toward exterior and somewhat recessed, pores open internally. Inner lamella wide: LOC and IM coincident, except posteriorly where a very narrow crescentic posterior vestibulum is present. Npcs few; 7 anterior and 6 posterior, simple, straight, widely spaced. Hinge gongylodont, robust; median element straight, in LV with oval, discrete denticulae becoming more quadrate distally and in RV discrete enclosed sockets and elongate, narrow denticles. Central muscle scars comprise 4 ovate adductor scars, dorsomedian scar more elongate, ventral scar more anteriorly disposed, frontal scar kidney-shaped, open anteriorly, at height of median adductor scars.

Dimensions.-

	Length	Height	Width
Holotype female LV, RT/SIR/443	0.54	0.37	
Paratype male C, RT/SIR/441	0.58	0.36	0.30
Paratype male RV, RT/SIR/445	0.63	0.39	
Paratype female C, RT/SIR/448	0.54	0.37	0.30
Male LV, RT/SIR/442	0.60	0.37	
Female RV, RT/SIR/444	0.53	0.37	
Male RV, RT/SIR/446	0.60	0.36	
Female LV, RT/SIR/447	0.54	0.38	
Male LV, RT/SIR/449	0.63	0.39	
Female RV, RT/SIR/450	0.55	0.38	
A-1 LV	0.46	0.30	

Mean Dimensions.-

	Length	Height	Width
7 Female C	0.55(0.51-0.59)	0.37(0.36-0.40)	0.30(0.29-0.31)
6 Male C	0.59(0.58-0.60)	0.37(0.36-0.38)	0.31(0.30-0.32)
14 A-1 LV	0.45(0.43-0.47)	0.29(0.28-0.31)	
8 A-1 RV	0.44(0.41-0.47)	0.28(0.27-0.29)	
1 A-1 LV	0.32	0.21	
1 A-2 RV	0.35	0.22	

Remarks.- The present species is similar to *L. mandviensis* Jain, 1978, from the Recent off Kutch, Western India, but is less strongly arched dorsally and more inflated laterally. The present species differs from *L.* sp. cf. *australis* Brady, 1880 of Hartmann, 1979, from the Recent eulittoral of Southwestern Australia, in being less caudate posteriorly, the female LV is arched dorsally, the anterior marginal keel is absent and the puncta less stellate. Puri and Hulings (1976) illustrated Brady' s original material of *L. australis* which is more inflated posterodorsally and is 0.15 mm longer than Hartmann's material and the present species. Although sexual dimorphism in the adults is manifest, precocious sexual dimorphism was not observed.

***Loxoconcha pumicosa* (Brady, 1880)**

(Fig. 4, Nos 7, 10; Pl. 2, Figs 1-9)

1880 *Loxoconcha pumicosa* sp. nov. Brady: 118, pl. 28, fig. 2a-d.

2001 *Loxoconcha pumicosa* Brady; Titterton *et al*: 38, pl. 2, figs 20-22. (*q. v.* for synonymy).

Material.- 40 valves and carapaces, adult to A-2 instars. Samples: 1, 2, 13-17, 29, 54-58 Guadalcanal.

Dimensions.-

	Length	Height	Width
Female C, RT/SIR/451	0.49	0.33	0.29
Male C, RT/SIR/452	0.53	0.32	0.30
Female LV, RT/SIR/ 453	0.50	0.33	
Female RV, RT/SIR/454	0.48	0.30	
Male RV, RT/SIR/455	0.52	0.31	
Male RV, RT/SIR/456	0.52	0.31	
Male LV, RT/SIR/457	0.53	0.31	
Male LV, RT/SIR/458	0.50	0.31	
Female LV, RT/SIR/459	0.51	0.33	

Mean Dimensions.-

	Length	Height	Width
1 Female C	0.49	0.34	0.29
15 Female LV	0.48(0.46-0.50)	0.32(0.30-0.35)	
7 Male LV	0.51(0.50-0.53)	0.31(0.31-0.32)	
4 A-1 RV	0.42(0.42-0.43)	0.28(0.27-0.28)	
1 A-2	0.34	0.21	

Distribution.- Recorded by Brady (1880) from the Recent of Booby Island and the Admiralty Islands, and from New Caledonia, Fiji and Samoa (Brady, 1890). It also occurs in the Recent around Pulau Seribu, Java Sea (Watson, 1988, MS).

Loxoconcha tumulosa **Hu, 1979**

(Fig. 4, Nos 9, 12; Pl. 2, Figs 10-17)

1978 *Loxoconcha* sp. Hartmann: pl. 10, fig. 6.
1979 *Loxoconcha tumulosum* Hu: 71, pl. 2, figs 17, 21, 22, 26, 27, 30, 31, text-fig. 10.
1981 *Loxoconcha heronislandensis* Hartmann: 117; text-figs 52-54; pl. 9, figs 1-6.
1984 *Loxoconcha tumulosum* Hu; Hu: pl. 4, figs 17, 18, 20.
1984 *Loxoconcha heronislandensis* Hartmann; Hartmann: 128, t.-figs 47, 48, pl. 7, figs 1-7.
1986 *Loxoconcha tumulosum* Hu; Zhao, Wang & Zhang: pl. 2, fig. 13.
1987 *Loxoconcha tumulosa* Hartmann; Whatley & Zhao: 350, pl. 5, fig. 12.
1990 *Loxoconcha tumulosa* Hu; Gou: 25, pl. 3, figs 45-47.
2006 *Loxoconcha tumulosa* Hu; Warne *et al*.: 125, pl. 4, figs 25, 26.

Material.- 489 valves and carapaces, A-2 to adult. Samples: 1, 2, 13-17, 20, 29, 30, 32, 40, 55, 57, 58, OS5, OS6 Guadalcanal and Shortland islands.

Dimensions.-

	Length	Height	Width
Female LV, RT/SIR/464	0.51	0.31	
Female C, RT/SIR/460	0.54	0.34	0.31
Male C, RT/SIR/461	0.59	0.34	0.31
Male LV, RT/SIR/462	0.58	0.33	
Male RV, RT/SIR/463	0.58	0.34	
Female RV, RT/SIR/465	0.51	0.31	
Male RV, RT/SIR/466	0.58	0.34	
Male LV, RT/SIR/467	0.58	0.35	
Female RV, RT/SIR/468	0.50	0.33	
A-1 RV, RT/SIR/469	0.46	0.27	

Mean Dimensions.-

	Length	Height	Width
10 Female C	0.53(0.51-0.54)	0.34(0.32-0.35)	0.31(0.29-0.32)
10 Male C	0.57(0.56-0.59)	0.34(0.33-0.36)	0.32(0.30-0.33)
15 A-1 LV	0.44(0.42-0.46)	0.27(0.25-0.27)	
15 A-1 RV	0.44(0.39-0.47)	0.26(0.23-0.27)	
13 A-2	0.32(0.31-0.33)	0.20(0.18-0.21)	

Distribution.- Large numbers of the living species were collected from algae from Heron Island, Eastern Australia by Hartmannn (1981) where it was more numerous on the protected inner reef than on the outer reef. Dead material was also found, in pools with coral detritus. Williams (1980, MS.) found this species in Quaternary brackish water sediments from the Indispensable Reefs and it is recorded by Zhao *et al*. (1986) from the South China Sea. Watson (1988, MS) found some 100 females specimens of this species (no males) from 12 samples on the islands in the Palau Seribu, Java Sea and Warne *et al.* found only 2 specimens at Shoal Bay, Northern Australia. The type material is fossil from Taiwan (Hu, 1979).

Remarks.- Hartmann (1981) compared *L. tumulosa* to *L. albaniensis* Hartmann, 1979, from the Recent eulittoral of Southwestern Australia and to *L. trita dunsboroughensis* Hartmannn, 1978, from the Recent eulittoral of Western Australia, as all three species were reticulate and possessed a prominent alar inflation. However, all three species differ in the size of the copulatory organ, outline of valve and in the detail of their reticulate ornament. The present species also resembles *Loxoconcha* sp. B of Jain, 1978, from the Recent of Western India, but the reticulae of the former are more irregular. Jain compared his species to *L. parallela* G. W. Muller, 1894 as figured by Bonaduce *et al.,* 1976, from the Recent of the Adriatic. Although sexual dimorphism is very conspicuous in the adults, precocious sexual dimorphism was not apparent.

Loxoconcha sp. A

(Pl. 1, Figs 1-2)

Material.- One adult right valve. Sample 65, Guadalcanal.

Diagnosis.- Subrhomboidal in lateral view. Anterior margin gently concave anterodorsally, becoming well rounded ventrally. Posterior margin slightly caudate; caudal process well above mid-height. Dorsal margin very gently arched. Ventral margin biconvex. Surface of valves ornamented by small, ovate puncta, concentric about midpoint. NPCs sieve-type. Inner lamella moderately wide: LOC and IM subparallel to OM. Very narrow anterior and posterior vestibulae. MPCs few; 8 anterior and 8 posterior canals.

Dimensions.-

	Length	Height
ARV RT/SIR/430	0.63	0.40

Remarks.- This species belongs to the same shape and ornamental group of the genus as the European species *L. rhomboidea* (Fischer, 1855). It is similar in size and ornament to *L. hendersonislandensis* Whatley *et al*. (2004) from Henderson Island in the Pitcairn group but differs in shape and in the details of the ornament.

Genus *Loxocorniculum* Benson & Coleman, 1963

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

Remarks.- Species are herein placed in this genus principally on shape and surface ornament. The usually characteristic pore conuli of *Loxocorniculum* occur only in *L. labyrinthos* sp. nov. but even those are small.

Loxocorniculum insulaecapricornensis (Hartmann, 1981)

(Fig. 4, Nos 13, 16; Pl. 3, Figs 1-10)

1981 *Loxoconcha insulaecapricornensis* Hartmann: 118, t.-figs 55-57; p1. 9, figs 7-17.
1984 *Loxoconcha insulaecapricornensis* Hartmann; Hartmann: 127, figs 42-46; pl. 6, figs 1-9.

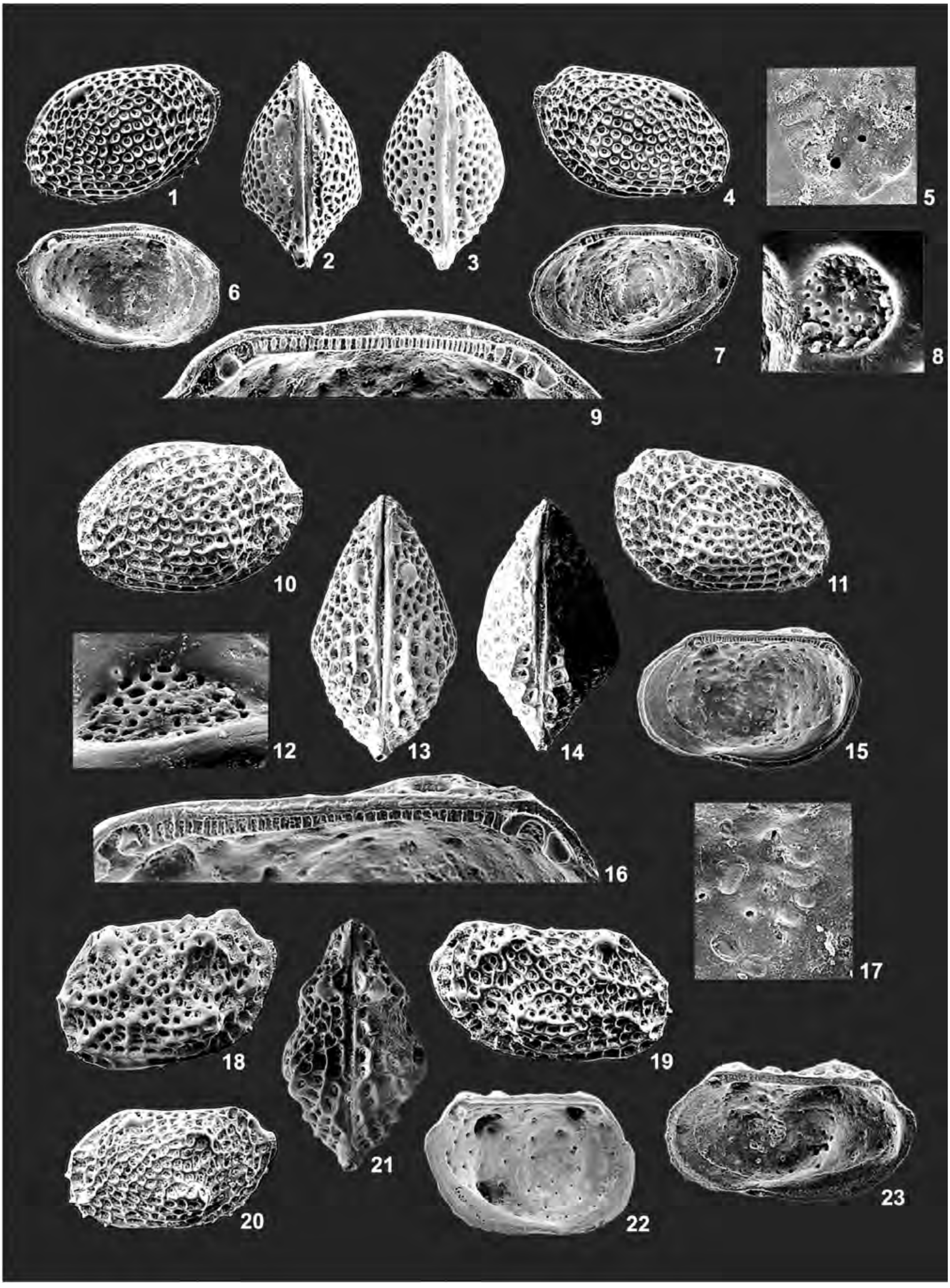
Material.- 159 valves and carapaces, A-2 to adult. Samples: OS5, OS6 Shortland Island.

Dimensions.-

	Length	Height	Width
Female C, RT/SIR/470	0.54	0.32	0.31
Male C, RT/SIR/471	0.63	0.32	0.30
Female RV, RT/SIR/472	0.53	0.30	
Female LV, RT/SIR/474	0.54	0.31	
Male RV, RT/SIR/473	0.63	0.33	
Male LV, RT/SIR/475	0.62	0.32	
Male RV, RT/SIR/476	0.62	0.33	
Female LV, RT/SIR/477	0.54	0.31	
Female RV, RT/SIR/478	0.54	0.31	
A-1 RV, RT/SIR/479	0.47	0.27	
Female RV, RT/SIR/480	0.53	0.30	
Male LV, RT/SIR/481	0.62	0.31	

Plate 2. *1-9, Loxoconcha pumicosa* (Brady, 1880) *1,* Female left valve RT/SIR/453 external lateral view x 68.0. *2,* Female carapace RT/SIR/451 dorsal view x 75.5. *3,* Male carapace RT/SIR/452 dorsal view x 71.7. *4, 8,* Male right valve RT/SIR/455 *4,* external lateral view x 67.3, *8,* detail of normal pore canal x 1511.3. *5, 6,* Male left valve RT/SIR/457 *5,* central muscle scars x 325.5, *6,* internal view x 67.9. *7,* Male right valve RT/SIR/456 internal view x 71.2. *9,* Female right valve RT/SIR/459 detail of hinge x 253.3. *10-17, Loxoconcha tumulosa* Hu, 1979 *10,* Female left valve RT/SIR/578 external lateral view x 78.4. *11,* Male right valve RT/SIR/581 external lateral view x 65.5. *12,* Male left valve RT/SIR/575, detail of normal pore canal x 1774.6. *13,* Male carapace RT/SIR/576, dorsal view x 78.0. *14,* Female carapace RT/SIR/576 dorsal view x 81.5.*15, 16, 17,* Male right valve RT/SIR/580 *15,* internal view x 69.0, *16,* detail of hinge x 221.3, *17,* central muscle scars x 263.3. *18-23, Sagmatocythere eridmatos* sp. nov. *18,* Holotype female left valve RT/SIR/488 external lateral view x 73.6. *19,* Paratype male right valve RT/SIR/482 external lateral view x 76.4. *20,* A-1 left valve RT/SIR/489 external lateral view x 77.1. *21,* Paratype male carapaceRT/SIR/484, dorsal view x 79.6. *22,* Female left valve RT/SIR/487 internal view x 77.6. *23,* Male right valve RT/SIR/483 internal view x 80.0.

Plate 2



Mean Dimensions. –

	Length	Height	Width
9 Female C	0.54(0.52-0.55)	0.33(0.32-0.33)	0.32(0.30-0.34)
10 Male C	0.62(0.59-0.66)	0.32(0.30-0.33)	0.31(0.29-0.33)
1 A-1 C	0.47	0.26	0.23
30 A-1	0.46(0.42-0.48)	0.26(0.24-0.28)	
4 A-2	0.35(0.34-0.36)	0.21(0.20-0.21)	

Distribution.- This very conspicuous species has been recorded from algae and coral sand from Heron Island, Eastern Australia (Hartmann, 1981). Watson (1988, MS) found some 230 adults and juveniles from 29 samples from the islands in the Palau Seribu, Java Sea.

Remarks.- This species is readily recognized by its large posterodorsal tubercle, large and pronounced ventrolateral tumidity, its weakly reticulate ornament with secondary papillae and some fine reticulation and with a narrowly open anteriorly C-shaped rib over the ventro-lateral inflation. It is similar in size and shape to *Loxoconcha antillea* Bold, 1946 as illustrated by Holden (1976, Pl.5, Figs.1-2 not Pl.4, Figs.10-11), from the Miocene of Midway Island, but is less strongly reticulate. *Loxoconcha antillea* Bold, 1946, from the Miocene of the Caribbean, is less strongly ribbed and the posteroventral inflation is situated less anteriorly than in the present species. *Loxocorniculum insulaecapricornensis* is similar in shape to *Sagmatocythere eridmatos* sp. nov. but the ornament of the latter is dominated by strong reticulo-punctation.

***Loxocorniculum labyrinthos* sp. nov.**

(Fig. 4, Nos 15, 18; Pl. 3, Figs 12, 14-17)

Derivatio nominis.- *Gr. laburinfos* - a labyrinth. With reference to labyrinthine nature of the reticulate and punctate ornament of this species.

Holotype.- LV, RT/SIR/493. Pl. 3, Figs 12, 14.

