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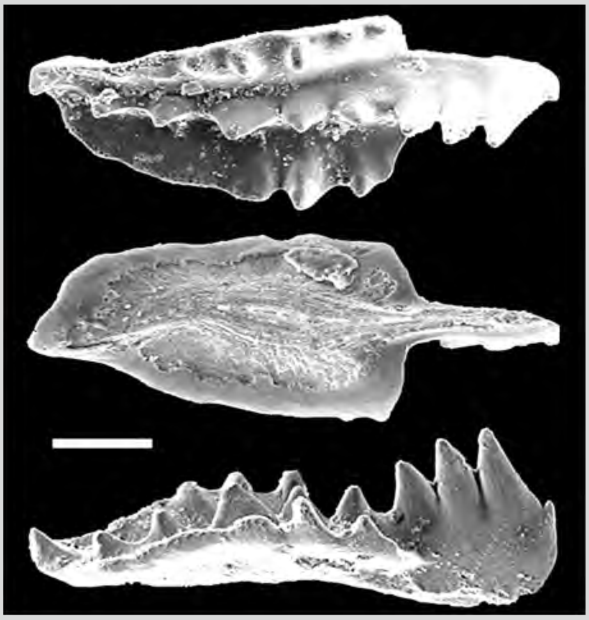

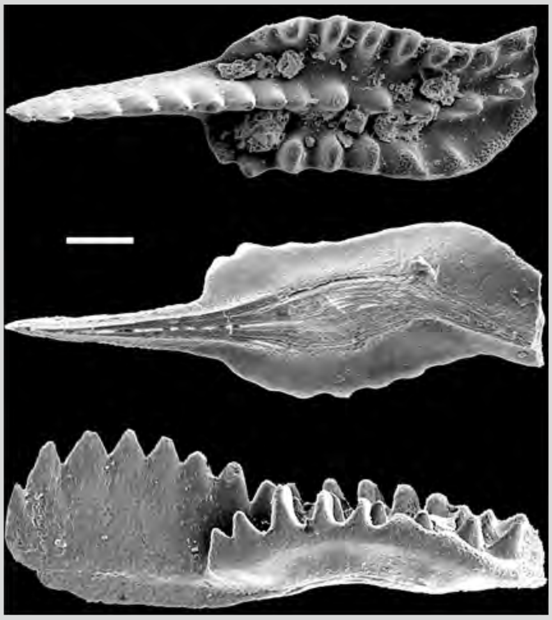

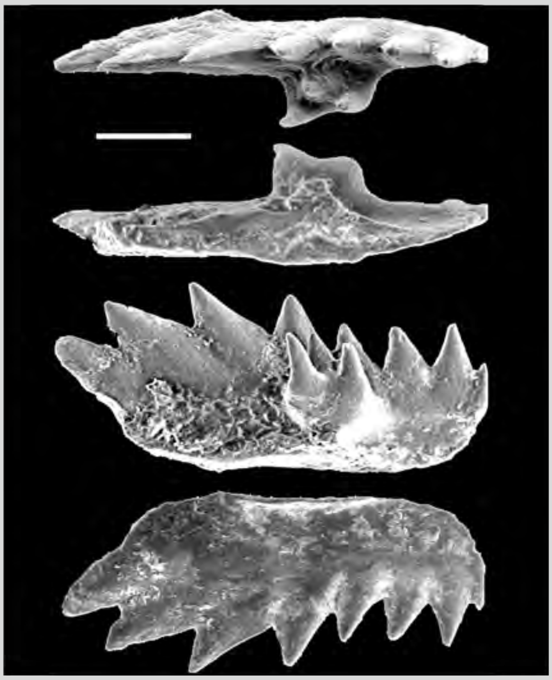

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Portada: Conodontos del Triásico Medio de Calanda (Teruel). Fotografías de P. Plasencia, A. Márquez-Aliaga y J. I. Valenzuela-Ríos. Escala gráfica: 100 µ.

Cover: Middle Triassic conodonts of Calanda (Teruel province, Spain). Microphotographies by P. Plasencia, A. Márquez-Aliaga and J. I. Valenzuela-Ríos. Scale bar: 100 µ.

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TAXONOMY AND EVOLUTIONARY SIGNIFICANCE OF SOME *GNATHODUS* SPECIES (CONODONTS) FROM THE MISSISSIPPIAN OF THE NORTHERN IBERIAN PENINSULA

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Abstract

A new species of *Gnathodus*, *G. joseramoni*, is defined and *Gnathodus cantabricus* Belka & Lehmann is revised from the study of some new conodont associations and analysis of previous data from the Cantabrian Mountains and the Pyrenees, North Iberian Peninsula. *G. cantabricus* is regarded as a junior synonym of *Gnathodus kiensis* Pazukhin from the Urals. Other occasional European findings of both taxa are indicated and stratigraphic middle Viséan to Arnsbergian ranges are established. Finally, the phylogenetic relations with other *Gnathodus* species are also outlined.

Key words: Conodont, systematic palaeontology, Mississippian, Cantabrian Mountains, Pyrenees.

Resumen

Se define una especie nueva de *Gnathodus*, *G. joseramoni*, y se revisa *Gnathodus cantabricus* Belka & Lehmann, a partir de nuevas asociaciones de conodontos y el análisis de los datos previos en la Cordillera Cantábrica y los Pirineos, norte de la Península Ibérica. *G. cantabricus* se considera un taxón sinónimo más moderno que *Gnathodus kiensis* Pazukhin de los Urales. Se indican otros hallazgos ocasionales en Europa de ambas especies y se establece su distribución estratigráfica entre el Viseense medio y el Arnsbergiense. Finalmente, se trazan las relaciones filogenéticas con otras especies de *Gnathodus*.

Palabras clave: Conodonto, paleontología sistemática, Misisípico, Cordillera Cantábrica, Pirineos.

INTRODUCTION

Gnathodus species are widely distributed in deep-water successions of the Mississippian age. Many species of this genus are used as indicators of the early Carboniferous standard conodont zones and, consequently, many papers focus on *Gnathodus*. Important studies on this genus have been carried out in the Cantabrian Mountains (Budinger, 1965; Adrichem Boogaert, 1967; Higgins & Wagner-Gentis, 1982; Park, 1983; Menéndez-Álvarez, 1991, unpublished) and the Pyrenees (Perret, 1993; Sanz-López, 1995, unpublished), in the northern part of the Iberian Peninsula.

Recently, *Gnathodus cantabricus* Belka & Lehmann (1998) was proposed as an upper Viséan species from the Cantabrian Mountains (Spain) and Styria (Austria). It was a minor component in studied conodont samples (less than five per cent of the total elements). Previously, Pazukhin (in Kulagina *et al.* 1992) described a Serpukhovian species *(Gnathodus kiensis)* from the South Urals that is very close to *G. cantabricus*.

Other materials recently assigned to *G. cantabricus* from the middle Viséan of the Cantabrian Mountains and the eastern Catalonian Pyrenees (García-López & Sanz-López, 2002b; Sanz-López, 1995, 2002) are also of interest because they constitute between twenty and forty per cent of total elements collected. Study and comparison of this Spanish material can play an important role providing a new background for discussing the status, biostratigraphic significance, and phylogenetic relationships of *"Gnathodus cantabricus"*.

GEOLOGICAL SETTING

The Cantabrian Zone and the Pyrenees are included in the south-western part of the European Variscan orogen. Both areas constitute foreland thrust and fold belts; the first is situated in the north of the Iberian Massif, and the latter lies outside this massif and is surrounded by Mesozoic and Tertiary cover (Fig. 1). A sedimentary high or block, the Cantabro-Ebroian massif (Carls, 1983), was located between the Cantabrian Zone and the Pyrenees in the Devonian, although marine rocks covered the massif from the uppermost Devonian up to the Carboniferous.

In the Cantabrian Zone, nodular cephalopod limestones of the Alba Formation (Comte, 1959) were deposited from upper Tournaisian to Serpukhovian. The Alba Fm. is 20-30 m thick and has yielded rich and diverse conodont associations. Most of the samples studied here (Fig. 1, Tabl. 1) come from the Fold and Nappe province (Julivert, 1971) of the Cantabrian Zone and were collected in the middle part of the Alba Fm. (Carranques, Millaró, Fig. 2, and Olleros de Alba sections, in García-López & Sanz-López, 2002a, b). Additional samples studied in this paper belong to the Dr. Menéndez-Álvarez's collection, deposited in the Department of Geology of the University of Oviedo (samples J-13 and J-5, from the Entrago section; J-53 and J-54, from the El Portillín section). Two other samples come from the Picos de Europa unit (Julivert, 1971): CPE-13, from the Cares River section (Blanco-Ferrera *et al.*, in press); and CPE-30, collected south of the Sotres village, in the River Duje valley (Blanco-Ferrera, 2002).

Rocks similar in facies, thickness and age to the Alba Fm. are known as the Aspe-Brousset Formation in the Pyrenees (Perret, 1993). A sample studied here, Co42, comes from the eastern Pyrenees and was collected at the comes de Das section, in the Cadí Alpine nappe (Sanz-López, 1995; 2002).

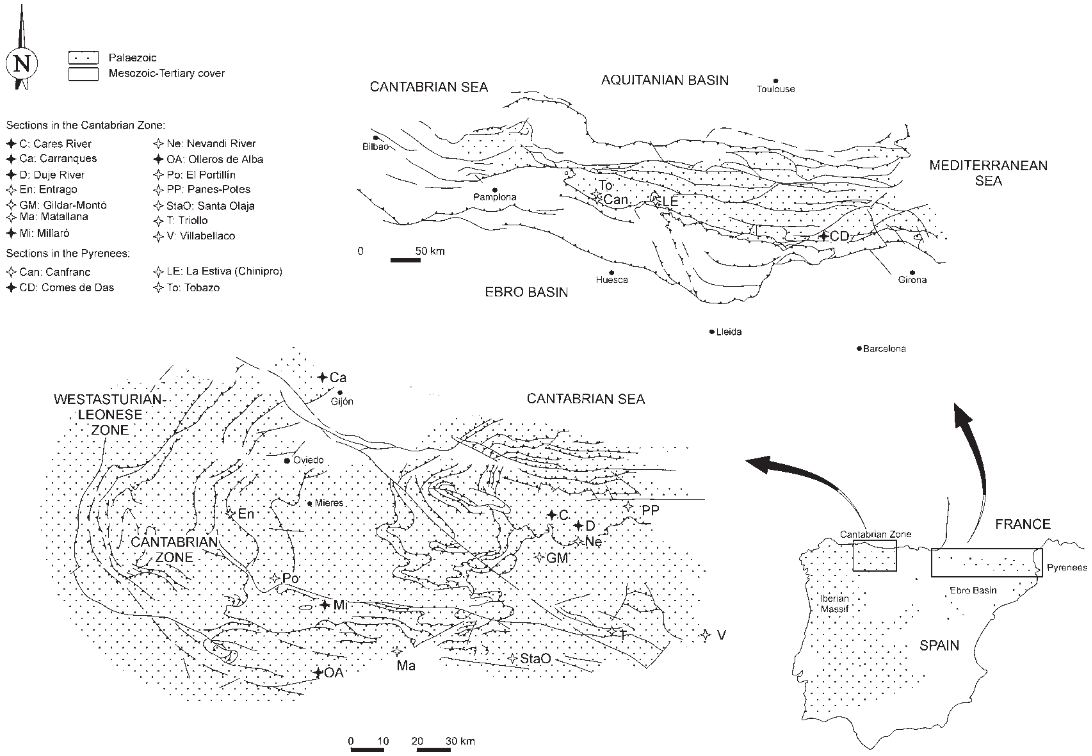


FIGURE 1–Geological sketch with the situation of the localities from the Cantabrian Mountains and the Pyrenees, with conodonts studied (black stars) and referred to in the text (grey stars).

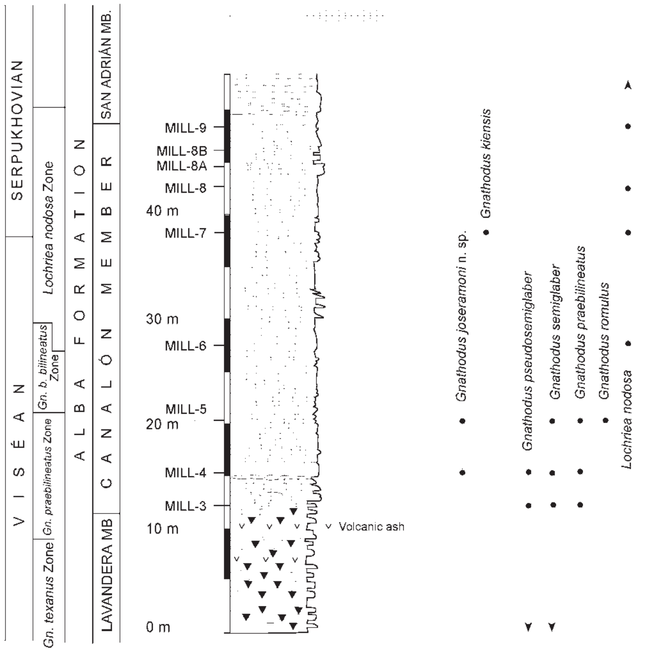


FIGURE 2–The lithostratigraphic units of the Alba Formation (except for the basal Gorguera Member and the uppermost part of the formation) are indicated in the Millaró stratigraphic section. The section included a sequence of samples that yielded much of the material discussed in this paper, as well as important conodont species.

REFERENCES TO *GNATHODUS CANTABRICUS* IN THE CANTABRIAN MOUNTAINS

Higgins (1962) and Budinger (1965) studied middle Viséan conodont associations containing *Gnathodus bilineatus* (Roundy), together with forms that these authors assigned to the Tournaisian species *G. delicatus* Branson and Mehl. Adrichem Boogaert (1967) continued to find these young occurrences of *G. delicatus* and included these Cantabrian associations in his *G. bilineatus-G. delicatus* s.l. Zone. However, Higgins (1974) considered those *"G. delicatus"* elements as a new subspecies of *G. bilineatus* (not described), which according to this author would range from the *G. bilineatus* Zone to his lower "unit" of the *L. nodosa* Zone (middle-upper Viséan). Higgins & Wagner-Gentis (1982) chose to include these forms in the variability of *G. bilineatus bilineatus*.

Menéndez-Álvarez (1991, unpublished) collected these "*G. delicatus*" elements from several Cantabrian sections and considered these forms (together with a younger morphotype) to belong to a new species. Earlier, Park (1983) described *Gnathodus* sp. A from the Santa Olaja de la Varga section. This potential new species was based on elements that only correspond to part of the variation included in the Menéndez-Álvarez's species. Belka & Lehmann (1998), from the upper Viséan to Serpukhovian strata of the Santa Olaja de la Varga section, formally described Park's morphotype as *Gnathodus cantabricus*.

SYSTEMATIC PALAEONTOLOGY

The systematic study is only based upon Pa elements, in spite of the multielement reconstruction preferred by conodont taxonomy. A great deal of information is contained in Pa elements at the specific level and the traditional practice is always based on them, while Pb, M and other elements are used for genera or subgenera assignment, which is not the aim of this paper. The terminology applied is shown in Fig. 3. The conodonts referred to are stored in the collections of the Department of Geology of the University of Oviedo.

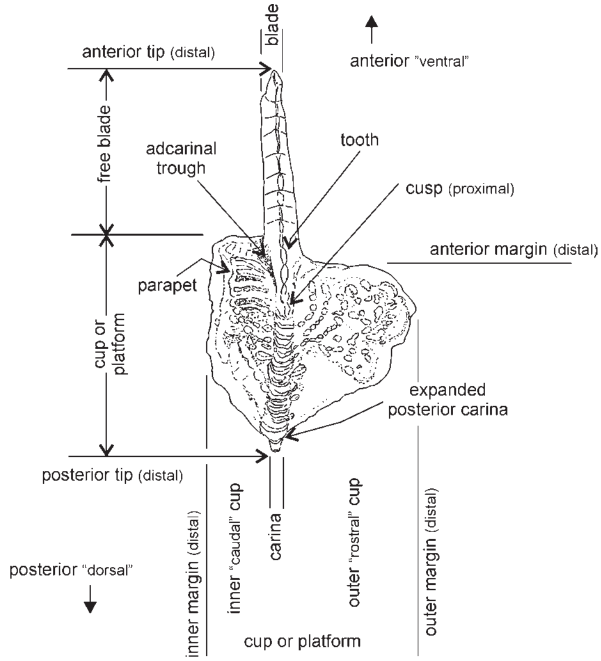


FIGURE 3–Terminology used for different morphologic parts on the oral surface of the Pa element of *Gnathodus* (P1 after the notation of Purnell *et al.,* 2000). Conventional orientation is accompanied by the biological orientation, surrounded by quotation marks, proposed in Purnell *et al.* (2000).

Localities	**1**			**2**	**3**	**4**	**5**	**6**
Conodonts ↓ samples →	**MILL-4**	**MILL-5**	**MILL-7**	**OLL-8**	**CQ-21**	**CPE-30**	**CPE-13**	**Co42**
Gnathodus joseramoni n. sp.	+	+				+		+
G. praebilineatus Belka	+	+				+	+	+
G. cf. *meischneri* Austin & Husri						+		
G. pseudosemiglaber (Thompson & Fellows)	+					cf.		
Geniculatus sp.						+		
Lochriea commutata (Branson & Mehl)	+	+	+	+	+	+	+	+
Pseudognathodus homopunctatus (Ziegler)	+		+			+		+
Ps. symmutatus Rhodes, Austin & Druce	+							+
Vogelnathus campbelli Rexroad	+					+		+
Gnathodus semiglaber Bischoff	cf.	+						
G. romulus Meischner & Nemyrovska		+						+
Gnathodus kiensis Pazukhin			+	+	+		+	
Gnathodus bilineatus (Roundy)			+	+	+		+	
Lochriea nodosa (Bischoff)			+	+			+	
L. mononodosa Rhodes, Austin & Druce			+	+			+	
L. ziegleri Nemyrov., Perret & Meischner			+		+		+	
L. cruciformis (Clarke)			cf.		+			
L. senckenbergica Nemy., Perret & Meischner				+				

TABLE 1–Conodonts from samples of the Millaró section (1), Olleros de Alba section (2), Carranques section (3), Duje River (4), Cares Rives (5), and the comes de Das section (6).

Genus *Gnathodus* Pander, 1856
Polygnathus bilineatus Roundy, 1926
Gnathodus joseramoni n. sp.
(Pl. 1, Figs. 3-16; Pl. 2, figs. 5-12; Text-Fig. 4.5-4.14)

±1959 *Gnathodus delicatus* Branson & Mehl. Voges, p. 283, Pl. 33, Fig. 33 (only).
1962 *Gnathodus bilineatus* (Roundy). Higgins, Pl. 3, Fig. 32.
1965 *G. delicatus* Branson & Mehl. Budinger, Pl. 2, Fig. 11 (only).
1967 *G. delicatus* Branson & Mehl. Adrichem Boogaert, Pl. 2, Fig. 15 (only).
1970 *G. bilineatus* (Roundy). Marks & Wensink, p. 258, Pl. 2, Figs. 9a, b, 11a and b (only).
1974 *Gnathodus* sp. indet. Mathews & Thomas, p. 384, Pl. 51, Figs. 1-3, 18? and 19.
±1977 *Gnathodus* sp. A.- Ebner, p. 471, Pl. 2, Figs. 5 and 7, 8-10? and 13?
1982 *G. bilineatus bilineatus* (Roundy). Higgins & Wagner-Gentis, pp. 328-329, Pl. 34, Fig. 3 (only).

1983 *Gnathodus semiglaber* Bischoff. Park, Pl. 2, Fig. 13 (only).
1983 *Gnathodus* n. sp. A Ebner, 1977. Park, pp. 84-85, Pl. 3, Figs. 1, 2, 3?, 4 and 5.
1991 *Gnathodus cantabricus* n. sp. Menéndez Álvarez, pp. 169-171 (part).
1993 Intermediate form between *G. semiglaber* and *G. praebilineatus*. Perret, Pl. CX, Fig. 3 (only; also illustrated by Perret *et al.*, 1994, Pl. 3, Fig. 18).
1993 *G. b. bilineatus* (Roundy) – (early representatives). Schönlaub & Kreutzer, Pl. 6, Fig. 14 (only; non Fig. 13= *G. praebilineatus*).
1993 *Gnathodus praebilineatus* Belka. Schönlaub & Kreutzer, p. 256, Pl. 6, Figs. 7-11.
1993 *G. semiglaber* Bischoff. Schönlaub & Kreutzer, Pl. 5, Fig. 17 (only).
v1995 *G. praebilineatus* Belka. Sanz-López, Pl. 57, Fig. 12 (only).
v1995 *G. cantabricus* Menéndez Álvarez. Sanz-López, Pl. 57, Fig. 13.
1996 *G. bilineatus* (Roundy). Rodríguez Cañero & Guerra-Merchán, p. 244, Pl. 1, figs. 3-4 and 8 (only).
1999 *G. delicatus* Branson & Mehl transitional to *G. praebilineatus* Belka. Meischner & Nemyrovska, Pl. 1, Fig. 11 (only).
v2002b *G. cantabricus* Belka. García-López & Sanz-López, pp. 182-183, Pl. 4, Fig. 10.
v2002 *G. cantabricus* Belka & Lehmann. Sanz-López, Tabl. 2.
2003 *G. bilineatus* (Roundy). Groves, Larghi, Nicora & Rettori, Fig. 3, 2a-c? and 4a-c (only).

Holotype.–A Pa element DPO 15.010 (Pl. 2, Fig. 8, illustrated previously as *Gnathodus cantabricus* Belka by García-López & Sanz-López, 2002b, Pl. 4, Fig. 10); paratypes DPO 15011-DPO 15014.

Type bed.–Bed of sample MILL-5, upper part of the *G. praebilineatus* Zone (Viséan), in the Canalón Member of the Alba Formation in the Millaró section (Fig. 2), Bernesga Valley, León province.

Material.–About 400 Pa elements, 60 elements from the eastern Pyrenees, sample Co42 (DPO 15.030-DPO 15.035) and the others from the Cantabrian Mountains: 25 elements from sample MILL-4 (DPO 15.004-DPO 15.007, Millaró section), about 200 elements from sample MILL-5 (DPO 15.010-DPO 15.015, Millaró section), 115 elements (many immature elements) from sample CPE-30 (Duje River, DPO 15.020-DPO 15.028), 1 element from the sample J-13 and 12 elements from sample J-53 (Menéndez-Álvarez's collection).

Derivation of name.–From Dr. José Ramón Menéndez-Álvarez, who studied and described elements of the new species in his unpublished Ph.D. thesis.

Diagnosis.–Pa elements with a short and often distally convex inner anterior parapet. The parapet can take up two thirds of the inner cup length, although its posterior part is composed of low nodes. Teeth from the posterior blade are only enlarged in mature elements. The cup is very asymmetrical, with the outer half wider at the anterior margin. The outer platform bears nodes that in many elements are arranged in roughly distinct concentric rows.

Description.–The specimens on hand have a short inner parapet that can take up two thirds of the inner cup length. The inner parapet is wider and higher at the anterior part and continues backwards through several low nodes near the carina. The anterior outline of the distal margin of the parapet is concave or straight, and afterwards convex (see elements from samples MILL-5 and CPE-30, Pl.1, Fig. 8; Pl. 2, Figs. 6 and 8, 10-12). The parapet is shorter in the earliest forms; these forms do not have isolated nodes behind the anterior high parapet. This is the case of a few elements of samples Co42 (Pl. 1, Figs. 15-16), MILL-4 (Pl. 1, Figs. 3-4) and MILL-5, where the parapet is located in the middle of the inner cup, the maximum width of the cup developing before that. The smaller elements have a few nodes (four or five) in the anterior part of the inner cup, the second of them being highest (Pl. 1, Fig. 6).

The posterior blade is composed of simple teeth, although the bigger (or mature) elements, from samples Co42, CPE-30, MILL-4 and MILL-5, show some expanded teeth at the posterior carina (Pl. 1, Figs. 14 and 16; PL. 2, Figs. 6, 8, 9 and 11).

The outer half of the cup is wider than the inner one, becoming more than three times wider in the mature elements, in which the widest point is located at the anterior margin. The anterior margin forms a right angle with the carina in the mature elements. In fact, such specimens have a triangular basal cavity. The asymmetry is less conspicuous in the small elements in which the outer anterior margin makes an acute angle with the blade.

The outer cup bears nodes that are usually arranged in distinct concentric rows. The elements from MILL-4 show poor development of the ornamentation (Pl. 1, Figs. 3-4) and it is lacking altogether in an element from sample Co42. Concentric rows of nodes are better developed in young samples (MILL-5, Fig. 4.9).

Some rare elements have an irregular pattern of ornamentation made of small, low nodes with a smooth posterior (or post-lateral) part of the outer cup (Pl. 1, Fig. 15; Pl. 2, Figs. 6 and 8). The immature specimens from samples Co42 and CPE-30 show a trend towards one or two rows of nodes (Pl. 1, Figs. 5-6 and 11).

Remarks.–Some elements show morphologies close to the *G. semiglaber* Bischoff, 1957. However, the short inner parapets in *G. joseramoni* n. sp. are slightly longer than in *G. semiglaber*. Furthermore, the small and medium-sized elements do not have the enlarged posterior teeth of the carina, a characteristic of *G. semiglaber,* and the big elements show moderate development of expanded teeth. In *G. joseramoni* the platform outline is less oval and more triangular than in *G. semiglaber* (Pl.1, Figs. 1-2), with a tendency to the *G. bilineatus* outline. The same tendency is observable for the ornamentation of the outer cup. There was a progressive increase in the distinguishable concentric alignment of the nodes, similar to *G. bilineatus*. However, a strong similarity can be still observed between *G. semiglaber* and some particularly large elements of *G. joseramoni*. The element illustrated as *G. semiglaber* by Park (1983, Pl. 2, Fig. 13, sample KANTV-5) is included in the range of variability of the new taxon. It is an element where the ornamentation of the outer cup is poorly developed.

Gnathodus sp. A of Ebner (1977, Pl. 2, Figs. 5 and 7) corresponds to immature elements of *G. joseramoni* n. sp. We are doubtful as to the inclusion of too many small elements from Ebner (1977, Pl. 2, Figs. 8-10 and 13) in the new species.

Some previously figured elements from the Rheinisches Schiefergebirge have morphologies very close to *G. joseramoni* n. sp. This is the case of the element from Sauerlandes illustrated by Voges (1959, Pl. 33, Fig. 33). It shows a convex inner parapet, which does not reach the posterior tip of the carina. Park (1983) considered an element from Velberter Sattel as *Gnathodus* n. sp. A Ebner (1977), but in our opinion this also belongs to *G. joseramoni* n. sp. Another element probably belonging to *G. joseramoni* is the specimen named as “*G. delicatus* transitional to *G. praebilineatus* Belka” by Meischner & Nemyrovska (1999, Pl. 1, Fig. 11). Unfortunately, in this specimen the outer cup is damaged and the inner parapet seems to have been blunted, thus hampering a comparison with our material.

Elements of *Gnathodus* sp. indet., figured by Mathews & Thomas (1974) from Devonshire (England), are sometimes identical to *G. joseramoni* n. sp. (see Mathews & Thomas, 1974, Pl. 51, Fig. 3), while other show long, high anterior parapets and narrow outer platforms (Pl. 51, Figs. 1-2, 18 and 19). In our opinion, they seem to be slender elements belonging to *G. joseramoni*.

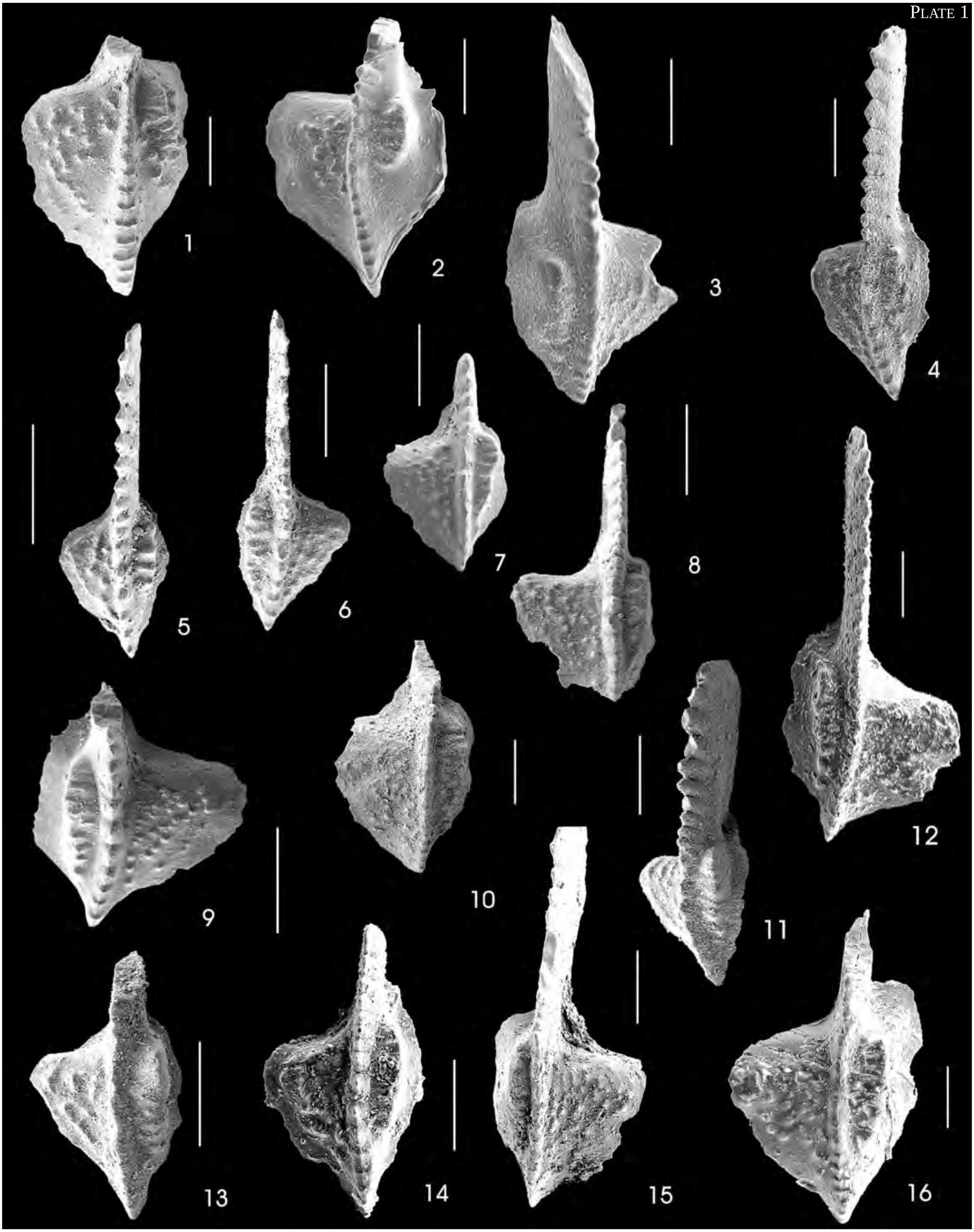
Elements from the Carnic Alps identified as “*G. praebilineatus”* by Schönlaub & Kreutzer (1993) show a posterior carina with nodes that are wider than in the Spanish elements and with an outer cup which is less enlarged (Fig. 4.5) than in the specimens described here. However, we think it is reasonable to include the Schönlaub & Kreutzer’s material in *G. joseramoni* n. sp., due to the characteristics of the inner parapet and outer ornamentation, as well as to the general architecture, which greatly resembles that of our species. In contrast, *G. praebilineatus* (Pl. 2, Figs. 1-4) has a long inner parapet formed by a row of nodes or cross ridges extending to, or near to, the posterior tip of the blade (Belka, 1985).

Other elements, considered by Schönlaub & Kreutzer (1993, Pl. 6, Fig. 14)) as early representatives of *G. b. bilineatus*, are similar to some rare elements from the samples Co42 and CPE-30 (Pl. 1, Figs. 13 and 14). Both the Spanish and the Carnic specimens have a shorter parapet than that of *G. praebilineatus* Belka but longer than the typical parapet of *G. joseramoni*, and an outer cup with a more triangular shape. However, in spite of all these differences, we are inclined to think that they should be considered co-specific with *G. joseramoni* n. sp., since they also have the anterior outer margin of the cup at an angle of 120 degrees to the carina (as is the case of *G. joseramoni).* Unfortunately, we have only collected a few elements in the associations studied.