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

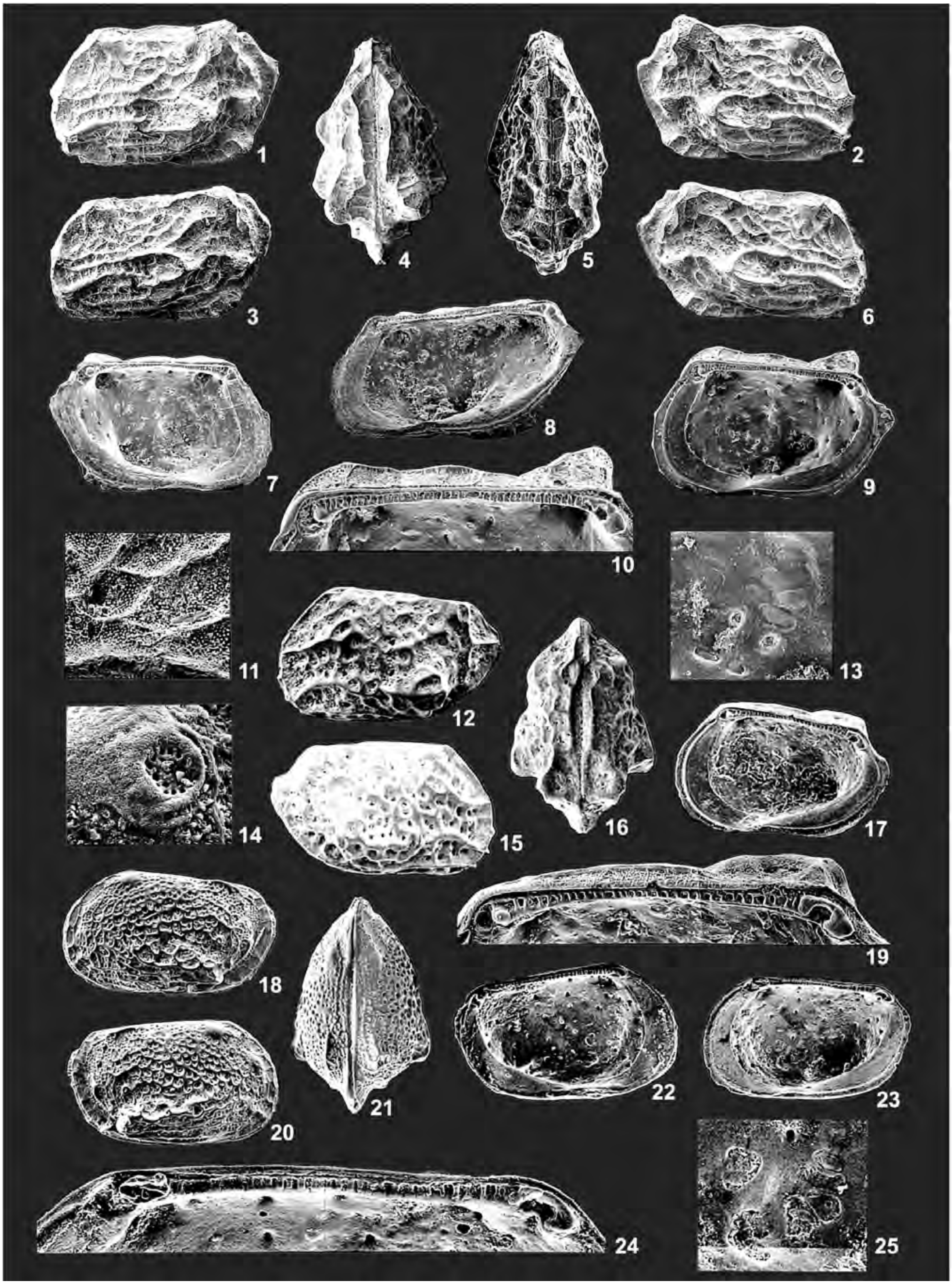
Material.- 116 valves and carapaces A-4 to adult. Samples: 1, 2, 13, 14, 17, 29, 32, 57, 58, OS5, OS6 Guadalcanal and Shortland islands.

Diagnosis.- A small species of *Loxocorniculum* distinguished by its subrectangular shape, strong ventrolateral ala in posterior third, irregular inflation just below the posterior cardinal angle and by the convoluted nature of the reticulate ornament within which is a delicate secondary ornament of fine papillae a fine secondary longitudinal ribbing along the primary muri.

Description.- Very small. Moderately thick-shelled. Opaque. Subrhomboidal in lateral view: bispinose in dorsal view. Anterior margin well rounded anteroventrally; becoming slightly oblique anterodorsally: extremity at mid-height. Posterior margin bluntly caudate well above mid-height, with a long gently convex posteroventral slope. Dorsal margin straight, cardinal angles. Ventral margin almost straight with very gentle oral concavity. Greatest length well above mid-height; greatest height at anterior cardinal angle; greatest width through ventrolateral alar projection. LV slightly larger than RV with small overlap along posterodorsal slope and at cardinal angles. Valves ventrolaterally alate in posterior third and also inflated below posterior cardinal angle into an irregular node. Eye-spot small but distinct, raised, ovate, glassy. Surface of valves very strongly and deeply reticulate and punctuate. Two irregular subparallel ribs extend laterally from anterior margin, the more ventral extending to the end of the ala. A vertical rib demarcates the proximal extent of the caudal process. A short rib extends laterally from the caudal process to meet the previously described rib at right angles. Very fine papillae occur within the

Plate 3. *1-10, Loxocorniculum insulaecapricornensis* (Hartmann) 1981 *1,* Female left valve RT/SIR/474 external lateral view x 74.1. *2,* Female right valve RT/SIR/472 external lateral view x 71.7. *3, 11,* Male left valve RT/SIR/475 *3,* external lateral view x 62.9, *11,* detail of ornament x 320.3. *4,* Female carapace RT/SIR/470 dorsal view x 74.1. *5,* Male carapace RT/SIR/471 dorsal view x 68.3. *6,* Male right valve RT/SIR/473 external lateral view x 63.5. *7,* Female left valve RT/SIR/477 internal view x 74.1. *8,* Male right valve RT/SIR/476 internal view x 69.4. *9, 10, 13,* Female right valve RT/SIR/478 *9,* internal view x 77.8, *10,* detail of hinge x 160.9, *13,* central muscle cars x 325.5. *12, 14-19, Loxocorniculum labyrinthos* sp. nov. *12, 14,* Holotype left valve RT/SIR/493 *12,* external lateral view x 102.6, *14,* detail of normal pore canal x 1455.9. *15,* Paratype right valve RT/SIR/494 external lateral view x 105.4. *16,* Carapace RT/SIR/492 dorsal view x 102.7. *17, 19,* Right valve RT/SIR/495 *17,* internal view x 97.4, *19,* detail of hinge x 276.0. *18-25, ?Sagmatocythyere microreticulata* sp. nov. *18,* Holotype left valve RT/SIR/499 external lateral view x 90.5, *20,* Paratype right valve RT/SIR/500, external lateral view x 72.5. *21,* Paratype carapace RT/SIR/498, dorsal view x 92.7. *22,* Left valve RT/SIR/501 internal view x 95.1. *23, 24, 25,* Paratype right valve RT/SIR/500 *23,* internal view x 90.2,*24,* detail of hinge x 301.9,*25,* central muscle scars x 354.2.

Plate 3



puncta and on the muri a fine longitudinal secondary ribbing. Npcs small, sieve-type; ovate, regularly distributed on muri, small pore conuli developed particularly anteriorly. Inner lamella wide: LOC and IM coincident and subparallel to OM. Mpcs few; 6 anterior and 5 posterior canals, most anterior canals typically branched, others simple, straight, well spaced. Hinge gongylodont, robust; median element straight with almost quadrate denticulae in RV. Central muscle scars comprise 4 ovate adductor scars and a V-shaped frontal scar open anteriorly.

Dimensions.-

	Length	Height	Width
Holotype LV, RT/SIR/493	0.39	0.24	
Paratype C, RT/SIR/492	0.37	0.22	0.25
Paratype RV, RT/SIR/494	0.37	0.21	
Paratype LV, RT/SIR/497	0.39	0.23	
RV, RT/SIR/495	0.39	0.22	
RV, RT/SIR/496	0.39	0.30	

Mean Dimensions.-

	Length	Height	Width
11 C	0.39(0.38-0.41)	0.23(0.22-0.24)	0.27(0.25-0.28)
17 LV	0.39(0.36-0.41)	0.23(0.22-0.24)	
10 A-1 LV	0.33(0.32-0.34)	0.19(0.18-0.21)	
10 A-1 RV	0.32(0.31-0.33)	0.19(0.17-0.21)	

Distribution.- Williams, 1980 found over 300 valves of *L. labyrinthos* in sediments of Quaternary age from the Indispensable Reefs, Solomon Islands.

*Remarks.-*This species resembles *L. lapidiscola* (Hartmann, 1959), from the Recent of El Salvador, because of its strongly caudate posterior margin, ornament of irregular ribs and small pore conuli. *Loxoconcha gilli* McKenzie, 1967, from the Recent of Southeastern Australia, is of a similar size and shape and is also reticulo-costate, but differs from *L. labyrinthos* in the detail of its ornament, particularly in lacking the two anterior, lateral ribs. Sexual dimorphism was not observed in the present species.

Genus *Sagmatocythere* Athersuch, 1976

Type species.- Loxoconcha napoliana Puri, 1963

Sagmatocythere eridmatos sp. nov.

(Fig. 4, Nos 14, 17; Pl. 2, Figs 18-23)

2006 *Loxocorniculum* sp. 2. Warne: Warne *et al.*, 128, pl. 5, figs 13, 14.

Derivatio nominis.- Gr. *εριδματος* eridmatos - strongly built. With reference to the thick-shelled and robustly ornamented carapace of this species.

Holotype.- Female LV, RT/SIR/488. Plate 2, Fig. 18.

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

Material.- 25 valves and carapaces, A-2 to adult. Samples: OS5, OS6 Shortland Island.

Diagnosis.- A thick-shelled, medium species of *Sagmatocythere* with subquadrate female and sub-rectangular male; bluntly sub-sagitate and bispinose in dorsal view. Surface of valves strongly reticulate; lateral muri dominant ventrally and antero-laterally and vertical muri dominant posteriorly and with blunt ala posteroventraly in posterior third and strong irregular tubercle posterolaterally, just below the dorsal margin. Dorsal margin very gently concave. Weakly crenulate median element.

Description.- Medium. Thick-shelled. Opaque. Sexual dimorphism conspicuous; male subrectangular, female subquadrate in lateral view; subsaggitate and bispinose in dorsal view. Anterior margin rounded in female anteroventrally, somewhat truncated in male; bearing 3 or 4 small well spaced marginal denticles; anterodorsal slope oblique, extremity above mid-height. Posterior margin with caudal process well above mid-height with a long gently convex posteroventral slope bearing some 5 small, well spaced marginal denticles and a short concave posterodorsal slope. Dorsal margin almost straight, cardinal angles well marked. Ventral margin almost straight, with gentle oral concavity. Greatest width well above mid-height; greatest height median; greatest width through ventrolateral ala. LV slightly larger than RV. Valves strongly inflated ventrolaterally with a strong irregular alar tubercle posteroventolaterally. Surface of valves deeply and strongly reticulate; reticula small, irregular, rather randomly distributed. Horizontal muri dominant ventrally and anterolaterally, with well developed median and ventrolateral ribs. Npc's moderately numerous, large, sieve-type, circular, recessed, evenly distributed. Eye-spot conspicuous, small, glassy. Inner lamella wide, particularly posteroventrally; LOC and IM coincident and subparallel to OM. Mpcs few; 9 anterior and 7 posterior canals, simple, straight, well spaced. Hinge gongylodont, median element in the LV with numerous very small oval denticulae to almost smooth in some specimens and with trace of lobation in posterior terminal element in RV. Central muscle scars comprise 4 closely spaced adductor scars, mediodorsal scar more elongate with a kidney-shaped frontal scar open anteriorly.

Dimensions.-

	Length	Height	Width
Holotype female LV, RT/SIR/488	0.53	0.31	
Paratype male RV, RT/SIR/482	0.55	0.30	
Paratype male C, RT/SIR/484	0.54	0.31	0.31
Paratype female RV, RT/SIR/486	0.53	0.31	
Paratype male LV, RT/SIR/490	0.56	0.30	
Male RV, RT/SIR/483	0.55	0.31	
Male LV, RT/SIR/485	0.57	0.30	
Female LV, RT/SIR/487	0.49	0.30	
A-1 LV, RT/SIR/489	0.48	0.27	
Female RV, RT/SIR/491	0.52	0.31	

Mean Dimensions.-

	Length	Height	Width
10 Female LV	0.51(0.49-0.54)	0.32(0.30-0.34)	
1 Male C	0.54	0.32	0.32
5 Male LV	0.56(0.54-0.57)	0.32(0.30-0.33)	
1 A-1	0.48	0.27	
3 A-2	0.43(0.42-0.43)	0.25	

Distribution.- Williams (1980, MS) found 2 valves of this species in sediments of Quaternary age from the Indispensable Reefs. Warne *et al.* (2006) encountered 6 specimens of this species from Shoal Bay, N Australia.

Remarks.- This species is somewhat similar to *Loxoconcha antillea* s.s. Bold, 1946 of Holden, 1976 (plate 4, figs.10-11 not plate 5, figs.1-2), from the Miocene of Midway Island, it differs, however, detail of the ornament and by the presence of the strong posterodorsal lateral inflation. This inflation also distinguishes the present species from *Loxoconcha longispina* Keij, 1953 of Holden (1976) also from Midway Island, which is also more strongly inflated posteroventrally than the present species. *Sagmatocythere eridmatos* is somewhat similar to *Loxoconcha* sp. cf. *L. variolata* Brady, 1878 of Hartmann, 1979, from the Recent eulittoral of Southern Australia but is less inflated posteroventerally and has a more strongly developed posterodorsal lateral inflation.

?*Sagmatocythyere microreticulata* sp. nov.

(Fig. 4, Nos 19, 20; Pl. 3, Figs 18-25)

Derivatio nominis.- L. For the delicate nature of the secondary punctation of this species.

Holotype.- LV, RT/SIR/499. Pl. 3, Fig. 18.

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

Material.- 79 valves and carapaces, A-1 to adult. Samples: OS5, OS6 Shortland Island.

Diagnosis.- A small species tentatively assigned to *Sagmatocythere*, subrectangular in lateral view, bluntly sagitate in dorsal view. Valves strongly inflated ventrolaterally in posterior quarter into blunt alae. Reticulate ornament with secondary reticulation within fossae, except subcentrally and on ala; secondary punctation becoming dominant peripherally, except ventrally. A short rib occurs posterodorsally.

Description.- Small. Moderately thick-shelled. Opaque. Subrectangular in lateral view, bluntly sagitate in dorsal view. Anterior margin well rounded becoming slightly oblique anterodorsally; extremity at mid-height. Posterior margin with small blunt caudal process well above mid-height, with a long, gently convex posteroventral slope and a very short posterodorsal slope. Dorsal margin almost straight. Ventral margin almost straight. Greatest length just above mid-height; greatest height through anterior cardinal angle; greatest width at posterior third. LV a little larger than RV, with slight overlap on posterodorsal slope. Valves strongly inflated ventrolaterally through the blunt alae. Surface of valves reticulate; reticulae very irregular, some muri more strongly developed into riblets, muri longitudinally aligned ventrally, particularly along alar process. Anterior and posteridor marginal rims almost smooth with very fine radiating riblets. Short, strong rib developed just anterior to posterior cardinal angle, parallel to dorsal margin. Secondary ornament of puncta developed within fossae except mediolaterally and on ala, becoming dominant antero- and posterodorsally behind marginal rims. Npcs moderate, sieve-type, small, circular, evenly distributed, Eye-spot conspicuous, low, small, circular, glassy. Inner lamella wide; LOC and IM coincident and sub-parallel to OM. Mpcs few; 9 anterior and 4 posterior canals, simple, straight, one or two short, false canals. Hinge gongylodont, delicate, median element straight and rather weakly crenulate. Central muscle scars comprise 4 elongate adductor scars in vertical row with a V-shaped frontal scar open anteriorly.

Dimensions.-

	Length	Height	Width
Holotype LV, RT/SIR/499	0.42	0.24	
Paratype C, RT/SIR/498	0.41	0.22	0.26
Paratype RV, RT/SIR/500	0.41	0.23	
Paratype LV, RT/SIR/503	0.40	0.23	
LV, RT/SR/501	0.41	0.24	
RV, RT/SIR/502	0.39	0.23	

Mean Dimensions.-

	Length	Height	Width
10 C	0.42(0.40-0.43)	0.24(0.23-0.25)	0.27(0.26-0.28)
13 LV	0.40(0.38-0.42)	0.24(0.22-0.25)	
1 A-1 C	0.35	0.19	0.22
11 A-1 LV	0.34(0.32-0.35)	0.20(0.19-0.20)	
9 A-1 RV	0.33(0.32-0.34)	0.19(0.19-0.20)	

Distribution.- Watson (1988, MS) found almost 200 individuals of this species from 26 samples from 3 islands in the Paau Seribu, Java Sea.

Remarks.- The present species is distinctive by its small size, subrectangular shape reticulate primary and punctate secondary ornament. It is unlike any other species recorded in the Pacific, except ?*S. dictyoklostos* (Whatley *et al.*, 2004) from the Pitcairn Island group and to which it probably related. The latter species, however, is notably larger (L=0.61-0.66) and has the central area dominantly punctate and the periphery reticulate, the reverse of the present species. It is similar in shape to *Loxoconcha dampierensis* Hartmann, 1978 from tropical western Australia. It is placed tentatively in *Sagmatocythere* on grounds of shape and its rather weak hingement. Sexual dimorphism not observed.

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Foraminíferos de marismas y llanuras de marea del estuario de Bahía Blanca, Argentina: distribución e implicaciones ambientales

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Resumen

El estuario de Bahía Blanca es un complejo sistema sedimentario y ecológico cuyos foraminíferos bentónicos recientes aún no han sido investigados en profundidad. Muestras superficiales tomadas en 3 sectores del estuario (2 correspondientes a la cabecera y 1 a la desembocadura) han sido analizadas a fin de establecer la distribución, abundancia y diversidad de estos organismos en función de las características ambientales de cada uno de los sectores. Fueron registradas 4 asociaciones microfaunísticas a partir del análisis de los ejemplares vivientes al momento del muestreo. La fauna dominante está constituida esencialmente por 4 especies de foraminíferos calcáreos hialinos (*Ammonia parkinsoniana, Ammonia tepida, Haynesina germanica* y *Elphidium gunteri*) y 2 de foraminíferos aglutinados (*Trochammina inflata* y *Jadammina macrescens*), los cuales se distribuyen a lo largo del estuario respondiendo a gradientes de salinidad, tiempo de exposición y tipo de marisma.

Palabras clave: Foraminíferos bentónicos, estuarios, marismas, salinidad, Bahía Blanca, Argentina, Océano Atlántico SW.

Abstract

[*Foraminifera in salt marshes and tidal flats from the Bahía Blanca estuary, Argentina: distribution and environmental implications*] The Bahía Blanca estuary is a complex sedimentary and ecological system which recent benthic foraminifera have not been investigated in depth. Surface samples taken in 3 sectors of the estuary (2 corresponding to the head and 1 to the mouth) have been analyzed in order to establish the distribution, abundance and diversity of these organisms, according to the environmental characteristics of each location. From the analysis of the living specimens at the moment of the sampling, 4 faunal assemblages were registered. The dominant microfauna is constituted essentially by 4 species of calcareous hyaline foraminifera (*Ammonia parkinsoniana*, *Ammonia tepida, Haynesina germanica* and *Elphidium gunteri*) and 2 species of agglutinated ones (*Trochammina inflata* and *Jadammina macrescens*), which are distributed along the estuary in response to salinity gradients, time of exposure and type of salt marsh.

Key words: Benthic foraminifera, estuaries, salt marshes, salinity, Bahía Blanca, Argentina, SW Atlantic Ocean.

1. INTRODUCCIÓN

Los foraminíferos actuales son organismos frecuentemente utilizados como indicadores para caracterizar el ambiente y así poder realizar reconstrucciones paleoambientales en secuencias fósiles. Sin embargo, el conocimiento de la biogeografía y ecología de los foraminíferos es aplicable también a ambientes modernos, debido a que son importantes indicadores de polución ambiental e impacto antrópico y permiten comparar faunas modernas contaminadas con aquellas fósiles que no han sido afectadas por contaminación (Armynot du Châtelet *et al.*, 2004).

Todas las aplicaciones que involucren a los foraminíferos bentónicos, tanto fósiles como actuales deberían incluir el estudio y comprensión de su ecología. Esto se debe a que los foraminíferos están estrechamente relacionados con su ambiente y pueden registrar variaciones muy leves de los parámetros ambientales. Por lo tanto, para poder realizar la reconstrucción de las condiciones paleoambientales de una región es indispensable comprender los procesos biológicos y sedimentológicos que condicionan la distribución de los foraminíferos actuales (Murray, 2006).

Existe mucha información sobre foraminíferos de ambientes restringidos, estuarios, llanuras mareales y marismas del hemisferio norte pero hasta el momento sólo algunos estudios han sido realizados en el hemisferio sur, especialmente en lo que respecta a Sudamérica. Entre estos trabajos se encuentran los de Boltovskoy (1954 a, b; 1957; 1965), Boltovskoy y Lena (1971), Boltovskoy *et al*. (1980), Bernasconi (2006), Cusminsky *et al*. (2006; 2009), Ferrero (2006), Calvo-Marcilese (2008), Calvo-Marcilese *et al*. (2007), Calvo-Marcilese y Pérez-Panera (2008) y Scott *et al*. (1990).

En este trabajo se propone aprovechar la variabilidad de ambientes intermareales existentes en el estuario de Bahía Blanca para hacer una primera aproximación al estudio de las condiciones biológicas y sedimentarias que determinan, en la actualidad, la presencia de las distintas asociaciones de foraminíferos en el área de estudio. A partir de esta primera contribución, se pretende colaborar con información actualizada, y circunscrita a los ambientes de marismas y llanuras de inundación que presentan distintas combinaciones de parámetros físicos y biológicos. En particular, se comparan las asociaciones de foraminíferos bentónicos de estaciones de muestreo ubicadas en los sectores interno y externo del Canal Principal, sometidos a diferentes niveles de inundación/exposición y caracterizadas por la presencia de distintos tipos de marismas.

Aunque este trabajo corresponde a un primer muestreo de sedimentos superficiales en el área de estudio para un momento dado, se prevé la toma de datos en forma estacional para suplir la falta de información y llevar un registro completo de las distribuciones y relaciones entre especies, a medida que se modifican las condiciones ecológicas. Esperamos que de la continuación de este trabajo surja la información de base necesaria para interpretar las variaciones del nivel del mar durante el Holoceno y la reconstrucción de paleoambientes a partir de registros fósiles. Además, como resultado del trabajo propuesto, podrían surgir valiosos indicadores para la detección de contaminación ambiental, en base a la abundancia, diversidad y características de la fauna de foraminíferos bentónicos hallada. Ningún estudio con estas características ha sido publicado para este área con anterioridad.

2. ÁREA DE ESTUDIO

El estuario de Bahía Blanca ocupa una amplia zona costera y se encuentra ubicado en el sudeste de la provincia de Buenos Aires. Es un sistema mesomareal cuya configuración regional se caracteriza por la presencia de 3000 km^2 de complejos canales de tipo meandriforme, separados por islas de relieve plano y extensas llanuras de mareas fangosas y arenosas (Piccolo *et al.,* 1988; Aliotta y Lizasoain, 2007).

El arroyo Napostá Grande, junto con el río Sauce Chico se constituyen como los principales aportes de agua dulce que recibe el Canal Principal del estuario de Bahía Blanca (Piccolo *et al.,* 1988). Dicho canal se encuentra ubicado en el extremo norte del estuario y su longitud es de aproximadamente 60 km. Posee una configuración de embudo, presentando una anchura máxima en su cabecera de 200 m, mientras que en la desembocadura alcanza los 4 km; su profundidad media es de 10 m (Perillo *et al*., 1987) (Figura 1).

Los flujos residuales en el estuario muestran la influencia de la geomorfología, las mareas asimétricas y los vientos. La presencia de extensas llanuras de marea conecta al Canal Principal con otros sectores del estuario, provocando balances no compensados a lo largo de los ciclos de marea y complicando el estudio de los parámetros oceanográficos. Si bien se ha estimado un tiempo medio de residencia de 28 días (Perillo *et al*., 1987), no se cuenta aún con estimaciones precisas de los flujos residuales y tasas de renovación de los distintos sectores del estuario.

La temperatura y la salinidad de las masas de agua son verticalmente homogéneas a lo largo del estuario, salvo en los sectores asociados a la desembocadura del arroyo Napostá, donde presentan una estratificación marcada. El promedio de salinidad superficial muestra un crecimiento exponencial desde la cabecera del estuario hasta la porción media, con valores que varían entre 15 y 30 ups, zona de aguas mixohalinas, presentando en el área distal valores entre 34 y 35 ups, zona de aguas eurihalinas (Piccolo *et al.,* 1988; Perillo *et al*., 1987; Gómez *et al*., 2005; Elías *et al.,* 2007). Las características geomorfológicas del estuario surgen como resultado del último evento transgresivo- regresivo, ocurrido durante el Holoceno (Aliotta y Lizasoain, 2007).

Figura 1. Localización geográfica del área de estudio y ubicación de las estaciones de muestreo. Estuario de Bahía Blanca (Modificado de Borel y Gómez, 2006).

Figure 1. Geographical setting of the study area and location of the sampling sites. Bahía Blanca estuary (Modified from Borel and Gómez, 2006).

2.1. Comunidades vegetales

La escasa disponibilidad de agua dulce y las altas tasas de evaporación en la franja de terreno que se encuentra por encima del nivel de la pleamar determinan salinidades extremadamente altas, tanto en los suelos como en el agua subsuperficial. Como resultado, en distintos sitios a lo largo de la zona costera de Bahía Blanca aparecen extensos saladares en los que sólo las plantas halófilas más tolerantes son capaces de sobrevivir (Verettoni, 1961; Nebbia y Zalba, 2003). Más allá del alcance de las mareas, tanto en la zona costera que bordea al estuario como en la porción central elevada de las islas, encontramos arbustales halófilos en los que aparecen especies típicas de estos ambientes, como *Cyclolepis genistoides* Gill. ex D.Don (Palo azul), *Suaeda spp*. Forsk (Vidriera), *Atriplex undulata* D.Dietr (Zampa crespa) y *Allenrolfea patagonica* Kuntze (Jume-Jume negro) (Lamberto *et al.*, 1997).

En la franja intermareal, las marismas de *Sarcocornia perennis* (Mill.) A. J. Scott (Jume) se desarrollan apenas por encima del nivel medio de las pleamares, donde el terreno se inunda únicamente durante las mareas más altas (aproximadamente 40 veces al año). En estos ambientes la vegetación se compone casi exclusivamente por *Sarcocornia perennis*, pero algunas matas de *Heterostachys ritteriana* Ung.-Sternb (Jumecillo) suelen aparecer en sitios un poco más elevados. Este tipo de marisma cubre aproximadamente 170 km^2, pero la vegetación en estos ambientes es escasa, con extensas zonas no vegetadas que presentan costras salinas entre las plantas (Cointre *et al.,* 2008).

Las marismas de *Spartina alterniflora* Brongn (Espartillo), son la vegetación dominante en la zona típicamente intermareal. Con una alta densidad de plantas, esta especie coloniza las llanuras de marea en elevaciones cercanas al nivel medio de las pleamares, por lo que soportan la inundación con agua de mar dos veces al día (Peláez *et al.*, 2008; Pratolongo *et al.,* 2009). Las llanuras de marea no vegetadas constituyen el ambiente más extenso dentro de la franja intermareal (578 km^2). Debido al gran estrés que provoca la inundación diaria, estos sedimentos no pueden sostener comunidades de plantas vasculares, sin embargo, soportan complejas comunidades de microorganismos fotosintéticos y fauna bentónica (Cointre *et al.,* 2008). Estos organismos juegan un papel clave en la dinámica del estuario y son los verdaderos soportes de la vida en las aguas costeras.

En este trabajo se seleccionaron tres zonas de muestreo que abarcan una interesante variabilidad de condiciones ambientales, tanto en función de sus características hidrológicas y sedimentarias como del ambiente biológico, caracterizado por el tipo de vegetación dominante. El balneario Villa del Mar (V) se encuentra en el sector externo del Canal Principal, en la transición entre los ambientes dominados por sedimentos finos y las costas arenosas. El patrón de zonación de la vegetación típico de esta zona del estuario incluye marismas de *S. alterniflora*, marismas de *S. perennis* y marismas mixtas de *S. perennis* y *Spartina densiflora* Loisel. En el sector interno del Canal Principal se trabajó en la zona denominada Club Almirante Brown (B), que presenta el patrón de zonación típico de la cabecera del estuario, con ausencia de vegetación en la zona intermareal y marismas de *S. perennis* colonizando elevaciones por encima del nivel de las mareas ordinarias. Finalmente, se recolectaron muestras en la zona de la boca del Canal Maldonado (M), que presenta la interesante particularidad de que allí crece la única marisma de *S. alterniflora* de la zona interna del estuario (Figura 1).

2.2. Escenario ambiental holoceno

A diferencia de los ambientes estuarinos mejor estudiados en Norteamérica y Europa, las costas del sur de Sudamérica, se caracterizan por un máximo transgresivo en el nivel del mar durante el Holoceno tardío. En las costas del norte de Argentina, el nivel del mar tuvo un máximo hace aproximadamente 6000 años, con una línea de costa que se encontraba entre 5 y 12 metros por encima del nivel actual (Schnak *et al.*, 2005). Esta historia transgresiva reciente modeló un paisaje costero muy particular, en el que es posible encontrar extensas superficies bajas que, aunque actualmente están desconectadas de las mareas, fueron marismas y llanuras de marea durante el Holoceno.

En este escenario, el estuario de Bahía Blanca ofrece una interesante diversidad de ambientes intermareales y perimarinos. Las marismas de *S. perennis* que hoy encontra-

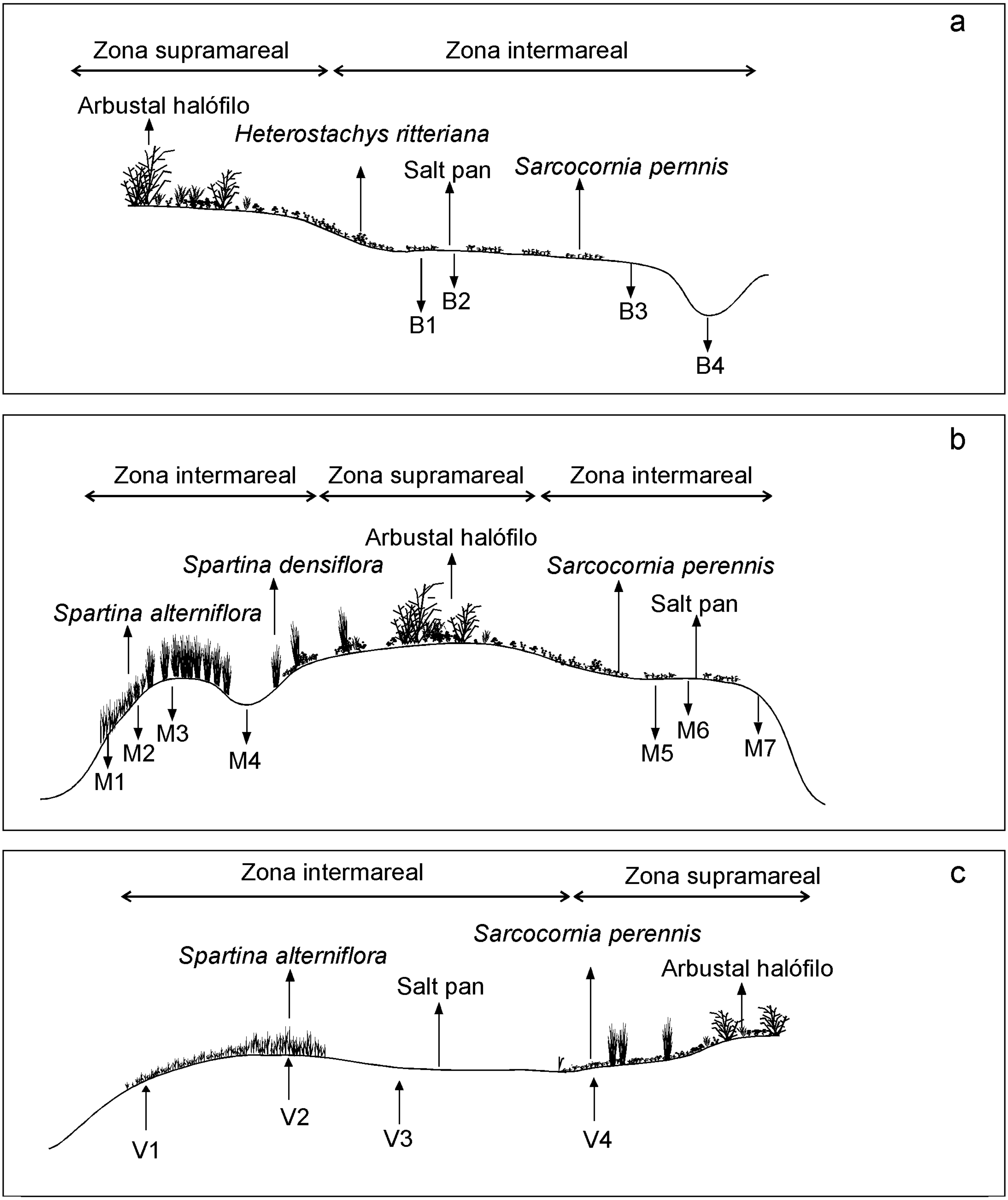


Figura 2 . a, Transecto Club Almirante Brown (B). b, Transecto Canal Maldonado (M). c, Transecto Villa del Mar (V).
Figure 2. a, Club Almirante Brown transect (B). b, Canal Maldonado transect (M). C, Villa del Mar transect (V).

mos en el estuario se establecen sobre viejos sedimentos muy compactos, que se depositaron durante la transgresión marina del Holoceno (Melo *et al.,* 2003; Melo, 2007). En este tipo de marismas, las plantas pioneras forman matas casi circulares, aisladas y levemente elevadas (Botté *et al.*, 2008). Además, durante el Holoceno tardío el clima en la región se volvió mucho más árido y los principales ríos que alimentaban al estuario migraron hacia el sur. Como resultado de este cambio climático e hidrológico, disminuyó el aporte de sedimentos al estuario y comenzó una etapa fuertemente erosiva (Melo, 2007). Desde entonces, las marismas de *S. perennis* de las islas y de gran parte del sector costero están sometidas a intensos procesos de erosión lateral y superficial. Parte del material removido se redistribuye y se deposita dentro del estuario, dando lugar a la aparición de nuevas marismas de *S. alterniflora* actualmente en expansión (Mazzon *et al.*, 2008; Pratolongo *et al.,* 2009). Una vez que estas marismas se establecen, las plantas modifican la hidrodinámica local, amortiguan la energía de olas y corrientes y facilitan la deposición de nuevos sedimentos, lo que a su vez retroalimenta el crecimiento vegetal (Elías *et al.*, 2007).

3. METODOLOGÍA

En agosto de 2008 fueron extraídas muestras superficiales para el estudio de foraminíferos en las zonas denominadas Villa del Mar (V), Almirante Brown (B) y Canal Maldonado (M). En cada una de las zonas se establecieron estaciones de muestreo, cubriendo la zona intermareal desde el nivel de bajamar hasta la parte superior de las marismas teniendo en cuenta cambios en la topografía y transiciones entre tipos de vegetación (Figuras 2 y 3).

Para la extracción de las muestras se utilizó un aro metálico de 10 cm de diámetro por 2 cm de alto, y se recogieron los 2 cm superficiales, luego el material fue vertido en un recipiente con etanol al 70%. Este procedimiento fue repetido en tres ocasiones a fin de evitar la distribución en manchas característica de los foraminíferos. El material recogido en los recipientes fue lavado con un set de tamices de 500 y 63 micrómetros de luz de malla a fin de eliminar la fracción gruesa y la fina, siguiendo las recomendaciones de Boltovskoy (1965). Una vez limpio, el residuo fue volcado en un vaso al que se le adicionó una solución de agua destilada con el colorante Rosa de Bengala (1gr/l). Al día siguiente las muestras fueron lavadas a fin de eliminar el exceso de colorante, y se dejaron secar a temperatura ambiente. Del sedimento obtenido se extrajo 1 gr de material que fue estudiado bajo lupa binocular. Los ejemplares con protoplasma, presuntamente vivos al momento del muestreo, adquirieron una coloración rosa muy marcada. Todos los foraminíferos presentes fueron separados mediante la técnica de picking, y ordenados en portamicrofósiles. Ambos grupos (coloreados y sin colorear) fueron utilizados para realizar estudios cualitativos y cuantitativos. Se recolectaron y analizaron 4 muestras en los transectos Villa del Mar (V) y Brown (B), y 7 muestras en el transecto Maldonado (M). Se hallaron aproximadamente un total de 1000 foraminíferos.

Las determinaciones sistemáticas se basaron en Boltovskoy (1954a ,1954b, 1957), Boltovskoy *et al*. (1980), Buzas-Stephens *et al*. (2002), Ferrero (2006), Loeblich y Tappan (1988) y Poag (1981). Los individuos de las especies más abundantes se fotografiaron utilizando el microscopio electrónico de barrido del Centro Atómico Bariloche (Philips, Modelo SEM 515).

En forma paralela a la extracción de muestras para el recuento de foraminíferos, se extrajeron muestras similares de sedimentos sobre las que se determinó la densidad aparente, contenido de materia orgánica (Loss on Ignition %), granulometría (Analizador láser Malvern Mastersizer), salinidad y pH (solución 1:2 de suelo seco en agua destilada).

3.1. Análisis de datos

En esta sección hemos realizado los análisis sobre el número de organismos vivientes hallados (Standing crop), teniendo en cuenta la abundancia total, relativa y diversidad desde las marismas hasta las llanuras de marea, evaluando su relación con los parámetros ambientales medidos. A su vez, se mencionan la presencia y abundancia de ejemplares muertos para cada una de las muestras.

El análisis de agrupamiento (Cluster) se realizó a partir de los contajes de individuos vivos de 13 muestras (las muestras M5 y M6 fueron excluidas del análisis por contener

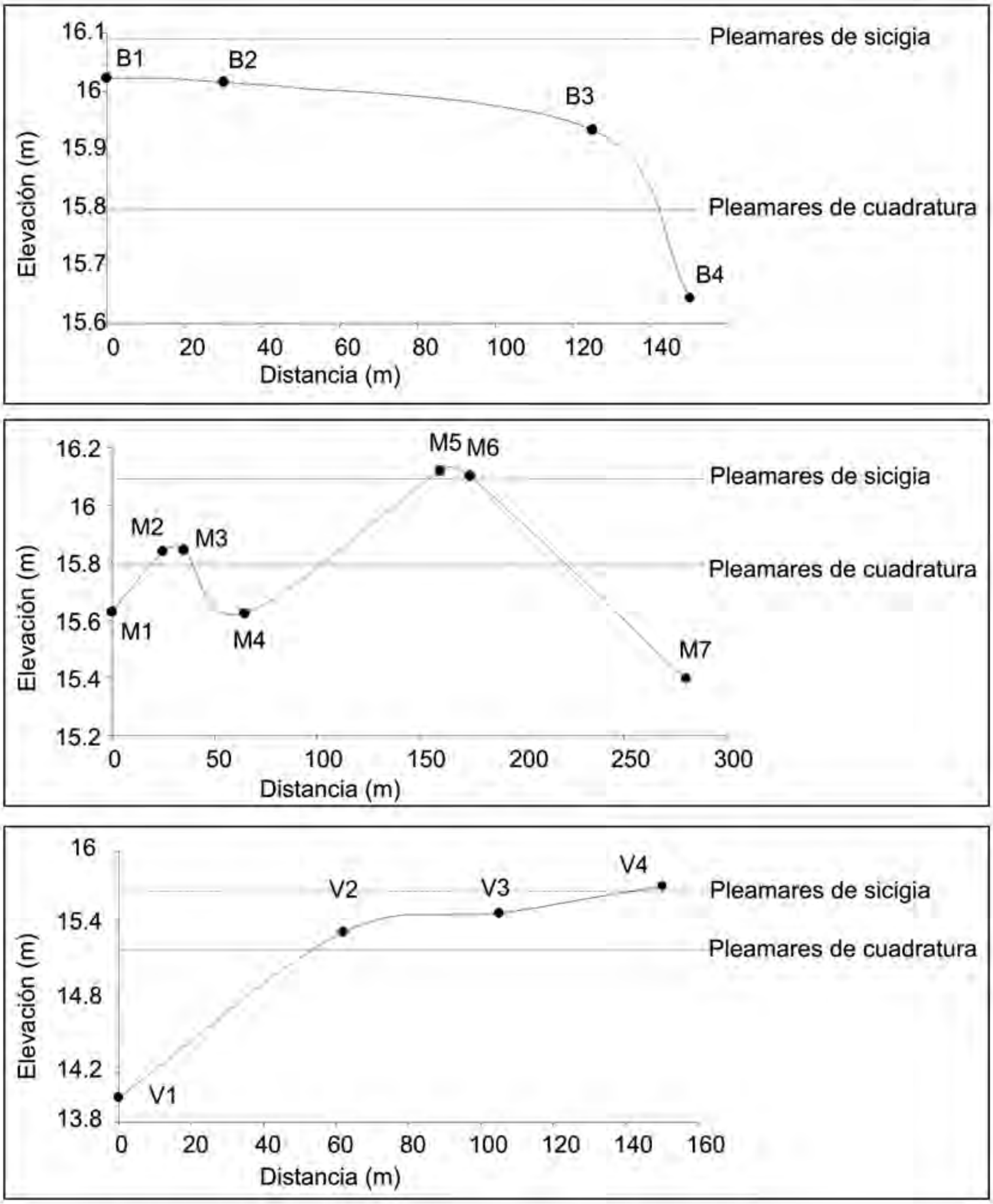


Figura 3. Ubicación y altura topográfica de las estaciones de muestreo.
Figure 3. Location and elevation of the sampling sites.