→

PLATE 1–Oral views of different Pa elements; graphic scale is 200 µm. *1-2, Gnathodus semiglaber* Bischoff, 1957, from samples MILL-2 and MILL-5 respectively (specimens DPO 15.002 and DPO 15.008, Millaró section); *1,* illustrated previously by García-López & Sanz-López, 2002b, Pl. 4, Fig. 5. *3-16, Gnathodus joseramoni* n. sp.; *3-4,* specimens DPO 15.005 and DPO 15.006 from sample MILL-4 (Millaró section); *5-11* and *13,* specimens DPO 15.020 to DPO 15.027 from sample CPE-30 (Duje River); *12* and *14-16*, specimens DPO 15.031 to DPO 15.034 from sample Co42 (comes de Das section).

PLATE 1



Finally, we also include in *G. joseramoni* n. sp. certain elements assigned to *G. bilineatus* by Rodríguez Cañero & Guerra Merchán (1996). These authors described them as small specimens showing shorter parapets than in the typical *G. bilineatus*.

Occurrence.–The oldest specimens of *G. joseramoni* n. sp. are from the Cantabrian Mountains (samples MILL-4 and CPE-30, Tabl. 1), the western Pyrenees (illustrated by Marks & Wensink, 1970; and Perret, 1993) and the eastern Pyrenees (sample Co42, Tabl. 1), and were found in the *G. praebilineatus* Zone (Figs. 1 and 2). Elements from the sample 1093 of Higgins (1962, basal part of the Alba Fm. at the Santa Olaja de la Varga section) may be of a similar age (middle Viséan?). The element figured by Budinger (1965, sample Gr2 at the Gildar-Montó) was collected in beds containing *Goniatites* cf. *stenumbilicatus* and was considered to belong to the Go α-β ammonoid unit. The samples from the Cima di Plotta section (Carnic Alps, Italy) studied by Schönlaub & Kreutzer (1993) are probably of a similar age. Finally, the elements of *Gnathodus* sp. A of Ebner (1977), considered here to be a synonym of *G. joseramoni*, were found in his *Gnathodus* sp. A Zone, from Styria (Austria), prior to the first appearance of *G. bilineatus bilineatus*.

Findings of *G. joseramoni* n. sp. in rocks of the *G. bilineatus* Zone are various: Adrichem Boogaert (1967, sample Tr4', Triollo section); Higgins & Wagner-Gentis (1982, sample 2902, Villabellaco section); Park (1983, –sample ES-8– Santa Olaja de la Varga section, –sample KANTV-5– Cervera de Pisuerga, and Velberter Sattels, Germany); Menéndez-Álvarez (1991, sample J-13 from the Entrago section and sample J-53 from the El Portillín section); and Rodríguez Cañero & Guerra-Merchán (1996, Betic Cordillera). Elements figured by Mathews & Thomas (1974) were found immediately below the *G. crenistria* Bed in reworked faunas with *G. bilineatus* from Devonshire (England). Another finding assigned to this age by Grooves *et al.* (2003) is located in the Greek island Chios.

Gnathodus kiensis Pazukhin, 1992
(Pl. 2, Figs. 13-14; Text-Fig. 4.15-4.26)

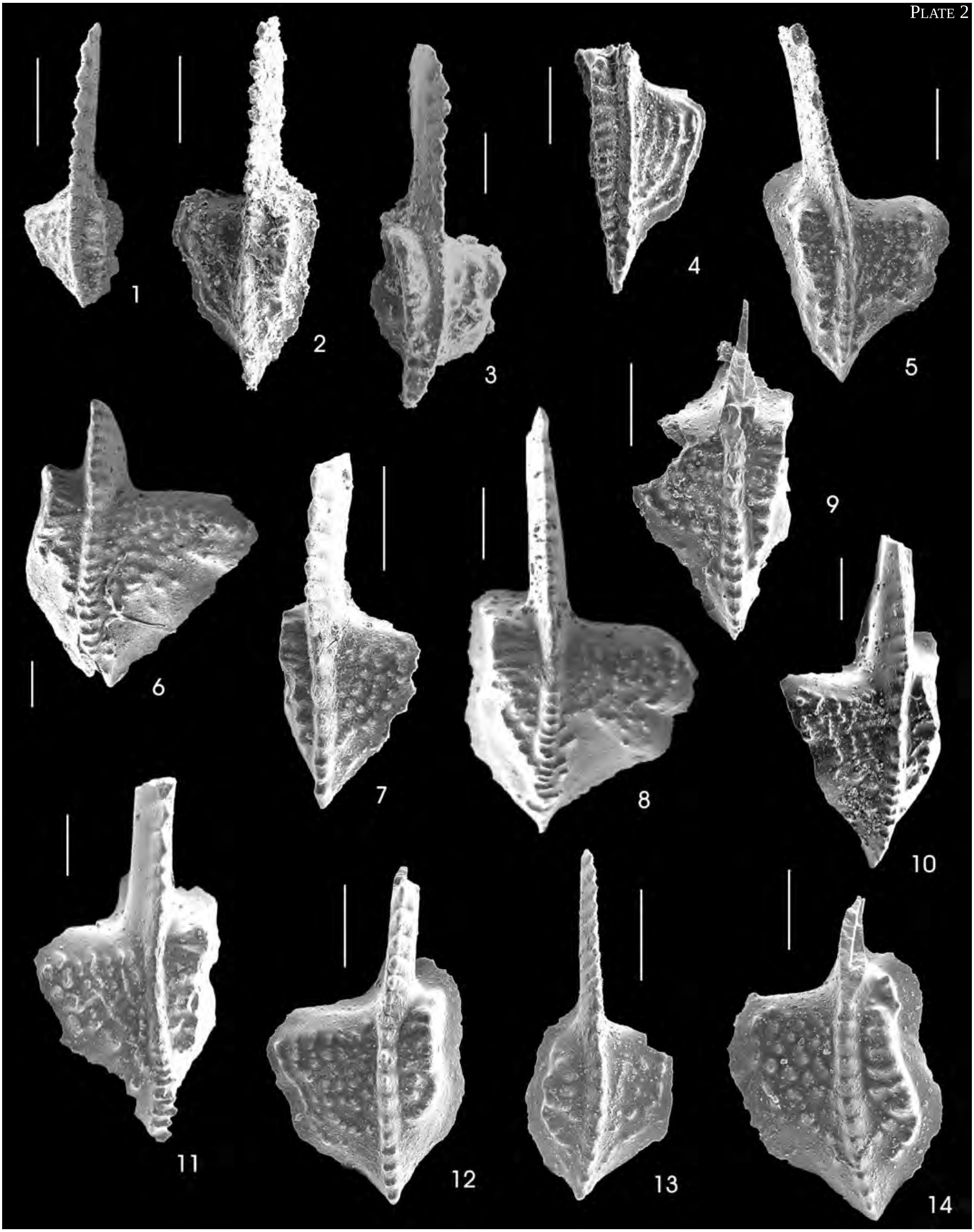
1962 *Gnathodus delicatus* Branson & Mehl. Higgins, Pl. 2, Fig. 23, 24?, Pl. 3, Fig. 33?
1965 *G. delicatus* Branson & Mehl. Budinger, Pl. 2, Figs. 9, 10, and 12 (only).
1973 *Gnathodus bilineatus* (Roundy). Durdanović, Pl. 4, Figs. 16a-b.
1981 *G. bilineatus* Roundy. Metcalfe, Pl. 3, Figs. 4a-d (only).
1983 *Gnathodus* n. sp. A. Park, pp. 86-87, Pl. 3, Figs. 18-21.
1991 *Gnathodus cantabricus* n. sp. Menéndez Álvarez, pp. 169-171 (partly), Pl. 23, Figs. 9, 12-13.
*1992 *Gnathodus kiensis* n. sp. Pazukhin (in Kulagina *et al.* 1992), p. 87, Pl. 28, Figs. 1-3.
1993 *G. bilineatus* (Roundy). Perret, pp. 329-333, Figs. 113 B, J, K and L (only).
1993 *G. bilineatus* cf. *bollandensis* Higgins & Bouckaert. Perret, lám. CX, Figs. 18-19.
1993 *Gnathodus b. bollandensis* Higgins & Bouckaert. Perret, lám. CX, Fig. 28 (only).
1996 *G. bilineatus* (Roundy). Rodríguez Cañero & Guerra-Merchán, p. 244, Pl. 1, Fig. 5 (only).
1998 *G. cantabricus* sp. n. Belka & Lehmann, pp. 37-38, Pl. 2, Figs. 1-3.
v2002a *G. cantabricus* Belka. García-López & Sanz-López, p. 152, Pl. 2, Fig. 20.
v2002 *G. cantabricus* Belka & Lehmann. Blanco-Ferrera, p. 28, Pl. 1, Fig. 20, Pl. 2, Fig. 1.

Material.–All samples were collected in the Cantabrian Mountains: 23 elements from sample MILL-7 (DPO 15017-DPO 15019, Millaró section), CQ-21 (Carranques section), 2 elements from sample OLL-8 (Olleros de Alba section), 16 elements from sample CPE-13 (Cares River); 59 elements from samples J-5, J-13 and J-54 in the Menéndez-Álvarez's collection.

→

PLATE 2–Oral views of different Pa elements; graphic scale is 200 µm. *1-4, Gnathodus praebilineatus* Belka, 1985; *1,* specimen DPO 15.029 from sample CPE-30 (Duje River); *2-4,* specimens DPO 15.036-DPO 15.038 from sample Co42 (comes de Das section). *5-12, Gnathodus joseramoni* n. sp.; *5,* specimen DPO 15.035 from sample Co42 (comes de Das section). *6,* specimen DPO 15.028 from sample CPE-30 (Duje River); *7-12,* specimens from sample MILL-5 (Millaró section), *8,* holotype DPO 15.009 illustrated previously by García-López & Sanz-López, 2002b, Pl. 4, Fig. 10; *7, 9-12,* paratypes DPO 15.010 to DPO 15.014 respectively. *13-14, Gnathodus kiensis* Pazukhin, 1992, specimens DPO 15.018 and DPO 15.019 from sample MILL-7 (Millaró section).

PLATE 2



Revised diagnosis.–In the original diagnosis of the species, Pazukhin (in Kulagina *et al.*, 1992) wrote in Russian: "the platform is wide and asymmetric with nodular and ribbed half-concentric ornamentation on the inner and outer sides of the element, and with a flat, low parapet". In addition, we feel the inner platform being widest at its mid-length, and, in particular, the parapet turning distally (outwards) at the posterior part, are important diagnostic features.

Description.–The spade-shaped platform is wide and asymmetric. The outer cup is wider than inner one, and is ornamented by rows of nodes, sometimes with a half-concentric arrangement, although other elements show nodes distributed at random. The inner cup has a triangular outline and displays a parapet of variable length, but always finishing before the posterior tip of the carina. The parapet is low and is not attached to the carina. It decreases in height towards the back, showing ramp morphology (Menéndez-Álvarez, 1991, Pl. 23, Fig. 9). At the same time, the parapet diverges from the carina. The big elements show a parapet margin with a convex-concave-convex trajectory. The space between parapet and carina is occupied by oblique rows of discrete low nodes. In medium-sized and immature elements, the parapet is parallel or convex with respect to the carina, and is followed backwards by isolated posterior nodes. Posterior concurrence with the carina is present when these nodes form an oblique row. Divergence between the posterior parapet and the carina is minimized in small elements.

The carina is composed of simple teeth, which are only slightly expanded in the biggest elements. The free blade is 1/2 to 2/5 of the total length of element. The anterior margins of the platform are in approximately opposing locations.

Remarks.–The original material of *Gnathodus kiensis* shows wide ornamented platforms, with the parapet becoming lower and nearly disappearing in adult specimens (Pazukhin in Kulagina *et al.*, 1992). The small forms have smaller ornamented platforms and more separated rows of nodes. They are located towards the limit of the specific variability that we accept now for *Gnathodus kiensis*. An element exactly like the holotype is not present in our samples, which display a too wide platform, a very low parapet, and maximum divergence between the carina and the posterior parapet. However, some elements from sample MILL-7 (Fig. 4.22-23) are similar to the medium-sized specimens of Pazukhin (in Kulagina *et al.*, 1992). Elements described by Park (1983) and Belka & Lehmann (1998) have a weak ornamentation on the outer cup made of randomly distributed nodes (Fig. 4.18), although concentric rows are visible in the holotype of *G. cantabricus* (see Belka & Lehmann, 1998, Pl. 2, Fig.1) (Fig. 4.17). We agree with Menéndez-Álvarez (1991), in that poorly ornamented cups are found together with elements where rows of nodes clearly occur, and together with intermediate elements. Blanco-Ferrera *et al*. (in press, Fig. 6.15) illustrated a young morph of *G. kiensis* with a short inner parapet composed of separated nodes isolated backwards (Fig. 4.19), and in which the outer cup only bears rare nodes.

Elements identical to the holotype of *G. cantabricus* Belka & Lehmann (1998) were found in sample J-54 from Menéndez-Álvarez (1991, lower part of the *L. nodosa* Zone). They are strongly ornamented elements with a high anterior parapet composed by ridges decreasing in height progressively towards the back.

G. joseramoni n. sp. has a shorter inner parapet than *G. kiensis*, and a different platform outline. The first species has a more enlarged triangular outer half of the cup, and the second a more oval outline, which is widest in the central platform. The parapet is convex in *G. joseramoni*, and shorter than in *G. kiensis*, and it is turned distally at the posterior part of the parapet in the second species.

Occurrence.–The oldest findings of *G. kiensis* are recorded in the *G. bilineatus* Zone of the Cantabrian Zone (sample J-13, Entrago section, Menéndez-Álvarez, 1991) and the Betic Cordillera (specimen illustrated by Rodríguez Cañero & Guerra-Merchán, 1996). *G. kiensis* seems to be rare in this biozone.

In contrast, there are far more abundant records in the overlying *L. nodosa* Zone. In the Cantabrian Zone, *G. kiensis* occurs in strata belonging to this biozone at the Matallana section (Higgins, 1962), Gildar-Montó and Panes-Potes sections (Budinger, 1965), Santa Olaja de la Varga (Park, 1983; Belka & Lehmann, 1998), El Portillín, Entrago, Olleros de Alba and Río Nevandi sections (Menéndez-Álvarez, 1991), Olleros de Alba and Millaró sections (García-López & Sanz-López, 2002b) (Fig. 2) and in the Cares River valley (Blanco-Ferrera *et al.*, in press). *G. kiensis* occurs together with *L. multinodosa* (Higgins) and *L. cruciformis* (Clarke), from beds of the Serpukhovian (Pendleian) age at the Santa Olaja de la Varga section (Belka & Lehmann, 1998) and the Carranques section, (García-López & Sanz-López, 2002a). Finally, *G. kiensis* coincides with the entry of *G. bilineatus bollandensis* Higgins at the Puente de Alba section after Menéndez-Álvarez (1991), in strata belonging to the Arnsbergian. However, Higgins & Wagner-Gentis (1982) maintained the lack of *G. b. bollandensis* in the Cantabrian Mountains.

Pyrenean elements considered *G. kiensis*, and illustrated by Perret (1993), were collected at the La Estiva/Chinipro section (Fig. 1) in samples (Chin 13 and Chin 13a JD) from the *L. nodosa* Zone. *G. kiensis* has also been reported from Dvor na Uni (Serbia, Durdanović, 1973), England (Metcalfe, 1981) and Styria (Austria, Belka & Lehmann, 1998). It must be noted that the original material of *G. kiensis* comes from the *G. b. bollandensis* Zone, Protvian Horizon (Nm_1b_2-Nm_1c_1, upper Pendleian to lower Arnsbergian, Serpukhovian) of the South Urals (Kulagina *et al.*, 1992). This material seems to correspond to the youngest finding so far known.

CONODONT DISTRIBUTION AND EVOLUTIONARY CONSIDERATIONS

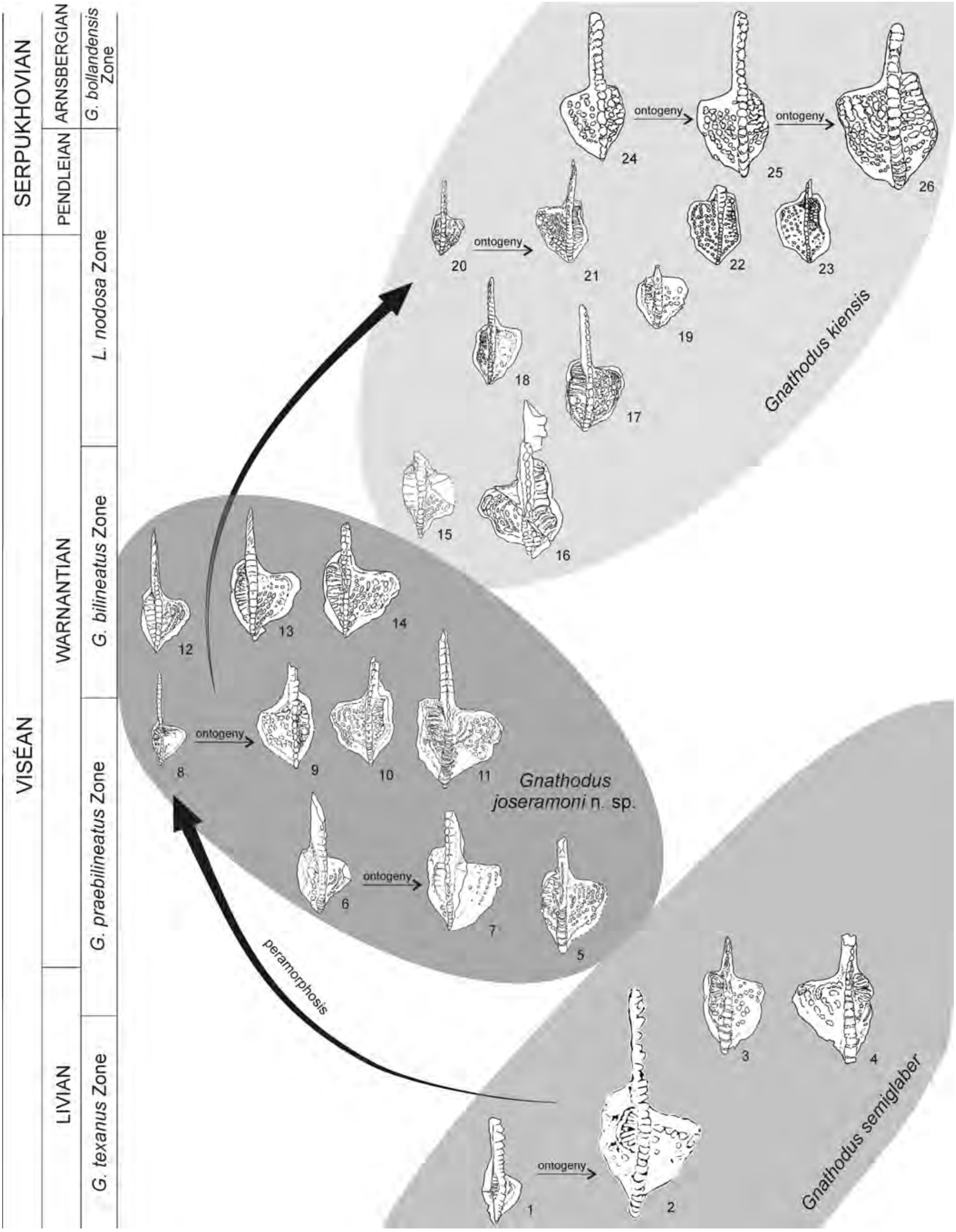
Elements identified here, as *Gnathodus joseramoni* n. sp. and *G. kiensis* were known long ago in the Cantabrian Mountains, but they have only occasionally been described, and the second species display a low abundance. Our relatively incomplete knowledge of these taxa hinders the understanding of their phylogeny, and of their relationships with other *Gnathodus* species. However, taking into account all the materials now available, we think that it is possible to trace some evolutionary trends based on the morphologic change observed in associations from the middle Viséan to the Serpukhovian (Fig. 4).

Older populations of *G. joseramoni* n. sp. from the Iberian Peninsula seems to be part of an innovative radiation episode of the *Gnathodus* species that took place at the *G. praebilineatus* Zone (Fig. 4). This conodont radiation replaced lower Viséan faunas dominated by species of the *G. punctatus* group of Lane *et al*. (1980). The conodont record of this radiation is known for a biozonal interval classically named as the "*anchoralis-bilineatus* Interregnum" (Voges, 1960) in Southern Europe, and frequently corresponding to an episode of chert deposition (Lavandera and Louron members in North Spain) together with the corresponding carbonate sedimentation (Fig. 2).

Belka (1985) proposed *G. praebilineatus* as ancestral species of *G. bilineatus*, and appearing at the base of his *G. austini* Zone. Menéndez-Álvarez (1991) defined the *G. praebilineatus* Zone between the occurrences of *G. praebilineatus* and *G. bilineatus* in the Cantabrian Mountains. After Belka (1985) and Belka & Korn (1994), *G. praebilineatus* was considered to originate from *G. semiglaber* Bischoff (a species of the *G. punctatus* group) through the development of the inner parapet and the reduction of the expanded posterior blade to the point of becoming a simple one (compare Pl. 1, Figs. 1-2 with Pl. 2, Figs. 2-4). According to Meischner & Nemyrovska (1999) in the Rheinisches Schiefergebirge, *G. praebilineatus* appeared below the *Entogonites nasutus* ammonoid Zone (lower Asbian), before other species of the *G. bilineatus* group such as *G. romulus* and *G. remus (E. grimmeri* Zone) and *G. b. bilineatus (Goniatites crenistria* Zone, upper Asbian).

Immature specimens of *G. praebilineatus* show low inner parapets that do not extend to the posterior tip of the blade, and an almost unornamented outer cup (Pl. 2, Fig. 1). Belka (1985) considered this morphology as probable for the forerunners or the earliest phylogenetic forms of *G. praebilineatus* in a heterochronic process, and it may correspond to the elements described as *Gnathodus* sp. A from Styria (Ebner, 1977) or from the Cantabrian Mountains (Park, 1983). We consider that most of these elements correspond to *G. joseramoni* n. sp. In contrast, early *G. praebilineatus* are probably the elements described by Belka & Korn (1994, Pl. 2, Figs. 11, Cantabrian Mountains) and Spalletta and Perri (1998, Pl. 3.1.1., Fig. 3, Carnic Alps). These two elements have three 3 rows of nodes in the small outer cup, and the inner parapet is long, although it does not reach to the posterior tip of the carina. Finally, we feel that after Meischner & Nemyrovska (1999), none of these elements should be attributed to *G. praebilineatus*, since they possess a short parapet. These authors indicated which transitional forms between *G. delicatus* and *G. praebilineatus* occur just below and together with *G. praebilineatus*. However, the observation of the phylogenetic link between both species is hindered by the existence of conodont gap between the strata yielding those "transitional" morphs, and older Tournaisian strata containing *G. delicatus*. In our opinion, most of the elements illustrated by Meischner & Nemyrovska (1999, Pl. 1, Figs. 6, 12 and 15; Pl. 2, Fig. 9) could correspond to immature *G. praebilineatus* specimens, since they are small in size and show poorly developed ornamentation on the outer cup.

G. joseramoni n. sp. seems to evolve from *G. semiglaber*. The typical material (Bischoff, 1957) of the ancestral species, *G. semiglaber,* shows nodes behind the high convex anterior inner parapet (Fig. 4.2, holotype); these nodes increase both in number and size in *G. joseramoni* n. sp. to give rise to a longer inner parapet (Fig. 4.5-4.7). They are early growing in the development of immature elements of *G. joseramoni* n. sp. (compare Figs. 4.1 and 4.8). The young elements of *G. joseramoni* have a morphology akin to


SERPUKHOVIAN
PENDLEIAN
ARNSBERGIAN
G. bollandensis Zone
L. nodosa Zone
VISÉAN
WARNANTIAN
G. bilineatus Zone
G. praebilineatus Zone
LIVIAN
G. texanus Zone
Gnathodus kiensis
Gnathodus joseramoni n. sp.
Gnathodus semiglaber
peramorphosis
ontogeny
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that of the big *G. semiglaber* elements (peramorphic heterocrony), with the exception of the expanded teeth of the posterior carina. Big elements of *G. joseramoni* n. sp. are similar to *G. semiglaber* because show fused ridges in the high convex parapet and, furthermore, an enlarged posterior carina (Figs. 4.5 and 4.11). Consequently, the expansion of the teeth was delayed during the growing of the element Pa of *G. joseramoni* n. sp., as a paedomorphic morphology (post-displacement process, McNamara, 2001). Supporting evidence also comes from certain Viséan elements considered a morph in the variation of *G. semiglaber*, and which could give rise to *G. joseramoni* n. sp. This morph (PL. 1, Fig. 1) coexists with typical *G. semiglaber* (Pl. 1, Fig. 2) in the Pyrenees and Millaró sections, and Schönlaub & Kreutzer (1993) illustrated a wide variability of similar elements from the Carnic Alps and classified them as *"G. punctatus"* (Pl. 4, figs. 10-15, 18-22). This morph of *G. semiglaber* shows nodes on the whole surface of the outer cup, and a few nodes behind the high inner parapet, characteristics not found in the typical morph of *G. semiglaber* but present in *G. joseramoni* n. sp. However, the morph is still differentiated from *G. joseramoni* by having the nodes homogeneously distributed on the outer cup, shorter inner parapets, and a more oval platform outline (Figs. 4.3 and 4.4).

As innovative characteristics, *G. joseramoni* n. sp. developed an asymmetric platform, with an increasing width on the anterior outer cup, and a half-concentric arrangement of the rows of nodes (Figs. 4.5 to 4.11). Both characteristics were also independently developed in another lineage, from *G. praebilineatus* to the cosmopolitan *G. bilineatus*. The morphologic resemblance between *G. joseramoni* and *G. praebilineatus* is notorious for small elements, which hinders their easy assignation. We find elements with a short parapet, considered as probably immature *G. joseramoni* (Pl. 1, Figs. 5-6 and 11); elements with a long parapet, but without meeting the posterior tip of the blade, considered as probably immature *G. praebilineatus* (Pl. 2, Fig. 1); and elements with intermediate type of parapet.

With respect to *G. kiensis*, Pazukhin (in Kulagina *et al.*, 1992), and later Belka & Lehmann (1998), mentioned the presence of transitional elements between this species and *G. bilineatus*, and interpreted this fact as an indication of a possible derivation of the first species from the second. However, the elements of *G. kiensis* from the *G. bilineatus* Zone studied here can hardly be distinguished from elements of *G. joseramoni*. These modern elements (sample J-53) of the last species have a longer parapet than that of typical elements (sample J-53, Figs. 4.12-4.14), and the anterior ridges of the parapet are higher and sometimes wider than the posterior ridges, as in *G. kiensis*. However, these elements of *G. joseramoni* do not display the divergence between the posterior parapet and the carina.

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FIGURE 4–Diagram showing the morphologic change on the oral surface of different Pa elements from the ancestral species *G. semiglaber* Bischoff to *G. joseramoni* n. sp. and *G. kiensis* Pazukhin. The vertical axis indicates age, series, stages and conodont zones. Magnifications are x 25. *1-4, Gnathodus semiglaber* Bischoff. *1,* Immature element from sample Co39 (comes de Das section). *2,* Holotype from Bischoff (1957, Pl. 3, Fig. 1). *3,* Ornamented element from sample 1044 A (Cima di Plota section, "*G. punctatus* Cooper" after Schönlaub & Kreutzer, 1993, Pl. 4, Fig. 18). *4,* Element with the anterior outer cup bearing rows of poorly developed nodes, from sample 1045 (Cima di Plota section, "*G. punctatus* Cooper" after Schönlaub & Kreutzer, 1993, Pl. 4, Fig. 15). *5-14, G. joseramoni* n. sp. *5,* Element with an increment on the number of nodes in the inner posterior cup in relation to *G. semiglaber,* and a concentric arrangement of nodes in the outer cup (sample 1047, Cima di Plota section, *G. praebilineatus* after Schönlaub & Kreutzer, 1993, Pl. 6, Fig. 7). *6-7,* Immature element and mature element with a triangular outline of the outer cup (sample MILL-4, Millaró section). *8-11,* Elements from sample MILL-5 (Millaró section); *8,* immature element; *9,* mature element where a slight distal divergence of the inner parapet with respect to the carina is perceptible; *10,* mature elements with asymmetric cup and half-concentric rows on the outer side; *11,* holotype of the species. *12-14,* Elements with different sizes and with a long inner parapet (sample J-53, El Portillín section). *15-26, G. kiensis* Pazukhin. *15-16,* Elements from sample J-13 (Entrago section); *15,* immature element; *16,* mature broken element with a spade-shaped platform where the parapet turns outward and the outer cup area decreases. *17,* Holotype of *G. cantabricus* Belka & Lehmann (1998, Pl. 2, Fig. 1, from sample 16, Santa Olaja de la Varga section), where the inner parapet has anterior high ridges and posterior parapet shows low discrete nodes. *18,* Medium-sized element from Belka & Lehmann (1998, Pl. 2, Fig. 2, sample 18, Santa Olaja de la Varga section). *19,* Immature element from sample CPE-13 (Cares River, Blanco-Ferrera *et al.*, in press). *20-21,* Immature element and holotype of *G. cantabricus* Ménendez-Álvarez (1991, Pl. 23, Fig. 9 and 12 respectively) from sample J-5 (Entrago section). *22-23,* Elements with oblique rows of nodes between the turned inner parapet and the carina from sample MILL-7 (Millaró section). *24-26,* Elements and holotype of *G. kiensis* (*26*) from sample 12 at the Kiya River (Pazukhin in Kulagina *et al.*, 1992, Pl. 28, Figs. 1-3).

Immature elements have a more convex parapet outline than big elements, parapet that is almost as long as the inner platform, indicating its early development during the growth of the element. Furthermore, the triangular morphology of the outer cup is accentuated during the growth (compare Figs. 4.12 and 4.14). Divergence and a decrease in height of the posterior inner parapet, together with a more rounded platform, are typical characteristics found in *G. kiensis*. They are present in some big elements from the *G. bilineatus* Zone (sample J-13), where, in addition, higher nodes are located at the parapet margin and a deep adcarinal trough lies right next to the carina (Fig. 4.16). The diverging inner parapet is not visible in immature elements of the same associations (Fig. 4.15).

In the same sense, small elements of younger associations of *G. kiensis* have not developed the spade-shaped platform, and the parapet has a convex morphology without the marked posterior carina-parapet divergence. Consequently, small elements of *G. kiensis* (Fig. 4.20) and some elements of *G. joseramoni* n. sp. (Fig. 4.9) exhibit very similar morphology. In accordance with what has been stated above, we consider that *G. kiensis* originated from *G. joseramoni*, although the speciation from a *G. bilineatus* ancestor should also be analyzed. Undoubtedly, many findings are necessary in order to prove any derivation, particularly those coming from the *G. bilineatus* Zone.

Early elements of *G. kiensis*, from the *L. nodosa* Zone, have a strong ornamentation and long parapet (sample J-54 and Fig. 4.17). They have a high anterior part, and a low wide posterior part of the parapet. The height of the parapet decreases in the younger associations, a feature already described in ontogenetic variation by Pazukhin (in Kulagina *et al.*, 1992). Distal outward deflection of the inner parapet also shows an accentuated development in the younger associations (Figs. 4.22 to 4.26).

So far *G. kiensis* has been only found in the Carboniferous western Palaeo-Tethys Ocean (Iberian Peninsula, Austria, England, Serbia and South Urals). Conodont provincialism during late Viséan *(L. nodosa* Zone) has been pointed out by Higgins (1981), who differentiated two “provinces”, Eurasian and Midcontinental. In this scheme, *G. kiensis* can be seen as a component of the deep-water faunas from the Eurasian province. With respect to the middle Viséan, species with restricted palaeogeographic distribution, such as that *G. joseramoni*, *G. praebilineatus*, *G. remus* and *G. romulus*, have so far only been found in the Eurasian province (see occurrences of the three last taxa in Meischner & Nemyrovska, 1999), which suggests certain endemicity in the distribution of the middle Viséan *Gnathodus* species, although the recognition of palaeobiogeographic units based on that distribution will be the object of future studies.

CONCLUSIONS

The study of new material from the Iberian Peninsula, as well as comparison with material previously described by different authors (and included in different species), allows us to describe the new species *Gnathodus joseramoni* n. sp. So far, the new species is known from cephalopod nodular limestones of the *G. praebilineatus* to the *G. bilineatus* zones (middle Viséan) in the Iberian Peninsula, Carnic Alps, England, Styria and Greece. Certain elements probably related to *Gnathodus joseramoni* were illustrated by several authors in the German Rheinisches Schiefergebirge. The taxon evolved from *G. semiglaber*, probably after the origin of *G. praebilineatus*.