únicamente ejemplares sin colorear). Con los valores estandarizados según el número total de individuos coloreados en cada muestra se construyó la matriz de distancia (distancia euclídea) y las asociaciones de muestras se definieron según el algoritmo de ligamiento simple, a través de la utilización del paquete estadístico R, de distribución gratuita. Para el análisis cuantitativo y para la caracterización de cada nivel se tuvo en cuenta el número y las frecuencias relativas de las especies halladas.

4. RESULTADOS Y DISCUSIÓN

4.1. Caracterización ambiental de las estaciones de muestreo

Las variables ambientales consideradas para la caracterización de las estaciones de muestreo se resumen en la Tabla 1. El número de individuos extraídos por gr de muestra se resume en la Tabla 2.

Muestras	Densidad aparente (g/cm^3)	Contenido de agua (%)	Materia orgánica (%)	Salinidad (ups)	pH	D50 (um)	Tipo de ambiente
B1	1.65	0.29	0.06	46.4	8.24	14.72	Salt Pan (Cubeta salina)
B2	2.26	0.31	0.07	24.3	7.96	9.47	Marisma alta (*S. perennis*)
B3	1.54	0.36	0.05	30.6	7.88	14.78	Llanura de marea
B4	1.46	0.51	0.05	30.6	7.93	18.48	Canal de marea
V1	0.98	0.55	0.06	18.8	7.96	11.96	Marisma baja (*S. alterniflora*)
V2	2.59	0.21	0.01	10.6	7.86	258.35	Marisma baja (*S. alterniflora*)
V3	1.87	0.27	0.05	34.0	8.24	168.52	Salt Pan(Cubeta salina)
V4	1.49	0.22	0.04	32.8	8.35	82.66	Marisma alta (*S. perennis*)
M1	1.39	0.54	0.09	21.4	7.95	19.97	Marisma baja (*S. alterniflora*)
M2	1.40	0.59	0.09	22.8	8.2	18.76	Marisma baja (*S. alterniflora*)
M3	2.37	0.38	0.07	17.6	7.89	17.69	Marisma media (*S. densiflora*)
M4	2.2	0.49	0.04	16.9	7.97	32.64	Canal de marea
M5	2.05	0.29	0.05	31.0	7.92	17.39	Marisma alta (*S. perennis)*
M6	2.46	0.30	0.06	34.8	8.28	17.89	Salt Pan (Cubeta salina)
M7	2.31	0.33	0.03	16.9	7.96	49.01	Llanura de marea

Tabla 1. Variables ambientales consideradas para la caracterización de las estaciones de muestreo.

Table 1. Environmental variables considered for the sampled sites.

En todos los transectos la salinidad tiende a aumentar con la elevación, alcanzando los valores más altos en los salt pans (cubetas salinas) que aparecen en elevaciones cercanas a las de las pleamares extraordinarias, donde la evaporación es máxima. Sin embargo, en las estaciones más elevadas, pero con cobertura de *S. perennis* la salinidad es notablemente menor que en las depresiones salinas vecinas, sugiriendo que la presencia de vegetación, y por consiguiente la disminución de la tasa de evaporación, tendría un efecto moderador de la salinidad.

4.2. Ordenamiento de las estaciones

El análisis de agrupamientos separó las muestras en 4 grandes grupos, uno de ellos dominado por la presencia de ejemplares aglutinados y los restantes predominantemente calcáreos (Figura 4).

4.3. Asociación de *Haynesina germanica* (Ehrenberg) y *Ammonia parkinsoniana* (d´Orbigny), HA

Está constituida por una gran cantidad de individuos de *Haynesina germanica* y *Ammonia parkinsoniana,* particularmente asociada a marismas de *S. alterniflora*. Las especies dominantes estás acompañadas por representantes aislados de *Ammonia tepida* (Cushman) y *Elphidium gunteri* Cole en la estación V1. Las especies *Trochammina inflata* y *Jadammina macrescens* (Brady) aparecen muy bien representadas en las estaciones M1 y M2, en la marisma de *S. alterniflora* que crece en la boca del canal Maldonado.

4.4. Asociación de *Haynesina germanica,* H

Similar a la asociación anterior, con *A. parkinsoniana* también presente, pero empobrecida (con menos especies acompañantes y menores abundancias). Aparece en sitios desprovistos de vegetación, con salinidades elevadas, pero que retienen humedad durante la bajamar.

4.5. Asociación de individuos calcáreos, C

Las estaciones M4, M7, V2, V4 y B3 son las que presentan las menores abundancias y asociaciones con menor riqueza específica (menos de 4 especies; en general *H. germanica* y/o *A. parkinsoniana* están presentes). Estas estaciones se ubican en ambientes con muy altas densidades de cangrejos, y una posible explicación para las bajas abundancias de foraminíferos es el efecto bioturbador de *Chasmagnathus granulatus*. Los cangrejos en tan altas densidades se comportan como importantes agentes mo-

TOTAL	*T. inflata*	*J. macrescens*	*H. germanica*	*B. frigida*	*E. aff. E.poeyanum Tipo I*	*E. excavatum*	*E. aff. E.poeyanum Tipo II*	*E. aff. E. clavatum*	*E. gunteri*	*A. tepida*	*A. parkinsoniana*	*B. elegantissima*	*Quinqueloculina sp*	*Q. seminulum*	*Cassidulina sp.*	*B. compacta*	*M. fusca*	**TOTAL ESPECIES**	**TOTAL INDIVIDUOS**
B1	1	0	7	1	0	1	0	1	16	3	7	0	0	4	0	1	0	**10**	**42**
B2	8	13	5	0	0	1	0	0	8	3	1	0	0	0	1	0	0	**8**	**40**
B3	0	0	15	1	0	0	1	0	12	8	6	1	0	0	1	1	0	**8**	**47**
B4	0	0	29	0	1	1	0	0	15	9	31	0	1	1	0	0	0	**8**	**88**
M1	32	100	75	0	0	0	0	0	5	17	32	0	0	2	0	0	9	**8**	**272**
M2	57	9	470	0	0	0	0	0	46	30	87	0	0	0	0	0	4	**7**	**703**
M3	8	2	12	0	0	0	0	0	12	4	4	0	0	0	0	0	0	**6**	**42**
M4	0	6	0	0	0	0	0	0	9	3	0	0	0	0	0	0	0	**3**	**18**
M5	0	0	2	0	0	0	1	0	3	0	0	0	0	0	0	0	0	**3**	**6**
M6	0	0	1	0	0	0	0	0	6	2	0	0	0	0	0	0	0	**3**	**9**
M7	0	0	5	0	0	0	0	1	10	0	1	0	0	0	0	0	0	**4**	**17**
V1	0	0	112	5	4	0	0	3	33	14	329	0	3	3	0	0	0	**9**	**506**
V2	0	0	3	0	0	0	0	1	3	2	11	0	0	0	0	0	0	**5**	**20**
V3	0	0	34	4	2	0	4	22	42	4	52	0	3	0	1	0	0	**10**	**168**
V4	0	0	12	5	10	0	3	9	22	4	31	0	0	1	0	0	0	**9**	**97**
VIVOS																			
B1	1	0	5	1	0	1	0	1	1	3	2	0	0	4	0	1	0	**10**	**20**
B2	8	7	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	**4**	**18**
B3	0	0	6	0	0	0	0	0	0	1	4	0	0	0	0	0	0	**3**	**11**
B4	0	0	20	0	0	0	0	0	1	3	9	0	0	0	0	0	0	**4**	**33**
M1	31	100	52	0	0	0	0	0	0	12	25	0	0	2	0	0	9	**7**	**231**
M2	22	3	197	0	0	0	0	0	1	23	85	0	0	0	0	0	0	**6**	**331**
M3	5	2	8	0	0	0	0	0	0	2	0	0	0	0	0	0	0	**4**	**17**
M4	0	3	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	**3**	**6**
M5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	**0**
M6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	**0**
M7	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**	**4**
V1	0	0	70	0	0	0	0	1	13	5	261	0	3	3	0	0	0	**7**	**356**
V2	0	0	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	**2**	**5**
V3	0	0	19	0	1	0	0	2	2	0	12	0	1	0	0	0	0	**6**	**37**
V4	0	0	5	0	0	0	0	0	0	1	5	0	0	0	0	0	0	**3**	**11**
MUERTOS																			
B1	0	0	2	0	0	0	0	0	15	0	5	0	0	0	0	0	0	**3**	**22**
B2	0	6	3	0	0	1	0	0	8	3	0	0	0	0	1	0	0	**6**	**22**
B3	0	0	9	2	0	0	1	0	12	7	2	1	0	0	1	1	0	**9**	**36**
B4	0	0	9	0	1	1	0	0	14	6	22	0	1	1	0	0	0	**8**	**55**
M1	1	0	23	0	0	0	0	0	5	5	7	0	0	0	0	0	0	**5**	**41**
M2	35	6	273	0	0	0	0	0	45	7	2	0	0	0	0	0	4	**7**	**372**
M3	3	0	4	0	0	0	0	0	12	2	4	0	0	0	0	0	0	**5**	**25**
M4	0	3	0	0	0	0	0	0	8	1	0	0	0	0	0	0	0	**3**	**12**
M5	0	0	2	0	0	0	1	0	3	0	0	0	0	0	0	0	0	**3**	**6**
M6	0	0	1	0	0	0	0	0	6	2	0	0	0	0	0	0	0	**3**	**9**
M7	0	0	1	0	0	0	0	1	10	0	1	0	0	0	0	0	0	**3**	**13**
V1	0	0	42	5	4	0	0	2	20	9	68	0	0	0	0	0	0	**7**	**150**
V2	0	0	1	0	0	0	0	1	3	2	8	0	0	0	0	0	0	**5**	**15**
V3	0	0	15	4	1	0	4	20	40	4	40	0	2	0	1	0	0	**10**	**131**
V4	0	0	7	5	10	0	3	9	22	3	26	0	0	1	0	0	0	**9**	**86**

Tabla 2. Contajes por estaciones de foraminíferos muertos, vivos y total presentes en 1 gr de sedimento.

Table 2. Counts for dead, living and total foraminifera in 1gr of sediment per each sampled site.

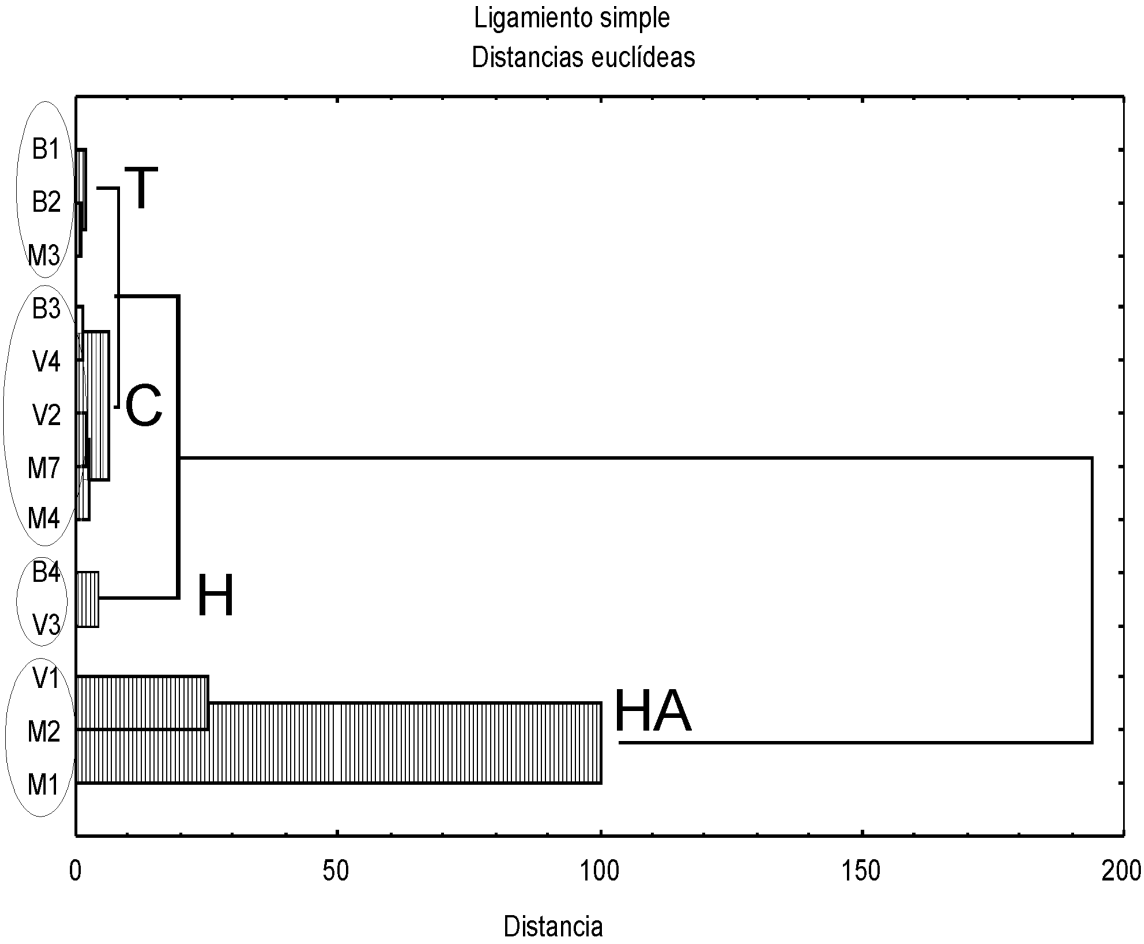


Figura 4. Dendrograma donde se observan las 4 asociaciones vivas resultantes del análisis de agrupamiento.

Figure 4. Dendrogram showing the 4 living assemblages from the cluster analysis.

deladores del paisaje debido a la gran cantidad de sedimentos que movilizan, además de su comportamiento como herbívoros y predadores de otros organismos bentónicos.

4.6. Asociación de *Trochammina inflata* (Montagu), T

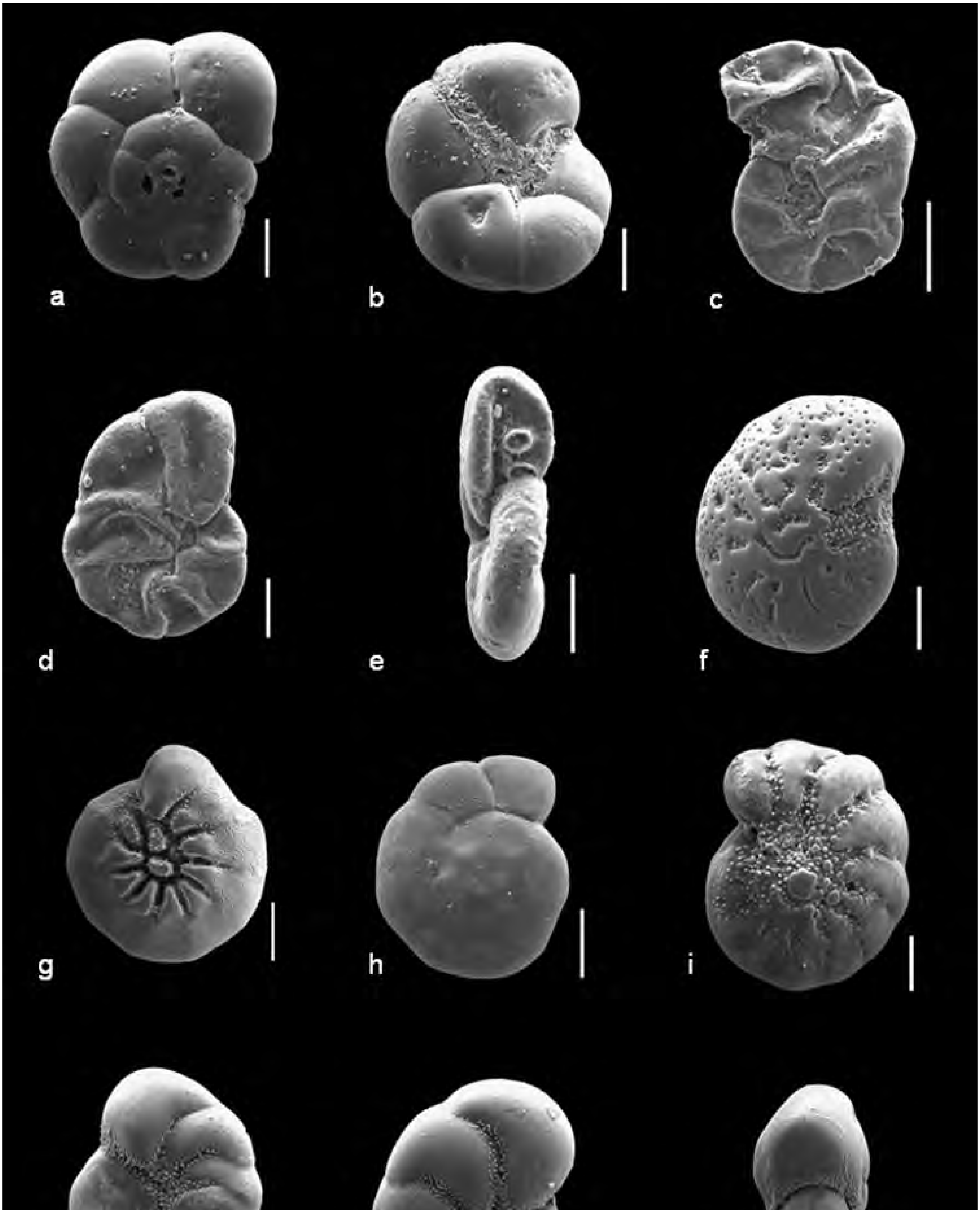
Las estaciones B1, B2 y M3 conforman esta asociación. Es una asociación con baja diversidad, que no supera las 5 especies, a excepción de la estación B1, donde se observa una inusual riqueza específica con un valor de 10 especies. La misma está caracterizada por la presencia de la especie aglutinada *T. inflata* en todas las muestras, que comúnmente se encuentra acompañada por *J. macrescens* (Lámina 1). Esta asociación suele desarrollarse en zonas que se ubican entre el nivel medio de pleamar (MHT) y el de mareas extraordinarias (SHT).

Cabe remarcar la presencia en la estación B1 de ejemplares (entre 1 y 4 individuos) característicos de asociaciones típicamente marino marginales, como *Elphidium gunteri, Elphidium* aff. *E. clavatum* Cushman*, A. tepida, A.*

Lámina 1. *a, Trochaminna inflata,* vista dorsal; *b, Trochaminna inflata,* vista umbilical*; c, Jadammina macrescens,* vista dorsal; *d, Jadammina macrescens,* vista umbilical*; e, Jadammina macrescens, vista apertural; f, Elphidium gunteri; g, Ammonia parkinsoniana,* vista umbilical*; h, Ammonia parkinsoniana, vista espiral; i, Elphidium* aff. *E. clavatum; j, Haynesina germanica; k, Haynesina germanica; l, Haynesina germanica,* vista apertural. Escala = 200 µm (figuras a, b, c, g, h, l); 100 µm (figuras d, e, f, i, j, k).

*Plate 1. a,*Trochaminna inflata, *dorsal view; b,*Trochaminna inflata, *umbilical view; c,* Jadammina macrescens, *dorsal view; d,* Jadammina macrescens, *umbilical view; e,* Jadammina macrescens, *apertural view; f,* Ephidium gunteri*; g,* Ammonia parkinsoniana*, umbilical view; h,* Ammonia parkinsoniana, *spiral view; i,* Elphidium *aff.* E. clavatum*; j,* Haynesina germanica*; k,* Haynesina germanica*; l,* Haynesina germanica, *apertural view. Scale bar = 200 µm (figures a, b, c, g, h, l), 100 µm (figures d, e, f, i, j, k).*

Lámina 1



parkinsoniana, Quinqueloculina seminula (Linneo), *Bolivina compacta* Sidebottom y *Buccella frigida* Cushman, los cuales probablemente hayan sido transportados desde la parte externa del estuario con las corrientes de marea.

Los puntos M3 a M7 tienen muy pocos individuos vivos. Si tenemos en cuenta las asociaciones muertas, y en contraste con la microfauna viva, es posible reconocer la presencia de ejemplares de *H. germanica, A. tepida* y *E. gunteri*, especies que actualmente son consideradas oportunistas en zonas con marcada contaminación e impacto antrópico (Armynot du Châtelet *et al.,* 2004; Cearreta y Leorri, 2000). Estas estaciones de muestreo se encuentran bajo la influencia directa del canal Maldonado, que desemboca en este sector del estuario después de recorrer una zona agrícola y atravesar la ciudad de Bahía Blanca. Asociada a esta descarga, se han registrado niveles elevados de diversos contaminantes y en particular de hidrocarburos aromáticos policíclicos (Arias *et al*., 2008) hecho que en un momento dado pudo haber provocado la proliferación de ejemplares de estas especies, pero que con el paso del tiempo y el aumento del foco contaminante, la elevada toxicidad podría haber impedido la supervivencia de las mismas.

Con respecto a los aglutinados, *T. inflata* y *J. macrescens* aparecen en M1 y M2, casi en el límite inferior de la marisma de *Spartina alterniflora*. En este caso, la presencia de los foraminíferos aglutinados parece estar asociada a la cabecera del estuario (Figura 5), en donde pueden ocupar elevaciones intermedias y bajas dentro de las marismas. En puntos con elevaciones similares en Villa del Mar, este tipo de microfauna no aparece. En la cabecera del estuario, la distribución de ambas especies se relaciona con la salinidad de las estaciones de muestreo, con un rango de ocurrencia entre 17 y 23 ups, aunque excepcionalmente, un individuo vivo de *T. inflata* fue encontrado en el punto B1, en un ambiente extremadamente salino (46 ups) (Figura 6).

En la gran mayoría de los trabajos realizados sobre marismas salinas del hemisferio norte, se registra la presencia

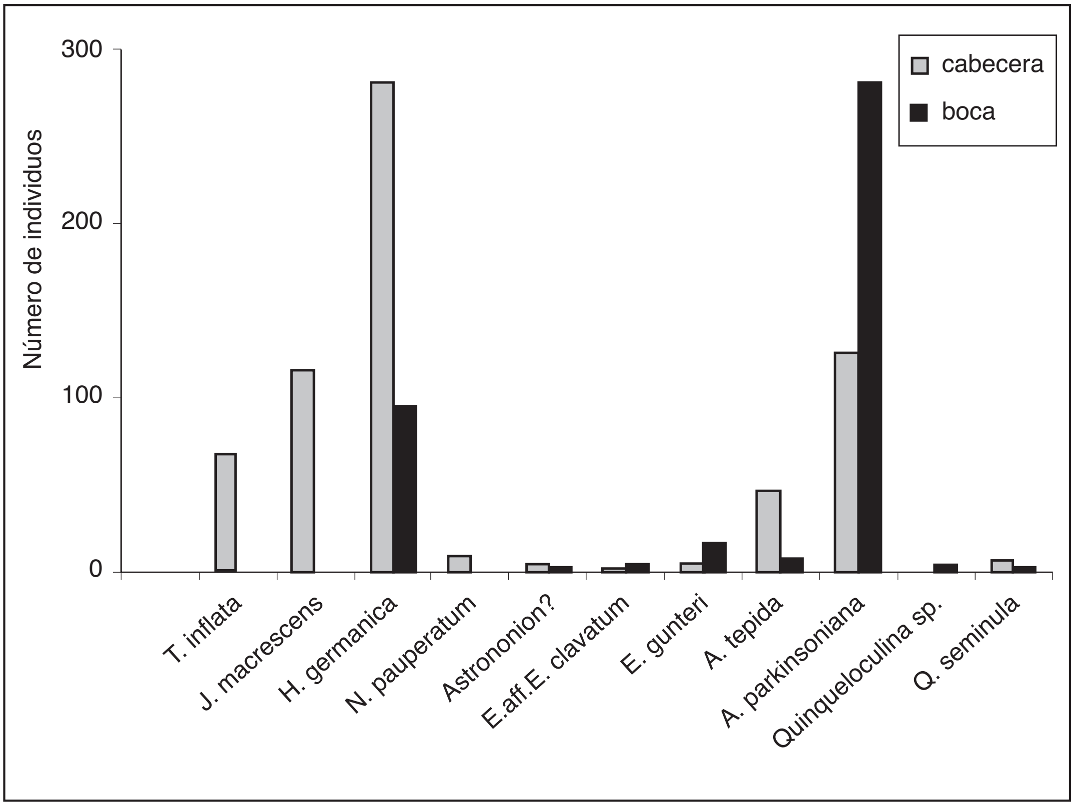


Figura 5. Distribución y abundancia de especies vivas en la cabecera y desembocadura del estuario de Bahía Blanca.
Figure 5. Distribution and abundance of living species in the head and the mouth of the Bahía Blanca estuary.

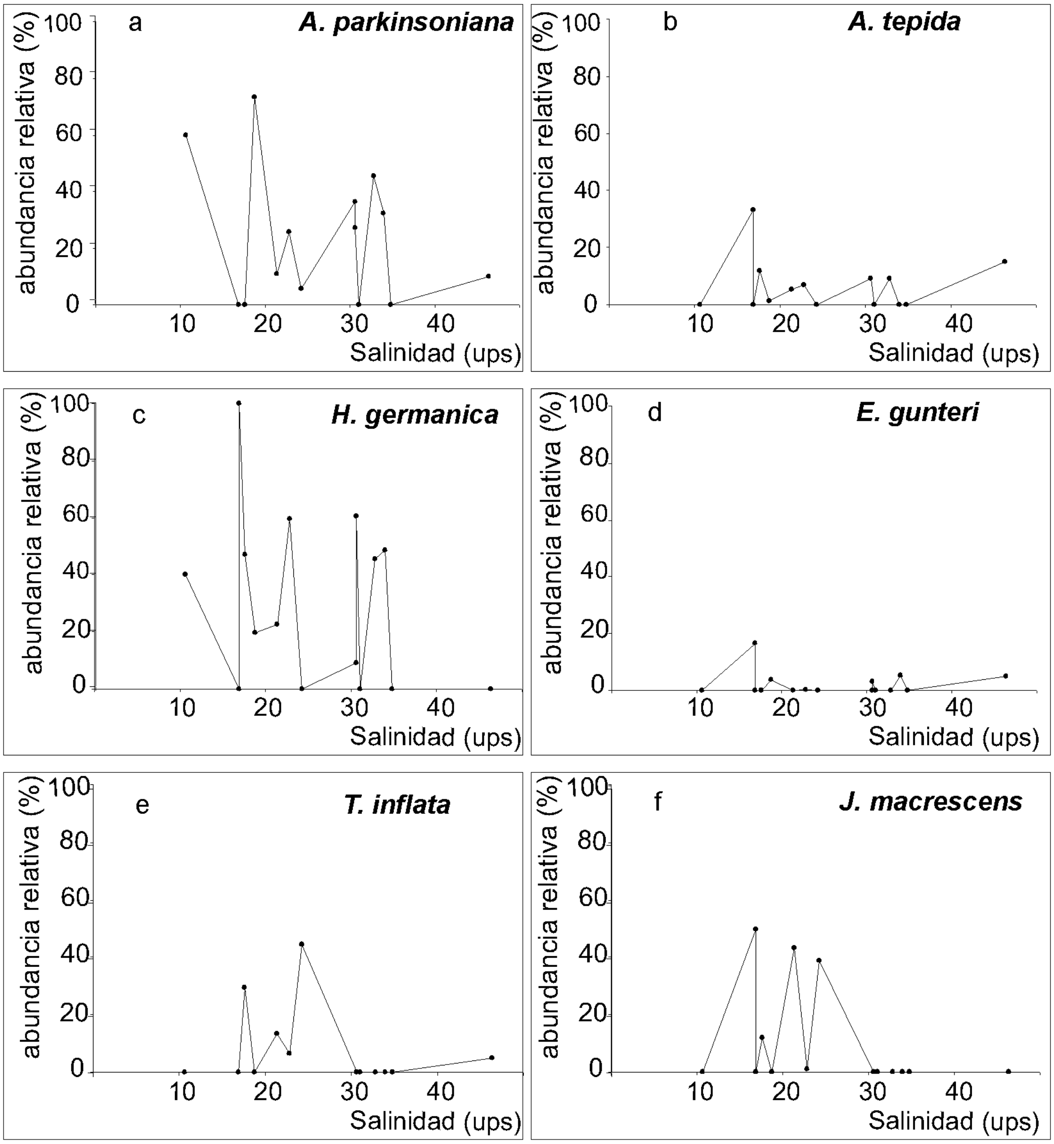


Figura 6. Abundancia relativa (%) versus salinidad (ups) para (a) *Ammonia parkinsoniana, (b) Ammonia tepida, (c) Haynesina germanica, (d) Elphidium gunteri, (e) Trochaminna inflata, (f) Jadammina macrescens.*

Figure 6. Relative abundance (%) against salinity (psu) for (a) Ammonia parkinsoniana*, (b)* Ammonia tepida*, (c)* Haynesina germanica*, (d)* Elphidium gunteri*, (e)* Trochaminna inflata*, (f)* Jadammina macrescens.

de foraminíferos aglutinados asociados exclusivamente a marismas altas o medias (Scott *et al.*, 1990; Hayward y Hollis, 1994; Horton *et al.*, 1999; Horton y Murray, 2007), mientras que en este trabajo hemos reconocido la presencia de *J. macrescens* y *T. inflata* asociadas predominantemente a zonas de marismas bajas, como ha sido reportado por De Rijk y Troelstra (1997) y por Southall *et al.* (2006). Cabe señalar que se han encontrado ejemplares aglutinados en las marismas altas aunque en bajo número (Figura 7).

Tanto *E. gunteri* como *H. germanica*, *A. tepida* y *A. parkinsoniana* se distribuyen en un rango muy amplio de salinidades, pero todas aparecen en mayor proporción en la marisma baja y ambientes submareales como señalan Hayward y Hollis, 1994; Horton y Murray, 2007 (Figura 7). Sólo *A. tepida* y *E. gunteri* aparecen relativamente bien representados en las marismas altas. La única especie que muestra preferencia por sitios elevados y de inundación menos frecuente (marismas altas y salt pans) es *Elphidium* aff. *E. clavatum*.

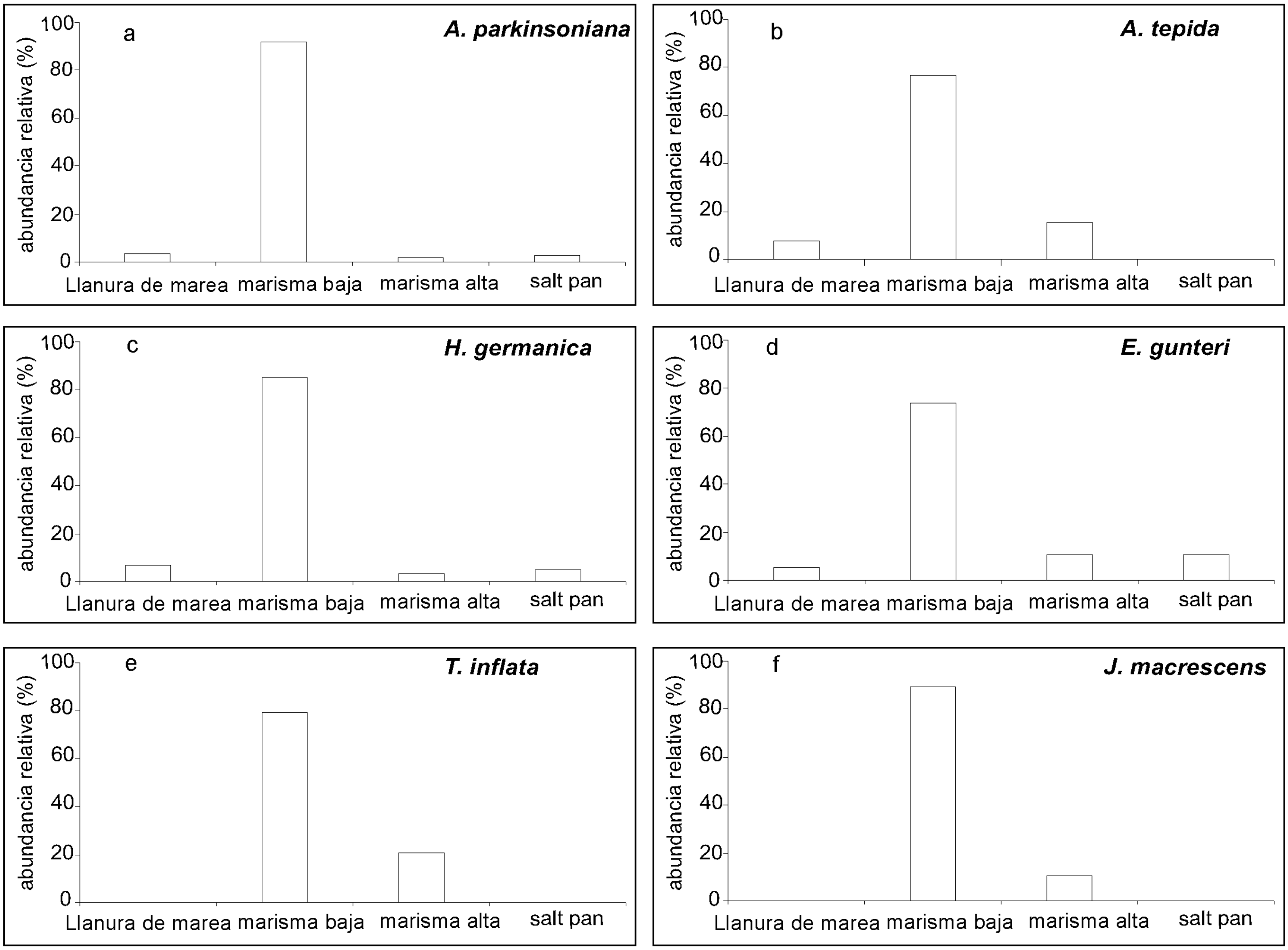


Figura 7. Abundancia relativa (%) versus ubicación espacial para (a) *Ammonia parkinsoniana, (b) Ammonia tepida, (c) Haynesina germanica, (d) Elphidium gunteri, (e) Trochaminna inflata, (f) Jadammina macrescens.*

Figure 7. Relative abundance (%) against location for (a) Ammonia parkinsoniana*, (b)* Ammonia tepida*, (c)* Haynesina germanica*, (d)* Elphidium gunteri*, (e)* Trochaminna inflata*, (f)* Jadammina macrescens.

Las estaciones de muestreo de Villa del Mar (V) son las que presentan mayor abundancia de foraminíferos y asociaciones dominadas por *A. parkinsoniana* y caracterizados por la presencia de *H. germanica* y *E. gunteri*. La excepción en este transecto es el punto V 2 que, aunque con similar composición, presenta abundancias notablemente menores. En el transecto del Club Almirante Brown (B), por el contrario, las abundancias son mucho menores y *A. parkinsoniana* ya no es la especie dominante. La excepción a este patrón es el punto B4, que con abundancias moderadas se asemeja en su composición a las estaciones de Villa del Mar. Además, en esta zona aparecen, aunque en bajo número, especies que no se encuentran en Villa del Mar, como *T. inflata*, *J. macrescens, B. elegantissima*, *B. compacta* y *Elphidium excavatum*.

4.7. Asociaciones muertas

Con respecto a las asociaciones muertas es posible observar que éstas difieren de las asociaciones vivas en mayor o menor grado, encontrándose caparazones vacíos en número variable en todas las muestras. Incluso de algunas especies sólo se hallaron ejemplares muertos y ningún representante viviente. Esto puede deberse principalmente al transporte post-mortem, ya que estas asociaciones se han formado a lo largo del tiempo manifestando efectos acumulativos y transporte desde áreas abiertas cercanas. Los caparazones vacíos de los foraminíferos son considerados sedimentológicamente como clastos y en consecuencia están sujetos a transporte, tanto en suspensión como en carga de fondo (Murray, 1991).

Muchos estuarios son cuencas de deposición de foraminíferos que viajan como carga en suspensión proveniente de la plataforma, debido a que estos ambientes marinos marginales poseen relativamente baja energía. En este caso el estuario de Bahía Blanca es un estuario de régimen mesomareal, lo que implica que al hacer una correlación entre el rango de mareas y los caparazones transportados puede considerarse que la proporción de caparazones exóticos es de moderada a alta (Murray, 1991). Por otro lado es conveniente considerar para éste y futuros trabajos en el área, aspectos relacionados con la contaminación del lugar de estudio, pudiendo ser estos factores causantes de la desaparición de muchas especies que en algún momento vivieron en el estuario.

En este estudio las especies dominantes representadas por caparazones vacíos son, para el sector interno (B), *E. gunteri* con 49 ejemplares, *A. parkinsoniana* con 29, *H. germanica* con 23 y *A. tepida* con 16. Las abundancias de las especies restantes no superan los 7 caparazones vacíos. Para la zona externa del estuario el número de individuos tiende a incrementarse, aquí las especies más frecuentes son *A. parkinsoniana* con 142 ejemplares, *E. gunteri* con 85, *H. germanica* con 65, *E.* aff. *E. clavatum* con 32 y *A. tepida* con 18. Es posible observar una leve tendencia al incremento de la diversidad y la abundancia desde el sector más interno del estuario hacia la desembocadura del mismo. No fueron hallados caparazones vacíos de foraminíferos aglutinados.

Considerando las características ambientales de las estaciones de muestreo en forma conjunta con los grupos resultantes del análisis de agrupamiento, puede observarse que las similitudes y diferencias en la composición específica de los puntos de muestreo no pueden explicarse por un único factor. En la cabecera del estuario, la alta salinidad podría ser un factor determinante del menor número de individuos. Sin embargo, la estación que presentó el mayor número de ejemplares en Almirante Brown no fue la de menor salinidad, sino la estación ubicada en la posición más baja y, por lo tanto, la que retiene la mayor cantidad de agua durante el periodo de exposición, sugiriendo que la desecación sería un factor limitante en esta zona. En el transecto de Villa del Mar, por el contrario, la estación con menor número de individuos fue aquella cuyos sedimentos presentaron las texturas más gruesas. Una mayor proporción de arena en el sedimento podría indicar condiciones de mayor energía en el ambiente hidrodinámico y, por consiguiente una restricción al desarrollo de las asociaciones de foraminíferos.

5. CONCLUSIONES

Este estudio tuvo como objetivo realizar un análisis preliminar de la distribución de los foraminíferos bentónicos en muestras superficiales del estuario de Bahía Blanca, y su posterior vinculación con las condiciones ambientales imperantes en el área. Las asociaciones registradas en las 3 zonas bajo estudio, reflejan una fuerte relación con la altitud mostrando zonaciones verticales que coinciden con estudios previos que sustentan el uso de los foraminíferos como potenciales indicadores de las variaciones del nivel del mar.

El análisis de agrupamiento separó las muestras en 4 asociaciones, una dominada por la presencia de especies aglutinadas como *T. inflata* y *J. macrescens* y tres asociaciones predominantemente calcáreas hialinas constituidas por *A. parkinsoniana, A. tepida, H. germanica* y *E. gunteri*. Las especies de foraminíferos aglutinados se hallaron esencialmente ocupando las partes bajas de las marismas, con algunos ejemplares en zonas de marisma alta; mientras que las especies calcáreas, con abundancias variables eran frecuentes en las marismas bajas y zonas de llanuras de marea. Estas asociaciones son características de ambientes similares templados y de latitudes medias, en ésta y otras regiones a nivel mundial. La baja diversidad también se corresponde con el desarrollo de un ambiente marino marginal bajo condiciones de estrés.

Probablemente el tiempo de exposición, la salinidad y la disposición de la vegetación se constituyan como elementos determinantes en la distribución de las asociaciones microfaunísticas. A su vez cabe recalcar que además de los factores previamente nombrados, la ubicación de las muestras dentro del estuario (cabecera-desembocadura) relacionada con el balance entre el aporte fluvial y marino, así como con las tasas de renovación de las aguas, sería el elemento condicionante de los demás parámetros ambientales.