Gnathodus cantabricus Belka & Lehmann is regarded as a junior synonym of *G. kiensis* Pazukhin. This species could have evolved from *Gnathodus joseramoni* n. sp., in the *G. bilineatus* Zone, although a derivation from *G. bilineatus* is also possible. The species is easily recognized and occurs frequently, although not abundantly, in the *L. nodosa* Zone, upper Viséan to lower Serpukhovian (Pendleian) in the Iberian Peninsula. Other occasional findings come from Austria, England, Serbia, and particularly the South Urals, where the species is known in strata as young as the upper Serpukhovian.

According to current data, *Gnathodus joseramoni* n. sp. and *G. kiensis* are endemic species with a geographic distribution restricted to areas included in the upper Viséan Eurasian conodont province of Higgins (1981).

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Part of the conodonts discussed in this paper, were observed from the Ménendez-Álvarez collection, through the courtesy of the Department of Geology in the University of Oviedo. Dr. Luis Carlos Sánchez de Posada and an anonymous reviewer provided very helpful reviews of the manuscript. We thank Dr. Alexandr S. Alekseev (Moscow State University) for the translation of the original data about *G. kiensis* from Russian, and Belén López Mosquera of the scanning electron microscopy service of the University of A Coruña. This paper was sponsored by the Spanish projects PB02-079 of the Consejería de Educación y Cultura del Principado de Asturias, BTE2003-01609, and BTE2002-03819 of the Ministerio de Ciencia y Tecnología and Fondo Europeo de Desarrollo Regional (FEDER). We thank Robin Walker for his revision of the English of the manuscript.

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PENNSYLVANIAN CONODONT ZONATION FOR MIDCONTINENT NORTH AMERICA

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Abstract

Most work on Pennsylvanian conodont biostratigraphy in Midcontinent North America is dispersed among papers on paleoecologic or taxonomic issues, often on limited geographic and stratigraphic scales. Here we provide a current summary of conodont zones that can be used to subdivide and correlate Pennsylvanian strata in Midcontinent North America. These zones are range zones, but several Midcontinent cyclothems are characterized by a unique combination of taxa that allow biostratigraphic recognition of individual eustatic cycles across the region. Lane and colleagues provided a detailed zonation for the Morrowan Stage that, with subsequent modifications, is widely accepted. Species of *Neognathodus* can be used to zone Morrowan, Atokan and Desmoinesian strata, but appear less useful for subdividing the late Desmoinesian than is commonly attempted. *Neognathodus* zones for the Morrowan through Desmoinesian are [ascending order]: *higginsi, symmetricus, bassleri, N.* n. sp. Lane 1977 (spans the Morrowan-Atokan boundary), *atokaensis, colombiensis, caudatus* (coincides with the base of the Desmoinesian), *asymmetricus, roundyi (sensu lato). Idiognathodus* and closely related genera like *Streptognathodus* remain underutilized, but will provide the best biostratigraphic resolution for Pennsylvanian strata once complex taxonomic relationships are resolved. Idiognathodid species currently provide the following zones for the Atokan and Desmoinesian: *I. incurvus* (approximates base of Atokan), *I. incurvus*-derived descendants, *I. obliquus/I. amplificus* (coincides with base of Desmoinesian), *I. iowaensis, I. delicatus, Swadelina neoshoensis, Sw. nodocarinata.* A radiation of *Idiognathodus* species in the early Missourian and a subsequent radiation of *Streptognathodus* species permit recognition of zones for the lower and middle Missourian: *I. eccentricus, S. cancellosus, S. confragus, S. gracilis.* The appearance of *I.* aff. *simulator* with *S. firmus* (a possible Eurasian immigrant) and descendants of both provide the basis for zones in upper Missourian through middle Virgilian strata: *I.* aff. *simulator, S. zethus* (coincides with base of Virgilian), *I. simulator (sensu stricto), S. virgilicus (sensu lato).* The first steps of the radiation of *Streptognathodus* species that lead to an Early Permian clade subdivide the uppermost Virgilian: *brownvillensis, wabaunsensis,* and, defining the base of the Permian, *isolatus.*

Key words: Conodonts, Pennsylvanian, biostratigraphy.

Resumen

La mayor parte de la información bioestratigráfica relativa al Pensilvaniense del Continente Medio de Norteamérica aparece dispersa en trabajos de carácter paleoecológico o taxonómico que, a menudo, se ocupan de ámbitos geográficos reducidos o de intervalos estratigráficos limitados. El presente trabajo proporciona una recopilación actualizada de las zonas de conodontos que permiten la subdividisión y correlación de las sucesiones pensilvanienses del Continente Medio de Norteamérica. Las zonas utilizadas son biozonas de extensión pero varios ciclotemas del Continente Medio presentan combinaciones características de taxones que permiten el reconocimiento en toda la región de determinados ciclos eustáticos. Lane y sus colaboradores han proporcionado una zonación detallada del Morrowiense que, con algunas modificaciones posteriores, ha sido ampliamente aceptada. Las especies de *Neognathodus* pueden ser usadas para establecer zonas en las sucesiones del Morrowiense, Atokaniense y Desmoinesiense, pero en la subdivisión de la parte alta de este último piso su utilidad parece ser bastante menor. Para el intervalo Morrowiense-Desmoinesiense, las zonas de *Neognathodus* son (en orden ascendente): *higginsi, symmetricus, bassleri, N.* n. sp. Lane 1977 (cruza el límite Morrowiense-Atokaniense), *atokaensis, colombiensis, caudatus* (su base coincide con la base del Desmoinesiense), *asymmetricus, roundyi (sensu lato). Idiognathodus* y géneros afines, como *Streptognathodus*, permanecen aún infrautilizados, pero, una vez que sus complejas relaciones taxonómicas hayan podido ser establecidas, no hay duda de que proporcionarán una excelente resolución estratigráfica en las sucesiones del Pensilvaniense. Actualmente, las especies de idiognathodidos permiten establecer las siguientes zonas para el Atokaniense y Desmoinesiense: *I. incurvus* (cuya base se sitúa próxima a la base del Atokaniense), descendientes de *I. incurvus, I. obliquus, I. amplificus* (su base coincide con la base del Desmoinesiense), *I. iowaensis, I. delicatus, Swadelina neoshoensis, Sw. nodocarinata.* La radiación de las especies de *Idiognathodus* al comienzo del Misuriense y la posterior radiación de las especies de *Streptognathodus* permiten el reconocimiento de zonas en el Misuriense inferior y medio: *I. eccentricus, S. cancellosus, S. confragus, S. gracilis.* La aparición de *I.* aff. *simulator* con *S. firmus* (este último un posible inmigrante euroasiático) y de los descendientes de *S. firmus* proporcionan las bases para el establecimiento de las siguientes zonas desde el Misuriense superior al Virgiliense medio: *I.* aff. *simulator, S. zethus* (su base coincide con la base del Virgiliense), *I. simulator (sensu stricto), S. virgilicus (sensu lato).* Las primeras etapas de la radiación de las especies de *Streptognathodus* (que conduciría a la formación de un clado en los primeros tiempos del Pérmico) subdividen el Virgiliense más alto con las zonas de *brownvillensis* y de *wabaunsensis*, y definen la base del Pérmico con la zona de *isolatus.*

Palabras clave: Conodontos, Pensilvaniense, bioestratigrafía.

INTRODUCTION

Pennsylvanian (late Carboniferous) conodont biostratigraphy in Midcontinent North America had progressed so little since the summary of Lane *et al*. (1971) that Sweet (1988) reported that there were “No widely recognized conodont zones” for post-Morrowan conodonts. Only in the past several years have North American Pennsylvanian conodont workers begun to consider the stratigraphic distribution of distinctive morphotypes in cyclothemic strata beyond paleoecological and biofacies studies. Swade (1985) was the first to recognize that the maximum transgressive deposits of many Desmoinesian cyclothems contain cycle-specific conodont faunas. This observation has been verified subsequently in Midcontinent Desmoinesian through Asselian (Lower Permian) cyclothems by several workers (e. g., Heckel, 1986, 1989, 1994, 2002; Lambert, 1988, 1992; Ritter, 1995; Barrick *et al.*, 1999) and extended into the western United States (Ritter *et al.*, 2002).

Here we present a conodont zonation for the Pennsylvanian of Midcontinent North America that represents our current understanding of the stratigraphic distribution of conodont taxa through this interval. This zonation is the result of a number of years of research by the authors and combines new information with that presented previously (Barrick & Heckel, 2000; Lambert *et al.*, 2001). Although taxonomic revision of many Pennsylvanian conodont taxa, especially *Neognathodus, Idiognathodus* and *Streptognathodus*, has not yet been completed, the most useful taxa are now sufficiently well described and illustrated such that the geological community can begin to use them to effect biostratigraphic correlations. Hopefully, this zonation will provide a framework for future studies in Pennsylvanian conodont biostratigraphy in North America, as well as for establishing a provisional standard by which correlations with Eurasia can be attempted in the hope that series and stage boundaries, once defined, can be correlated on a global basis. A preliminary correlation of late Desmoinesian through early Virgilian conodont faunas of Midcontinent North American cyclothems with the conodont succession in Eurasia was presented by Heckel *et al.* (1998), but the complications of provincialism (Barrick *et al.*, 2000) will make global correlation difficult for some parts of the Pennsylvanian.

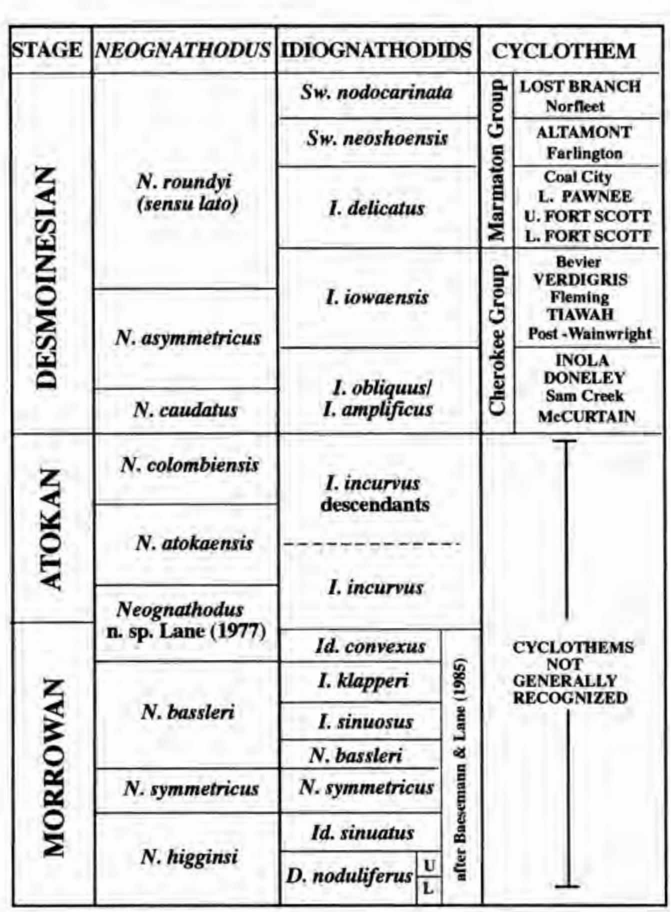
The plates that accompany this paper illustrate many of the more important Morrowan through Virgilian conodont species used in the Midcontinent zonation (Plates 1-5). These taxa include species that have been poorly illustrated in the past, species that are undergoing revision for which there are new or revived names, and species that we retain in open nomenclature. Most of the significant Morrowan and Virgilian species are well illustrated in the papers discussed below.

EARLY AND MIDDLE PENNSYLVANIAN

The pioneering efforts of Lane (1967, 1977) and colleagues led to a detailed zonation for Morrowan strata, which are largely restricted to the foredeep-influenced continental margin of southern North America and the more significant epicontinental margins. Atokan deposits are somewhat more widespread. Uncertainty over stratigraphic relations in its type area has hindered development of an Atokan conodont zonation (Lane & West, 1984). Despite this, studies by Grayson (1979, 1984; Grayson *et al.* 1989; 1990) and Lambert (1992; Lambert & Heckel, 1990) have begun to resolve problems of the placement and correlation of the Morrowan-Atokan and Atokan-Desmoinesian boundaries. By the Desmoinesian, classic cyclothemic sequences became increasingly well developed and widespread across the Midcontinent. Ranges of significant conodont taxa can be plotted against the cyclothemic succession and utilized in identifying and correlating cyclothems in the Midcontinent region and the Illinois and Appalachian basins (Heckel, 1989, 1994, 1999, 2002). Because the Subcommission on Carboniferous Stratigraphy has not yet selected global stage and series boundaries for the Pennsylvanian Subsystem, the positional series terms are used in their traditional informal sense to supplement the North American regional stage names in the discussion below.

Morrowan Stage (lower Pennsylvanian): The Mid-Carboniferous (Mississippian-Pennsylvanian Subsystem) boundary was placed at the first appearance of *Declinognathodus noduliferus* (Ellison & Graves, 1941) in Arrow Canyon, Nevada (Lane *et al.*, 1999), a horizon that also defines the concurrent base of the regional Morrowan Stage. Morrowan conodont zones first proposed by Lane (1967) were modified by Lane & Straka (1974), Lane (1977), Lane & Baesemann (1982), and Baesemann & Lane (1985) (Fig. 1).

The base of the *Declinognathodus noduliferus*-*Rhachistognathus primus* Zone is defined by the first occurrence of either *D. noduliferus* or *R. primus* Dunn 1966, the latter restricted to western North America. The *noduliferus-primus* Zone is subdivided into a lower subzone where *Gnathodus girtyi simplex* Dunn 1966 and *G.* cf. *G. bollandensis* Higgins & Bouckaert 1968 overlap with the nominate species, and an upper subzone above the overlap (Brenckle *et*



STAGE	*NEOGNATHODUS*	IDIOGNATHODIDS			CYCLOTHEM	
DESMOINESIAN	*N. roundyi (sensu lato)*	*Sw. nodocarinata*			Marmaton Group	LOST BRANCH Norfleet
		Sw. neoshoensis				ALTAMONT Farlington
		I. delicatus				Coal City L. PAWNEE U. FORT SCOTT L. FORT SCOTT
	N. asymmetricus	*I. iowaensis*			Cherokee Group	Bevier VERDIGRIS Fleming TIAWAH Post -Wainwright
	N. caudatus	*I. obliquus/* *I. amplificus*				INOLA DONELEY Sam Creek McCURTAIN
ATOKAN	*N. colombiensis*	*I. incurvus* descendants			CYCLOTHEMS NOT GENERALLY RECOGNIZED	
	N. atokaensis	*I. incurvus*				
MORROWAN	*Neognathodus* n. sp. Lane (1977)	*Id. convexus*		after Baesemann & Lane (1985)		
	N. bassleri	*I. klapperi*				
		I. sinuosus				
		N. bassleri				
	N. symmetricus	*N. symmetricus*				
	N. higginsi	*Id. sinuatus*				
		D. noduliferus	U			
			L			

FIGURE 1–Conodont zones for Morrowan, Atokan, and Desmoinesian strata in Midcontinent North America. Ranges of species are not shown because taxonomic and nomenclatural problems remain unsettled. Zones are plotted opposite Desmoinesian cyclothems as discussed in text. Lower Desmoinesian cyclothems below Fleming are summarized from Boardman *et al*. (2002). Major cyclothems are denoted by all capital letters; intermediate cyclothems by upper and lower case letters. See text for discussion of names shown here. *D. = Declinognathodus; I. = Idiognathodus; Id. = Idiognathoides; N. = Neognathodus; Sw. = Swadelina.*

al., 1977; Baesemann & Lane, 1985). In the Midcontinent, this zone is called the *noduliferus* Zone and has been reported from the Rhoda Creek Formation in southern Oklahoma (Grayson *et al.*, 1985; Grayson, 1990) and from the Marble Falls Formation in the Llano region of central Texas (Dunn, 1970; Grayson *et al.*, 1987).

In the Midcontinent, the first appearance of *Idiognathoides sinuatus* (Harris and Hollingsworth 1933) defines the base of the *sinuatus* Zone of Lane (1977). For sections in western North America, Lane and Baesemann (1982) modified this zone by adding *Rhachistognathus minutus* (Higgins and Bouckaert 1968) as an index, and renaming the zone the *sinuatus-minutus* Zone. Although the *sinuatus-minutus* Zone appears to represent an insignificant stratigraphic interval between the *noduliferus-primus* Zone and the overlying *Neognathodus symmetricus* Zone in western North America, the *sinuatus* Zone occupies several meters of strata in southern Oklahoma (Lane, 1977) and northwestern Arkansas (Baesemann and Lane, 1985). Grayson (1990) proposed the *Neognathodus higginsi* Zone, based on the appearance of *N. higginsi* (Grayson *et al.*, 1985), to replace the *noduliferus* and *sinuatus* zones in the southern Midcontinent, which offers the possibility of a *Neognathodus*-based zonation that could extend from the base of the Morrowan through the Desmoinesian.

The *Neognathodus symmetricus* Zone and the subsequent *N. bassleri* Zone are defined by the first occurrence of *N. symmetricus* (Lane 1967) and *N. bassleri* (Harris & Hollingsworth, 1933), respectively, and have been applied consistently since originally proposed (Lane, 1967; Lane & Straka, 1974). These two mid-Morrowan conodont zones have been reported from a number of localities across North America. No consistent zonation has been developed for Morrowan conodonts above the *bassleri* Zone. In many papers, the next zone is the *Idiognathodus sinuosus* Zone, defined by the range overlap of *N. bassleri* and *I. sinuosus* Ellison & Graves 1941 (Lane & Straka, 1974; Baesemann & Lane, 1985).

The overlying *Idiognathodus klapperi* Zone of Lane & Straka (1974) was defined by the presence of *I. klapperi* Lane & Straka 1974. Typical *I. klapperi* occurs only in the caprock of the Baldwin coal (Dye Formation) in southern Oklahoma, and Pa elements identical to the type material of *I. klapperi* have not been recovered elsewhere. Grayson *et al.* (1989; 1990) expanded the concept of *I. klapperi* to include Pa elements in which the anterior extensions of adcarinal ridges have been incorporated into the platform. Using this definition, they applied the name *I. klapperi* to a series of distinctive late Morrowan Pa elements that had been called *I. delicatus* previously. The first appearance of *I. klapperi* was retained by Grayson *et al.* (1990) to mark a datum above the *sinuosus* Zone.

The base of the overlying *Idiognathoides convexus* Zone was tentatively defined as the range of *Id. convexus* (Ellison & Graves, 1941) below the appearance of *Idiognathoides* n. sp. (Lane *et al.*, 1972) by Lane & Straka (1974). This zone has been applied and labeled in an inconsistent manner, but is most often indicated by the first occurrence of *Id. convexus* following the appearance of *N. bassleri*, and usually *I. sinuosus*, whether or not *I. klapperi* is present below.

One alternative to the existing zones would be to expand the *bassleri* Zone to include the *sinuosus* and *klapperi* zones in a *Neognathodus*-based zonation. Because the appearance of *I. klapperi* (in the sense of Grayson *et al.)* is a distinctive event in *Idiognathodus*, *I. klapperi* could be used to subdivide the expanded *bassleri* Zone into two subzones. The *bassleri* Zone contains additional morphotypes of *Neognathodus*, most of which are poorly circumscribed in North America. They include *N.* sp. A and *N.* sp. B (part) of

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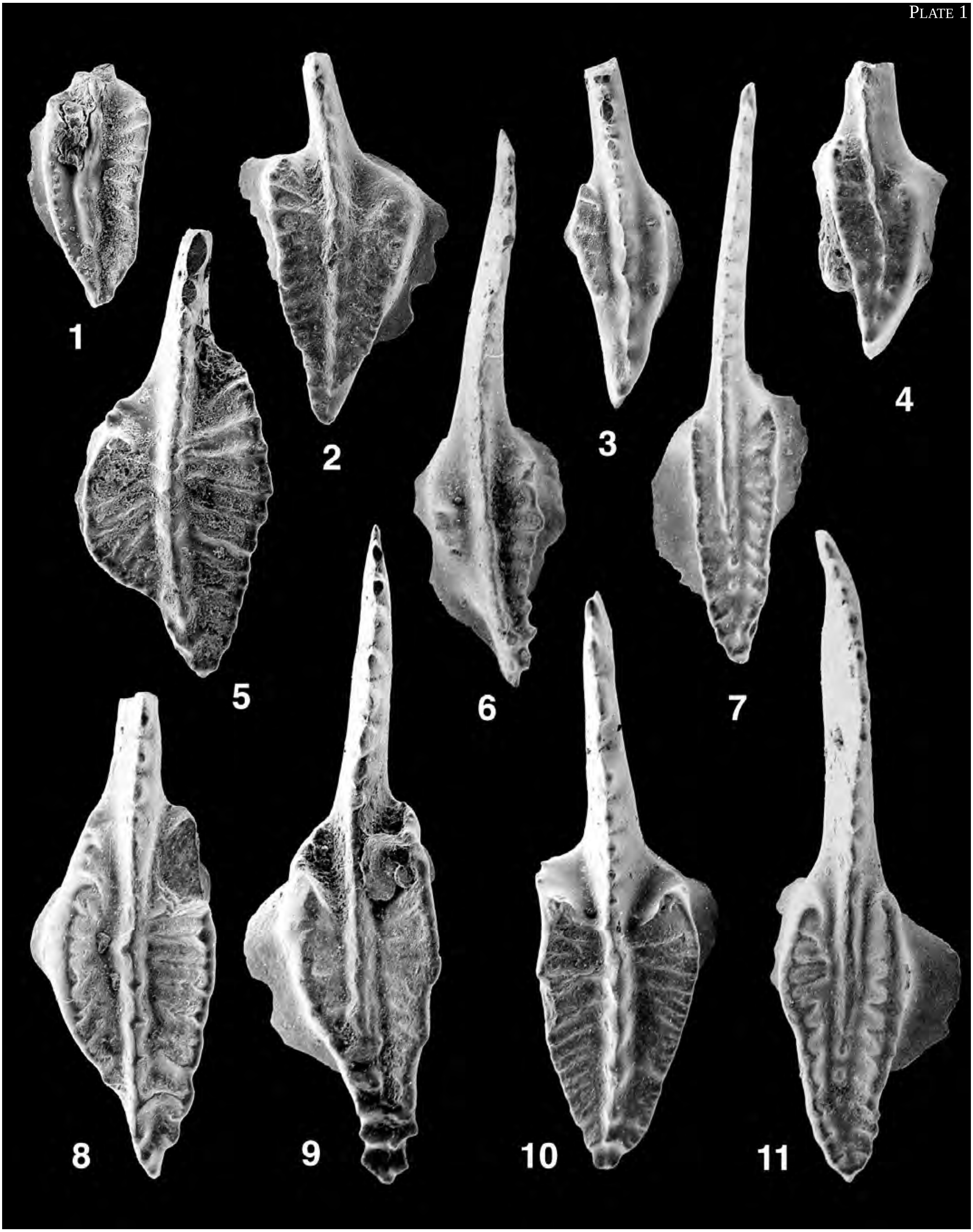
PLATE 1–All figures x 60; all are upper views of Pa elements. SUI – University of Iowa, OU – University of Oklahoma. *1*, *Neognathodus asymmetricus* Stibane 1967. SUI 100567, lower Floris Formation, Iowa. *2, Neognathodus caudatus* Lambert 1992. Holotype, SUI 61543, upper Kalo Formation, Iowa. *3, Neognathodus roundyi* (Gunnell, 1931), late variety. SUI 100568, Lost Branch cyclothem, Missouri. *4, Neognathodus higginsi* (Grayson *et al.*, 1985). SUI 100569, upper Rhoda Creek Formation, Oklahoma. *5, Neognathodus* n. sp. Lane 1977. SUI 100570, Unnamed Unit 2, upper Golf Course Formation, Oklahoma. *6, Neognathodus roundyi* (Gunnell, 1931), middle variety. SUI 100571, Pawnee cyclothem, Iowa. *7, Neognathodus symmetricus* (Lane, 1967). SUI 100572, basal Marble Falls Formation, Texas. *8, 9. Neognathodus atokaensis* Grayson 1984. *8,* Transitional with *N.* n. sp. Lane 1977, SUI 100573, middle Bostwick Member, Lake Murray Formation, Oklahoma; *9,* OU 10,027, upper Atoka Formation, Oklahoma. *10, Neognathodus colombiensis* Stibane 1967. SUI 100574, Seville Limestone, Illinois. *11, Neognathodus bassleri* (Harris and Hollingsworth, 1933). SUI 100575, uppermost Barnett Formation, Texas.

PLATE 1



Grayson (1990), which may or may not be conspecific with some Eurasian species described from Bashkirian and Moscovian strata.

The next conodont zone has never been consistently defined. Zones based on *Idiognathoides* n. sp. (Lane & Straka, 1974), *Neognathodus* n. sp. (Lane, 1977) and *Idiognathoides ouachitensis* (Harlton, 1933) (Grayson, 1979; 1984; Lane & Baesemann, 1982; Baesemann & Lane, 1985) have been used. We propose the *Neognathodus* n. sp. Zone be used, the base of which is defined by the first appearance of *N*. n. sp. of Lane (1977). This form is widespread in western North America, the Midcontinent and the Appalachian Basin, but its presence is commonly obscured by mis-assignment to Desmoinesian species. Detailed taxonomic work with the *Idiognathoides*-*Declinognathodus* clades (Grayson *et al*., 1990) has not been pursued in North America, as it has been recently in Europe and Russia. More research is needed to evaluate the biostratigraphic utility of those lineages in North America, and whether or not provincialism affects their potential for intercontinental correlation.

Atokan Stage (lower middle Pennsylvanian): The Morrowan-Atokan boundary has variously been assigned to lie at the base, top, and within the *Neognathodus* n. sp. Zone. When the base of the Atokan is identified on the appearance of the foraminifer *Eoschubertella* (Groves, 1986), the boundary falls within this zone (Fig. 1). Some workers had used the appearance of *Diplognathodus* to identify the Morrowan-Atokan boundary (e. g., Dunn, 1976; Lane, 1977; Bender, 1980), but that genus has since been demonstrated to range significantly lower (von Bitter & Merrill, 1990). *Idiognathodus* Pa elements that Grayson *et al*. (1989) and Grayson (1990) assign to *I. incurvus* Dunn 1966 appear at or near the base of the Atokan, according to Grayson *et al*. (1989).

The *Neognathodus atokaensis* Zone of Grayson (1984) extends from the first occurrence of *N. atokaensis* Grayson 1984 to its last occurrence, and represents the middle Atokan. The upper boundary of this zone will be better defined once the taxonomy of the several co-occurring and overlying *Neognathodus* morphotypes is stabilized. Coeval strata produce morphotypes named *N. kashiriensis* Goreva 1982 and *N. uralicus* Nemirovskaya & Alekseev 1994, among others. *Neognathodus uralicus* is a distinctive morphotype that is common in the southern Midcontinent, but has been referred incorrectly to *N. medadultimus* Merrill 1972 and *N. medexultimus* Merrill 1972 (e. g., Manger & Sutherland, 1984).

A short-lived acme of gondolellids occurs within the *atokaensis* Zone in the southern Midcontinent and western North America. Mesogondolelloids typically assigned to *Mesogondolella clarki* (Koike, 1967) are common both early and late in the *N. atokaensis* Zone (von Bitter & Merrill, 1977). So-called ‘naked’ gondolellids usually assigned to *Gondolella gymna* Merrill & King 1971 are often limited to the same acme zone in the lower *atokaensis* Zone.

The *Neognathodus colombiensis* Zone overlies the *N. atokaensis* zone. Its base is defined by the appearance of *N. colombiensis* Stibane 1967, which is characterized by morphotypes with a relatively flat, symmetrical upper surface. Grayson (1990) has referred these morphotypes to (in implied sequence) *N. ‘prebothrops’*, *‘bothrops’*, and *bothrops* Merrill 1972, and other workers have forced them into younger *Neognathodus* species. The name *N. colombiensis* has priority among these symmetrical forms. During the time represented by the *colombiensis* zone, *Declinognathodus* and *Idiognathoides* dwindled to extinction in North America. Neither genus has been recovered above the latest Atokan in the northern Midcontinent, or possibly the earliest Desmoinesian in Texas and western North America.

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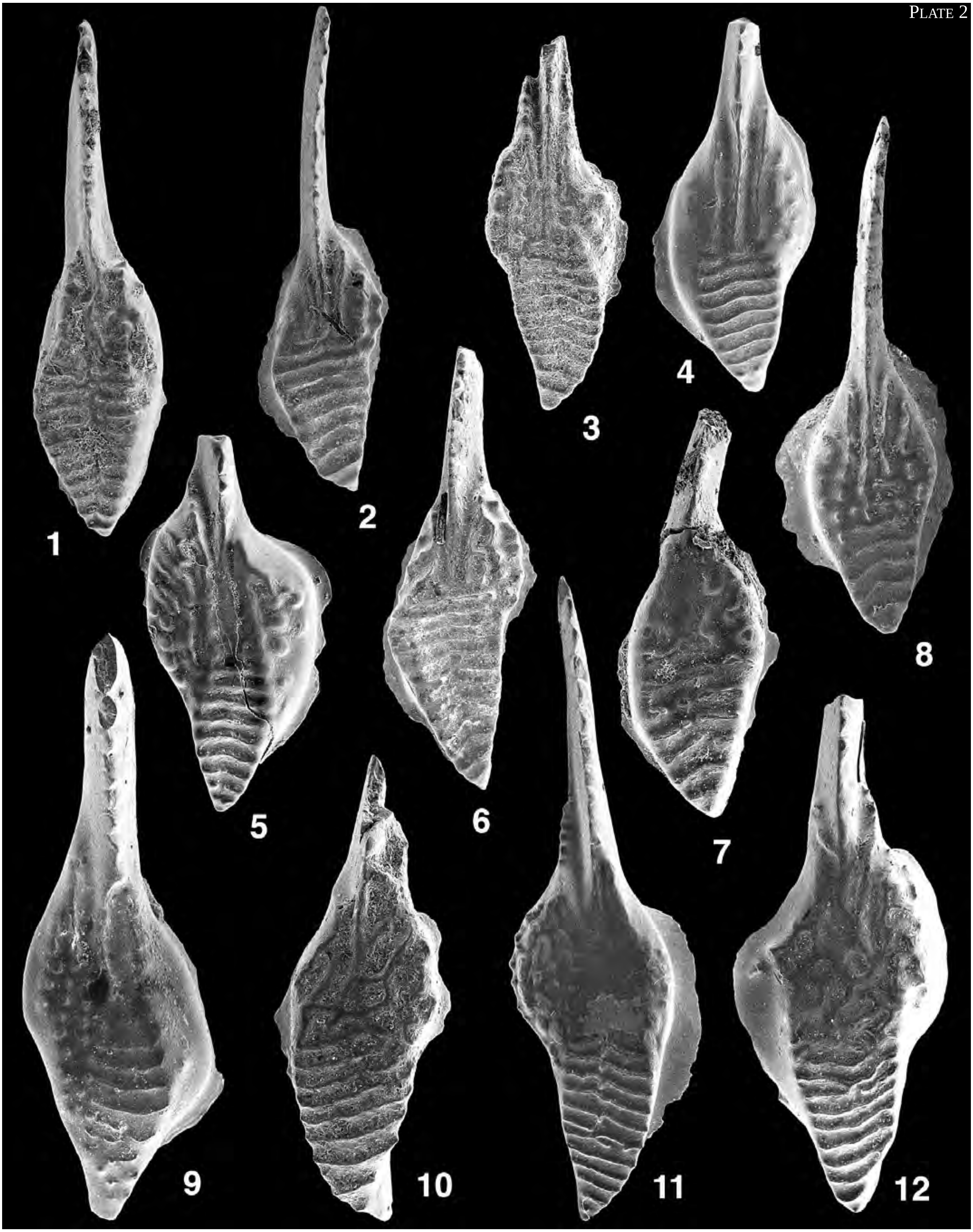
PLATE 2–All figures x 60; all are upper views of Pa elements. SUI – University of Iowa. *1, Idiognathodus gibbus* Lambert 1992. Holotype, SUI 61580, upper Kilbourn Formation, Iowa. *2, 6*, *Idiognathodus sinuosus* Ellison and Graves 1941? *2,* SUI 100576, upper Bloyd Formation, Arkansas; *6,* SUI 100577, upper Bloyd Formation, Arkansas. *3*, *Idiognathodus incurvus* Dunn 1967. SUI 100578, mid (46 m above base) “Middle” Magdalena Formation, Texas. *4, 5, 11*, *Idiognathodus incurvus* Dunn 1967 descendants. *4*, SUI 100579, Ladden Branch Limestone, Missouri; *5,* SUI 100580, Ladden Branch Limestone, Missouri; *11*, SUI 100581, upper (90 m above base) “Middle” Magdalena Formation, Texas. *7, 8*, *Idiognathodus klapperi* sensu Grayson *et al.* (1989, 1990). *7,* SUI 100582, upper Bloyd Formation, Arkansas; *8,* SUI 100583, lower (16 m above base) “Middle” Magdalena Formation, Texas. *9, Idiognathodus* sp. B Lambert 1992. SUI 61534, upper Kalo Formation, Iowa. *10, 12, Idiognathodus* sp. A Lambert 1992. *10,* SUI 61589, middle Kilbourn Formation, Iowa; *12*, SUI 61591, middle Kilbourn Formation, Iowa.

PLATE 2



Desmoinesian Stage (upper middle Pennsylvanian): The exact position of the Atokan-Desmoinesian boundary remains unresolved, but it is commonly equated with the base of the *Fusulinella/Fusulina (Beedeina)* Zone (Lane & West, 1984; Lambert and Heckel, 1990). The basal Desmoinesian in its type region possesses a conodont fauna that includes the first occurrence of *Neognathodus caudatus* Lambert 1992, *Idiognathodus amplificus* Lambert 1992, and *Idiognathodus obliquus* Kozitskaya & Kossenko 1978 (verified by T. Nemyrovska, personal communication, 2003). *Neognathodus caudatus* is a widely distributed taxon, and has been recovered from the marine interval above the Cliffland Coal in the type region, the subsurface Hugoton Embayment of western Kansas, the Lester Limestone in southern Oklahoma, and various localities across Eurasia. Because *N. caudatus* may provide a reliable marker for the basal Desmoinesian, we use the *caudatus* Zone, the base of which is defined by the first appearance of this species (Fig. 1).

Some North American workers have instead relied upon *Idiognathodus amplificus* to correlate lower Desmoinesian strata (Rice *et al.*, 1994; Ritter *et al.*, 2002). *Idiognathodus obliquus* and related morphotypes (e. g., *I. praeobliquus?)* are common in the lower Cherokee Group in northeastern Oklahoma, where the succession is more continuous (Boardman *et al.,* 2002), as well as in Iowa (Lambert 1992). We therefore now recognize an equivalent *I. obliquus* zone, which may be more useful for global correlation because this species occurs in Eurasia.

The next Desmoinesian zone is defined by the first occurrence of *Neognathodus asymmetricus* Stibane 1967. Most North American workers have ignored *N. asymmetricus* and have inconsistently split morphologies that should be assigned to this species between *N. medadultimus* Merrill 1972 and *N. medexultimus* Merrill 1972, based on a hypothetical terminal paedomorphocline (Merrill, 1975a, 1975b, 1999). Additional *Neognathodus* morphotypes occur in the *asymmetricus* zone, but are rare and poorly circumscribed. *Gondolella* species in the *asymmetricus* Zone had not developed the crenulated platform edges characteristic of the genus in the late Desmoinesian, and can be loosely assigned to *G. ex. gr. laevis,* followed by *G. pohli* von Bitter & Merrill 1998 in the base of the next higher zone.

The lowest widely recognized cyclothem in the Midcontinent is the Verdigris cyclothem of the upper Cherokee Group. It contains the youngest non-crenulated gondolellid, *G. pohli,* and the first occurrence of *Neognathodus roundyi* (Gunnell 1931) *(sensu lato),* which defines the base of the *roundyi* Zone. Only a single *Neognathodus* zone, based on the occurrence of *N. roundyi,* can be consistently recognized in the overlying Marmaton Group. A variety of names has been proposed for the numerous *Neognathodus* morphotypes that characterize this interval (Jones, 1941; Youngquist and Downs, 1949; Merrill, 1975a, 1975b), but *N. roundyi* has priority. Lambert and Grayson (1993) inferred that developmental constraints on parapet morphology in *Neognathodus* may have weakened with an apparent loss of ecological competition following the extinction of partially homeomorphic *Declinognathodus* and *Idiognathoides*. That would account for the broad variability in platform development of neognathodid populations following the Atokan, and which became especially pronounced through the middle and late Desmoinesian.

Continuing study of *Idiognathodus* species from the upper Cherokee Group has shown that several previously overlooked taxa named from the Midcontinent (Youngquist & Heezen, 1948; Youngquist & Downs, 1949) and the Appalachians (Sturgeon & Youngquist, 1949) are valid and useful for zonation of the

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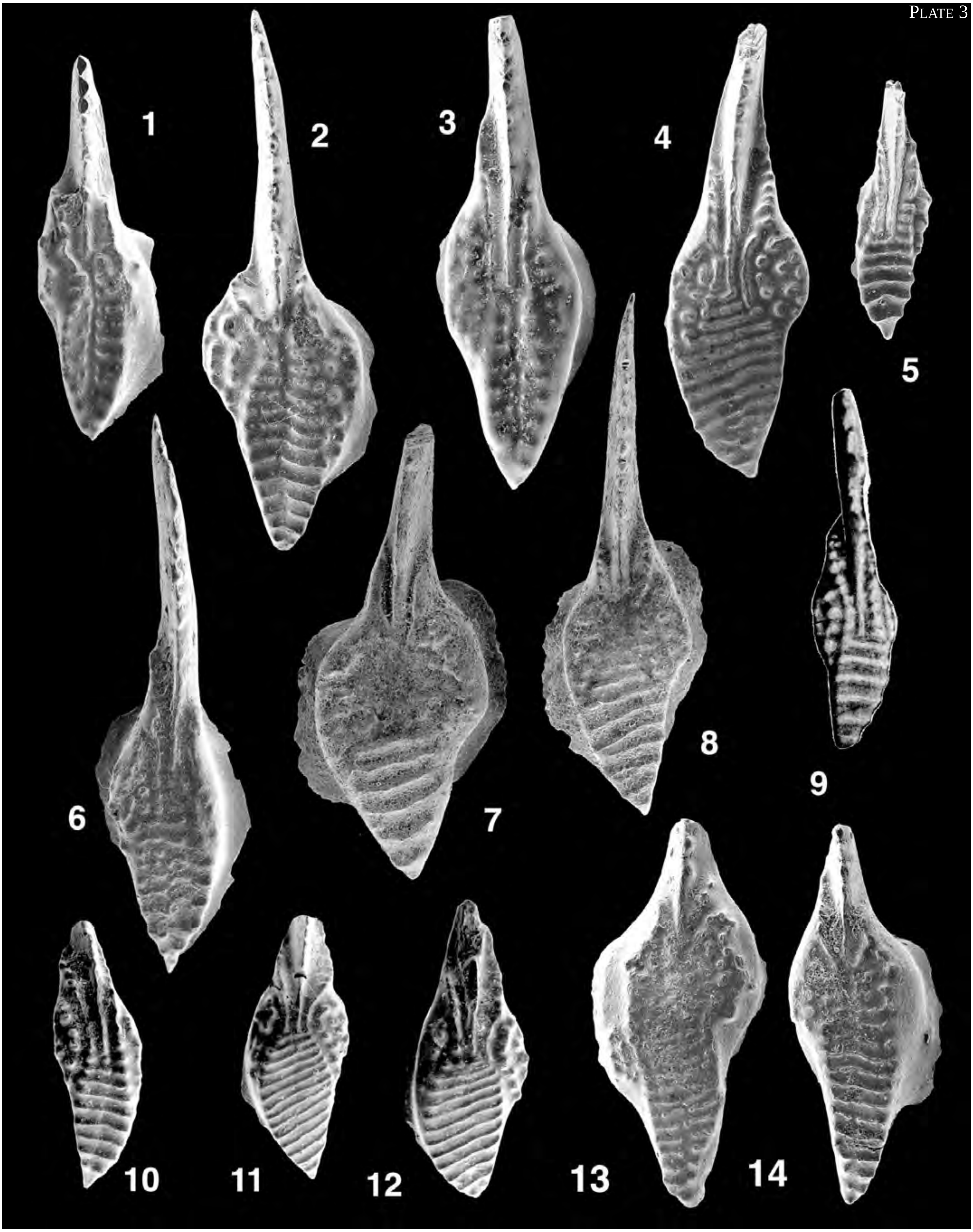
PLATE 3–All figures x 60; all are upper views of Pa elements. SUI – University of Iowa, UC – University of Chicago, UM – University of Missouri. *1, 2, Swadelina nodocarinata* (Jones 1941). *1,* Holotype, UC 44667, Lost Branch cyclothem, Oklahoma; *2,* SUI 99435, Lost Branch cyclothem, Kansas. *3, Swadelina neoshoensis* Lambert, Heckel & Barrick 2003. Holotype, SUI 99442, Altamont cyclothem, Iowa. *4, Idiognathodus expansus* Stauffer & Plummer 1932. SUI 100584, Lost Branch cyclothem, Kansas. *5, 7-9, Idiognathodus delicatus* Gunnell 1931. *5,* UM 488-1, lectotype, Coal City cyclothem, Missouri; *7,* SUI 100585, Coal City cyclothem, Kansas; *8,* SUI 100586, Coal City cyclothem, Kansas; *9,* UM 488-1?, lost holotype?, plate 29, fig. 23 of Gunnell (1931), Coal City cyclothem, Missouri; see Barrick & Walsh (1999) for discussion. *6, Idiognathodus iowaensis* Youngquist & Sturgeon 1948. Holotype, SUI 4162, Verdigris cyclothem, Iowa. *10, Idiognathodus praeobliquus* Nemyrovska, Perret-Mirouse & Alekseev 1999? SUI 100587, McCurtain cyclothem, Oklahoma. *11, 12, Idiognathodus obliquus* Kozitskaya & Kossenko 1978. *11,* SUI 100588, Sam Creek cyclothem, Oklahoma; *12,* SUI 100589, Doneley cyclothem, Oklahoma. *13, 14, Idiognathodus amplificus* Lambert 1992. *13,* Holotype, SUI 61563, upper Kalo Formation, Iowa; *14,* SUI 61569, upper Kalo Formation, Iowa.

PLATE 3



middle Desmoinesian. The Verdigris is the cyclothem from which Youngquist & Heezen (1948) named *Idiognathodus iowaensis*, a taxon that is sufficiently abundant in the upper Cherokee Group that we now recognize the *I. iowaensis* zone for this interval. Further detailed study may delineate additional zones in both the lower and upper parts of the Cherokee Group.

A zonation of the upper Desmoinesian Marmaton Group is accomplished using species of *Idiognathodus* and *Swadelina* Lambert, Heckel & Barrick, 2003a. Marmaton strata (specifically the Coal City cyclothem: see Heckel *et al.,* 2003) contain the genotype of *Idiognathodus, I. claviformis* Gunnell 1931, and the holotype of *I. delicatus* Gunnell 1931, of which the latter has been used indiscriminately for lobed flat morphotypes throughout the Pennsylvanian. These early-named taxa are currently undergoing detailed study to better characterize both their morphological and stratigraphic ranges (Lambert *et al.,* 2003b). Here we recognize the *I. delicatus* zone for the Lower Fort Scott through Coal City cyclothems, a zone spanning the lower and middle Marmaton Group.

The next two zones are based on the successive first occurrences of two species of *Swadelina,* a troughed clade of idiognathodids that preceded the appearance of *Streptognathodus* in the early Missourian (Lambert *et al.,* 2003a). In the Midcontinent, the *neoshoensis* Zone appears just above the Coal City cyclothem with the first appearance of *Sw. neoshoensis* Lambert, Heckel & Barrick 2003a in the Farlington cyclothem (Heckel, 1999, 2002), and includes the overlying Altamont cyclothem. The *nodocarinata* Zone is defined by the entry of *Sw. nodocarinata* (Jones, 1941) in the Norfleet cyclothem, and includes the uppermost Desmoinesian Lost Branch cyclothem.

The platformed lineage of *Gondolella* attains its characteristic upper Desmoinesian platform crenulation in the Lower Fort Scott cyclothem at the base of the Marmaton Group, coincident with the base of the *delicatus* Zone. These forms were referred to *G. bella* Stauffer and Plummer 1932 by Merrill (1975a). Although not found through most of the Marmaton, *Gondolella* reappears as the more ornately crenulate *G. magna* Stauffer & Plummer 1932, along with the non-platformed *G.* cf. *G. denuda* Ellison 1941 in the Lost Branch cyclothem.

LATE PENNSYLVANIAN

Merrill (in Lane *et al.*, 1971) proposed a set of four zones for the late Pennsylvanian based on faunas from the Appalachian Basin. These zones, which were distinguished by the peaks or epiboles of the name-givers, have not been widely used. More recently, Ritter (1995) published a series of range zones extending from the middle Missourian into the Lower Permian.

Missourian Stage: For purposes of correlation, Heckel *et al.* (2002) recommended that the base of the Exline cyclothem be used as a reference position for the base of the regional Missourian Stage in the Midcontinent. The Exline level is slightly above the traditional base of the Missourian, which is the unconformity at the base of the Pleasanton Group in Kansas and the laterally equivalent base of the Seminole Formation in Oklahoma. The level of the Exline cyclothem was chosen because it contains the first appearance of *Idiognathodus eccentricus* (Ellison 1941) above the first appearance of its ancestor, *I. sulciferus* Gunnell 1933. Because it is the first new species of *Idiognathodus* to appear above the traditional boundary, the first appearance of *I. eccentricus* serves as a biostratigraphic marker by which basal Missourian strata can be identified in the Midcontinent region.

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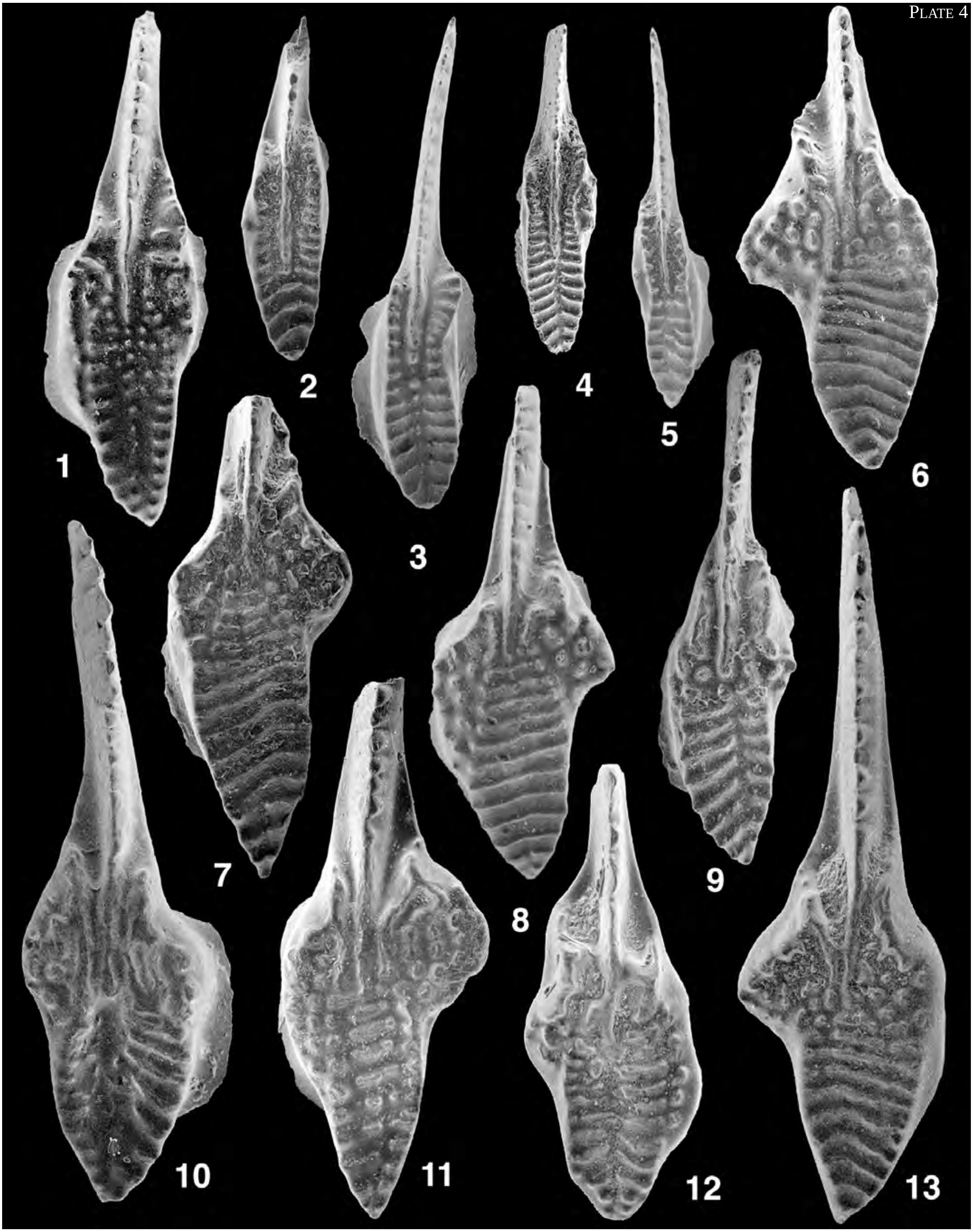
PLATE 4–All figures x 60; all are upper views of Pa elements. BEG- Texas Memorial Museum; SUI- University of Iowa; UM- University of Missouri. *1, Streptognathodus cancellosus* (Gunnell, 1933). Holotype. UM491-2. Swope cyclothem, Kansas. *2, Streptognathodus confragus* (Gunnell, 1933). Holotype, UM 498-1, Dennis cyclothem, Kansas. *3, Streptognathodus elegantulus* Stauffer & Plummer 1932. Holotype, BEG 19166, Wolf Mountain Shale, Texas (equivalent to Iola cyclothem). *4, Streptognathodus corrugatus* Gunnell 1933. Holotype, UM 506-1, Cherryvale cyclothem, Kansas. *5, Streptognathodus gracilis* Stauffer & Plummer 1932. Holotype, BEG 19169, PP3 shale member, Posideon Formation, Texas (equivalent to Dewey cyclothem). *6-8. Idiognathodus magnificus* Stauffer & Plummer 1932. *6,* Cotype, lectotype of Barrick & Walsh (1999), BEG 19164, PP3 shale member, Posideon Formation, Texas. *7,* Cotype, BEG 20927, PP3 shale member, Posideon Formation, Texas. *8,* Cotype, BEG 20926, PP 3 shale member, Posideon Formation, Texas. *9, Idiognathodus eccentricus* (Ellison, 1941). Holotype, UM 560-1, Swope cyclothem, Kansas. *10, Streptognathodus excelsus* Stauffer & Plummer 1932. Holotype, BEG 19168, Wolf Mountain Shale, Texas. *11, Idiognathodus* sp. A. SUI 100590, Mound City cyclothem, Oklahoma. *12, Idiognathodus clavatulus* (Gunnell, 1933). Holotype, UM 491-1, Swope cyclothem, Kansas. *13, Idiognathodus sulciferus* Gunnell 1933. Holotype, UM 492-4, Swope cyclothem, Kansas.

PLATE 4



The thin marine cyclothem recognized in the Checkerboard Limestone and the South Mound Shale, which occurs above the traditional base of the Missourian but underlies the first appearance of *I. eccentricus* in the Kansas-Oklahoma border region, has yielded non-diverse conodont faunas characterized by *I. sulciferus*. The *eccentricus* Zone extends from the first appearance of the nominate species up to the first appearance of *Streptognathodus cancellosus* (Gunnell, 1933). Within the upper part of the *eccentricus* Zone, the more nodose species, *I.* n. sp. A and *I. clavatulus* (Gunnell, 1933) appear at the level of the Hertha cyclothem (Barrick *et al.*, 1996).

In eastern Kansas, the *eccentricus* Zone includes (in ascending order) the intermediate Exline cyclothem, the minor Critzer cyclothem, and the major Hertha cyclothem. The Scottville Limestone of the Illinois Basin contains *Idiognathodus eccentricus*, which allows correlation with the Exline cyclothem (Heckel, 1999, 2002). The next higher Cramer marine unit (Trivoli cyclothem) of the Illinois basin contains *I. clavatulus*, which allows correlation with the Hertha cyclothem (Heckel & Weibel, 1991; Heckel, 1999, 2002), and with the upper part of the *eccentricus* Zone. In north-central Texas, *I.* n. sp. A and *I. clavatulus* occur in the Dog Bend cyclothem (Barrick & Boardman, 1989), which also has been correlated with the Hertha cyclothem (Boardman & Heckel, 1989). The *eccentricus* Zone has been identified in upper Honaker Trail Formation in the Paradox Basin of Utah, a short distance above beds bearing Desmoinesian conodonts and fusulinids (Ritter *et al.*, 2002). More recently, the Eurasian species *I. sagittalis* Kozitskaya 1978 has been recognized in the Exline and and possibly also the Hertha cyclothems of the *eccentricus* zone in Kansas and Oklahoma.

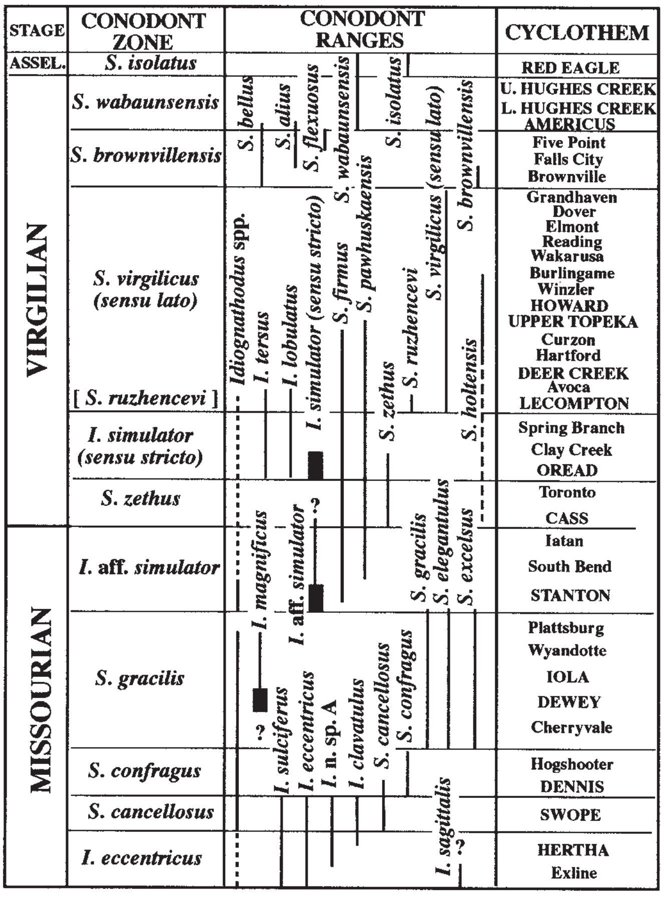


FIGURE 2–Conodont zones for Missourian and Virgilian strata in Midcontinent North America. Ranges of better-known and significant species are shown plotted against cyclothems as discussed in text. Major cyclothems are denoted by all capital letters; intermediate cyclothems by upper and lower case letters. *I. = Idiognathodus; S. = Streptognathodus.*

The appearance of the distinctive species *Streptognathodus cancellosus* in the major Swope cyclothem marks the divergence of the lineage that leads to the diverse *Streptognathodus* faunas of the later Missourian (Barrick *et al.*, 1996). The *cancellosus* Zone ranges from the first appearance of the nominate taxon up to the first appearance of *Streptognathodus confragus* Gunnell 1933. The *cancellosus* Zone used here is not the same as the Eurasian *cancellosus* Zone of Barskov (1984) and other authors, because the species identified in Eurasia as *S. cancellosus* is a different species from the Midcontinent North American taxon. All *Idiognathodus* species occurring in the *eccentricus* Zone range into the *cancellosus* zone, and some additional unnamed forms may also be present. The *cancellosus* Zone includes the major Swope cyclothem in the Midcontinent region, and has been identified in the Appalachian basin ('Lower' Brush Creek marine unit: Heckel, 1994, which is where Merrill, in Lane *et al.*, 1971, recognized a similar zone), the Illinois basin (Macoupin cyclothem, which is next above the Trivoli: Heckel & Weibel, 1991), north-central Texas (Upper Salesville Shale: Boardman & Heckel, 1989), as well as in the Paradox basin of Utah (upper Honaker Trail Formation: Ritter *et al.*, 2002).

The first appearance of *Streptognathodus confragus* defines the base of the *confragus* Zone, which ranges up to the first appearance of *S. gracilis* Stauffer & Plummer 1932. The *confragus* Zone includes the minor Mound Valley cyclothem, the major Dennis cyclothem and the overlying Hogshooter-upper Winterset cyclothem. Some *Idiognathodus* and

Streptognathodus Pa elements in the Dennis fauna appear to be transitional to forms occurring in later Missourian cyclothems. This zone has been recognized in the Appalachian basin (the equivalent 'Upper' Brush Creek and Pine Creek marine units: Heckel, 1994), the Illinois basin (Shoal Creek cyclothem: Heckel & Weibel, 1991), and north-central Texas (Palo Pinto Limestone: Boardman & Heckel, 1989), as well as in the Paradox basin of Utah (upper Honaker Trail Formation: Ritter *et al*., 2002).

Ritter (1995) proposed the *Streptognathodus gracilis* Zone to extend from the first appearance of the nominate species to the first appearance of *S. firmus* Kozitskaya 1978. The *gracilis* Zone includes a large part of middle to upper Missourian strata in the Midcontinent region, extending from the intermediate Cherryvale cyclothem through the lower part (Captain Creek Limestone) of the major Stanton cyclothem and includes five major to intermediate cyclothems (in ascending order, Cherryvale, Dewey, Iola, Wyandotte and Plattsburg) and several minor cycles (Heckel, 1999, 2002). The *gracilis* Zone is characterized by the radiation and dominance of a closely related group of *Streptognathodus* species in the Midcontinent: *S. gracilis, S. elegantulus* Stauffer & Plummer 1932, *S. excelsus* Stauffer & Plummer 1932, and *S. corrugatus* Gunnell 1933. *Idiognathodus* Pa elements are usually assigned to *I. magnificus* Stauffer & Plummer 1932, but preliminary studies of the *Idiognathodus* faunas indicate that other species are present as well.

Subdivision of the *gracilis* Zone is not yet possible using range data alone. Heckel (1999) has used the acme of a prominently lobed and delicately ribbed morphotype, *I. magnificus sensu stricto* to identify the Quivira Shale of the Dewey cyclothem. This acme has been used to correlate the Dewey with the mid-Posideon Shale (PP3, the type stratum of the species) in north-central Texas (Boardman & Heckel, 1989) and with the Flat Creek cyclothem in the Illinois Basin (= "Fithian" cyclothem of Heckel & Weibel, 1991). In the Muncie Creek Shale of the next higher Iola cyclothem, a closely related *Idiognathodus* morphotype with a reduced lobe (= informal "postmagnificus": Heckel *et al.*, 1998; Heckel, 1999, 2002) is characteristic and has been used to correlate it with the La Salle/Lower Millersville cyclothem in the Illinois basin (Heckel & Weibel, 1991), and with the lower Wolf Mountain Shale in north-central Texas (Boardman & Heckel, 1989). Heckel (1999, 2002) reported that a morphotype of *Streptognathodus* with a bent trough axis (probably = *S*. sp. A of Ritter, 1995) occurs in the intermediate Wyandotte and Plattsburg cyclothems in the Midcontinent, and it also has been found in two equivalent cyclothems above the LaSalle/Lower Millersville cyclothem in the central Illinois Basin, near the top of the *gracilis* Zone. Above the 'Upper' Brush Creek/Pine Creek marine unit in the Appalachian Basin, the conodont faunas of the Cambridge/Nadine and the Portersville/Woods Run marine units are dominated by the *S. gracilis* group, placing them into the *gracilis* Zone (these are the units in which Merrill *in* Lane *et al*. 1971 recognized a similar zone).

Ritter (1995) proposed the *Streptognathodus firmus* Zone to extend from the first appearance of the nominate species in the upper Missourian to the first appearance of *S. pawhuskaensis deflectus* Ritter 1995, well up in the lower Virgilian. We split the *firmus* Zone into three zones, the lower one of which is called temporarily the *Idiognathodus* aff. *simulator* Zone. Its lower boundary is defined by the first appearance of the ancestor to *I. simulator,* which is being described as a new species, and the upper boundary is defined by the first appearance of *S. zethus* Chernykh 1987. Both *I.* aff. *simulator* and *S. firmus* first appear in the Eudora Shale, the core shale of the Stanton cyclothem, so the lower boundary of the *I.* aff. *simulator* Zone is essentially the same as that of the *firmus* Zone of Ritter (1995). We hesitate to use *S. firmus* as a zonal index in the Midcontinent because it may have immigrated into the Midcontinent from Eurasia (Barrick *et al.*, 2000). Pa elements that could be ancestral to *S. firmus* are common in earlier Kasimovian Eurasian faunas, where most of them are assigned to *"S. oppletus"*, a taxon that is different from true *S. oppletus* Ellison 1941, which was described from the Quivira Shale of the Midcontinent region in the *gracilis* zone. In contrast, *I.* aff. *simulator* is derived from Midcontinent forms of *Idiognathodus,* and transitional forms between *I.* aff. *simulator* and typical flat-topped older *Idiognathodu*s Pa elements occur in the Eudora Shale. *Streptognathodus firmus* does reliably appear at the top of the Eudora Shale and its equivalents in the Midcontinent, making it a useful species for correlation of shallower-water facies in eastern North America.

Species of *Idiognathodus* are rare in most cyclothems above the Stanton. Through the next three cyclothems (the intermediate South Bend and Iatan cyclothems, and the minor Westphalia cyclothem), *Streptognathodus firmus* occurs in decreasing numbers as the closely related species *S. pawhuskaensis* (Harris & Hollingsworth, 1933) rises to dominance. Keairns (2002) suggests that it may be possible to separate the South Bend and Iatan cyclothems, as well as equivalent cyclothems in Texas, based on relative abundances of two morphotypes transitional between *S. firmus* and *S. pawhuskaensis*. The Iatan cyclothem also contains forms of *S. pawhuskaensis* with a few irregularly distributed marginal nodes.

The Stanton cyclothem has been correlated with the Little Vermilion cyclothem of the Illinois basin (Heckel & Weibel, 1991) and the upper Winchell/Merriman Limestone of north-central Texas (Boardman & Heckel, 1989) based on the co-occurrence of *Idiognathodus* aff. *simulator* and *Streptognathodus firmus*, and with the Noble Limestone of Ohio (above the Portersville marine unit) based on the presence of *S. firmus* (Heckel, 1994, 2002). Ritter *et al*. (2002) correlated the Schafer Limestone at Honaker Trail, Utah, with the South Bend cyclothem, based on the co-occurrence of *S. firmus* and *S. pawhuskaensis*.

Virgilian Stage: The base of the Virgilian Stage has been placed at different levels in the Midcontinent, as discussed by Boardman *et al.* (1994). Most state geological surveys have placed the boundary within or at the top of the South Bend cyclothem, which lacks a sufficiently distinctive conodont fauna. The level that we use here to mark the base of the Virgilian is the base of the Cass cyclothem (= 'Haskell-Cass' of Heckel *et al.*, 1998) in the middle of the Douglas Group in Kansas. This level coincides with the first appearance of the species *Streptognathodus zethus* in the Midcontinent region (Heckel, 1999). The top is defined by the first appearance of *Idiognathodus simulator* Ellison 1941 *(sensu stricto)*. Recognition of the *zethus* Zone outside of Kansas is complicated by the presence of similarly noded Pa elements that occur below *S. zethus*. Hence, the report of *S. zethus* by Boardman & Barrick (1989) from the Lower Colony Creek cyclothem in north-central Texas is now less certain. Heckel & Weibel (1991) identified *S. zethus* from the Omega marine unit in the Illinois basin and correlated it with the Cass cyclothem.