Esperamos que esta primera contribución sea un nuevo aporte para el establecimiento de análogos modernos, útiles para la interpretación de las variaciones del nivel del mar durante el Holoceno en Sudamérica, y para la reconstrucción de paleoambientes a partir de la comparación con el registro fósil. A su vez, apoyar la utilización de material micropaleontológico, como herramienta válida para la detección y monitorización de contaminación ambiental e impacto antrópico en Argentina.

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ANEXO I:

Lista de especies encontradas

Astrononion sp. Cushman y Edwards, 1937.
Ammonia parkinsoniana (d´Orbigny) = *Rosalina parkinsoniana,* 1839.
Ammonia tepida (Cushman) = *Rotalia beccarii* (Linneo) var. *tepida* Cushman, 1926.
Bolivina compacta Sidebottom = *Bolivina robusta* Brady var. *compacta*-Sidebottom, 1905.
Buccella frigida (Cushman) = *Pulvinulina frigida* Cushman, 1922.
Buliminella elegantissima (d' Orbigny) = *Bulimina elegantissima* d' Orbigny, 1839.
Cassidulina sp. d' Orbigny.
Elphidium excavatum (Terquem) = *Polystomella excavata* Terquem, 1876.
Elphidium aff. *E. clavatum* Cushman.
Elphidium gunteri Cole = *Elphidium gunteri* Cole, 1931.
Elphidium aff. *E. poeyanum* (d' Orbigny) Tipo1.
Elphidium aff. *E. poeyanum* (d' Orbigny) Tipo 2.
Jadammina macrescens (Brady)= *Trochammina inflata* (Montagu) var. *macrescens* Brady,1870.
Milliamina fusca (Brady)= *Quinqueloculina fusca* Brady, 1870.
Haynesina germanica (Ehrenberg) = *Nonion germanicum* 1798.
Nonion pauperatum Balkwill y Wright = *Nonion pauperata* Balkwill y Wright*,* 1885.
Quinqueloculina sp. d' Orbigny.
Quinqueloculina seminula (Linneo) = *Serpula seminulum* Linneo, 1758.
Trochammina inflata (Montagu)= *Nautilus inflatus* Montagu, 1808.

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Estudio polínico de una laguna endorreica en Almenara de Adaja (Valladolid, Meseta Norte): cambios ambientales y actividad humana durante los últimos 2.800 años

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Resumen

El análisis de microfósiles polínicos y no polínicos de una secuencia obtenida en una laguna endorreica en Almenara de Adaja (Valladolid, Meseta Norte) muestra este registro como sensible tanto a cambios de naturaleza climática como antrópica durante los últimos 2800 años. Se han detectado los momentos de variabilidad climática que se han descrito para esta cronología como el período frío del final de la Edad del Hierro (850-75 cal BC), el Período Cálido Romano (*ca.* 75 cal BC-300 cal AD), el Período Frío Altomedieval (*ca.* 300-800 cal AD), el Período Cálido Bajomedieval (*ca.* 800-1450 cal AD) y la Pequeña Edad del Hielo (*ca.* 1450-1800 cal AD). Además, se han observado distintos grados de antropización en el paisaje en relación con las pautas de asentamiento en la zona. Aunque es desde la época romana cuando se establecieron las transformaciones del paisaje que han conformado el paisaje actual, que está caracterizado por ser un espacio muy agrícola y ganadero.

Palabras clave*:* Polen, microfósiles no polínicos, historia de la vegetación, cambios climáticos, impacto humano, Valladolid, España.

Abstract

[*Pollen study of an endorheic lagoon in Almenara de Adaja (Valladolid, Northern Meseta): environmental changes and human activity during the last 2800 years*] The analysis of pollen and non-pollen palynomorphs in a sequence from an endorreic lake in Almenara de Adaja (Valladolid, Northern Plateau) shows the sensibility of this record to both climatic and anthropogenic changes during the last 2800 years. All the phases of climatic variability described for this chronology have been detected, as the cold period at the end of the Iron Age (850-75 cal BC), the Roman Warm Period (*ca.* 75 cal BC-300 cal AD), the Dark Ages (*ca.* 300-800 cal AD), the Medieval Warm Period (*ca.* 800-1450 cal AD) and the Little Ice Age (*ca.* 1450-1800 cal AD). Besides, different human pressure degrees have been observed in the landscape in connection with the local settlement guidelines. Although since Roman times is when started the landscape modifications that created the current landscape, characterized by agricultural and pastoral activities.

Key words*:* Pollen, non-pollen palynomorphs, vegetation history, climatic changes, human impact, Valladolid, Spain.

1. INTRODUCCIÓN

En la actualidad, la información de tipo ambiental de los últimos milenios referida a la Meseta Norte, especialmente la que hace mención a la dinámica de su vegetación y a las pautas de antropización de los ecosistemas, es ciertamente reducida, lo cual se debe a dos razones fundamentales (Franco Múgica *et al*., 2005): (1) el enorme grado de alteración de todo el área, sujeta a un proceso continuado de degradación forestal que apenas ha permitido la supervivencia de la vegetación natural, y (2) la falta de registros ambientales que permitan estudiar la historia de su vegetación.

En referencia a este segundo punto, la mayor parte de los datos ambientales de los últimos milenios conocidos en la Meseta Norte proceden de estudios palinológicos realizados sobre turberas o lagos de zonas montañosas, particularmente del Sistema Central y Sistema Ibérico (p.e. Peñalba *et al*., 1997; Franco Múgica *et al*., 1998; Sánchez-Goñi & Hannon, 1999; Ruiz Zapata *et al*. 2003; Gómez González, 2007); así como de los cada vez más numerosos estudios de índole arqueopalinológica emprendidos en yacimientos de diversos periodos crono-culturales en el área considerada (Mariscal, 1995; Ruiz Zapata, 1995; Yll, 1995). Estos segundos tienen, no obstante, la limitación de comprender 'ventanas cronológicas cerradas', impidiendo estudios de dinámica vegetal en un sentido diacrónico (López Sáez *et al*., 2003).

En los últimos años, sin embargo, son cada vez más frecuentes los registros ambientales en zonas de fondo de valle, cuya tipología se sustenta básicamente en entornos lacustres o suelos de naturaleza higroturbosa. En este sentido las secuencias de Espinosa del Serrato (Palencia) y El Carrizal (Segovia) (Franco-Múgica *et al*., 2001, 2005) son las únicas bien datadas y estudiadas a alta resolución en las zonas no montañosas de la Meseta Norte, cubriendo casi por completo el período cronológico del Holoceno, haciendo una muy buena descripción de los bosques que poblaron la Meseta Norte y demostrando el origen autóctono de las formaciones pinariegas. Sea como fuere, este tipo de información es aún muy limitada, y en este sentido la provincia de Valladolid se encuentra completamente inédita.

En la mitad norte de la Península Ibérica se han realizado numerosos estudios de reconstrucción ambiental del Holoceno sobre distintos tipos de sedimentos y utilizando muy diversos *proxies*, algunos de ellos efectuados en la propia Meseta Norte (Franco-Múgica *et al*., 2001, 2005). Aunque el número de trabajos en referencia a la variabilidad climática y al impacto humano durante los últimos milenios en la mitad septentrional de la Península Ibérica (Holoceno final) es bastante exiguo, reúnen una información muy interesante y valiosa. Los más reseñables son el de Martínez Cortizas *et al*. (1999) en una turbera gallega (Penido Vello), el de Luque & Julià (2002) en un sondeo corto del lago de Sanabria, los de Desprat *et al*. (2003) y Muñoz Sobrino *et al*. (2007) en la Ría de Vigo, los de Riera *et al*. (2004, 2006) en el lago de Estanya y el de López-Sáez *et al*. (2009) en la Bahía de Portlligat; siendo también importante citar el de Gil García *et al*. (2006) en las Tablas de Daimiel aunque se ubique en la Meseta Sur. En algunos de ellos se detectan una o varias fases de los momentos de variabilidad climática que han sido descritos en otras partes de Europa durante el Holoceno más reciente: el período frío y seco del final de la Edad del Hierro, el Período Cálido Romano de características cálidas y más húmedas, el Período Frío Altomedieval algo más frío y más seco, el Período Cálido Bajomedieval de características cálidas y con una tendencia al incremento de la humedad, la Pequeña Edad del Hielo de características frías, y el período más cálido y húmedo en el que vivimos en la actualidad. Sin embargo, la cronología y duración de cada una de las fases es ligeramente diferente en cada uno de los registros.

El depósito que se presenta en este trabajo es un bodón o lavajo de origen endorreico. Las características hidrológicas estacionales e irregulares de este tipo de sistemas acuáticos los hacen muy interesantes como captadores de cambios ambientales. Por lo tanto, en el presente estudio se muestra el primer análisis ambiental de los últimos *ca*. 2.800 años, de índole palinológica, emprendido en Valladolid en el seno de un contexto natural no arqueológico, caso del bodón o laguna endorreica de Almenara de Adaja, situado en el entorno inmediato de la Villa Romana de Almenara de Adaja (Fig.1). Este registro ha demostrado ser muy sensible tanto a cambios ambientales como climáticos.

2. ÁREA DE ESTUDIO

La zona de estudio (41°11’31.01”N; 4°40’5.07”W) se localiza en la Meseta Norte, en la cuenca del Duero, a una altitud de 784 m snm, cercana a las localidades de Almenara de Adaja y Puras, ambas en la provincia de Valladolid (Fig.1) y en lo que es conocido como ‘Tierra de Pinares’. El punto en donde se efectuó el sondeo se localiza en un pequeño lavajo de carácter endorreico, de apenas 20 x 10 m, con una pequeña lámina de agua de carácter esporádico, cuya vegetación característica está formada por pastizales hidro-higrófilos de juncáceas y ciperáceas, mientras que en los alrededores se localizan cultivos de cereal. La vegetación regional corresponde a paisajes dominados por pinares, tal y como alude el nombre de ‘Tierra de Pinares’ de la comarca. En general, los pinos (*Pinus pinaster* y *P. pinea*, principalmente; y *P. nigra* y *P. sylvestris* de carácter más relicto) crecen sobre sustratos arenosos plio-cuaternarios, si bien las frondosas (*Quercus ilex* y *Q. faginea*, y de manera esporádica *Q. pyrenaica*) lo hacen sobre sustratos terciarios (Franco-Múgica *et al.*, 2005).

3. MATERIAL Y MÉTODOS

El bodón de Almenara de Adaja está situado en las inmediaciones de la Villa Romana del mismo nombre (Fig.1), por lo que es de esperar que la ocupación de esta villa tenga reflejo en los espectros polínicos. En la orilla del bodón se procedió a la obtención de un registro ambiental mediante el empleo de una sonda industrial hidráulica, obteniéndose un testigo sedimentario de 610 cm de potencia, cuya descripción sedimentológica queda recogida en la Tabla 1.

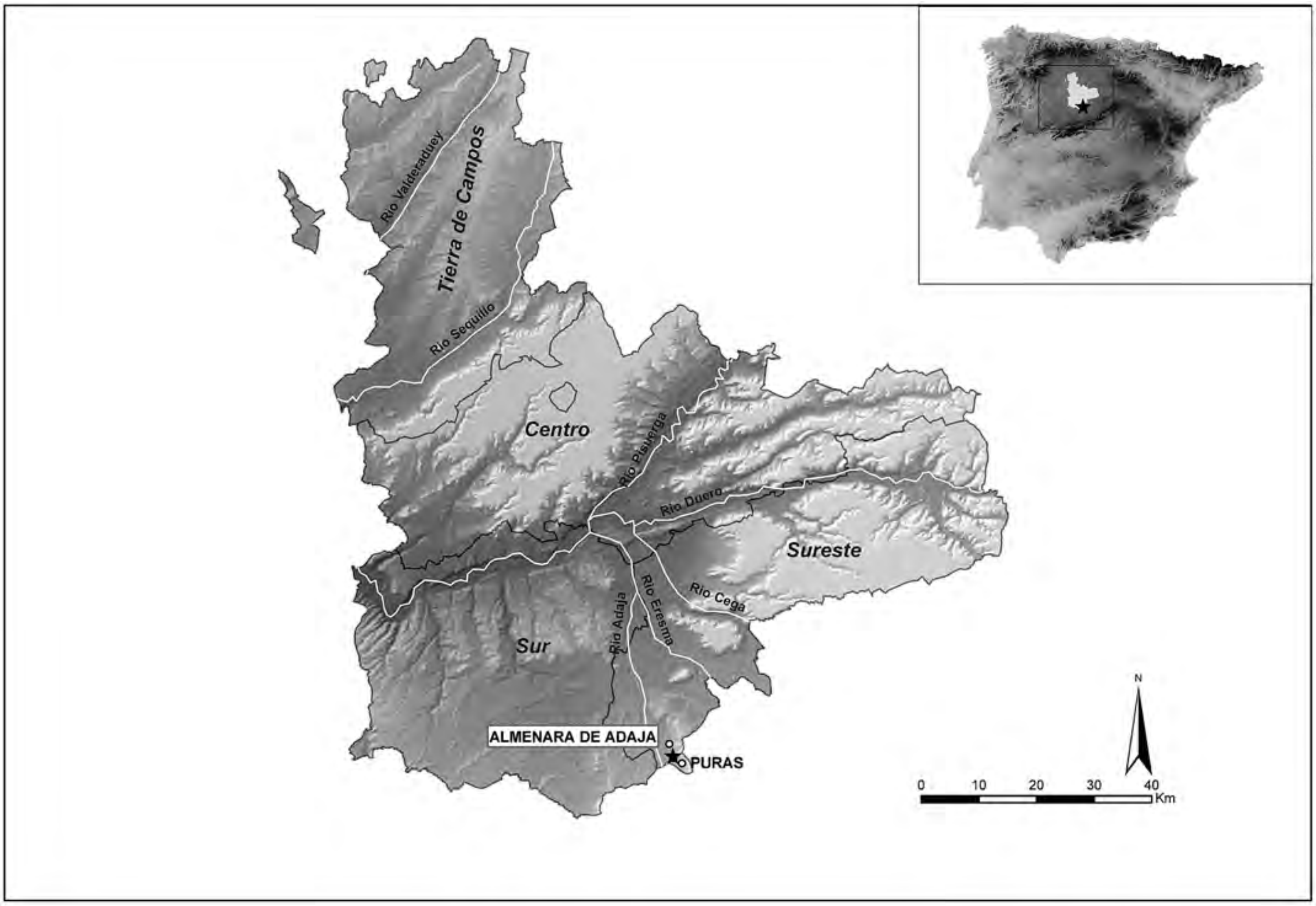

Figura 1. Localización del área de estudio y del punto de muestreo de la secuencia de Almenara de Adaja (Valladolid).

Figure 1. Location of the study area and sample point in the Almenara de Adaja (Valladolid) sequence.

Profundidad (cm)	Descripción
0-40	Limo humificado con detritus herbáceos, color pardo oscuro.
40-240	Limo amarillo claro con arenas finas.
240-610	Limo amarillo-grisáceo con arenas muy gruesas.

Tabla 1. Descripción sedimentológica de la secuencia ambiental de Almenara de Adaja.

Table 1. Sedimentological description of the environmental sequence at Almenara de Adaja.

Se efectuaron seis dataciones radiocarbónicas (AMS) para la totalidad del sondeo. Desafortunadamente cuatro de ellas, comprendidas entre los 240 y 610 cm, no contuvieron la cantidad de materia orgánica necesaria para ser datadas, a pesar de haberse procedido mediante la técnica AMS que apenas precisa un miligramo (López Sáez, 2005). En cambio, para el tercio superior del registro sedimentario (0-240 cm) sí fue posible obtener dos dataciones ^{14}C, que quedan recogidas y calibradas en la Tabla 2. Para la calibración de las mismas se utilizó el programa CALIB 5.0.2, que trabaja con los datos de la curva INTCAL04 (Reimer *et al.*, 2004). Con los datos obtenidos se elaboró un modelo de edad-profundidad para el registro, que presupone una tasa de sedimentación constante entre las dos dataciones y escoge los intervalos de mayor probabilidad, considerando el techo de la secuencia como la actualidad (Fig.2).

Las muestras para el análisis polínico se estudiaron cada 10 cm. Un total de 61 muestras se sometieron a procedimientos químicos en el laboratorio. Desafortunadamente, del total analizado tan sólo las correspondientes a los 240 cm superiores del sondeo resultaron fértiles a nivel polínico, mientras que el resto del testigo (240-610 cm) fue estéril. Estos datos polínicos concuerdan con lo anteriormente expuesto acerca de la imposibilidad de obtener dataciones AMS para este tramo sedimentario de la secuencia. Es probable que la naturaleza del sedimento, limos con arenas gruesas, haya sido la causa de la falta de contenido polínico (eliminado por abrasión), así como de otro resto de materia orgánica susceptible de ser datado. El método químico utilizado para la extracción de polen, esporas y microfósiles no polínicos (MNPs) fue el tradicional en este tipo de sedimentos (Faegry & Iversen, 1989; Moore *et al.*, 1991), consistente en un ataque al sedimento mediante ácidos y bases. El residuo obtenido fue sometido a técnicas de enriquecimiento, separación densimétrica de los palinomorfos polínicos y no polínicos, mediante la concentración del polen por flotación en licor de Thoulet (Goeury & Beaulieu, 1979), y añadiendo un marcador exógeno (*Lycopodium*) para calcular las concentraciones (Stockmarr, 1971).

El tratamiento de datos y representación gráfica (diagrama polínico: Figs. 3-4) se realizó con ayuda de los programas TILIA y TGview (Grimm, 1992, 2004). Para el cálculo de los porcentajes de cada taxón (frecuencia relativa) del diagrama polínico, los taxa hidro-higrófilos y los MNPs fueron excluidos de la suma base, por ser considerados de carácter local o extra-local y estar fuertemente sobrerrepresentados (Wright & Patten, 1963), aunque su porcentaje relativo se ha calculado respecto a ésta. Con el fin de facilitar la visualización de los datos se ha elaborado un diagrama polínico sintético en función de la cronología obtenida (Fig.5), en donde se han agrupado los taxa relacionados con la antropización en dos grupos: comunidades nitrófilas antrópicas (resultado de la suma de los

Código	Profundidad (cm)	Datación ^{14}C	Edad cal BP (1σ)	Edad cal BC/AD (1σ)
Ua-24520	95-100	1550 ± 40 BP	1423-1394 cal BP (29.6%) 1444-1430 cal BP (12.4%) 1526-1457 cal BP (**58.1%**)	527-556 cal AD (12.4%) 506-520 cal AD (12.4%) 434-493 cal AD (**58.1%**)
Ua-24521	234-240	2675 ± 100 BP	2627-2623 cal BP (0.9%) 2928-2714 cal BP (**99.1%**)	678-674 cal BC (0.9%) 979-765 cal BC (**99.1%**)

Tabla 2. Dataciones radiocarbónicas obtenidas en la secuencia de Almenara de Adaja y calibración de las mismas.

Table 2. Radiocarbon datings at the Almenara de Adaja sequence, with their calibration.

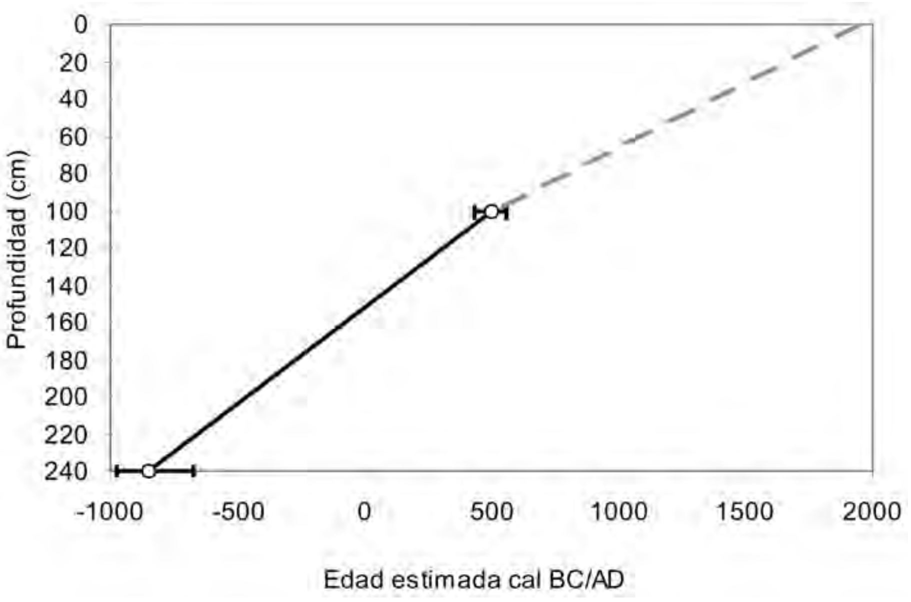

Figura 2. Modelo de edad-profundidad de la secuencia de Almenara de Adaja (ver el apartado de Material y métodos para su explicación). Las barras de error representan los intervalos de calibración a 1σ.