Now that we differentiate *Idiognathodus* aff. *simulator*, which dominates the Eudora Shale in the Stanton cyclothem and occurs sparsely in the South Bend and Cass cyclothems, from *I. simulator (sensu stricto)*, we recognize the *I. simulator (sensu stricto)*Zone starting at the base of the Heebner Shale, the core shale of the Oread cyclothem, from which the holotype of *I. simulator* was collected. The first appearance of *I. tersus* Ellison 1941, and the last appearance of *I. simulator (sensu stricto)*, are also in the Oread cyclothem (Heckel, 1989; Ritter, 1995). *Idiognathodus simulator (sensu stricto)* has been used to correlate the Oread cyclothem with cyclothems in north-central Texas (Finis cyclothem: Boardman & Heckel, 1989), the Illinois basin (Shumway cyclothem: Heckel & Weibel, 1991), and the Appalachian basin (Ames limestone: Heckel, 1994). Although Ritter (1995) erected the *deflectus* Zone to encompass the interval from the first appearance of the nominate subspecies to the first appearance of *S. virgilicus* Ritter 1995, this subspecies has not been found in recent intensive collecting in southern Kansas and Oklahoma. Therefore, we do not recognize the zone, and include the two intermediate cyclothems it encompassed (Clay Creek and Spring Branch) in the *simulator (sensu stricto)* Zone. *Idiognathodus lobulatus* Kozitskaya 1978 also appears in the Oread and ranges up into the next zone.

The *virgilicus* Zone of Ritter (1995) includes a significant proportion of middle into late Virgilian time, spanning approximately 30 cyclothems of all scales as recognized by Boardman (1999). Its base is defined by

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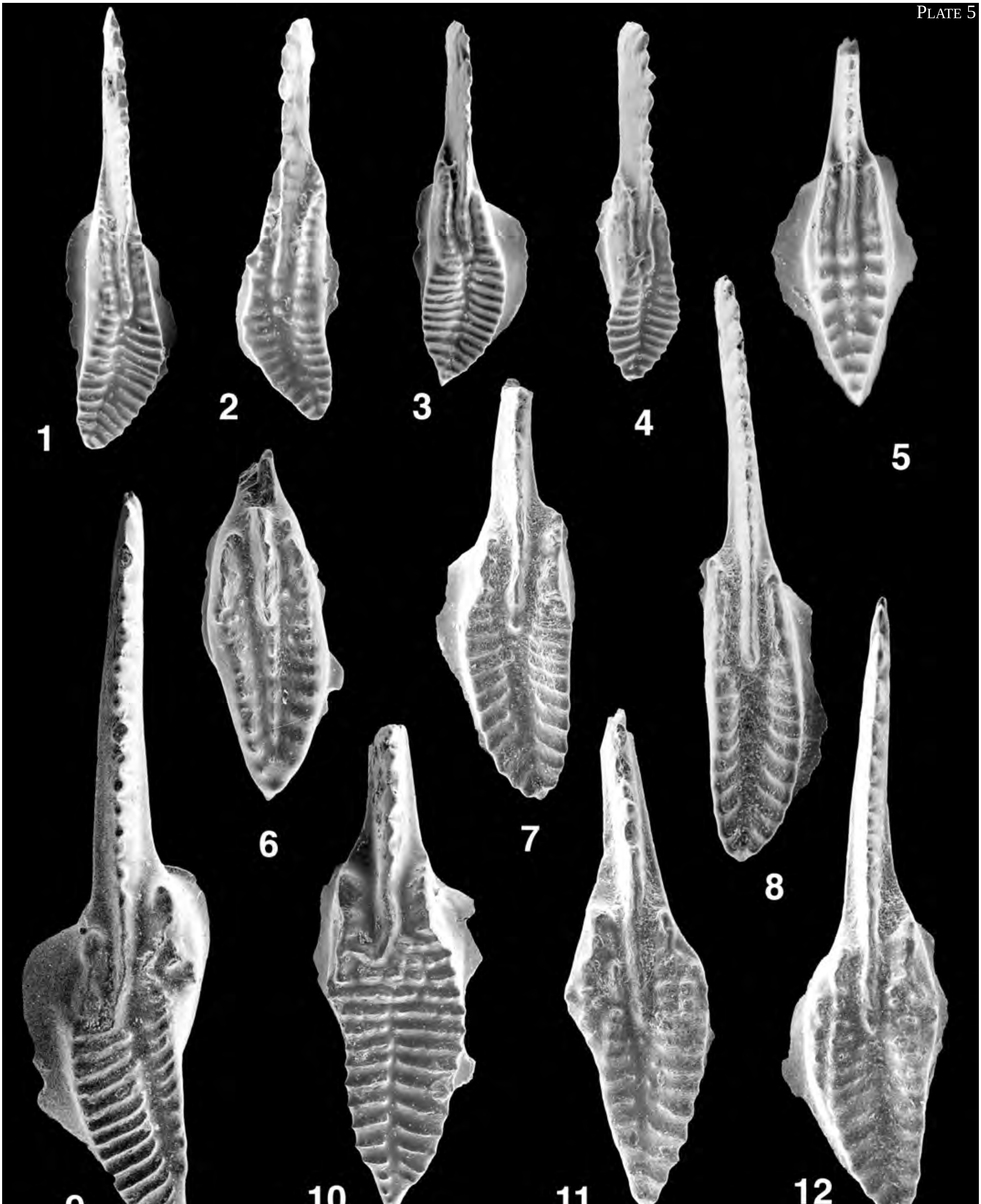
PLATE 5–All figures x 60; all are upper views of Pa elements. SUI – University of Iowa. *1, Streptognathodus wabaunsensis* Gunnell 1933. SUI 100598, Americus cyclothem, Kansas. *2, Streptognathodus brownvillensis* Ritter 1994. SUI 100599, Brownville cyclothem, Kansas. *3, Streptognathodus flexuosus* Chernykh & Ritter 1997. SUI 100600, Five Point cyclothem, Kansas. *4, Streptognathodus alius* Akhmetshina 1990. SUI 100601, Falls City cyclothem, Kansas. *5, Streptognathodus ruzhencevi* Kozur 1977. SUI 56353, Necessity Shale, Texas (equivalent to Lecompton cyclothem). *6, Streptognathodus firmus* Kozitskaya 1978. SUI 100591, South Bend cyclothem, Kansas. *7, 8, Streptognathodus pawhuskaensis* (Harris & Hollingsworth 1933); *7,* SUI 100592, Cass cyclothem, Kansas; *8,* SUI 100593, Cass cylothem, Kansas. *9, Idiognathodus simulator* (Ellison, 1941) *(sensu stricto)*. Holotype, UM 257-5, Oread cyclothem, Kansas. *10, Idiognathodus* aff. *simulator*. SUI 100594, Stanton cyclothem, Kansas. *11, 12, Streptognathodus zethus* Chernykh 1987*; 11,* SUI 100595, Cass cyclothem, Kansas; *12,* SUI 100596, Cass cyclothem, Kansas.

PLATE 5



the first appearance of the nominate species at the base of the Lecompton cyclothem, and its top is defined by the first appearance of *Streptognathodus brownvillensis* Ritter 1994 at the base of the Brownville cyclothem. Because Ritter (1995, p. 1148-1149, Fig. 10-11) illustrated only a "transition specimen between *S. pawhuskaensis* and *S. virgilicus"* from the sparse *S. virgilicus* fauna he reported from the Queen Hill Shale in the basal cyclothem (Lecompton) of the zone, we prefer to call this zone the *virgilicus (sensu lato)* Zone. Thus far, except for the Lecompton, mostly long-ranging species have been reported from this zonal interval. Species of *Idiognathodus (I. tersus* and *I. lobulatus)* and *Gondolella* (in any abundance) have their highest Midcontinent occurrence in the Lecompton (Ritter, 1995). The highest occurrence of *I. tersus* has been used to correlate the Queen Hill Shale of the Lecompton cyclothem with the Necessity Shale of north-central Texas by Boardman & Heckel (1989) and with the Bogota cyclothem of the Illinois basin by Heckel & Weibel (1991). We now have identified the first appearance of the Eurasian species *S. ruzhencevi* Kozur 1977 in the Queen Hill Shale in Kansas and Oklahoma. This is useful for global correlation because in Russia the *ruzhencevi* zone directly overlies the *simulator* zone (Ritter, 1995, p. 1149). We also have lowered the first appearance of *Streptognathodus holtensis* Ritter 1995 to the Hartford cyclothem, and possibly as low as the Cass Cyclothem. Because *S. virgilicus* has not been identified outside of Kansas, the value of this zone remains to be fully resolved.

Ritter (1995) proposed the *brownvillensis* Zone to include the interval between the first appearance of *Streptognathodus brownvillensis* at the base, and the first appearance of *S. wabaunsensis* Gunnell 1933 at the top. As Ritter (1995) and Chernykh & Ritter (1997) have used the zone, the base of the zone lies at the base of the Brownville cyclothem and includes strata up to the base of the Falls City cyclothem, where they reported the first appearance of *S. wabaunsensis*. Boardman (1999) reported that *S. bellus* Cherynkh & Ritter 1997 and the fusulinid *Leptotriticites* also appear in the Brownville cyclothem.

From the level of the Brownville cyclothem and higher, a rapid diversification in *Streptognathodus* produced a number of short-ranged species, many of which could be used to create a detailed zonation extending from the latest Pennsylvanian into the earliest Permian. However, the taxonomy and stratigraphic distribution of these *Streptognathodus* species are still unresolved (Chernykh & Ritter, 1997; Boardman *et al.*, 1998; Boardman, 1999). The *wabaunsensis* Zone of Ritter (1995) extends from the first appearance of *S. wabaunsensis* in the Falls City cyclothem up to the first appearance of *Streptognathodus* aff. *S. barskovi* Kozur 1976 in the Burr Limestone Member of the Grenola Formation of the Council Grove Group. Boardman (1999) indicated that *S. wabaunsensis* actually first appears five cyclothems (mostly minor ones) higher in the section, in the Americus Limestone at the base of the Foraker megacyclothem complex. In the Falls City cyclothem, Boardman (1999) reported the species *S. alius* Akhmetshina 1990, and in the Five Point cyclothem, he reported *S. flexuous* Chernykh & Ritter 1997, two taxa that are similar to *S. wabaunsensis.* We place the first appearance of *S. wabaunsensis* and thus the base of the *wabaunsensis* Zone at the base of the Americus cyclothem.

When Ritter (1995) proposed his zonation, the position of the base of the Permian had not been formally decided, but he indicated that the proposed level of the base of the Permian would lie within his *wabaunsensis* Zone in the Red Eagle Limestone. Subsequently, Chernykh *et al.* (1997) proposed the new species, *Streptognathodus isolatus*, for the taxon that appears at the base of the Permian in the Aidaralash Creek global stratotype, and Chernykh & Ritter (1997) erected a new zone for the base of the Permian, the *S. isolatus* Zone, based on the first appearance of this species. Because *S. isolatus* first appears in the Glenrock Limestone Member of the Red Eagle Limestone in Kansas (Chernykh & Ritter, 1997), we use it to identify the position of the base of the Permian in the Midcontinent region. It is significant for global correlation that Chernykh and Ritter (1997) also showed the succession of first appearance of *S. bellus, S. flexuosus*, and *S, wabaunsensis* below *S. isolatus* at Aidaralash, which is identical to the succession of first appearance in the Midcontinent of *S. bellus* in the Brownville cyclothem, *S. flexuosus* in the Five Point cyclothem, and *S. wabaunsensis* in the Americus cyclothem below *S. isolatus* at the base of the Permian in the Red Eagle cyclothem.

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MIDDLE TRIASSIC CONODONTS OF CALANDA (IBERIAN RANGE, SPAIN)

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Abstract

In the Calanda Anticline a stratigraphic section comprising Muschelkalk rocks has yielded *Pseudofurnishius murcianus* Van den Boogaard and *Sephardiella mungoensis* (Diebel), whose joint presence, in several levels, dates this Middle-Triassic section as Ladinian (Longobardian). Occurrences of conodonts match sedimentological and paleoecological interpretations. The jointly occurrence of *P. murcianus* and *S. mungoensis* happens in a more open marine platform environment. The sole presence of *P. murcianus* correspond with subtidal marine environment. Last occurrence of *S. mungoensis* coincides with the beginning of a markedly regression.

Key words: Biochronostratigraphy, conodonts, systematic paleontology, Muschelkalk, Ladinian, Triassic, Spain.

Resumen

Una sección estratigráfica levantada en los materiales del Muschelkalk del Anticlinal de Calanda (Teruel) contiene elementos de *Pseudofurnishius murcianus* Van den Boogaard y *Sephardiella mungoensis* (Diebel). La presencia conjunta de estos taxones de conodontos permite la atribución de estos materiales al Triásico Medio y más concretamente a la parte terminal del Ladininese (Longobardiense). Su presencia permite interpretaciones tanto sedimentológicas como paleoecológicas. Los niveles con *P. murcianus* y *S. mungoensis* se corresponden con un ambiente marino de plataforma abierta, la presencia en solitario de *P. murcianus* con un ambiente marino submareal. La última aparición en la sección de *S. mungoensis* coincide con el comienzo de una marcada regresión.

Palabras clave: Biocronoestratigrafía, conodontos, paleontología sistemática, Muschelkalk, Ladiniense, Triásico, España.

INTRODUCTION

Calanda is a small village located in the north of the Teruel province, which is situated in the northeast of Spain. The stratigraphic section studied herein belongs to the Muschelkalk sequences of the Calanda Anticline, which is composed of Early Triassic (Buntsandstein facies) to Paleogene rocks. This Anticline is sitted in the central part of the Aragonian branch of the Iberian Range, close to the joint of three major geological structures: Iberian Range to the south, Catalonian Coastal Ranges to the northeast and Ebro Domain to the northwest (Fig. 1). Its especial situation makes this Anticline an important place to understand the relationships between the Iberian Range and Catalonian Coastal Ranges during Middle Triassic.

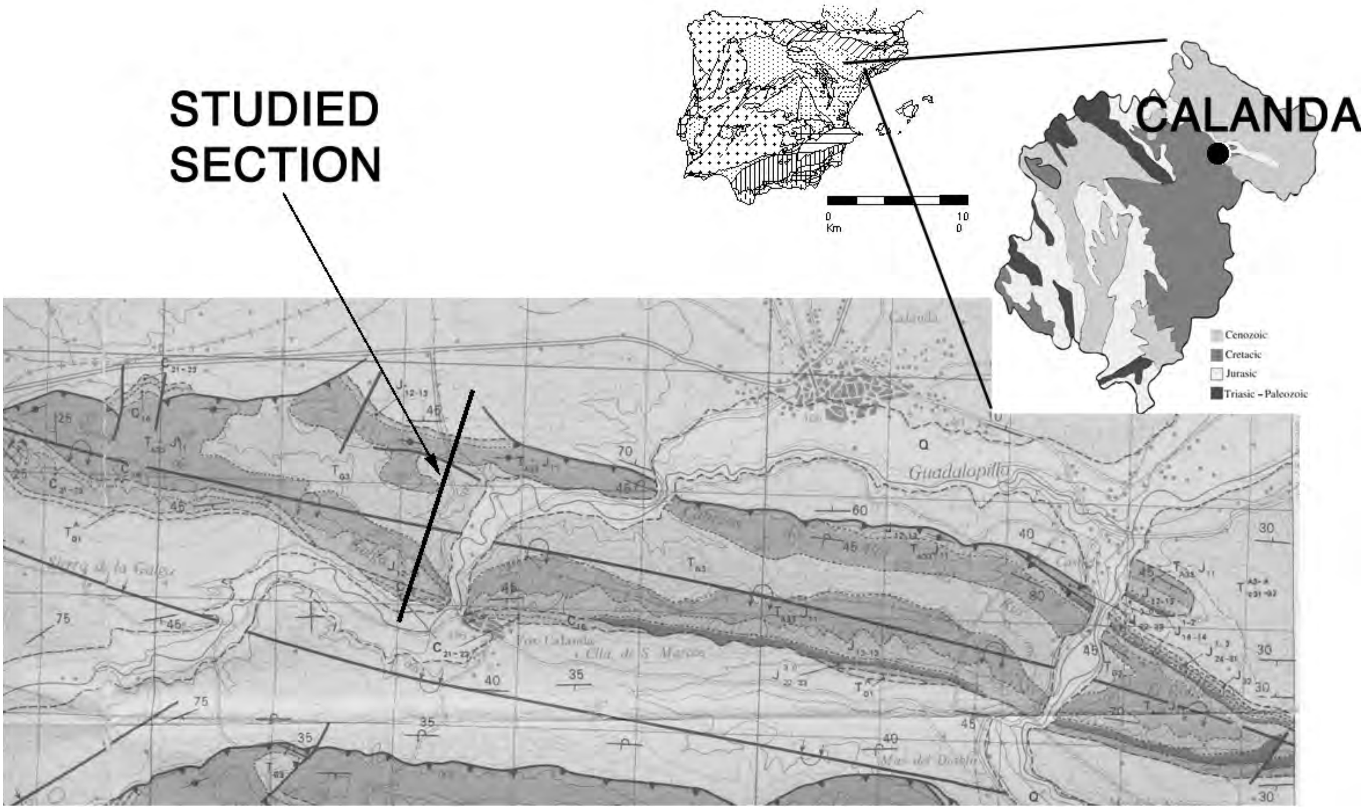

FIGURE 1–Geographical and geological setting of Calanda Anticline.

Geological and paleontological papers refered to the Muschelkalk of Calanda Anticline are scarce; among them, the works by Fallot & Bataller (1927) describing by first time the Muschelkalk facies from Calanda and Gálvez (1956) who noting the presence of Muschelkalk in Calanda stand out. After them, Anadón & Albert (1973) realized a comprehensive study on the Muschelkalk facies, describing the presence of typical Middle Triassic fossils such as *Protrachyceras* and *Daonella*. Márquez-Aliaga *et al.* (1987) reported the presence of Upper Ladinian ammonites, foraminifers, bivalves and conodonts, *Pseudofurnishius murcianus* Van den Boogaard and *Sephardiella mungoensis* (Diebel). Subsequently, the paleontological work of Márquez-Aliaga *et al.* (1994) confirmed the Upper Ladinian age in the sequence. Regarding conodonts from Calanda section, March (1986, 1991) studied the genera *Pseudofurnishius* and *Sephardiella* in a few levels.

The main goal of this paper is to realise a throughout study of the distribution of these conodont taxa and to study the different morphologies of Pa elements of *Pseudofurnishius* from Calanda.

METHODOLOGY

We have followed the techniques described by Plasencia *et al.* (1999), but using acetic instead of formic acid. The scanning electronic microscope used was ESEM-Phillips XL-30, hosted in the "SCSIE", of the University of Valencia. Four digital images were obtained for each Pa element: upper, lower, outer and inner views; this documentation intents to create a quick visual reference of the conodont morphological variability that could be used to compare elements of different morphologies or from several localities.

LITHO-, BIO- AND CRONOSTRATIGRAPHY

Muschelkalk of the Calanda Anticline was caracterized as a marine platform sedimentary environment, with different mareal subenvironments (Márquez-Aliaga *et al.*, 1994). The lower part represents the most marine part of the section, and changes from subtidal shoals to lagoons, sometimes with open sea influences

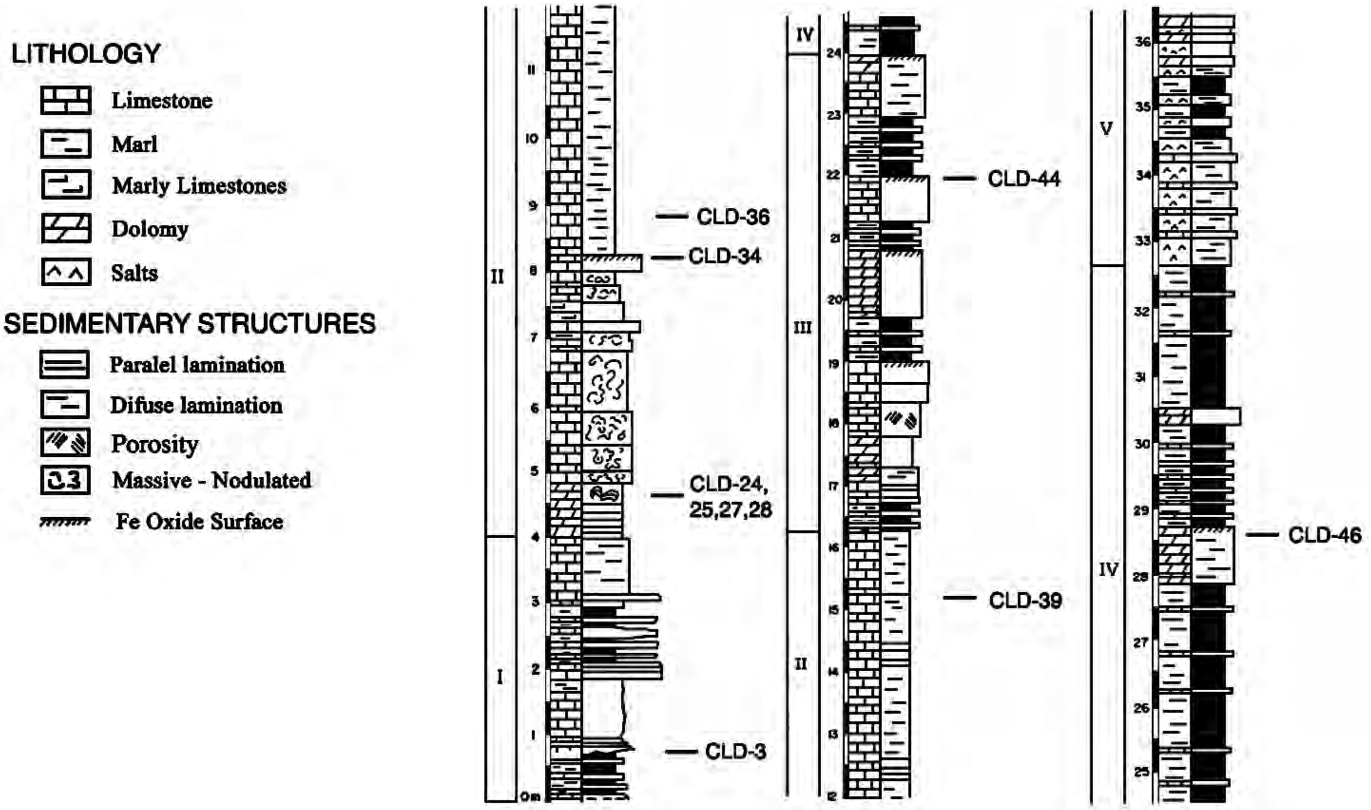

FIGURE 2–Stratigraphic section of Calanda.

and sometimes with bioconstructions. The upper part of the section is clearly regressive and changes from lagoonal environments to uppertidal ones in the uppermost part. The section (Fig. 2) was divided into 5 units:

Unit I

Represents the first 4 meters of the section, and consists of 1 m thick packs built up by mudstones interbedded with packstones and grainstones and a few marls. Macrofossils include echinoids, crinoids, brachiopods, gastropods, bivalves and bioclasts, and microfossils include foraminifera, echinoderms, ostracods and the conodonts *Pseudofurnishius murcianus* and *Sephardiella mungoensis,* which have been found by first time in sample CLD-3. The joint occurrence of the two taxa indicates a Middle-Upper Ladinian age.

Unit II

This unit has a 12.3 m thickness and contains different lithologies. It starts with a 1 m thick dolomite pack, followed by 2.35 m of limestones that are overlaid by a 8.2 m of mudstones. Macrofossil remains consist of bivalves and gastropods. Microfossils consist of foraminifera, echinodermata and conodonts. 1 m above the base of the unit there is a 35 cm thick reef bioconstruction where samples CLD-24, 25, 26 and 28 where obtained, all of them yielded *Pseudofurnishius murcianus*.

3.5 m above the bioconstruction, sample CLD-34 was taken. It contains *Pseudofurnishius murcianus* and *Sephardiella mungoensis*. Sample CLD-36 furnished *Pseudofurnishius murcianus* and *Sephardiella mungoensis;* and sample CLD-39, which is located near the top of the unit, has a “S” element of difficult assignation.

The joint presence of *Pseudofurnishius murcianus* and *Sephardiella mungoensis* date this unit as Middle-Upper Ladinian as well.

Unit III

This unit is 7.7 m thick and it is formed by four 1.35 m thick similar sequences that are composed of marls and mudstones in the lower third, and the upper two thirds are composed of mudstones and wackstones. Macrofossils include bivalves and foraminifera and conodonts represent microfossils. Sample CLD-44, 5.5 meters above the base of the unit, contains well-preserved specimens of *Pseudofurnishius murcianus* and *Sephardiella mungoensis*.

Unit IV

This unit is 8.7 m thick, and it is composed by green and gray marls interbedded with very thin levels of mudstones. Bivalves, and conodonts have been firstly found in sample CLD-46, which lies 5 m above the base of the unit, and yielded a broken and very bad preserved platform assigned to *Pseudofurnishius murcianus*.

Unit V

The last 3 m of the section are composed of levels of 35-40 cm of salts, with intercalations of 10-20 cm of limestones. In this unit the studied samples are barren. This unit represents the most regressive part of the section.

PALAEONTOLOGY

Most of the Calanda fossil record belongs to Molusca. Bivalves are common and diverse, with 16 species belonging to 10 genera. Gastropods are common, but very difficult to identify. Ammonites are few and bad preserved, but very important for biostratigraphy. The following species have been described: *Protrachyceras* cf. *hispanicum* (Mojsisovics), *Protrachyceras vilanovae* (Anadón & Albert), *Iberites* sp., *Nannites mambrini* (Schmidt), *Eotrachyceras* sp., and *"Protrachyceras"* sp. The microfossil record is mainly composed of conodonts, fish remains and foraminifera. Other groups, like briozoan, echinoderm and poriferan, are scarce.

Conodont specimens are generally well preserved and the number of elements is good regarding the standard Spanish Triassic record. Two species have been identified: *Pseudofurnishius murcianus* Van den Boogaard and *Sephardiella mungoensis* (Diebel), which are described below.

SYSTEMATICS

Family GONDOLELLIDAE Lindström, 1970
Subfamily NEOGONDOLELLINAE Hirsch, 1995
Genus *Pseudofurnishius* Van den Boogaard, 1966
Pseudofurnishius murcianus Van den Boogaard, 1966
(Pl. I Figs. 3-4; Pl. II, Figs. 1-4; Pl. III, Figs. 1-4;
Pl. IV, Figs. 2, 4)

1966 *Pseudofurnishius murcianus* n. sp. Van den Boogaard, Pl. I, Figs. 6-8; Pl. II, Figs. 1-5.
1973 *Pseudofurnishius murcianus* Van den Boogaard. Van den Boogaard & Simon, Pl. 1, Figs. b, d, e, f; Pl. 2, Figs. f, g, k, l.
1974 *Pseudofurnishius murcianus* Van den Boogaard. Eicher & Mosher, Pl. I, Figs. 1-14, 17, 19, 23, 33, 35-38, 41-44; Pl.II, 1-5.
1974 *Pseudofurnishius murcianus* Van den Boogaard. Hirsch & Gerry, Pl. 1, Figs. 2-3.
1978 *Pseudofurnishius murcianus* Van den Boogaard. Krivic & Stojanovic, Pl. 1, Figs. 1-4; Pl. 2, Fig. 1.
1978 *Pseudofurnishius murcianus* Van den Boogaard. Ramovs, Pl. 1, Figs. 1-2.
1981 *Pseudofurnishius murcianus* Van den Boogaard. Rakus, Pl. 1, Figs. 1-2.
1981 *Pseudofurnishius murcianus* Van den Boogaard. Nicora, Pl. 1, Figs. 1-3.
1985 *Pseudofurnishius murcianus* Van den Boogaard. Bandel & Waksmundzki, Pl. 4, Figs. 1-7; Pl. 5, Figs. 1-5; Pl. 6, Figs. 1-6.
1986 *Pseudofurnishius murcianus* Van den Boogaard. March, Pl. I, Figs. 4-5; Pl. VI, Figs. 1-4; Pl. X, Fig. 1; Pl. XI, Fig. 4; Pl. XII, Fig. 7; Pl. XIII, Fig. 4; Pl. XIV, Fig. 2, 9; Pl. XV, Fig. 6; Pl. XVI, Fig. 3, 7; Pl. XVII, Fig. 8; Pl. XVIII, Fig. 6; Pl. XIX, Figs. 2-3.

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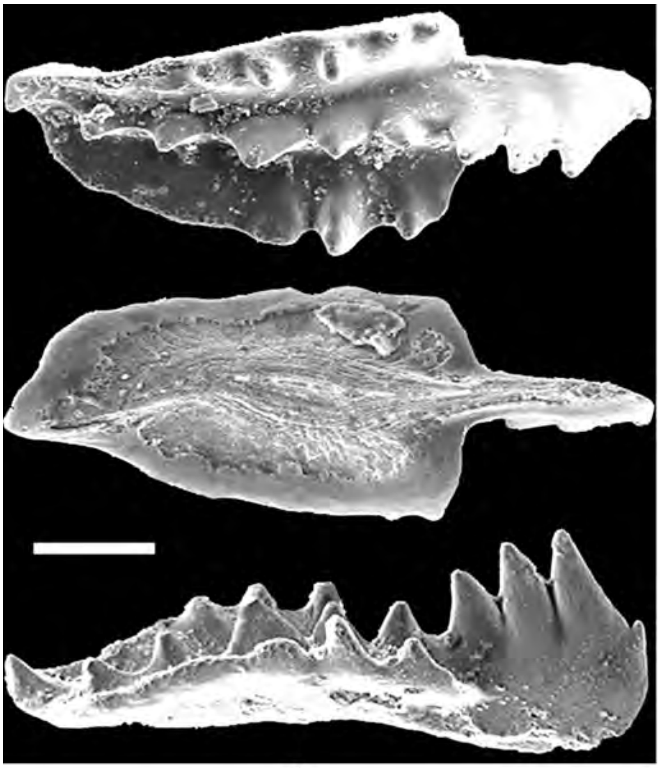
PLATE I–*1, Sephardiella mungoensis* (Diebel). Right Pa element, with upper, lower and inner views. CLD-3 01. Calanda, Teruel. Ladinian. *2, Sephardiella mungoensis* (Diebel). Left Pa element. with upper, lower and inner views. CLD-3 02. Calanda, Teruel. Ladinian. *3, Pseudofurnishius murcianus* Van den Boogaard. Left Pa element, with upper, lower and inner views. This element broke during manipulation and external view couldn't be photographed. CLD-3 03. Calanda, Teruel. Ladinian. *4, Pseudofurnishius murcianus* Van den Boogaard. Left Pa element, with upper, lower, inner and outer views. CLD-3 04. Calanda, Teruel. Ladinian. Scale bar: 100 µ.

Plate I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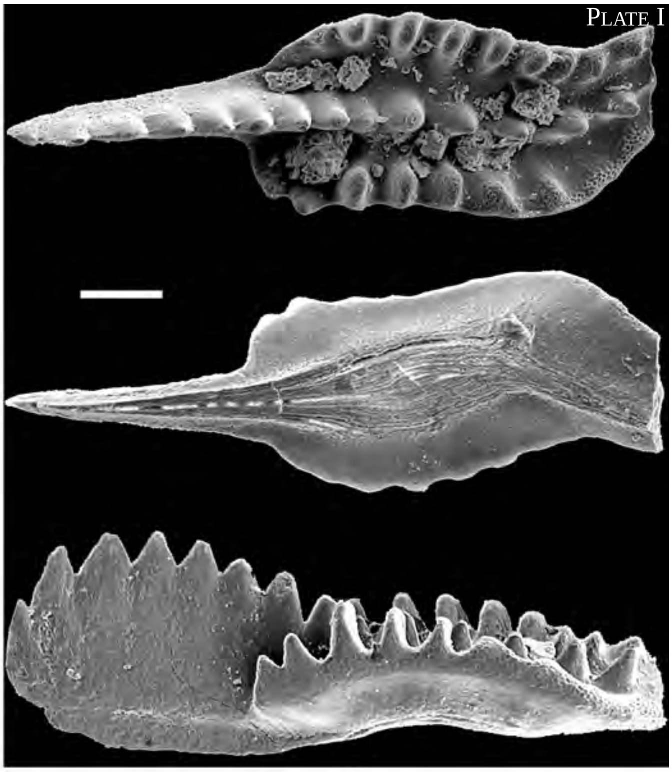
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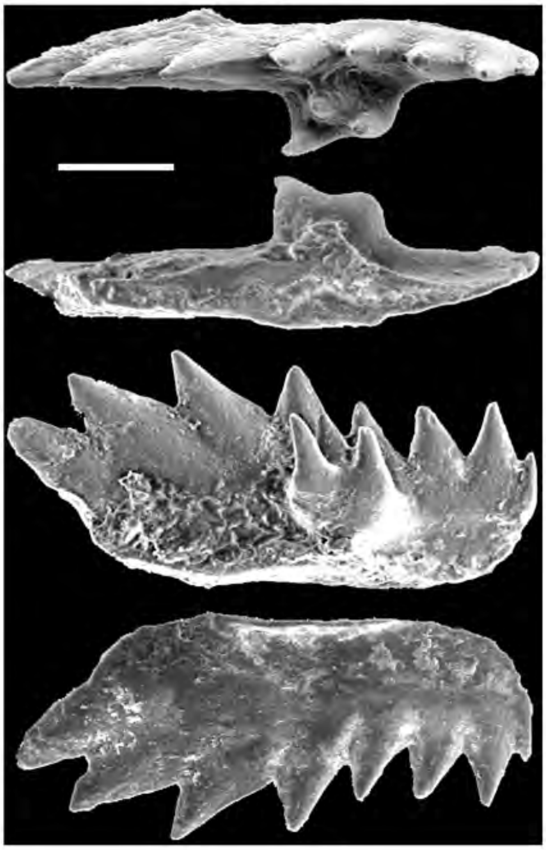
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1987 *Pseudofurnishius murcianus* Van den Boogaard. Márquez-Aliaga *et al.*, Pl. II, 2.
1989 *Pseudofurnishius murcianus murcianus* Van den Boogaard. Gullo & Kozur, Pl. 1, Fig. 10.
1990 *Pseudofurnishius murcianus murcianus* Van den Boogaard. Catalano *et al.*, Pl. 3, Figs. 3-4, 6.
1990 *Pseudofurnishius murcianus* Van den Boogaard. Saddedin, Pl. 4, 1-6; fig. 4, 1.
1991 *Pseudofurnishius murcianus* Van den Boogaard. March, Pl. III, Figs. 13-15.
1991 *Pseudofurnishius murcianus murcianus* Van den Boogaard. Gullo & Kozur, Pl. 5, Figs. 3-6.
1993 *Pseudofurnishius murcianus* Van den Boogaard. Kozur, Pl. I, Fig. 6.
1996 *Pseudofurnishius murcianus* Van den Boogaard. Márquez-Aliaga *et al.*, Pl. 1, Figs. 1-5.
1999 *Pseudofurnishius murcianus* Van den Boogaard. Plasencia *et al.*, Pl. I, Figs. 1-3, Pl. II, Figs. 1-4.
1999 *Pseudofurnishius murcianus* Van den Boogaard. Márquez-Aliaga *et al.*, Fig. 2.
2002 *Pseudofurnishius murcianus* Van den Boogaard. Plasencia *et al.*, Pl. I, Figs. 4-6, 9-11.

Description.–Blade laterally compressed, straight or slightly curved. In the inner side presents a small, denticulated and discreet platform that is variable in shape; this wide morphological variability mostly depends on the specimen stage of development: the juvenile elements present only one erected denticle; many adult elements show frequently three denticles: one central, near the blade and the other two diverging around 45º. In mature forms, platform denticles number increases up to 8, developing a complex distribution pattern. In the outer side, some specimens present 1 to 4 denticles, which rest on a weak ledge in the posterior half of the blade.

The blade is composed by a group of 4-5 to 16 aligned denticles, fused at their bases. Denticles of the anterior carina procline progressively from the cusp to the anterior margin, and the anteriormost denticle lies parallel to the base or forms an acute angle with it. Posterior carina is composed of up to 4 denticles erected or slightly inclined, similar in size except the posteriormost, which is germinal.

In inner view, the platform often lies at the anterior part of the posterior half, and some specimens show denticles behind the platform that can be connected to it. In outer view, surface is flat or with one up to four denticles. In all cases, a small ledge runing longitudinally along the blade is well developed. Denticles can grow from any point of this line, especially at the posterior part of the unit.

In lower view, a long, broad and asymmetrical basal cavity occupies most of the base, with a restricted, but open, lateral expansion that extends beneath the platform; the basal cavity continues anteriorly and posteriorly in acute or rounded grooves. Pit sits in the middle of the element, and, in some specimens, the basal cavity overgrows the outer side of the blade.

Remarks.–Several specimens would fall in *Pseudofurnishius murcianus praecursor* Gullo & Kozur (1991). For instance, the Pa element CLD 24 01 (Pl. II, Fig. 1) bears a well-developed outer denticle; which is very similar to the one figured by Mastandrea *et al*. (1997: Plate 2, Fig. 4) identified as *Pseudofurnishius murcianus praecursor*. But because *Pseudofurnishius murcianus* is a taxon with a great morphological variability and because outer denticles are more common in mature specimens (thus, related to ontogenic development), we are not sure about the reliality of that subspecies, and until a deeper study on this genus could be achieved, we prefer to tentatively include these specimens within the variability of *Pseudofurnishius murcianus*.

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PLATE II–*1, Pseudofurnishius murcianus* Van den Boogaard. Right Pa element, with upper, lower, inner and outer views. CLD-24 01. Calanda, Teruel. Ladinian. *2, Pseudofurnishius murcianus* Van den Boogaard. Left Pa element, with upper, lower, inner and outer views. CLD-24 02. Calanda, Teruel. Ladinian. *3, Pseudofurnishius murcianus* Van den Boogaard. Left Pa element, with upper, lower, inner and outer views. CLD-24 03. Calanda, Teruel. Ladinian. *4, Pseudofurnishius murcianus* Van den Boogaard. Right Pa element, with upper, lower, inner and outer views. CLD-24 04. Calanda, Teruel. Ladinian. Scale bar: 100 µ.

Plate II

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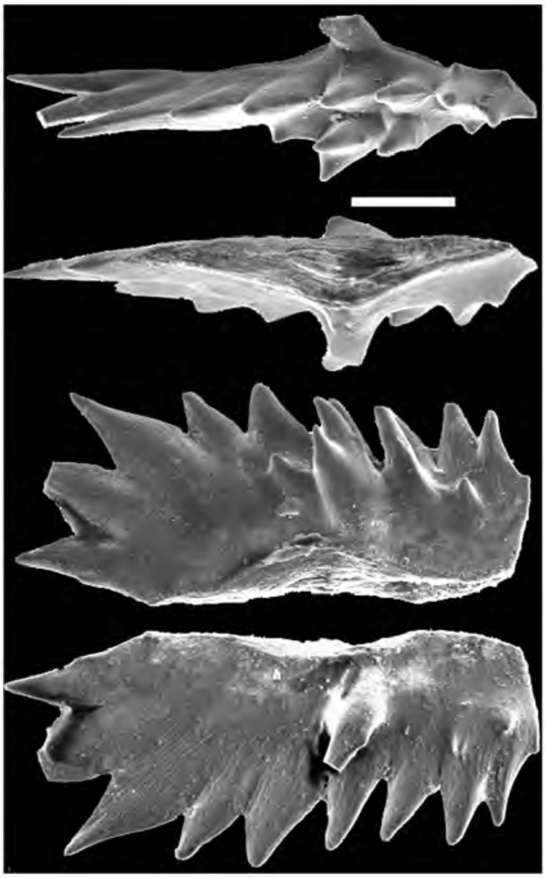

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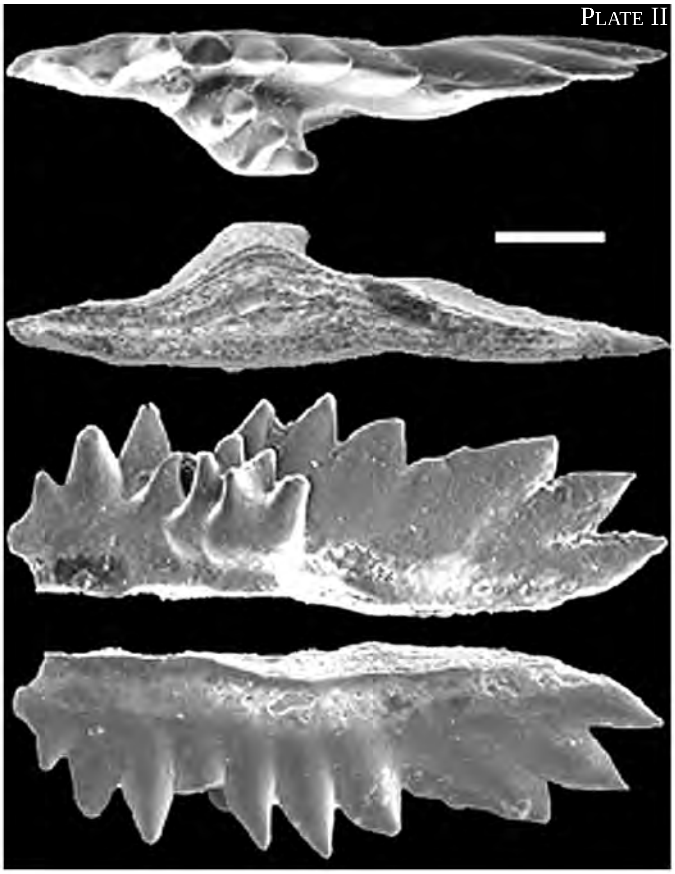

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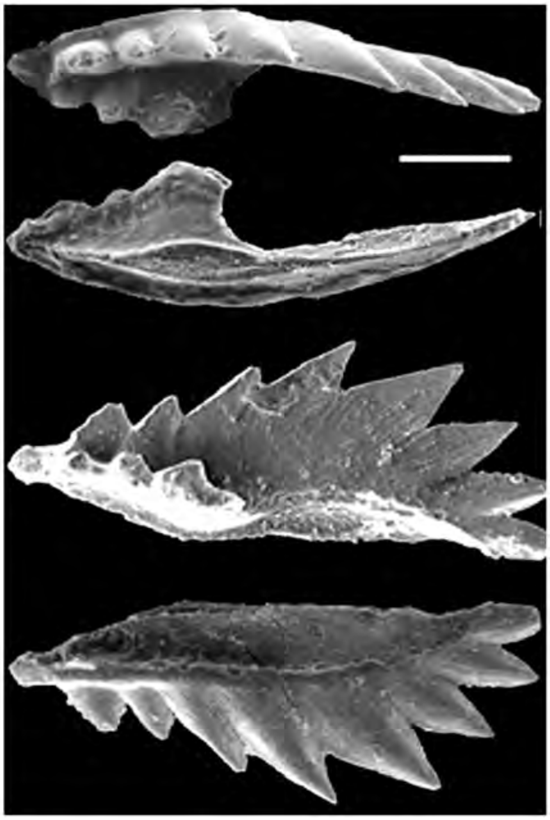

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Taxa	***P. murcianus***	***S. mungoensis***	***Non assigned elements***	
Samples	**Pa**	**Pa**	**M**	**S**
CLD-3	2	2	2	-
CLD-24	7	-	5	2
CLD-25	-	-	-	3
CLD-27	4	-	-	2
CLD-28	-	-	-	1
CLD-34	6	4	2	5
CLD-36	2	2	1	6
CLD-39	-	-	-	1
CLD-44	2	1	-	-
CLD-46	1	-	2	2
Total	**24**	**9**	**12**	**22**

TABLE 1–Number of conodont elements in the different studied samples.

Material.–24 Pa elements from the following localities: CLD-3 (2), CLD-24 (7), CLD-27 (4), CLD-34 (6), CLD-36 (2), CLD-44 (2), CLD-46 (1).

Occurences.–This species that ranges from Middle to Upper Fassanian to Lower Cordevolian (Middle part of Early Ladinian to Carnian) has been found in Spain (Iberian, Catalonian, Prebetic and Betic Ranges), Italy (Sicily, Southern Alps), Hungary, Jordan, Israel, Sinai and Palestine.

Genus *Sephardiella* March *et al.*, 1990
Sephardiella mungoensis (Diebel, 1956)
(Pl. I, Figs 1-2; Pl. IV, Figs. 1, 3)

1966 *Gondolella catalana* Hirsch. Hirsch, Pl. 1, Figs. 1-4.
1967 *Polygnathus mungoensis* Diebel. Pomesano Cherchi, Pl. 16, Figs. 5-17.
1973 *Tardogondolella mungoensis mungoensis* (Diebel). Van den Boogaard & Simon, Pl. I, Fig. c; Pl. II, Figs. a-b.
1974 *Epigondolella mungoensis* (Diebel). Eicher & Mosher, Pl. I, Figs. 29.
1974 *Epigondolella mungoensis* (Diebel). Hirsch & Gerry, Pl. 1, Fig. 1.
1976 *Carinella mungoensis* (Diebel). Budurov, Pl. II, Figs. 1-5.
1982 *Metapolygnathus mungoensis* (Diebel). Mietto, p. 2, Figs. 1-3.
1985 *Metapolygnathus mungoensis* (Diebel). Bandel & Waksmundzki, Pl. 1, Figs. 3-5; Pl. 2, Figs. 1-5.

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PLATE III–*1, Pseudofurnishius murcianus* Van den Boogaard. Right Pa element, with upper, lower, inner and outer views. CLD-27 01. Calanda, Teruel. Ladinian. *2, Pseudofurnishius murcianus* Van den Boogaard. Left Pa element, with upper, lower, inner and outer views. CLD-27 02. Calanda, Teruel. Ladinian. *3, Pseudofurnishius murcianus* Van den Boogaard. Right Pa element, with upper, lower, inner and outer views. CLD-27 03. Calanda, Teruel. Ladinian. *4, Pseudofurnishius murcianus* Van den Boogaard. Right Pa element, with upper, lower, inner and outer views. CLD-27 04. Calanda, Teruel. Ladinian. Scale bar: 100 µ.

PLATE III

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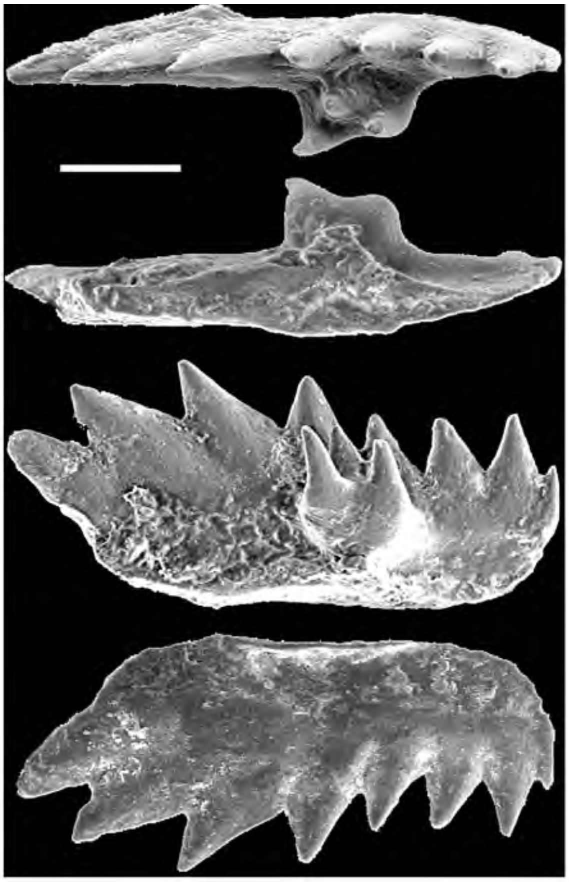

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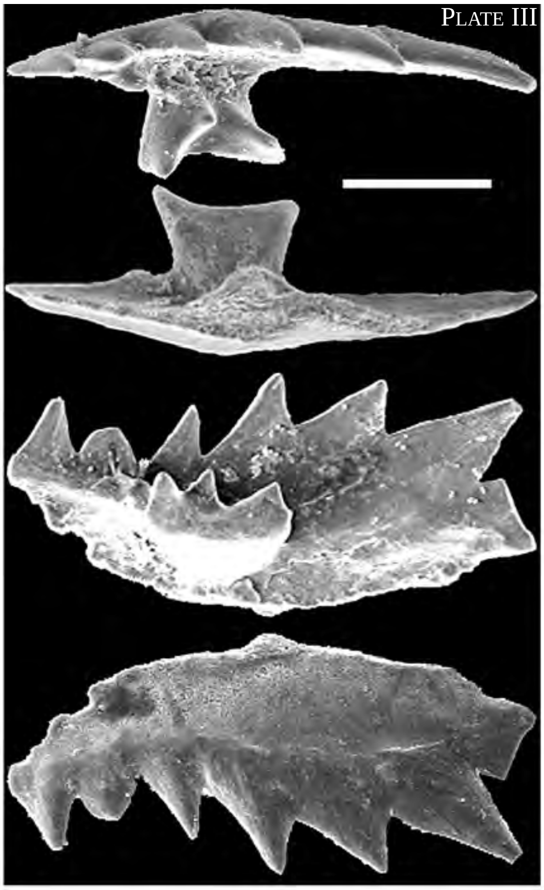

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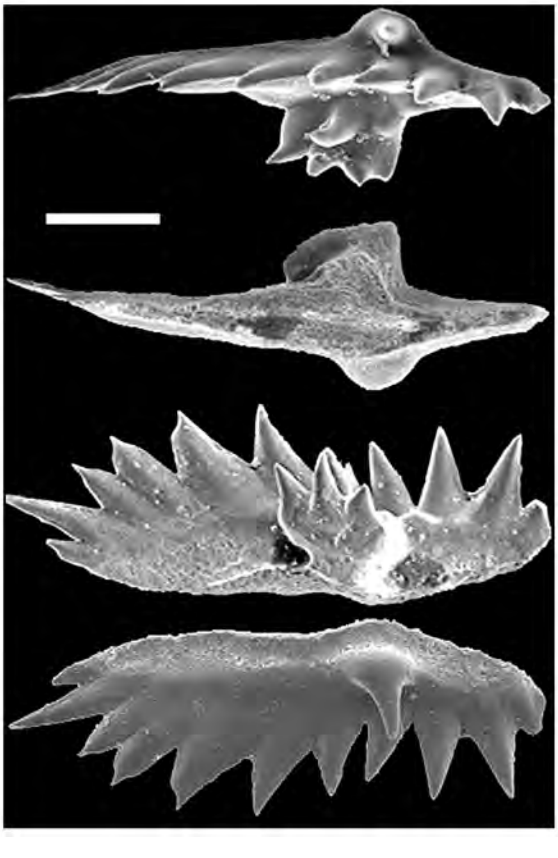

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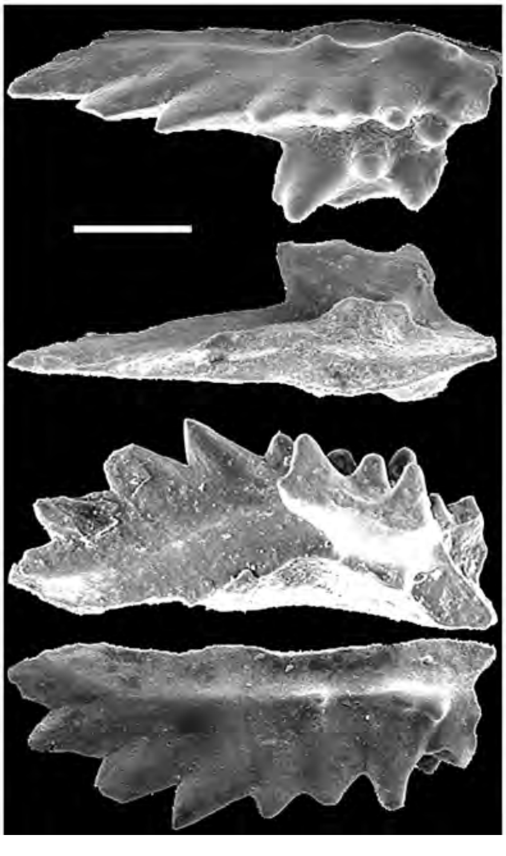


1986 *Metapolygnathus mungoensis* (Diebel). March, Pl. I, Figs. 1-2; Pl. II, Figs. 1-5; Pl. III, Figs. 1-5; Pl. IV, Figs. 1-5; Pl. V, Fig. 7; Pl. VII, Figs. 4, 6; Pl. VIII, Fig. 7; Pl. IX, Figs. 2, 6; Pl. X, Fig. 7; Pl. XI, Fig. 1; Pl. XII, Fig. 1, Pl. XIII, Fig. 2; Pl. XVIII, Fig. 4.
1987 *Metapolygnathus mungoensis* (Diebel). Márquez-Aliaga *et al.*, Pl. II, Fig. 1.
1990 *Budurovignathus mungoensis* (Diebel). Catalano *et al.*, Pl. 1, Fig. 8.
1990 *Sephardiella mungoensis* (Diebel). March *et al.*, Pl. 1, a-p.
1990 *Budurovignathus mungoensis* (Diebel). Saddedin, Pl. I, Fig. 5, 2-3.
1991 *Sephardiella mungoensis* (Diebel). March, Pl. II, Fig. 4-12.
1991 *Budurovignathus mungoensis* (Diebel). Gullo & Kozur, Pl. II, Figs. 6-7.
1994 *Budurovignathus mungoensis* (Diebel). Neri *et al.*, Pl. I, Fig. 1.
1995 *Budurovignathus mungoensis* (Diebel). Neri *et al.*, Pl. II, Figs. 7-9.
1997 *Budurovignathus mungoensis* (Diebel). Mastandrea *et al.*, Pl. I, Figs. 9.
1998 *Budurovignathus mungoensis* (Diebel). Mastandrea *et al.*, Pl. I, Fig. 5.
1999 *Sephardiella mungoensis* (Diebel). Plasencia *et al.*, Pl. III, Figs. 3-4.
1999 *Budurovignathus mungoensis* (Diebel). Meço, Pl. 1, Figs. 6, 9.
2000 *Budurovignathus mungoensis* (Diebel). Balini *et al.*, Pl. 2, Fig. 1.
2002 *Sephardiella mungoensis* (Diebel). Plasencia *et al.*, Pl. I, Figs. 2-3.

Description.–Long, narrow and asymmetric platform that occupies 2/3 of the element; blade with 9 to 15 denticles that it is divided into a free blade which forms a carina with 3-7 denticles and reaches up to the cusp, and a line of 6-8 insolated denticles on the platform behind the cusp. Platform with marginal nodes turns downwards in the posterior end. The inner posterior part usually bears more nodes than the outer one. These nodes and the surrounding surface present a crenulated pattern, which could be related to the inner structure of the element.

In lateral view, the free blade has 3-4 free and very high pointed denticles in juvenile specimens, that in mature ones seem to be lower, as they are fused up to 4/5 of their height. Usually, the anteriormost denticle is germinal and the rest are of similar size. Blade progressively reduces its height up to the apical denticle, where it integrates with the platform; posterior denticles are conical or triangular, and decrease in size to the posterior part; marginal nodes are also higher in the anterior part. Platform shows a convex profile; it starts at the lower margin, rises up to the middle of the blade, and lowers again.

Basal cavity is narrow and extends longitudinally, with long open grooves that pointed both anteriorly and posteriorly. Posterior groove deflects in the posterior part, following the shape of the platform. Pit is situated in the middle of the unit.

Remarks.–Our specimens fully coincide with the types. Our best preserved *Sephardiella* are those of Plate I, Figs. 1-2. Figure 2 presents the typical morphology of a well developed element, with a high free blade that contains several small and rounded denticles. On the contrary, Figure 1 is related to a juvenile form, it has bigger and pointed denticles, with a smaller free blade that contains less denticles.

Material.–9 Pa elements from the following localities: CLD-3 (2), CLD-34 (4), CLD-36 (2), CLD-44 (1).

Occurrences.–This taxon ranges from Longobardian to Cordevolian (Late Ladinian) and has been recorded from Spain (Iberian, Catalonian, Prebetic and Betic Ranges), Italy (Southern Alps, Sardinia), Jordan, Israel, Sinai and Palestine.

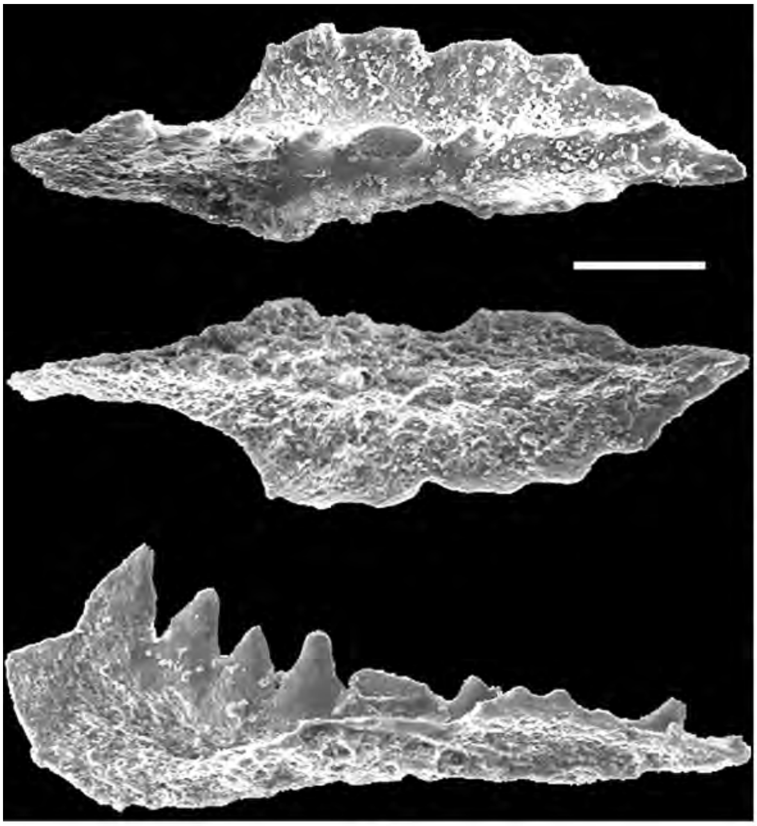
DISCUSSION OF RESULTS AND CONCLUSSION

The joint presence of *Pseudofurnishius murcianus* and *Sephardiella mungoensis* in some samples dates this section as Upper Ladinian. This agrees with data obtained from other groups, such as ammonites (with the presence of *Protrachyceras hermitei* and *P. hispanicum*, which characterize the *Hispanicum* Zone of Goy (1995).

→

PLATE IV–*1, Sephardiella mungoensis* (Diebel). Right? Pa element, with upper, lower and inner views. CLD-34 01. Calanda, Teruel. Ladinian. *2, Pseudofurnishius murcianus* Van den Boogaard Right Pa element, with upper, lower, inner and outer views. CLD-34 04. Calanda, Teruel. Ladinian. *3, Sephardiella mungoensis* (Diebel). Left? Pa element, with upper, lower and inner views. CLD-36 01. Calanda, Teruel. Ladinian. *4, Pseudofurnishius murcianus* Van den Boogaard. Right Pa element, with upper, lower, inner and outer views. CLD-36 02. Calanda, Teruel. Ladinian. Scale bar: 100 µ.

PLATE IV



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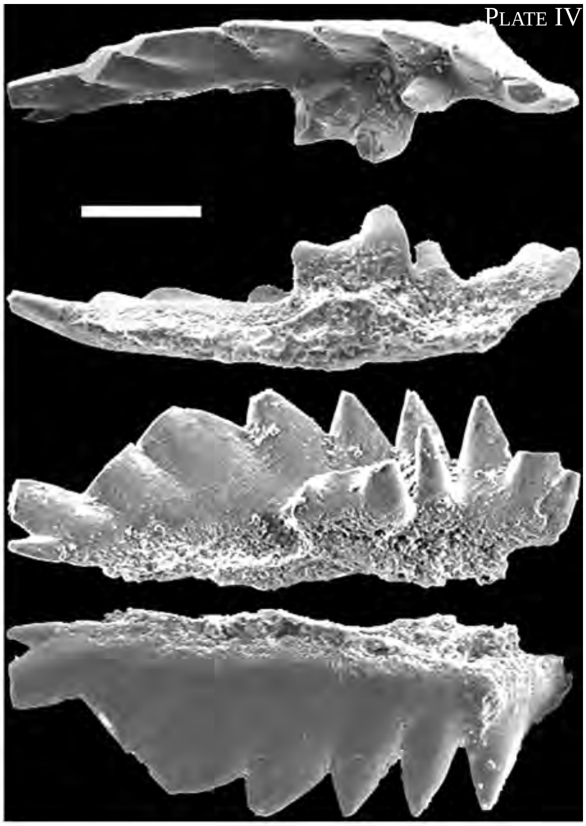

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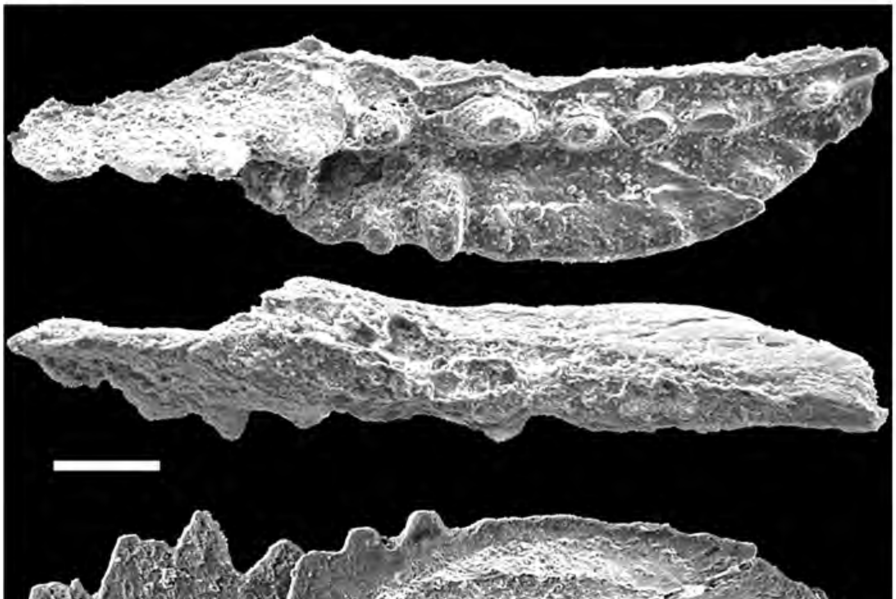

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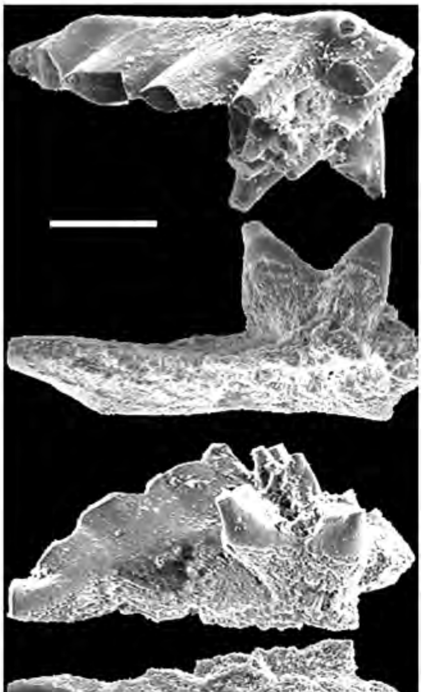

The preservation of the conodonts is quite good. The joint presence of *Pseudofurnishius murcianus* and *Sephardiella mungoensis* in some samples, which is not very common in the Iberian Range, makes possible some paleoecological interpretations: the presence of *Sephardiella mungoensis* is interpreted as an indicator of an open platform marine paleoecological environment, and this is confirmed by the joint occurrence of ammonites. On the contrary, *Pseudofurnishius murcianus*, which occurs together with bivalves such as *Pseudocorbula gregaria*, has been interpreted as an indicator of subtidal marine environment (Hirsch *et al.*, 1987). The joint occurrence of both species in some of our samples can be interpreted as a position close to the subtidal, but still in the inner platform. This interpretation agrees with the sedimentological data of the section. Units I and II testify the most transgressive interval and unit III indicates the beginning of a regression, coinciding with the last appearence of *Sephardiella mungoensis*.

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FASCIELLA AND *PRAEDONEZELLA* (MISSISSIPPIAN-EARLY PENNSYLVANIAN ALGAE): REVISION AND NEW SPECIES

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Abstract

Several species of the genera *Fasciella* and *Praedonezella* have been published by previous authors. Due to the particular kind of growth of these genera, their species are considered as in synonymy. However, *Praedonezella primitiva* n. sp., *Fasciella crustosa* n. sp. and *Fasciella scalaeformis* n. sp. are created from upper Viséan to Serpukhovian rocks in western Palaeo-Tethyan basins. Taxonomic characters which allow these species to be distinguished do not depend on the type of section, and are also reinforced by their particular stratigraphic record, independent of other species of *Fasciella* and *Praedonezella*.

Key words: Algae, taxonomy, biostratigraphy, Carboniferous, Mississippian, Pennsylvanian, Palaeotethys.