Figure 2. Age-depth model of the Almenara de Adaja sequence (see the "material and methods" section for further explanation). The error bars represent calibration intervals at 1σ.

porcentajes de *Aster* tipo, Cardueae, Cichorioideae y Boraginaceae) y pastizales antropozoógenos (resultado de la suma de Poaceae, *Urtica dioica* tipo, *Plantago lanceolata* tipo y Chenopodiaceae/Amaranthaceae).

4. RESULTADOS

El diagrama polínico de la secuencia de Almenara de Adaja (Figs. 3-4), que cubre los últimos 2800 años, se ha dividido en seis zonas polínicas (AD-1 a AD-6), cuya descripción y características quedan resumidas en la Tabla 3. En general se observan fluctuaciones en los porcentajes arbóreos y en la curva de Cyperaceae, siendo las zonas polínicas impares (AD-1, AD-3 y AD-5) características por descensos en los porcentajes arbóreos y de Cyperaceae, y las pares (AD-2, AD-4 y AD-6) por el incremento de ambos. Gracias a las curvas arbóreas, de las ciperáceas y de los MNPs se han podido identificar distintos períodos climáticos con alternancia entre episodios más térmicos y favorables con episodios menos favorables y más fríos, cuyas características quedan descritas en el apartado de Discusión y pueden observarse en el diagrama sintético de la Fig.5. Adicionalmente, de la base al techo de la secuencia polínica se observan indicadores antrópicos y de actividades pastoriles, aunque en distinto grado, al igual que un diferente desarrollo de los cultivos cerealísticos. Aunque estos síntomas antrópicos se detecten desde la Edad del Hierro, es desde la época romana cuando se establecen las transformaciones del paisaje que conformarán de una manera paulatina esta zona como un espacio altamente agrícola y ganadero.

5. DISCUSIÓN

5.1. Cambios ambientales durante los últimos 2.800 años

En la secuencia de Almenara de Adaja pueden reconocerse las características de los eventos anteriormente comentados en el apartado de Introducción, suponiendo una nueva evidencia, a este respecto, de la variabilidad climática durante los últimos milenios del Holoceno, normalmente enmascarada por el impacto humano y por la escasa resolución de los registros para el Holoceno final (Desprat *et al.*, 2003). Aunque en el diagrama polínico se observan síntomas de antropización del paisaje desde el inicio, como se discutirá en el siguiente apartado, el uso

Zona polínica	Profundidad (cm)	Edad estimada cal BC/AD (cal BP)	Polen	Hidro-higrófilas y MNPs
AD-6	0-10	1800 cal AD-actualidad (150 cal BP-actualidad)	Los porcentajes arbóreos muestran un ligero aumento, llegando a casi el 50%, siendo *Pinus* el elemento mayoritario. Este paisaje abierto estaría dominado por formaciones herbáceas de carácter antrópico, donde los campos de cultivo de cereal (25%) sería lo más sobresaliente del paisaje, tal como puede verse en la actualidad.	La desaparición de *Closterium idiosporum* (T60) muestra una nueva elevación de las temperaturas de la lámina de agua. El bodón posee características meso-eutróficas (*Spirogyra*), mientras que la ocurrencia de incendios disminuye. Se siguen detectando altos procesos erosivos que, al igual que en la zona anterior, pueden relacionarse con la intensidad de los cultivos.
AD-5	10-35	1450-1800 cal AD (500-150 cal BP)	Los porcentajes arbóreos rompen con la dinámica de recuperación arbórea detectada en AD-4, mostrando un ligero retroceso, afectando mayoritariamente a las formaciones pinariegas. Los síntomas de antropización del paisaje continúan, siendo las prácticas agrícolas (cereal) más intensas que en AD-5.	La curva de Cyperaceae también rompe con la dinámica de crecimiento comenzada en la zona anterior. La aparición de *Closterium idiosporum* (T60) indica de nuevo enfriamiento del agua; mientras que *Glomus* cf. *fasciculatum* (T207) habla de un importante aumento de los procesos erosivos y *Chaetomium* (T7A) de la ocurrencia de incendios locales. Las condiciones continúan siendo meso-eutróficas (*Spirogyra*).
AD-4	35-80	800-1450 cal AD (1150-500 cal BP)	Se produce una lenta recuperación arbórea del 25 al 40%, sobre todo de *Pinus sylvestris* tipo y de *Pinus pinaster*, aunque las comunidades herbáceas son los elementos mayoritarios. Los tipos polínicos indicadores de antropización y pastoralismo continúan siendo tan abundantes como en AD-3, mientras que la presencia de polen de cereal se hace más abundante, indicando una intensidad similar a la detectada en AD-2.	Se produce un aumento paulatino de los porcentajes de Cyperaceae paralelo a la recuperación arbórea. La presencia de *Spirogyra* sigue haciendo referencia a unas condiciones meso-eutróficas, mientras que el T119 indica la existencia local de humedad. La bajada de *Closterium idiosporum* (T60) indica una mayor temperatura de la lámina de agua.
AD-3	80-120	300-800 cal AD (1650-1150 cal BP)	Los porcentajes arbóreos sufren un nuevo descenso, estando en torno al 20%. La mayor bajada la experimentan *Pinus sylvestris* tipo y *Quercus* perennifolio, mientras que *Quercus* caducifolio desparece. En cambio, se registra incrementos de *Juniperus* tipo y *Pinus pinaster*. Las plantas antrópicas incrementan sus porcentajes, sobre todo Cichorioideae y Chenopodiaceae/Amaranthaceae. Los cultivos de cereal continúan estando presentes, aunque con menor intensidad que en la zona AD-2.	Cyperaceae muestra una gran disminución de sus porcentajes, que ahora rondan el 20%. Los MNPs *Spirogyra* y *Closterium idiosporum* (T60) muestran condiciones meso-eutróficas, y éste último además prefiere las aguas frías, mientras que T200 sigue indicando la persistencia de encharcamiento estacional en la zona. *Sordaria* (T55A) revela pastoreo de manera local, aunque de forma menos intensa que en AD-2.
AD-2	120-160	75 cal BC-300 cal AD (2025-1650 cal BP)	La curva AP aumenta sus valores (20-50%), siendo los tipos arbóreos más importantes *Pinus sylvestris* tipo y *Quercus* perennifolio, y la aparición de *Quercus* caducifolio. *Juniperus* tipo pierde importancia. Los indicadores antrópicos y de actividades pastorales continúan teniendo altos valores, uniéndose a ellos Cardueae y *Rumex obtusifolius* tipo. Los cultivos de cereal comienzan a ser permanentes.	Cyperaceae incrementa sus porcentajes (45-75%) y junto con la presencia de T200 y T179 muestra la persistencia de encharcamiento estacional en la zona, y el último de los MNPs además el paso a unas condiciones eutróficas. El pastoreo se intensifica de manera local como indica *Sordaria* (T55A) y se constata la existencia de incendios (*Chaetomium*, T7A).
AD-1	160-240	850-75 cal BC (2800-2025 cal BP)	Los porcentajes arbóreos (AP) disminuyen del 45 al 20%. Estos porcentajes están dominados por *Quercus* perennifolio, aunque también hay presencias de *Pinus sylvestris* tipo, *Pinus pinaster* y *Juniperus* tipo. Los porcentajes herbáceos (NAP) son los predominantes (65-80%), siendo Poaceae el mayoritario y acompañado de indicadores de antropización como Cichorioideae, *Aster* tipo, y de indicadores de pastoralismo como *Plantago lanceolata* tipo y *Urtica dioica* tipo. Puede detectarse presencia esporádica de cultivos de cereal.	Cyperaceae muestra porcentajes variables entre 15-40%. El MNP T119 indica la existencia local de una zona húmeda, y tendría características meso-eutróficas como indica la presencia de *Spirogyra*. Se constatan procesos erosivos con la presencia de *Glomus* cf. *fasciculatum* (T207).

Tabla 3. Descripción de las zonas polínicas de Almenara de Adaja.

Table 3. Description of the pollen zones at Almenara de Adaja.

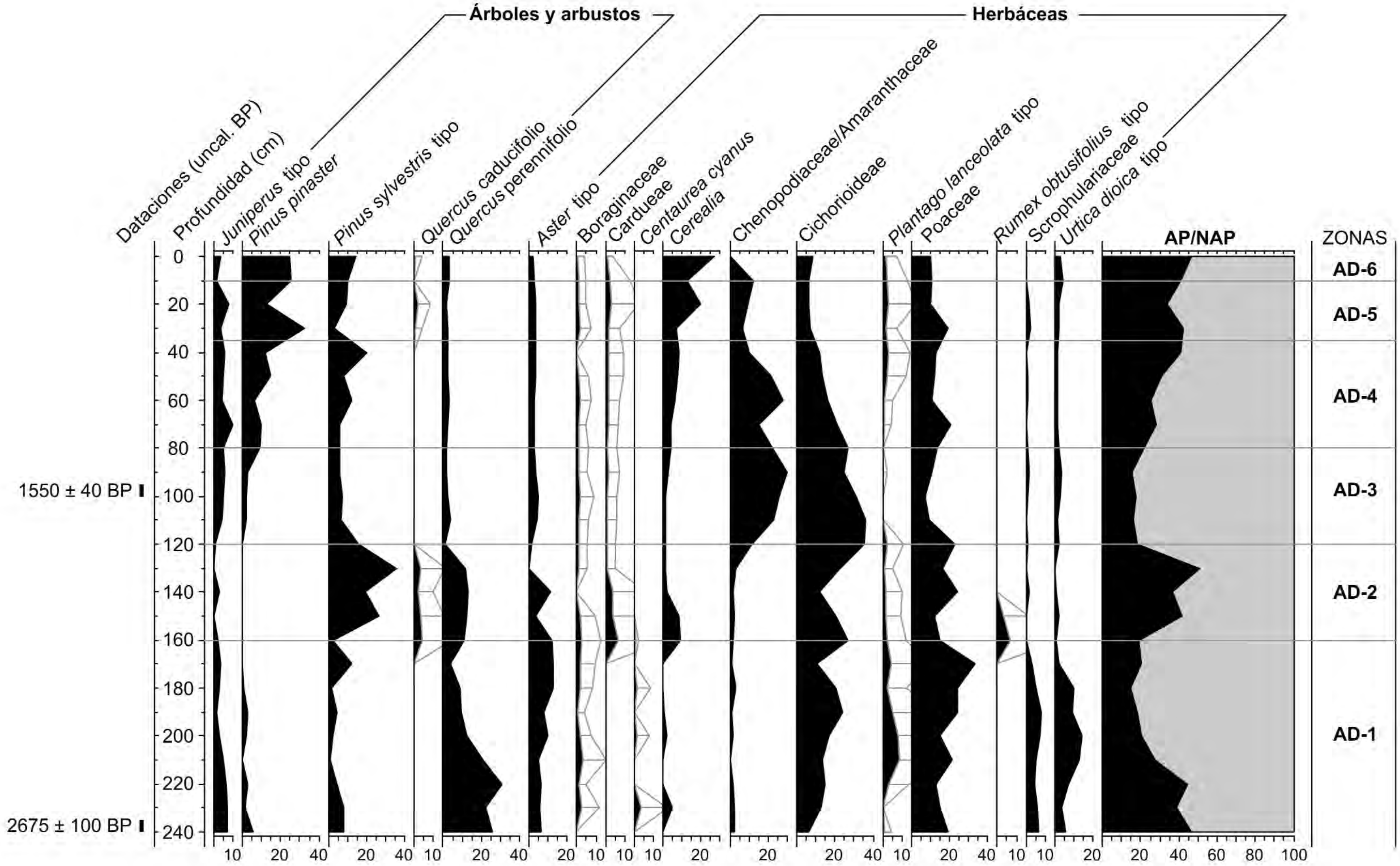

Figura 3. Diagrama polínico de árboles, arbustos y herbáceas de Almenara de Adaja (Valladolid). La magnificación de algunos taxa es de 5 veces.

Figure 3. Pollen diagram for trees, bushes and herbs in Almenara de Adaja (Valladolid). Some taxa have been magnified 5 times.

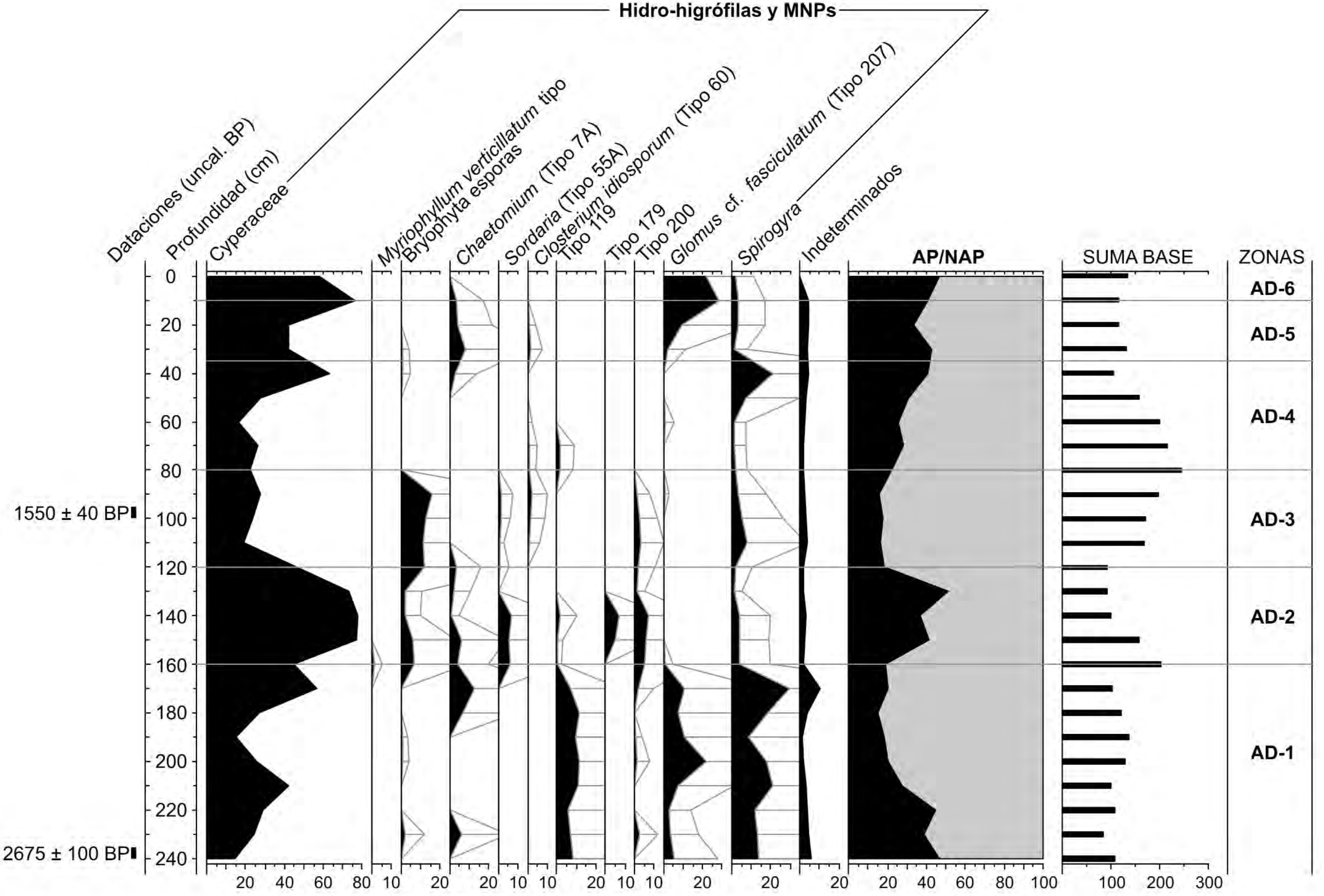

Figura 4. Diagrama polínico de hidro-higrófilas y microfósiles no polínicos (MNPs) de Almenara de Adaja (Valladolid). La magnificación de algunos taxa es de 5 veces. Se presenta la Suma Base Polínica.

Figure 4. Pollen diagram for hydro-higrophytes and non-pollen palynomorphs (MNPs) from Almenara de Adaja (Valladolid). Some taxa have been magnified 5 times. Also presented is the pollen sum.

de la presencia de taxa locales en el ambiente del bodón, tales como Cyperaceae y los MNPs, ha mostrado ser de mucha utilidad para detectar cambios climáticos (Fig.5).

Durante la Edad del Hierro (AD-1) se observa una disminución progresiva del estrato arbóreo, que aun así es bajo durante toda la secuencia (Fig.5). La presencia del Tipo 119, un MNP de estructura globosa y origen desconocido (Pals *et al.*, 1980; López Sáez *et al.*, 1998), indica la existencia local de una zona húmeda, por lo que puede considerarse que el bodón ya poseería las características que tiene en la actualidad: una pequeña lámina de agua de carácter esporádico, que tendría unas características meso-eutróficas, tal y como indica la existencia de zigósporas de *Spirogyra*, alga filamentosa que habitualmente vive en aguas de características superficiales (van Geel *et al.*, 1981, 1989). Cyperaceae, dentro del componente hidro-higrófilo, muestra porcentajes bajos y variables, indicando un ambiente menos húmedo que el que se observa en la fase inmediatamente posterior (Fig.5). En un bodón de las características del estudiado en este trabajo, el que haya un cinturón de ciperáceas bien desarrollado alrededor del mismo indicaría unas condiciones de mayor humedad edáfica, que demostraría que la lámina de agua es relativamente estable en el tiempo permitiendo el desarrollo de pastos hidro-higrófilos. Por lo tanto, el paulatino descenso de los porcentajes arbóreos que se observa *ca.* 850-75 cal BC (2800-2025 cal BP, AD-1), junto con el indicio de que el bodón poseería una comunidad de ciperáceas poco desarrollada, podría estar indicando la existencia de un período desfavorable en relación con unas temperaturas bajas y unas precipitaciones menores que en épocas posteriores. Estas mismas características se han descrito en otras secuencias, como en la Ría de Vigo *ca.* 975-250 cal BC (Desprat *et al.*, 2003) y Las Tablas de Daimiel anterior a 150 cal BC (Gil García *et al.*, 2006).

En la siguiente fase (AD-2), ya en época romana, se observa un fuerte incremento tanto del componente arbóreo como de las ciperáceas, que muestran los valores más altos de toda la secuencia polínica en una cronología *ca.* 75 cal BC-300 cal AD (2025-1650 cal BP, AD-2) (Fig.5). El hecho de que *Quercus* caducifolio y perennifolio incrementen sus porcentajes en detrimento de los de *Juniperus* tipo podría estar haciendo referencia al tránsito a unas condiciones más húmedas y térmicas; mientras que la desaparición de *Pinus pinaster* y el aumento de la presencia de *Pinus sylvestris* tipo quizás esté haciendo relación a una gestión antrópica del territorio. De hecho, la presencia del Tipo 200, MNP de origen fúngico (van Geel *et al.*, 1989; Kuhry, 1997), y del Tipo 179, un MNP de aspecto vasiforme y que probablemente esté relacionado con algún invertebrado acuático (van Geel *et al.*, 1983, 1989) (Fig.5), ponen de manifiesto la permanencia de una lámina de agua de características estacionales. Esta lámina de agua poseería un cinturón ribereño de ciperáceas mucho más desarrollado que en la época anterior, por lo que este tramo cronológico poseería unas características más húmedas. Una mayor humedad y un aumento de las temperaturas, relacionadas con la fase climática denominada Período Cálido Romano, también han sido descritas en las secuencias anteriormente citadas: en la Ría de Vigo *ca.* 250 cal BC-450 cal AD (Desprat *et al.*, 2003), en Las Tablas de Daimiel su cronología es de *ca.* 150 cal BC-250 cal AD (Gil García *et al.*, 2006), mientras que en la turbera gallega de Penido Vello se extiende *ca.* 0-500 cal AD y con una temperatura estimada de 2,2ºC superior a la registrada en la actualidad (Martínez Cortizas *et al.*, 1999).