Resumen

Algunas especies pertenecientes a los generos *Fasciella* y *Praedonezella* han sido publicadas previamente. Estas especies se consideran como sinónimas y relacionadas debido a su particular tipo de crecimiento. Sin embargo, en el presente trabajo se describen *Praedonezella primitiva* n. sp., *Fasciella crustosa* n. sp. y *Fasciella scalaeformis* n. sp., que se han identificado en rocas del Viseense superior y Serpujoviense de diferentes cuencas del Paleotethys occidental. Los caracteres taxonómicos que permiten definir estas especies no dependen del tipo de sección. Además, estos tipos de crecimientos y caracteres taxonómicos aparecen en rangos estratigráficos determinados, lo que refuerza su validez como caracteres independientes dentro de los generos *Fasciella* y *Praedonezella*.

Palabras clave: Algas, taxonomía, biostratigrafía, Carbonífero, Mississippiense, Pennsylvaniense, Palaeotethys.

INTRODUCTION

The genus *Fasciella* Ivanova, 1973 is one of the most commonly documented alga in Viséan rocks (e. g. see synonymy list in Mamet, 2002), and several species have been proposed [e. g. *F. multiplex*, *F. ivanovae*, *F. kizilia*, *F. fusus* (as *Shartymophycus*)]. However, it exhibits a typical encrusting growth, secondary erected. As with most "encrusters" (such as algae, foraminifera), taxonomic characters cannot be based on the final morphology, because it ultimately depends on the substrate shape. Mamet (1991) considered the different species of *Fasciella* previously described in the literature as synonymous (synonymy accepted here). Thus, formerly described species can be only considered as morphotypes of a single species, *Fasciella kizilia* Ivanova, 1973 (which has priority). This species exhibits basically three morphotypes (Fig. 1), related to the presence of a substrate, and internal 'pivot' or the occurrence of ramifications. *Fasciella* is a common taxon in the late Viséan throughout western Europe, although its first occurrence is much older, close to base of the Viséan Stage (see stratigraphic range of *Fasciella* in Systematics section). In some basins though, its stratigraphic range appears to be more restricted, as in Ireland, where its first occurrence was used to defined the uppermost late Asbian (Jones & Somerville, 1996). Work in progress in Ireland and northern England allows us to recognise two new species of *Fasciella, F. crustosa* n. sp. and *F. scalaeformis* n. sp. The latter species seems to exhibit a more restricted geographic distribution and it is rare. However, the former species is very common, not only in Britain and Ireland, but in most western Tethyan basins (e. g. Spain, Poland), and mostly, for the latest Asbian-Brigantian interval. Taxonomic characters used to define these new species are the internal division of the 'pivot', the development of a laminar encrusting habit (determining the shape), and the number of stacked laminae. These particular species are especially interesting, because they show a similar morphology to other groups of problematic algae in the Mississippian (e. g. *Claracrustinae, Calcifoliaceae*, palaeoberesellids), which links one group to another. Detailed analysis of their phylogeny in still in progress, and will be dealt with in a forthcoming paper elsewhere.

Nevertheless, revised analyses of the Montagne Noire limestones (Vachard and Aretz, in press), allows us to recognise common specimens of *Praedonezella primitiva* n. sp. This new taxon can be distinguished from the typical and larger species in this genus, *P. cespeformis* Kulik, 1973, but also, it clarifies the stratigraphic range of both species. This new species is also common in Spain, and, as in France, also occurs in late Asbian rocks. Phylogenetically more interesting, is the occurrence of some unusual specimens which exhibit morphological convergences with the genus *Frustulata*.

SYSTEMATICS

Kingdom PLANTAE
Phylum, Class, Order INCERTAE SEDIS
Family CALCIFOLIACEAE G. Termier, Termier & Vachard, 1977
Tribe FASCIELLEAE Shuysky, 1999 nomen translat. pro Fasciellaceae
Genus *Fasciella* Ivanova, 1973

Type species.–*Fasciella kizilia* Ivanova, 1973.

Synonym.–*Shartymophycus* Kulik, 1973 (partim, probably a composite taxon corresponding to *Fasciella* and *Frustulata*).

Diagnosis.–Elongate, stacked, irregular to concentric encrusting laminae surrounding a cylindrical 'axis/substrate' [bioclasts, lithoclasts, "strezhnen" (in Russian) = pivot], or a pivot, microsparitized whitish or with divisions. Hyaline, yellowish, originally calcitic crusts separated by minute dark intervals.

Composition.–*Fasciella kizilia* (= *Shartymophycus fusus* Kulik, 1973 = *Fasciella ivanovae* Saltovskaya, 1984 = *F. ramosa* Saltovskaya, 1984; according to Mamet, 1991, 2002 = ? *Shartymophycus multiplex* Kulik, 1973; Fig. 1), *Fasciella crustosa* n. sp., *Fasciella scalaeformis* n. sp.

Remarks.–The typical specimens, representative of the type species, seem to encrust a short cylindrical microsparitic pivot (bacillar substratum, spicule, central siphon?), and other species are encrusting skeletal remains or lithoclasts (Gallagher, 1992, 1998; Skompski, 1996; Somerville, 1999; Cózar *et al.*, 2003), or exhibit internal divisions of the axis (Fig. 1).

Distribution.–Very rarely present in the late early Viséan 'V1b' from Belgium (thin-section Dinant 42/38; RC 5566, already cited by Vachard *et al.*, 1991b) and in the early middle Viséan 'V2a' from Montagne Noire (Vachard, 1974, 1977a, and erroneously 'V2b' in Vachard, 1977b); common in the late Viséan-Serpukhovian, and up to the Bashkirian. Cosmopolitan, but scarce in North America and Japan (Roux, 1985; Groves, 1986; Mamet, 1991, 2002; Groves *et al.*, 2003), e. g. Russian Platform, southern Urals, Donbass, southern Spain, southern France, Great Britain, Ireland, Belgium, the Netherlands, Germany, Poland, Austria, Greece; Algeria, Morocco, Afghanistan (Hindu Kush), Tadzhikistan, Japan, Idaho, Québec, Alaska. Documented in the early Moscovian from Algeria by Sebbar & Mamet (1999), but not illustrated. Rarely recorded in Turkey, *Fasciella* is present in the Balya-Maden area, samples B 34 to 37 (D. Vachard, unpublished data; location in Argyriadis *et al.*, 1976 and Vachard & Argyriadis, 2002).

Fasciella kizilia Ivanova, 1973
Pl. 1, Figs. 2, 4

1973 *Fasciella kizilia* Ivanova, p. 39, Pl. 21, Fig. 2, Pl. 27, Figs. 1-6, Pl. 34, Fig. 4.
2002 *Fasciella kizilia*, Mamet, p. 501-502, Pl. 7, Fig. 9 (with detailed synonymy).

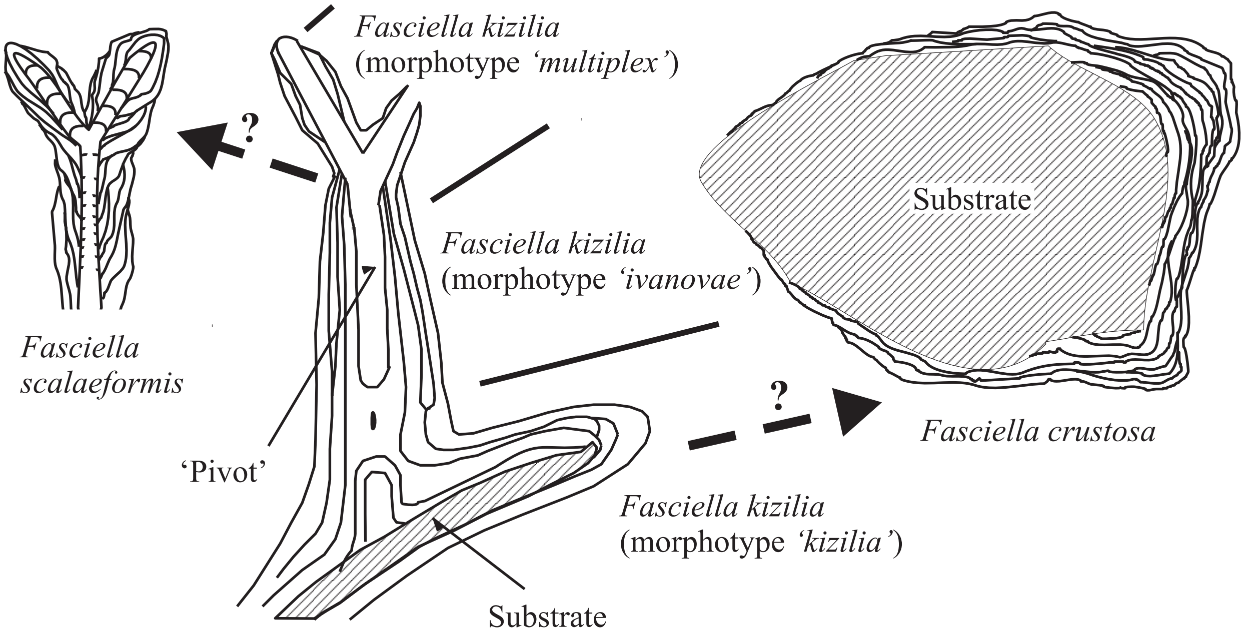


FIGURE 1–Comparative cartoon of the species of *Fasciella* and morphotypes of *F. kizilia*. Discontinuous lines are the inferred phylogeny between the species (not to scale).

The synonymy list of Mamet (2002) is almost complete but needs the following remarks: (a) the specimens of Crousilles *et al.* (1976), Bless *et al.* (1976), and Vachard *et al.* (1991a) are true *Fasciella*; (b) the specimen illustrated by Mamet & Roux (1975, Fig. 2) is questionable; (c) add to this list of *F. kizilia*:

? 1973 *Shartymophycus multiplex* Kulik, 1973, Pl. 3, Fig. 7.
1977 *Fasciella kizilia*, Mamet & Roux, p. 246, Pl. 14, Fig. 7.
? p. 1978 *Fasciella kizilia*, Mamet *et al.*, p. 364-365, Pl. 6, Fig. 5 (not Figs. 4, 6 = *F. crustosa* n. sp.).
1980 *Shartymophycus fusus* Kulik, Buchroithner *et al.*, p. 27-28, Pl. 3, Figs. 1, 8, Pl. 4, Fig. 9.
? 1984 *Fasciella* aff. *kizilia*, Igo *et al.*, text-fig. 3B, p. 457.
? 1984 *Fasciella kizilia*, Chuvashov *et al.*, p. 34, 62, 63, 66, 84 (no illustration).
? 1987 *Shartymophycus fusus* Kulik, Aizenverg *et al.*, p. 10, 12, 23, 26, 31, 34, 35, 36, 37, 42 (no illustration).
? 1988 *Fasciella kizilia*, Poletaev *et al.*, Tabl. 1, p. 68 (no illustration).
v. 1991b *Fasciella kizilia*, Vachard *et al.*, p. 253-254, Pl. 1, Fig. 11.
? 1992 *Fasciella kizilia*, Mamet, p. 192 (no illustration).
v. 1998 *Fasciella kizilia*, Delvolvé *et al.*, p. 366 (no illustration).
1999 *Fasciella kizilia*, Sebbar & Mamet, Pl. 1, Fig. 7.
2000 *Fasciella kizilia*, Sebbar, Pl. 2, Fig. 13.
v. 2002 *Fasciella* cf. *kizilia*, Krainer & Vachard, Pl. 3, Figs. 4, 10.
2003 *Fasciella kizilia*, Groves *et al.*, Fig. 6.6-8.

Diagnosis.–See Ivanova (1973), Mamet (2002), and here the generic diagnosis.

Remarks.–The most common morphotype in southern France *('F. ivanovae')* is centred upon white, microsparitized, rectilinear internal structure or 'pivot'. The typical morphotype *(F. kizilia)* is devoid of this pivot. Small and ramose specimens *('F. ramosa'* and *'F. multiplex')* can correspond to the extremities of thalli (Fig. 1).

Distribution.–As for the genus.

Fasciella crustosa n. sp.
Pl. 1, Figs. 1, 3, 5-8

? 1972 *Stacheoides* cf. *S. spissa*, Petryk & Mamet, p. 785, 787, Pl. 5, Fig. 8.

? p. 1975 *Fasciella kizilia*, Mamet & Roux, Pl. 14, Fig. 2 (or *Claracrusta)*.
? p. 1978 *Fasciella kizilia*, Mamet *et al.*, Pl. 6, Figs. 4, 6.
1983 "Composite sparry laminae", Bowman, Fig. 3 b?, c, d? (non Fig. 3 a, e-f = indeterminate species).
1985 *Fasciella kizilia*, Mamet & Pinard, Pl. 2, Figs. 13, 17.
p. 1990 *Fasciella kizilia*, Bogush *et al.*, Pl. 17, Fig. 4 (non Fig. 5-7 probably a consortium *Frustulata/Fasciella)*.
v. 1991a *Fasciella kizilia*, Vachard *et al.*, Pl. 1, Fig. 1.
1992 *Fasciella kizilia*, Gallagher, Pl. 9, Figs. 7, 9, Pl. 16, Fig. 2.
1996 *Fasciella* sp., Skompski, Pl. 14, Figs. 1-2.
1997 *Fasciella kizilia*, Gallagher & Somerville, Fig. 9z.
1998 *Fasciella*, Gallagher, Fig. 8.6.
1999 *Fasciella kizilia*, Sebbar & Mamet, Pl. 1, Fig. 7.
1999 *Fasciella*, Somerville, Figs. 3.28, 5.21.
2003 *Fasciella* sp., Cózar *et al.*, Pl. 4, Fig. 12, Pl. 5, Fig. 6.

Derivatio nominis.–*Crustosa*, i.e. with encrusting growth habit.

Locus typicus.–EG9B (Locality 15 in Gallagher, 1992), North Co. Cork, Southwest Republic of Ireland (ROI).

Stratum typicum.–Liscarrol Limestone Formation (early Brigantian = Lower Cf6δ = 'Lower V3c').

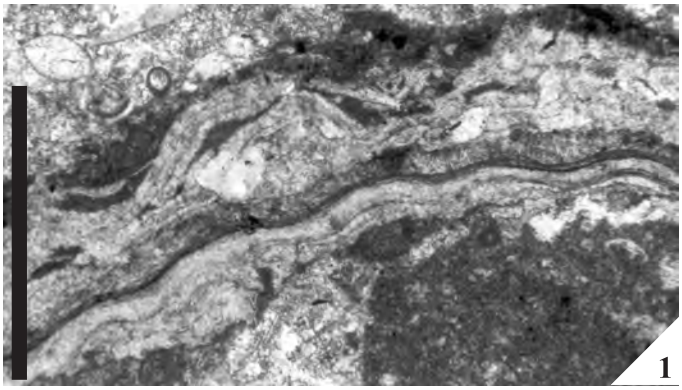
Holotype.–Pl. 1, Figs. 3 and 6 (thin-section UCD-EG9T).

Paratypes.–Tens of specimens in the locus typicus (location in Gallagher, 1992); – tens of specimens from the Slievenaglasha Formation (Burren succession, Co. Clare, southwestern R. Ireland, thin-sections GSI-781475, 781478, 781482, e. g. Pl. 1, Figs. 7-8; location in Gallagher, 1992); – tens of specimens from the Deer Park Formation at Deer Park South section (Kingscourt, Co. Meath, northeastern R. Ireland, thin-sections UCD-DPS132a-b, e. g. Pl. 1, Figs. 1 and 5; location in Somerville, 1999); at Cookstown quarry section (Co. Tyrone, Northern Ireland, thin-sections UCD-CKQ34, CKQ38; location in Somerville, 1999); and Poulmore Scarp section (Kingscourt, Co. Meath, northeastern R. Ireland, thin-section UCD-PH8; location in Somerville, 1999); – tens of specimens from the Clogrenan Formation (Co. Carlow and Kilkenny, southeastern R. Ireland, thin-sections PC-8/8/9, 8/8/42, 8/8/44, 20/8/13, 20/8/15, 20/8/40, 9/8/50; location in Cózar & Somerville in press); – tens of specimens from northern England, from the Gordale Limestone up to the Five Yard Limestone (thin-sections BGS-AH31, 43, 55, 57, 59, 60 (Allenheads boreholes), BGS-RH318', 465', 467', 588', 602', 1120' (Rookhope Borehole), BGS-BS4, 13, 15, 27, 36, 48, 52 (Back Scar Borehole), BGS-ARE1301, 1298, 1320, 1321, BGS-KR3101, 3079 (Janny Wood section; location in Strank, 1981, White, 1992, Cózar & Somerville, 2004); – hundreds of specimens from SW Spain (Sierra del Castillo and San Antonio-La Juliana units, Guadiato Area, thin-sections PC-636 to 637, 639, 641 to 642, 644, 653 to 655, 658, 661, 663, 665, 670 to 671 (San Antonio Section), PC-690, 704, 714, 758 (El Collado section), PC-1784, 1791, 1796 (Sierra del Castillo section), PC-1925 to 2002, PC-2116 to 2197, PC-SA/2-2 (San Antonio Section), PC-COR/6g, COR/11e, COR2/1 (La Cornuda section), PC-CAR/4 (La Caridad Section), PC-MIN/1d, MIN/8a, MIN/8c (Lavadero de la Mina section), PC-CCB (Cerro Cabello section); location in Cózar & Rodríguez, 1999a, 2004; Cózar *et al.*, 2003; Cózar & Vachard, in press).

→

PLATE 1–*1, 3, 5-8, Fasciella crustosa* n. sp. (scale bar = 0.5 mm). *1,* Brachiopod as substrate, micrite filling interlaminae spaces, note that laminae are discontinuous. Same horizons as in Fig. 5. *3,* Holotype. Intraclastic substrate, thin-section UCD-EG9T, locality EG9B, Liscarrol Limestone Formation, North Co. Cork, southern R. Ireland (location in Gallagher 1992), early Brigantian. *5,* Intraclastic substrate, c. 20 laminae are observed, micrite is sometimes filling the inter-lamina space. Thin-section UCD-DPS132b, Deer Park South section, Deer Park Formation, Kingscourt, Co. Meath, northeastern R. Ireland (location in Somerville 1999), early Brigantian. *6,* The holotype is observed in the lower right corner (as in Fig. 3). *7,* Same specimen as in Fig. 8. (encased area). *8,* Close-up view of the laminae of specimen in Fig. 7. Thin-section GSI-781369, Slievenaglasha Formation, the Burren section, locality 781, Co. Clare, southwestern R. Ireland (location in Gallagher 1992), Brigantian. *2, 4, Fasciella kizilia* Ivanova, 1973 (scale bar = 0.5 mm). *2,* Transverse section. Thin-section DV 293C, near Roquessels, Montagne Noire (location in Vachard 1977b), Brigantian. *4,* Transverse section with an included *Eotuberitina/Diplosphaerina* (compare with the specimen Pl. 27, Fig. 4 of Ivanova 1973 and Pl. 7, Fig. 4 of Herbig 1984). Thin-section DV 130A, Saint Rome (Cabrières), Montagne Noire (location in Vachard 1977b), Brigantian.

Plate 1



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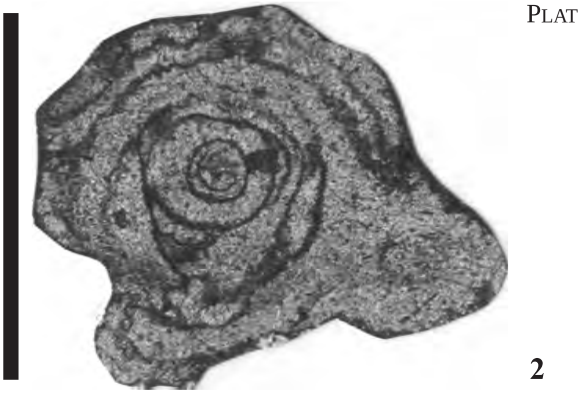

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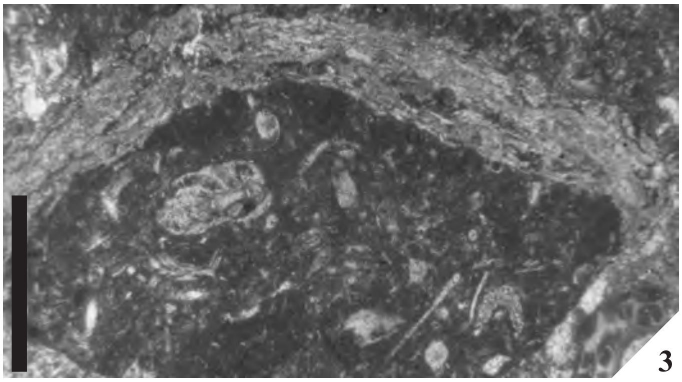

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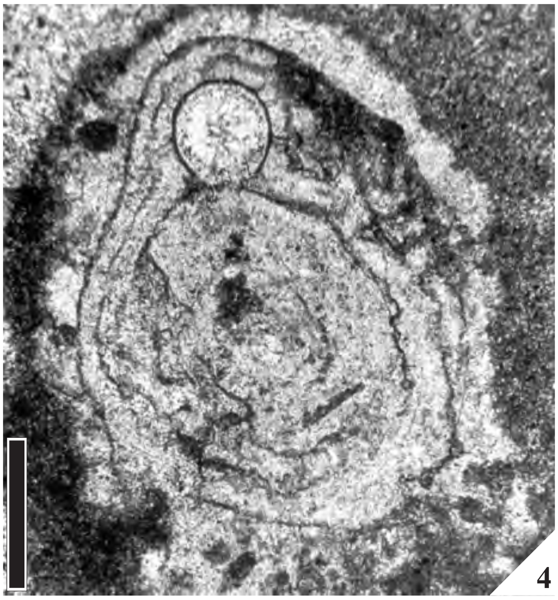

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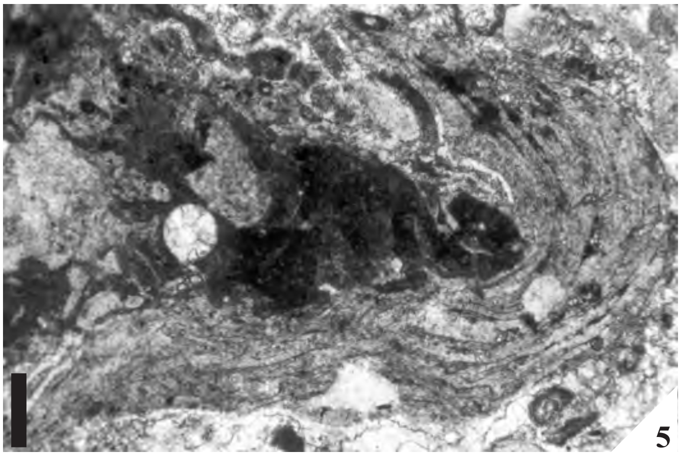

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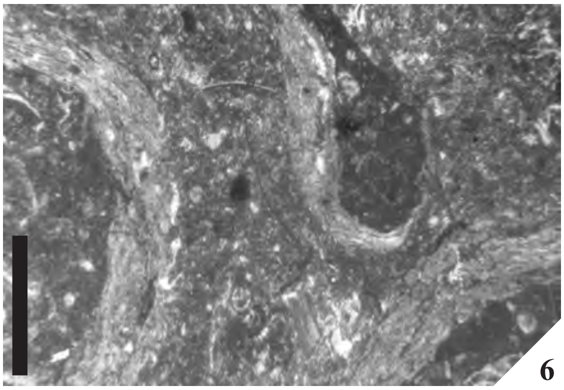

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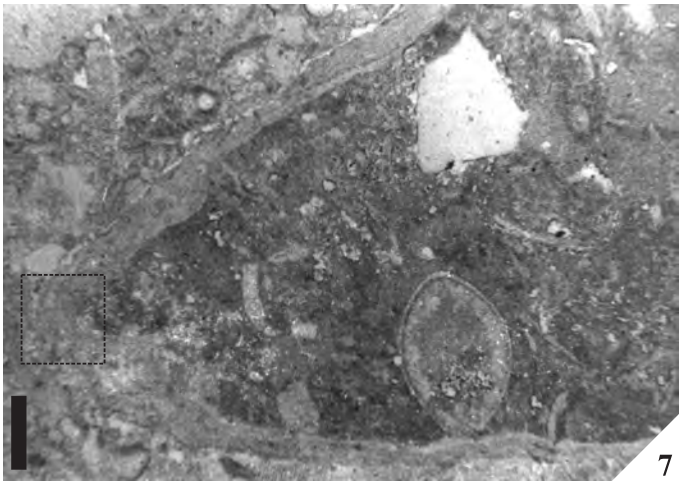

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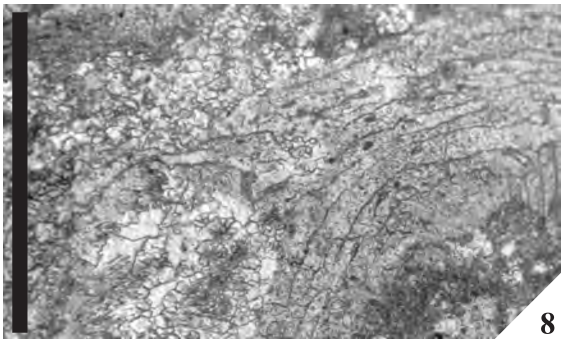

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Repository of the types.–Material from the Republic of Ireland and Northern Ireland are housed in the Department of Geology, University College Dublin (UCD), except the material from the Burren succession, which is stored in the Geological Survey of Ireland, Dublin (GSI). Material from England is housed in the British Geological Survey, Palaeontological Unit, Keyworth (BGS). Material from SW Spain is housed in the Department of Palaeontology, Universidad Complutense de Madrid (PC).

Diagnosis.–*Fasciella* with a rather wide substrate, and/or numerous laminae.

Description.–Long stacked laminae composed of yellowish calcite encrusting intraclasts, bioclasts and unknown or dissolved substrates. The number of laminae is variable, and specimens with only 4 or 5 are recorded, but also up to 20 stacked (Pl. 1, Fig. 5). Individual thickness of the laminae varies between 10 µm and 70 µm. The size of the specimens depends on the size of the substrate, thus, specimens from the Liscarrol Limestone Formation reach 2-2.5 mm, but up to 6 mm in the Slievenaglasha Formation (intraclastic substrates). Some specimens of dissolved substrate reach 2-3 mm, and specimens incrusting bioclasts (Pl. 1, Fig. 1) up to 3 mm. Some specimens from SW Spain, which are encrusters in oncoidal coatings, reach up to centimetric size (see Cózar *et al.*, 2003). Lateral extension of the individual lamina can cover entirely the substrate or not (Pl. 1, Fig. 6). Laminae can develop also as stacked lumps in some parts of the specimens (Pl. 1, Fig. 5), and they can be continuous for hundreds of microns, or discontinuous (Pl. 1, Fig. 1). Micrite accumulation is commonly observed in between laminae (Pl. 1, Figs. 1, 5), as well as encrustation by other organisms (cyanobacteria in the specimens from SW Spain). More compacted laminae show microstylolitized contacts, or with a slight concentration of iron oxides or micrite.

Comparison.–Differs from other species of *Fasciella* by the large size of the stacked laminae, emplacement of large substrate, the discontinuous development of the laminae, and the common interlamina space filled by micrite or encrusted by organisms.

Differs from *Claracrusta* (= *Berestovia*) by the massive calcitic mineralization of the laminae, in which, internal cavities or divisions are not observed.

Differs from the encrusting morphotype of *Calcifolium* (?) *punctatum* Maslov, by the absence of internal filaments (see Cózar & Vachard, in press). However, it is difficult to distinguish recrystallized encrusting *Calcifolium* (?) from *Fasciella crustosa*.

Remarks.–Specimens illustrated by Bowman (1983, Fig. 3b-d) from Bashkirian-Moscovian San Emiliano Fm. of NW Spain, were interpreted by Cózar *et al.* (2003) as of algal origin, such as recrystallized *Fasciella*, *Claracrusta* or even *Berestovia*. However, the higher quality of the illustration in Skompski (1996) allows the interpretation of his specimens as representatives of the genus *Fasciella*, and assigned to this new species.

Distribution.–Specimens from Ireland and England are recorded in Brigantian rocks, usually from a few metres above the base of this stage. However, one specimen is found in the latest Asbian (20 m below the boundary in Janny Wood; Cózar & Somerville, 2004). Specimens from SW Spain first occur in the late Asbian, but its acme is in the Pendleian. Other specimens occur in the late Asbian-Serpukhovian from the Urals, Poland, Morocco and Algeria, and questionably in Canada. The imprecise location of the samples of Bowman (1983), compared to the accurate biozonations of Ginkel & Villa (1996), does not allow to confirm the extension of *Fasciella* to the early Moscovian, as documented by Sebbar & Mamet (1999).

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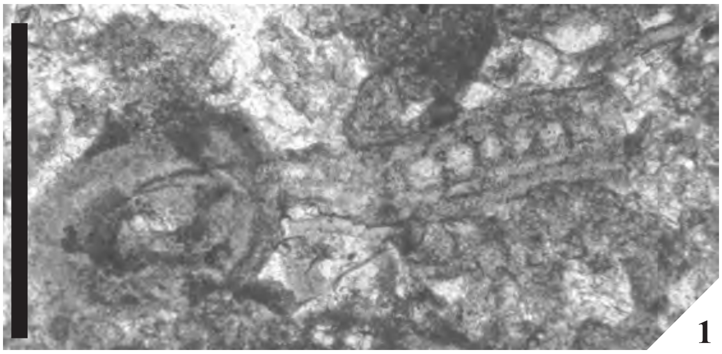
PLATE 2–*1-9*, *Fasciella scalaeformis* n. sp. *1-2*, *4-6*, *8* from the thin-section BGS-BS90, Gordale Limestone, Back Scar Borehole, northern England (location in White 1992), late Asbian; *3* and *7* from the thin-section BGS-ARE1323, Smiddy Limestone, Janny Wood section, northern England (location in Strank 1981), early Brigantian (scale bar = 0.5 mm, except for Fig. 6 = 0.25 mm). *1,* Holotype, tangential section. *2,* Longitudinal section. *3,* Longitudinal section, note the clear colour of the inner lamina. *4,* Longitudinal section. *5,* Longitudinal section, note that the internal divisions are marked in the upper part, and not in the lower part. *6,* Close-up view in longitudinal section. *7,* Longitudinal section, note the poor development of the internal divisions and the clear nature of the inner lamina. *8,* Longitudinal section of a ramification. *9,* Longitudinal section with the segmented internal part, as nucleus of an oolith. Thin-section DV431E, Mounio-Cabrières (location in Vachard 1977b). Montagne Noire. Brigantian. (x 100).