En la zona polínica AD-3 (*ca.* 300-800 cal AD; 1650-1150 cal BP) se observa cómo los porcentajes arbóreos disminuyen con respecto a la fase descrita como el Período Cálido Romano (Fig.5), siendo ahora los más importantes *Juniperus* tipo y *Pinus pinaster*, que son taxa que viven bajo unas condiciones más secas. Las ciperáceas también muestran una reducción importante de sus porcentajes, indicando una fase más seca que la anterior, aunque el Tipo 200 sigue indicando la persistencia de encharcamiento estacional, por lo que el sistema acuático no desaparecería. Las condiciones pasarían de eutróficas en AD-2 a meso-eutróficas en esta zona, tal y como indican los MNPs *Spirogyra* y *Closterium idiosporum* (Tipo 60). Este último microfósil, correspondiente a zigósporas, además de indicar condiciones meso-eutróficas, tiene preferencia por aguas frías (van Geel, 1976; van Geel *et al.*, 1981; Kuhry, 1985), por lo que se constata una disminución de las temperaturas con respecto a la fase anterior. Este episodio climático más frío y seco, detectado en esta secuencia *ca.* 300-800 cal AD (Fig.5), ha sido también descrito como correspondiente al Período Frío Altomedieval en la Ría de Vigo *ca.* 450-950 cal AD (Desprat *et al.*, 2003), en Las Tablas de Daimiel *ca.* 270-950 cal AD (Gil García *et al.*, 2006), y en el lago de Estanya en el Pre-Pirineo en un cronología *ca.* 160-820 cal AD (Riera *et al.*, 2004).

Entre *ca.* 800-1450 cal AD (1150-500 cal BP, AD-4) se asiste a una lenta recuperación arbórea, que va en paralelo también con un paulatino incremento de los porcentajes de Cyperaceae (Fig.5). Estos hechos podrían estar indicando la vuelta a unas condiciones climáticas más favorables, en términos de aumento de la humedad y las temperaturas. En este sentido, el Tipo 119 sigue indicando la permanencia de un sistema acuático más o menos estacional, mientras que la desaparición de *Closterium idiosporum* (Tipo 60), durante el intervalo cronológico comentado, señalaría una subida de las temperaturas de la lámina de agua, que podrían estar relacionadas con el trasvase a unas condiciones más térmicas. El hecho de que tras la época climáticamente desfavorable del Período Frío Altomedieval se produzca una recuperación climática ha sido descrito en otras secuencias como el Período Cálido Bajomedieval. Estas condiciones más térmicas y con tendencia hacia un aumento de la humedad poseen una cronología *ca.* 950-1400 cal AD tanto en la Ría de Vigo (Desprat *et al.*, 2003) como en Las Tablas de Daimiel (Gil García *et al.*, 2006), mientras que en la turbera gallega de Penido Vello es de *ca.* 750-1000 cal AD y con una temperatura estimada de 1,9ºC más que en la actualidad (Martínez Cortizas *et al.*, 1999).

Tras el Período Cálido Bajomedieval se ha descrito la ocurrencia de la fase de la Pequeña Edad del Hielo (Bradley & Jones, 1993). En Las Tablas de Daimiel se manifiesta con una alternancia de períodos cálidos y fríos posteriores a 1400 cal AD (Gil García *et al.*, 2006), mientras que en el lago de Estanya se observa como una fase constantemente fría, pero con alternancia de períodos secos y húmedos: *ca.* 1490-1580 cal AD es húmedo, *ca.* 1580-1760 es seco, y se vuelve a condiciones más húmedas *ca.* 1760-1870 cal AD (Riera *et al.*, 2004). Desprat *et al.* (2003) la definen también como una época fría con una cronología entre 1400-1850 cal AD y Muñoz Sobrino *et al.* (2007) entre 1500-1750 cal AD, ambos en la Ría de Vigo. En el lago de Sanabria Luque y Julià (2002) la fechan entre 1300-1585 cal AD, y en la turbera gallega de Penido Vello se refleja *ca.* 1400-1800 cal BP, estimando una temperatura de aproximadamente 1,7ºC menor que en la actualidad según Martínez Cortizas *et al.* (1999). En la secuencia presentada en este trabajo, el bodón de Almenara de Adaja, se constata *ca.* 1450-1800 cal AD (500-150 cal BP) una disminución de la temperatura del sistema acuático en la zona polínica AD-5, como puede inferirse con la nueva presencia de *Closterium idiosporum* (Tipo 60) (Fig.5), mientras que la curva de ciperáceas fluctúa, mostrando una fase más seca entre dos húmedas, tal y como describe Riera *et al.* (2004). Aunque en este caso la cronología de las fases húmedas es *ca.* 1450-1500 cal AD y 1650-1800 cal AD, y la de la fase más seca es de *ca.* 1500-1650 cal AD, esta última coincidente con una ligera bajada de los porcentajes arbóreos.

Desde 1800 cal AD hasta la actualidad (AD-6) sólo hay dos muestras, pero parece que se estabilizan las curvas de arbóreos y ciperáceas, mientras que la desaparición de *Closterium idiosporum* (Tipo 60) marcaría una subida de las temperaturas (Fig.5). El paso hacia unas condiciones más estables y cálidas desde finales de la Pequeña Edad del Hielo hasta la actualidad ha sido igualmente descrito en la Ría de Vigo por Desprat *et al.* (2003) desde 1850 cal AD y en el lago de Estanya por Riera *et al.* (2004) desde 1870 cal AD.

5.2. Actividad antrópica durante los últimos 2.800 años

El área vallisoletana de la zona de Almenara de Adaja debe su fama arqueológica a la existencia de una villa romana con ricos mosaicos, bajo la cual existen numerosas huellas de una ocupación humana más o menos interrumpida entre el Neolítico y la Edad del Hierro (Delibes & Moure, 1973; Balado Pachón, 1989; Delibes *et al.*, 1995; Delibes & Guerra, 2004). La secuencia palinológica presentada en este trabajo tiene su origen en los momentos iniciales de la Edad del Hierro *ca.* 850 cal BC (Fig.5). Este momento es sumamente interesante debido a que en toda Europa se producen una serie de transformaciones de gran calado, entre las que podemos citar el aumento numérico y de tamaño de los poblados, la creciente jerarquización social y el desarrollo de la tecnología metalúrgica del hierro (Collis, 1997) que asimismo se ven reflejadas en el registro arqueológico de la Meseta Norte (Romero *et al.*, 2008). Los datos procedentes del bodón (zona polínica AD-1) concuerdan con diversos análisis palinológicos llevados a cabo en yacimientos vallisoletanos de la Primera

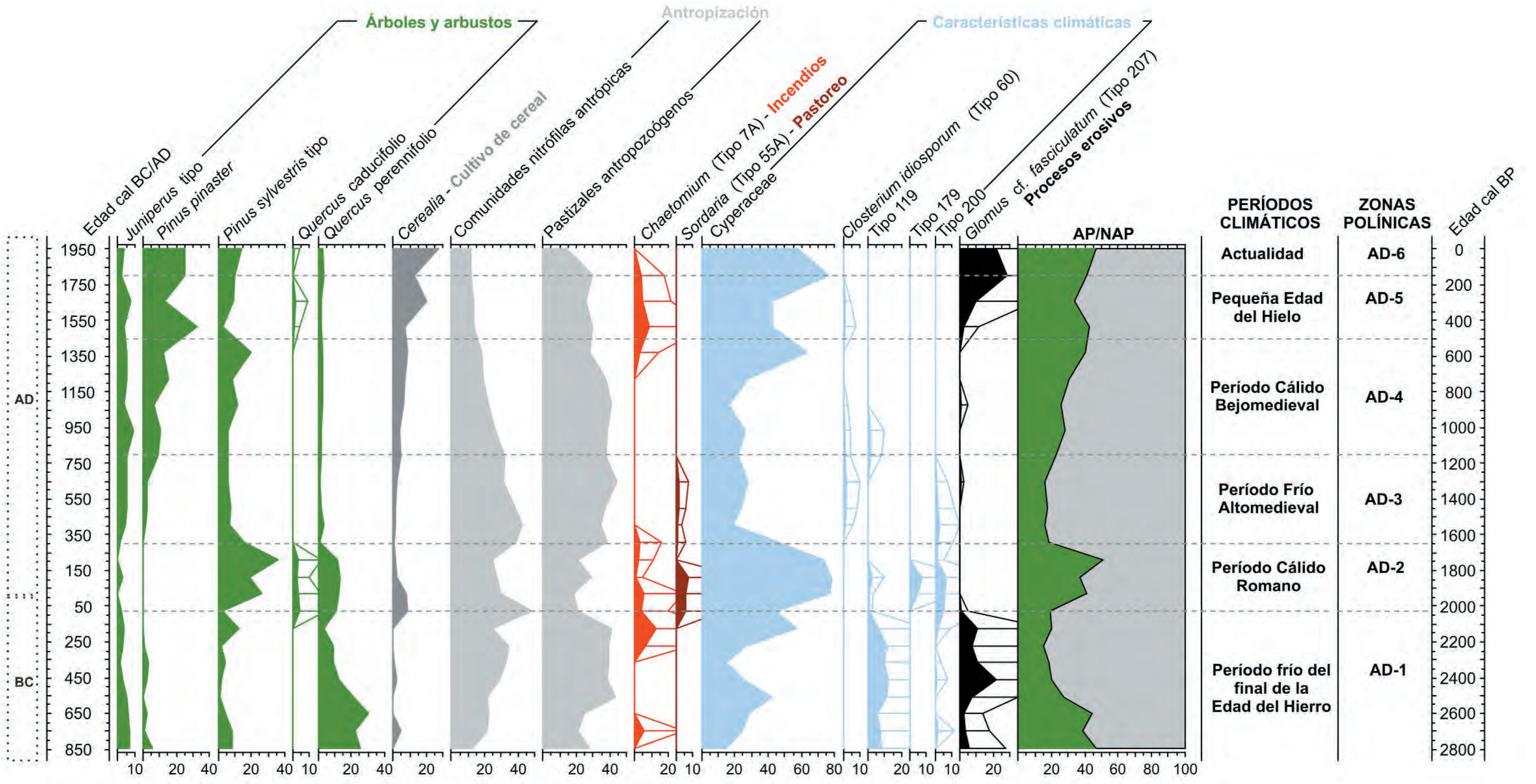

Figura 5. Diagrama polínico sintético de Almenara de Adaja en función de la edad. El grupo de comunidades nitrófilas antrópicas es el resultado de la suma de los porcentajes de *Aster* tipo, Cardueae, Cichorioideae y Boraginaceae; mientras que el grupo de pastizales antropozoógenos es el resultado de la suma de Poaceae, *Urtica dioica* tipo, *Plantago lanceolata* tipo y Chenopodiaceae/Amaranthaceae.

Figure 5. Synthesized pollen diagram from Almenara de Adaja based on age. The group of nitrophilous communities is the sum of the percentages of different types like Aster *type, Cardueae, Cichorioideae and Boraginaceae, while the group of anthropozoogenous pasture is the sum of Poaceae,* Urtica dioica *type,* Plantago lanceolata *type and Chenopodiaceae/Amaranthaceae.*

y Segunda Edad del Hierro, en concreto con los de El Soto de Medinilla, El Cerro de La Mota y La Era Alta (Mariscal, 1995; Ruiz Zapata, 1995; Yll, 1995), los cuales, *grosso modo*, también dan cuenta de un paisaje sumamente deforestado de dominancia herbácea, con abundancia de pastos graminoides y nitrófilos, presencia de pino haciendo referencia al paisaje regional, palinomorfos indicativos de presión pastoral, documentación palinológica más o menos esporádica de cerealicultura, bajo porcentaje de pastos húmedos y un clima fundamentalmente seco (Fig.5). La aparición de cereal, además también queda confirmada por estudios carpológicos (Hopf, 1973; Cubero Corpas, 1995; Romero & Cubero, 1999).

Para la época romana (zona polínica AD-2), aunque muy importante en la zona debido a la existencia de la villa, no se poseen estudios ambientales. La villa romana de Almenara de Adaja data de la segunda mitad del siglo IV cal AD, aunque se construyó en un solar previamente ocupado por las instalaciones de una ocupación agrícola de otra villa del siglo III y primera mitad del IV cal AD. Pero incluso se han recuperado algunos restos cerámicos anteriores, concretamente de los siglos I y II cal AD (García Merino, 2008). Todos estos datos ponen de manifiesto la ocupación de este territorio durante todo el período romano (Alto y Bajo Imperio) siendo, además, las estructuras relacionadas con asentamientos de carácter agropecuario los elementos de ocupación más importantes. El carácter agropecuario de los asentamientos romanos queda refrendado polínicamente por el hecho de que la curva de polen de cereal se hace constante, y no intermitente como durante la Edad del Hierro (Fig.5). Otro hecho que ratifica el carácter agropecuario de estas villas es que se constata la persistencia de la ganadería detectada durante la Edad del Hierro, pero mucho más intensificada. Esta intensificación puede inferirse de la presencia de las esporas de *Sordaria* (Tipo 55A) (Fig. 5), hongo coprófilo que vive sobre las heces (van Geel, 1978; van Geel *et al.*, 1983, 2003) y que indica que el establecimiento de las cabañas ganaderas en este momento es local, que no regional (López Sáez *et al.*, 2000; López Sáez & López Merino, 2007). El uso agropecuario del paisaje queda, pues, demostrado. Este uso también puede estar relacionado con la generalización de la ocurrencia de esporas de *Chaetomium* (Tipo 7A) (Fig. 5), hongo de ecología carbonícola que se usa como indicador de incendios (van Geel, 1978; Kuhry, 1985), probablemente antrópicos cuando, como en este caso, hay una relación muy estrecha entre su presencia y la antropización del paisaje (López Sáez *et al.*, 1998, 2000).

Tras la caída del Imperio se produjo el abandono de las estructuras de esta villa y de otras cercanas, aunque se ha podido constatar una continuidad en su ocupación posterior, no obstante de manera bastante precaria y con persistencia de los usos agrícolas (García Merino, 2008). En el diagrama polínico (Fig. 5) se observa que, aunque las actividades agropecuarias continúan (zonas polínicas AD-3 y AD-4), se produce un descenso de la importancia de las mismas hasta época ya más reciente (zonas polínicas AD-5 y AD-6). Hace unos *ca.* 450 años es cuando pueden apreciarse de nuevo las evidencias de indicadores de incendios (*Chateomium*); incendios que servirían para la apertura de los paisajes (que estaría relacionada con la proliferación de las clamidosporas de *Glomus* cf. *fasciculatum*, indicador de procesos erosivos; van Geel *et al.*, 1989) y utilización de esos espacios para la proliferación de los campos de cultivo, creando los paisajes que podemos observar hoy día tan típicos de las llanuras castellanas.

El uso del fuego para la apertura del espacio forestal se detecta desde el inicio del diagrama, aunque se intensifica en dos períodos. El primero de ellos es en cronología romana, donde la apertura de espacios se ha utilizado tanto para la instalación de campos de cultivo de cereal como para crear pastos de uso ganadero, como muestran los altos porcentajes de polen de cereal y de hongos coprófilos. Mientras que en el segundo de los períodos, ya en época reciente, la apertura del paisaje ha creado espacios tanto para la intensificación de los cultivos de cereal como para repoblaciones forestales, tal y como muestran de nuevo los altísimos porcentajes de polen de cereal y la proliferación moderna de *Pinus pinaster* (Fig. 5).

6. CONCLUSIONES

El análisis tanto de microfósiles polínicos como de no polínicos de una secuencia extraída de una laguna endorreica de carácter superficial y estacional en Almenara de

Adaja (Valladolid) ha demostrado una sensibilidad tanto a cambios climáticos como antrópicos:

Los MNPs relacionados con la existencia de unas condiciones acuáticas junto con las fluctuaciones en las curvas de las ciperáceas y de los elementos arbóreos han revelado la existencia de distintos ciclos climáticos durante los últimos 2.800 años: i) una fase fría y seca entre 850-75 cal BC (AD-1), ii) la más cálida y húmeda del Período Cálido Romano entre 75 cal BC-300 cal AD (AD-2), iii) una nueva etapa desfavorable (Período Frío Altomedieval) *ca*. 300-800 cal AD (AD-3), iv) el retorno a unas condiciones más térmicas y húmedas del Período Cálido Bajomedieval *ca*. 800-1450 cal AD (AD-4), y iiv) las condiciones más frías de la Pequeña Edad de Hielo entre 1450-1800 cal AD, con una fase seca entre dos húmedas (AD-5).

Además, el diagrama polínico muestra síntomas antrópicos desde su comienzo en la Edad del Hierro, pero es la época romana la que estableció las bases de las transformaciones paisajísticas para entender el paisaje actual de la zona de estudio, convirtiendo la zona en un espacio altamente agrícola y ganadero.

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La *Revista Española de Micropaleontología* publica manuscritos originales, relacionados con cualquier aspecto micropaleontológico. Solamente aquellos remitidos de acuerdo con las normas editoriales, serán enviados para su revisión a un mínimo de dos revisores.

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La revista acogerá para su publicación trabajos en español o inglés. Excepcionalmente se aceptarán en otro idioma (en este caso con resúmenes también en español e inglés). En caso de que el autor no escriba en su lengua nativa, los manuscritos deberán estar corregidos lingüísticamente antes de ser remitidos al editor.

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El *resumen* no deberá superar las 300 palabras y debe dar una idea clara del contenido del trabajo; deberá mencionar en su caso las nuevas determinaciones sistemáticas. También, se incluirá un resumen en inglés, junto con 4 a 6 palabras clave en ambos idiomas.

En el *apartado sistemático,* el nivel del taxón más elevado queda a discreción del autor, pero deben estar acompañados de autor y año, de acuerdo con los siguientes ejemplos:

Orden FORAMINIFERIDA Eichwald, 1830
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Género *Thomasinella* Schlumberger, 1893
Thomasinella punica Schlumberger, 1893

Las *tablas* irán en páginas independientes, aunque se intercalarán en el lugar que les corresponda en el texto. Se proyectarán teniendo en cuenta el formato de la página (180 mm) y de la columna (85 mm), y sus explicaciones deberán in en hoja aparte.

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Bengston, P. 1988. Open Nomenclature. *Palaeontology,* 31, 223227.

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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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Articles should be written in Spanish or English. Other languages may occasionally be accepted (with abstracts also provided in Spanish and English). Typescripts should be submitted on a good-quality paper of International A4 size and prepared on a word processor. Authors writing in other than their own native language are requested to have their manuscripts thoroughly checked linguistically before submission to the Editor.

Title page should include the name(s) of the author(s), affiliation(s) and e-mail address(es). In case of more than one author, please indicate to whom the correspondence should be addressed. The *title* should be short but informative, with indications about the fossil group, the age and the geographic area. It should not include the names of new taxa.

A concise *abstract* of no more than 300 words should summarize results of the paper and must mention all new systematic names. Abstract should be written in English and Spanish. Also provide 4 to 6 *keywords* placed beneath the abstract.

In the *systematic work,* the level of the highest taxon is at the discretion of the author, but must always be accompanied by authority and date. Example:

Order FORAMINIFERIDA Eichwald, 1830
Family THOMASINELLIDAE Loeblich & Tappan, 1984
Genus *Thomasinella* Schlumberger, 1893
Thomasinella punica Schlumberger, 1893

Use italics rather than underlining for genus/species names.

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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Bengston, P. 1988. Open Nomenclature. *Palaeontology,* 31, 223227.

Bolli, H., Beckmann, J. P. and Sanders, J. 1994. *Benthonic foraminiferal biostratigraphy of the South Caribbean Region.* Cambridge University Press, Cambridge, 408 pp.

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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