PLATE 2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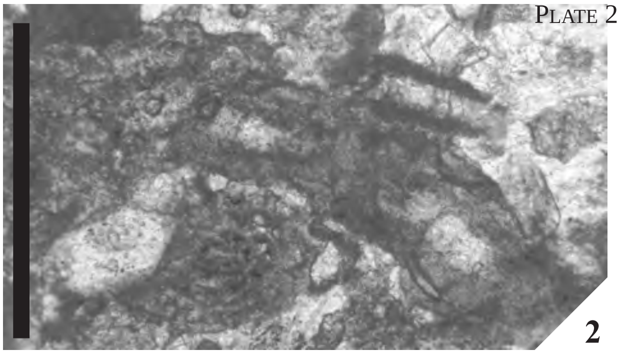
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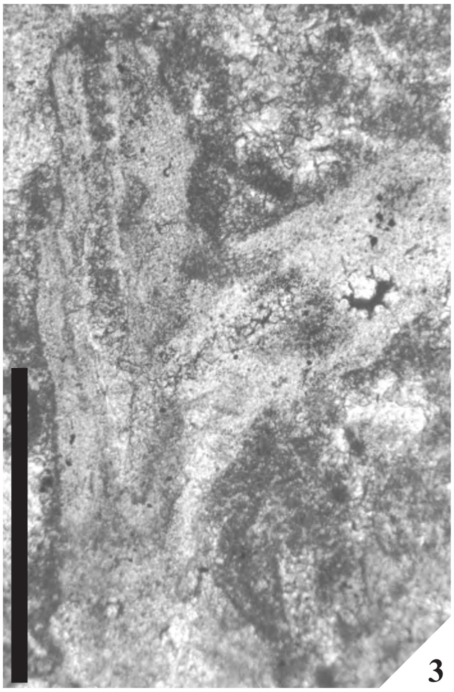
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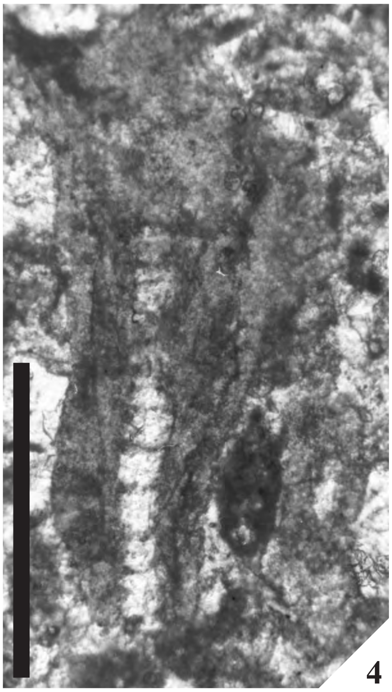
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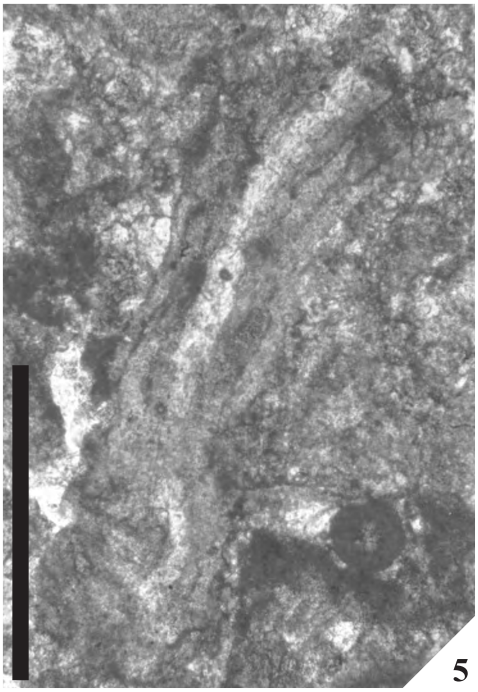
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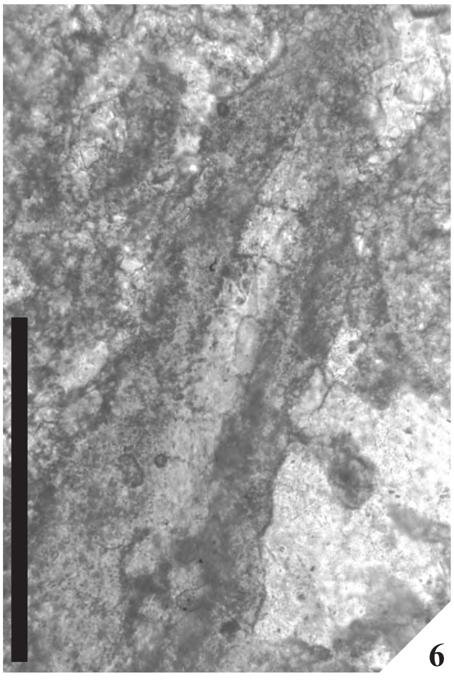
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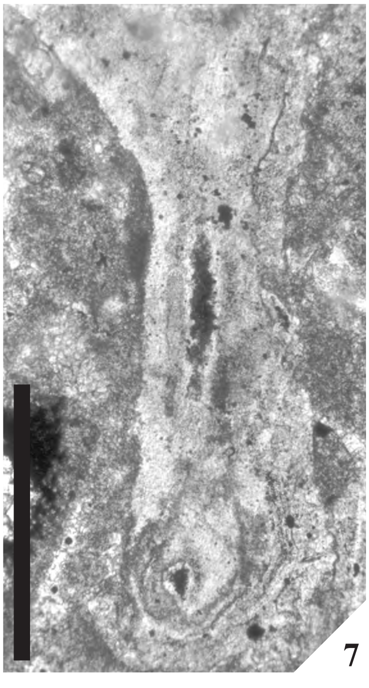
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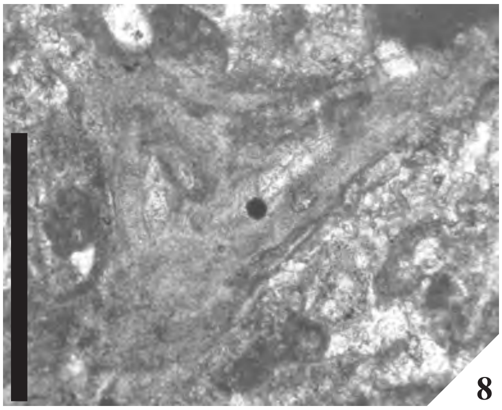
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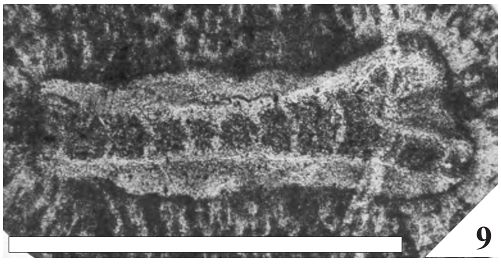
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Fasciella scalaeformis n. sp.

Pl. 2, Figs. 1-9

? v. 1991 *Kamaenella*? sp., Vachard & Tahiri, Pl. 3, Fig. 17.

Derivatio nominis.–*Scalaeformis*, ladderlike, due to the septate internal divisions of the axis.

Locus typicus.–Back Scar Borehole (Askrigg Block, northern England).

Stratum typicum.–Gordale Limestone (late Asbian = Cf6γ = 'V3bγ').

Holotype.–Pl. 2, Fig. 1 (thin-section BGS-BS90).

Paratypes.–Tens of specimens in the thin-section BGS-BS90 (e. g. Pl. 2, Figs. 2, 4-6, 8), and three specimens in the Smiddy Limestone (early Brigantian), at Janny Wood section (thin-section BGS-ARE1323).

Repository of the types.–British Geological Survey, Palaeontological Unit (Keyworth), Back Scar Borehole (BS90, location in White, 1992), and Janny Wood section (ARE1323, location in Strank, 1981).

Diagnosis.–*Fasciella* intensely branched and the axis shows a scalariform tube.

Description.–Small specimens with an inner pivot divided regularly, every 30-60 µm, the axis is filled by microspar. Tangential sections only show an inner microsparitized axis (as in '*Fasciella ivanovae*', Pl. 2, Fig. 9), longitudinal sections show the divided axis (e. g. Pl. 2, Figs. 1-6, 8). Externally, several laminae, typical of *Fasciella*, are observed, but not numerous. Some specimens exhibit a less marked division of the axis (Pl. 2, Figs. 5, 7), usually related to a closer position to the unbranched thallus. Thallus commonly branched. The growth of the lamina seems to be oblique to the axis in longitudinal section (Pl. 2, Fig. 4), and concentric in tangential section (Pl. 2, Fig. 9). Wall yellowish, calcite, in some specimens slightly clearer in the axis (Pl. 2, Figs. 1, 3, 7, 9).

Dimensions.–Maximum length of the preserved specimens: 500 µm-1200 µm. Maximum width of the preserved thalli (not ramified): 160 µm-300 µm. Maximum number of stacked laminae: 3-5. Inner diameter of the axis: 40 µm-55 µm.

Comparison.–Differs from *Kamaenella* by the outer laminae, more close and regular divisions of the axis, and the angle of ramification, which never shows 'nodes' as in *Kamaenella*. Differs from other species of *Fasciella* by the segmented axis.

Remarks.–The similar species *Shartymophycus multiplex* was previously attributed to *Kamaenella* (see Mamet & Roux, 1975; Roux, 1985) and *Kulikaella* (see Berchenko in Aizenverg *et al.*, 1983). The original diagnosis of *S. multiplex* does not indicate the presence of a segmented tube, and thus, it has been considered as the final ramified parts of *F. kizilia*. Therefore, *F. scalaeformis* is considered as an independent species due to the presence of the segmented tube.

The species could be interpreted as a *Kamaenella* encrusted by *Fasciella*, but paucity of the divisions, and the angle and type of bifurcations are distinct. Furthermore, horizons containing this species in northern England (BGS-BS90 and BGS-ARE1323), do not contain *Kamaenella* (Cózar & Somerville, 2004). Thus, the encrustation by *Fasciella* of an 'non-existant' taxon in these horizons seems to be unlikely.

The presence of this segmented axis is considered as a clue for further investigation of other algae in the Carboniferous, because it potentially links the Fascielleae, and thus the Calcifoliaceae, with the Moravamminale/Palaeosiphonocladales.

Distribution.–Late Asbian (Cf6γ) northern England in the Askrigg Block (Gordale Limestone, Back Scar Borehole); it also occurs in the early Brigantian (Cf6γ) in the Stainmore Trough (Smiddy Limestone, Janny Wood Section); Cózar & Somerville, 2004. Questionably in the Late Viséan ('V3bγ' = Cf6γ) from Morocco. Locally common in the 'V3bγ'-'V3c' (Cf6γ-Cf6δ subzones) from Montagne Noire (Vachard & Aretz, unpublished material from Castelsec, and collection D. Vachard: Mounio de Cabrières, thin-section DV413; Pl. 2, Fig. 9).

Genus *Praedonezella* Kulik, 1973

Type species.–*Praedonezella cespeformis* Kulik, 1973.

Synonyms.–Principally *Donezella* Maslov, 1929 (partim), and *Kulikaella* Berchenko, 1981 (partim). Other less cited synonyms are indicated in the list of the described species.

Diagnosis.–Initial part similar to *Fasciella*, encrusting a cylindrical support, followed by short, more or less tetrahedric, erect and segmented skeletal elements, regrouped in a nodular colony. Yellowish calcite wall with internal cavities diversely preserved, generally not communicated with the exterior.

Composition.–*Praedonezella primitiva* n. sp., *P. cespeformis* (= *P. catenuliformis* Ivanova in Bogush *et al.*, 1990). *P.* (?) sp.

The two following taxa belong to another genus: (1) *Praedonezella tenuissima* Berchenko, 1982 (type species of *Pseudodonezella*). The taxonomical problem is probably very complex, because

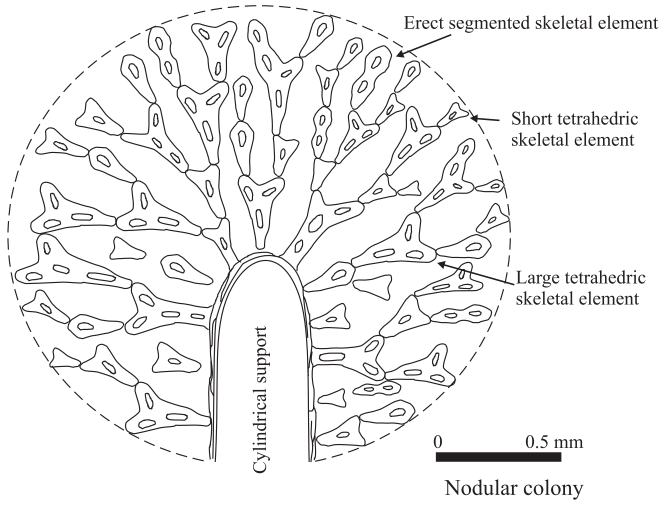

FIGURE 2–Reconstructive scheme of *Praedonezella* (according to Perret & Vachard, 1977, Fig. 23; modified).

Praedonezella tenuissima is morphologically, closely related to *Donezella delicata* Berchenko, 1982, the type species of *Masloviporidium* Groves & Mamet, 1985 (see discussions in Vachard & Maslo, 1996); (2) *Praedonezella* sp. (sensu Vachard, 1990, Pl. 2, Fig. 14; another fasciellacean genus).

Remarks.–After diagenesis, the colony appears as a ramified yellowish skeleton, with the open spaces filled by micrite, with shelter porosities (Pl. 3, Figs. 3, 9) or not (Pl. 3, Figs. 1-2). Despite this spongy aspect, *Praedonezella* was created as a Rhodophycean Gigartinales similar to *Donezella* (Kulik, 1973), and successively transferred to the Pharetronida Calcifoliida (Perret & Vachard, 1977), the Porifera Moravammida Donezellinae (H. Termier *et al.*, 1977; Vachard, 1991), the Chlorophyta Palaeosiphonocladales Beresellaceae Donezelleae (Chuvashov *et al.*, 1987), and the Siphonocladales Palaeoberesellaceae Donezelleae (Bogush *et al.*, 1990). *Praedonezella* is attributed here to the Fascielleae, because of the initial stage described and illustrated by Perret & Vachard (1977, text Fig. 22F, Pl. 8, Fig. 3, Pl. 9, Fig. 4-5) newly illustrated here: Pl. 3, Figs. 6, 10; Fig. 2). Due to the preservation of the delicate skeletal elements and the absence of cyanobacterial coatings (Pl. 3, Figs. 1-3, 11), the habit can be interpreted as infaunal or semi-infaunal (Vachard & Aretz, in press). In this case, the different thalli of the colony, or ramifications of the thallus constitute a bindstone and/or bafflestone.

Distribution.–Late Viséan (‘V3bγ’–‘V3c’, Vachard, 1974)-early Bashkirian: southern France (Montagne Noire, Pyrénées), northern Spain, southwestern Spain (P. Cózar, unpublished data), Greece (Evvia Island, De Bono *et al.*, 1998), southern Urals, Kazakhstan (Brenckle & Milkina, 2003), Afghanistan (Hindu Kush, thin-sections ML 4311, ML 4315 to 4319; D. Vachard, unpublished data), Japan (Mamet, 2002), Austria (collection Amler, slide PR 125-1), Donbass (Aizenverg *et al.*, 1987). Unpublished data in the Pendleian of Balya Maden area (western Turkey, samples B 34 to B 37, located in Argyriadis *et al.*, 1976 and Vachard & Argyriadis, 2002). Questionably in the late Serpukhovian of Algeria (Sebbar, 2000, re-interpreted). In Ireland, its presence was suggested by Vachard *et al.* (1989), due to an erroneous interpretation of *Shartymophycus fusus* of Mamet & Roux, 1975 (Pl. 11, Fig. 2) (see above *Fasciella crustosa*). In fact, *Praedonezella* seems to be absent in Ireland and northern England (P. Cózar & I. D. Somerville, unpublished data).

Praedonezella primitiva n. sp.
Pl. 3, Figs. 4-5

v. 1974 *Hikorocodium* (?) sp., Vachard, p. 186, Pl. 6, Fig. 1.
1981 Donezellid bafflestone, Mamet & Martínez, Pl. 1, Fig. 5.

Derivatio nominis.–*Primitivus*, primitive, i.e. suggesting the first appeared species.

Locus typicus.–Tourière (Montagne Noire, southern France).

Stratum typicum.–‘calcaires à *Productus*’ (‘V3c’ = Cf6δ Brigantian).

Holotype.–Pl. 3, Fig. 4 (thin-section DV 341).

Paratypes.–Pl. 3, Fig. 5 (six other sections in the locus typicus, two sections at Les Pascales DV 601, five sections in Castelsec, collection M. Aretz: 10, 10-6, 10-7, 10-10, 11-4).

Repository of the types.–University of Lille, Laboratoire LP3.

Diagnosis.–Small colonies with small and closely spaced skeletal elements.

Description.–Thallus is nodular, hemisphaerical or rounded elongate. Skeletal elements are filiform, tetrahedric, smooth and inflated at the extremities, densely packed, randomly disposed, and rounded in transverse section. No internal cavities are visible. The open spaces of the colonies are occupied by micrite.

Dimensions.–General dimensions of thallus = 1.60-3.00 mm. Length of skeletal elements = 0.10-0.15 mm. Width of skeletal elements = 0.015-0.020 mm.

Comparisons.–Differs from *Praedonezella cespeformis* by the small skeletal elements and the narrow cavities. The species can be confused with recrystallized *Kamaenella*, from which it differs by the size of the skeletal elements and its type of bifurcation.

Distribution.–The outcrops containing the material from southern Spain were assigned to a 'zone 13 or younger' (Mamet & Martínez, 1981); i. e. Holkerian or Asbian. After the re-examination of Cózar & Rodríguez (1999b, P. Cózar, unpublished data), these outcrops were attributed to zones 14 to 16 (Holkerian to Brigantian). Material illustrated by Mamet & Martínez (1981) seems to be Asbian in age.

Brigantian (and not 'V3bγ' = late Asbian, as indicated by Vachard, 1974)-early Serpukhovian (Vachard & Aretz, in press) from Montagne Noire (southern France). Late Asbian-early Brigantian from the Guadiato Basin in southern Spain (P. Cózar, unpublished data). Brigantian or Pendleian from Austria (collection Amler, thin-sections PR 116-1, 116-4, 116-6, 125-1).

Praedonezella ex gr. *cespeformis* Kulik, 1973
Pl. 3, Figs. 1-3

1973 *Praedonezella cespeformis* Kulik, p. 47-48, Pl. 3, Figs. 5-6.
2002 '*Praedonezella*' *cespeformis*, Mamet p. 496, Pl. 1, Fig. 3 (erroneously indicated Fig. 4 by inversion with *Paramitcheldeania nakamurae* Mamet; with detailed synonymy).

The synonymy list of Mamet (2002) needs three comments: (a) *Praedonezella* is a perfectly valid genus and not a synonym of *Donezella*, as indicated by Mamet (1991, 1992); (b) all the specimens of Perret & Vachard (1977) belong to the same species; (c) the specimens attributed to *P. cespeformis* by Pajic & Filipovic (1995) belong probably to *Donezella*, whereas those of *Praedonezella* sp. of the same authors (Pl. 45, Fig. 1) belong possibly to *Frustulata*.

To Mamet's synonymy list, add:

v. 1977a *Praedonezella cespeformis* - Vachard, Tabl. 1 (no illustration).
? p. 1979 *Donezella*, Bowman, Fig. 6a (non Fig. 6b: true *Donezella/Goksuella*).
? 1984 *Donezella lutuginii* Maslov, Racz, Fig. 3d.
? 1984 *Praedonezella cespeformis*, Chuvashov *et al.*, p. 34, 62, 63, 64, 66, 76, 84 (no illustration).
? 1987 *Praedonezella cespeformis*, Aizenverg *et al.*, p. 18, 48 (no illustration).
v. 1989 *Praedonezella carbonica* (Racz), Vachard *et al.*, p. 706-707, Pl. 1, Fig. 10, Pl. 4, Figs. 5, 7-8.
? 1990 *Praedonezella catenuliformis* Ivanova in Bogush *et al.*, p. 84, Pl. 5, Figs. 8-9.
? 1990 *Kulikaella partita* Ivanova in Bogush *et al.*, p. 121-122, Pl. 18, Figs. 5-7.
v. 1991 *Praedonezella carbonica*, Vachard & Beckary, p. 324, Pl. 2, Fig. 6.
v. 1991b *Praedonezella cespeformis*, Vachard *et al.*, Pl. 1, Fig. 13.
? 1992 *Kulikaella partita* Ivanova, Ivanova & Bogush, Pl. 49, Figs. 10-11.

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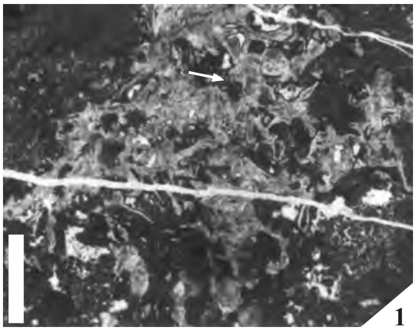
PLATE 3–*1-3*, *Praedonezella* ex gr. *cespeformis* Kulik, 1973 (collection Aretz, Cologne) (scale bar = 2 mm). *1,* Longitudinal section. Some skeletal elements with dark and clear zones (white arrow). La Serre (Montagne Noire). Early Serpukhovian. Thin-section GIK 1809. *2,* Compared with Fig. 3, the skeleton is more compact and thicker. La Serre (Montagne Noire). Early Serpukhovian. Thin-section GIK 1809. *3,* Longitudinal section, with shelter porosities. La Serre (Montagne Noire). Early Serpukhovian. Thin-section GIK 1818. *4-5*, *Praedonezella primitiva* n. sp. (scale bar = 0.5 mm). *4,* Holotype. Transverse section.Tourière, Montagne Noire (location in Vachard 1977b). Brigantian. Thin-section DV 341A. *5,* Paratype. Longitudinal section. Les Pascales, Montagne Noire (location in Vachard 1977b). Brigantian. Thin-section DV 601A. *6-10, Praedonezella cespeformis* Kulik, 1973 (location in Perret & Vachard 1977: all the magnifications indicated by these authors in the legend of the plates must be divided by 90%). Ardengost (Pyrénées). Late Serpukhovian (Arnsbergian) (scale bar = 0.5 mm). *6,* Initial encrusting stage. Thin-section AH 2a (collection M. F. Perret). *7,* Detail of a tetrahedric skeletal element. Thin-section GER 10-11b (collection M. F. Perret). *8,* Scalariform skeletal elements (rows of cells?). Thin-section AH 11a (collection M. F. Perret). *9,* Well preserved longitudinal section. Thin-section GER 10-11b (collection M. F. Perret). *10,* Initial encrusting part passing to an erect secondary part. AH 2b (collection M. F. Perret). *11-12, Praedonezella* (?) sp. (scale bar = 0.5 mm). *11,* Skeletal elements morphologically heralding *Frustulata* or *Calcifolium*. La Serre (Montagne Noire). Early Serpukhovian. Thin-section GIK 1807 (collection Aretz). *12, Praedonezella* (?) sp. Skeletal elements with cavities (left) filled with internal micritic sediment and peloids and tetrahedric connections (right). Early Serpukhovian. Thin-section LS 2028 (collection Aretz). La Serre (Montagne Noire).

PLATE 3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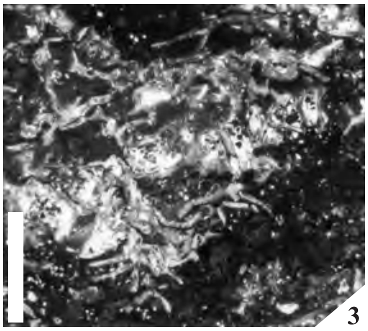
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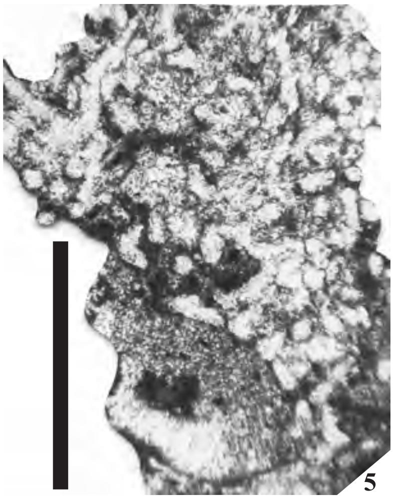
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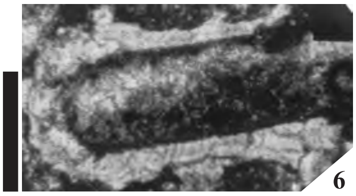
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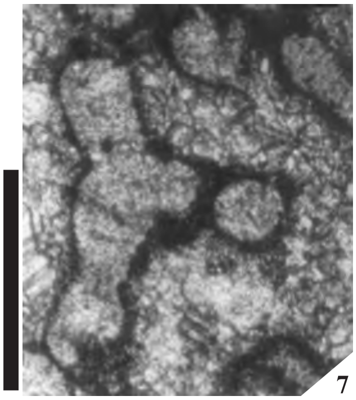
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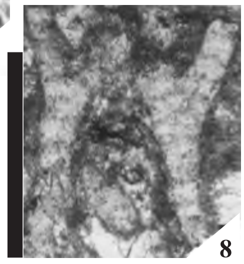
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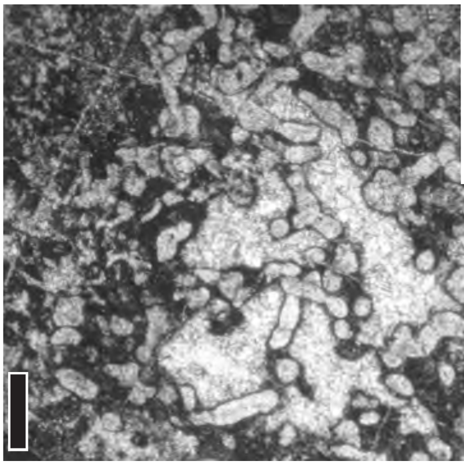
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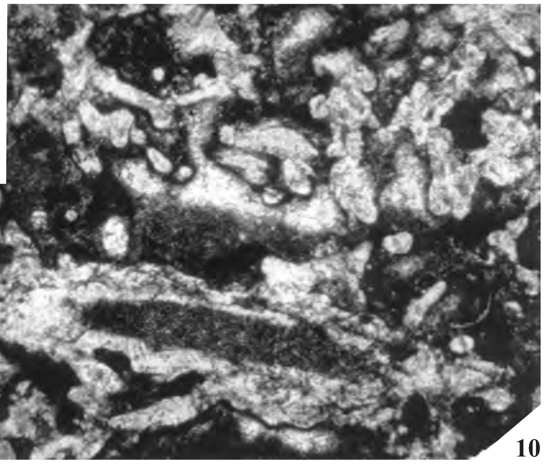
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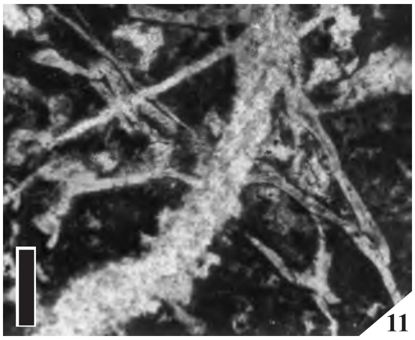
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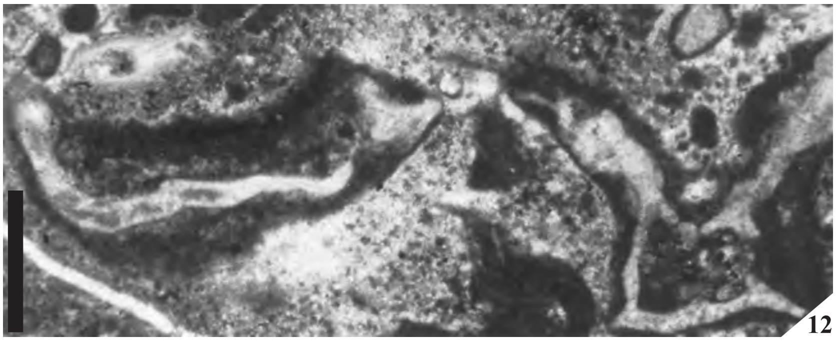
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1992 *Donezella cespeformis*, Mamet, p. 191 (no illustration).
? 1993 *Kulikaella partita* Ivanova, Chuvashov *et al.*, Pl. 1, Fig. 7.
1995 *Girvanella ducii* Wethered, Pajic & Filipovic, Pl. 47, Fig. 1.
1995 *Girvanella* sp., Pajic & Filipovic, Pl. 47, Fig. 2.
1998 *Praedonezella cespeformis*, Delvolvé *et al.*, p. 366, 367 (no illustration).
v. 1998 *Praedonezella*, De Bono *et al.*, p. 20 (no illustration).
? 2000 *Pseudokamaena armstrongi* Mamet, Sebbar, Pl. 2, Fig. 9.
2003 *Praedonezella cespeformis*, Brenckle & Milkina, Pl. 6, Fig. 11, 15.
2003 *Praedonezella carbonica*, Fontaine *et al.*, Pl. 9, Fig. 5, 12.
in press *Praedonezella* ex gr. *cespeformis*, Vachard & Aretz, Fig. 12. 1-6.

Description.–Same as the genus, with an average diameter of the skeletal elements of circa 0.100 mm (see detailed description, with a diameter of 0.040-0.180 mm, in Perret & Vachard, 1977). However, some morphotypes are larger (Pl. 3, Fig. 3-5), or smaller (i. e. *'Praedonezella carbonica'* sensu Vachard *et al.*, 1989). The limits of the morphotypes or possible species are insufficiently established until now.

Distribution.–Serpukhovian - early Bashkirian from southern France, northern Spain, Greece (Evvia), southern Urals, Donbass, western Turkey, Kazakhstan, Afghanistan, Malaysia, Japan. ? Earliest Bashkirian, western Algeria.

Praedonezella (?) sp.
Pl. 3, Figs. 11-12

? p. 1980 *Donezella lutuginii* Maslov?, Buchroithner *et al.*, p. 25-26, Pl. 5, Figs. 7-9 (not Pl. 2, Fig. 5 = *Frustulata).*
? 1991 *Praedonezella carbonica*, Vachard & Beckary, p. 324, Pl. 2, Fig. 6.

Description.–Some elements present in the early Serpukhovian of La Serre, where *Praedonezella* ex gr. *cespeformis* is common (Pl. 3, Figs. 1-3), are different. They are longer, slender, and rather isolated (i. e. poorly grouped in colonies).

Remarks.–These forms are difficult to understand. Morphologically, they seem to be intermediate between *Praedonezella* and *Frustulata* but the biostratigraphy actually known does not confirm this possible phylogeny.

Distribution.–Early Serpukhovian of La Serre, Montagne Noire (location in Vachard & Aretz in press). Serpukhovian of southern Spain. ? Early Bashkirian of northern Spain.

CONCLUSIONS

Three new species of algae have been described: *Fasciella crustosa* n. sp., *Fasciella scalaeformis* n. sp. and *Praedonezella primitiva* n. sp.

Taxonomic characters for *Fasciella* allow us to recognise only three species in this genus: *Fasciella kizilia* Ivanova, 1973, *Fasciella crustosa* n. sp. and *Fasciella scalaeformis* n. sp. The species *Shartymophycus fusus* Kulik, 1973, *Fasciella ivanovae* Saltovskaya, 1984, *F. ramosa* Saltovskaya, 1984 and *Shartymophycus multiplex* Kulik, 1973, are considered as morphotypes of *F. kizilia*.

The genus *Praedonezella* is considered as being composed of *Praedonezella primitiva* n. sp., *P. cespeformis* (= *P. catenuliformis* Ivanova in Bogush *et al.*, 1990), and questionably *Praedonezella* (?) sp.

The three new species are excellent markers for the late Asbian/Brigantian interval. They are widely distributed, and they can occur in East European basins (e. g. Urals, Poland), but they are commonly found in Ireland, England (except for *Praedonezella*), France and Spain, and more rarely in Morocco and Algeria. In consequence, they are mostly western Tethyan taxa.

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PALINOESTRATIGRAFÍA DEL GRUPO PIZARROSO-CUARCÍTICO DEL SECTOR MÁS ORIENTAL DE LA FAJA PIRÍTICA IBÉRICA, SO DE ESPAÑA

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Resumen

Este trabajo consiste en el análisis palinoestratigráfico de las pizarras de la parte inferior del Grupo PQ del sector más oriental de la Faja Pirítica Ibérica. Los palinomorfos son poco abundantes y suelen presentar un estado de conservación deficiente. La asociación incluye esporas trilete, acritarcos y algas prasinofíceas. La presencia de *Chelinospora concinna, Cristatisporites triangulatus, Geminospora lemurata, Retusotriletes rugulatus, Aneurospora greggsii* y *Verrucosisporites scurrus* sugiere una edad Givetiense superior-Frasniense inferior? para estas rocas, edad más antigua reconocida en la FPI. La asociación de palinomorfos indica un medio sedimentario marino próximo al área fuente.

Palabras clave: Palinoestratigrafía, esporas, acritarcos, algas prasinofíceas, Faja Pirítica Ibérica, Devónico.

Abstract

[Palynostratigraphy of the Phyllite-Quartzite Group in the easternmost sector of the Iberian Pyrite Belt, SW Spain]. Palynostratigraphical analysis of shales sampled from the lower levels of the PQ Group, in the easternmost area of the Iberian Piryte Belt, reveals the presence of a generally sparse and poorly preserved assemblage of trilete spores, acritarchs and prasinophyte phycomata. The presence of *Chelinospora concinna, Cristatisporites triangulatus, Geminospora lemurata, Retusotriletes rugulatus, Aneurospora greggsii* and *Verrucosisporites scurrus,* suggests an upper Givetian-lower Frasnian? age for these rocks, which is the oldest age recognized for the IPB. The palynomorph assemblage indicates a marine environment, highly continental-influenced.

Key words: Palynostratigraphy, spores, acritarchs, prasinophyte phycomata, Iberian Pyrite Belt, Devonian.

INTRODUCCIÓN

La Faja Pirítica Ibérica (FPI) constituye la mayor parte, y también la más representativa, de la Zona Surportuguesa, que es la más meridional de las unidades que conforman el Macizo Hercínico Ibérico (Julivert *et al.,* 1974). Además, la FPI es una de las provincias metalogénicas de sulfuros masivos más importantes del mundo. Contiene más de un centenar de mineralizaciones, destacando distritos mineros tan conocidos como Riotinto, Tharsis, Sotiel, Aznalcóllar, Aljustrel y Neves-Corvo, entre otros muchos (Fig. 1).

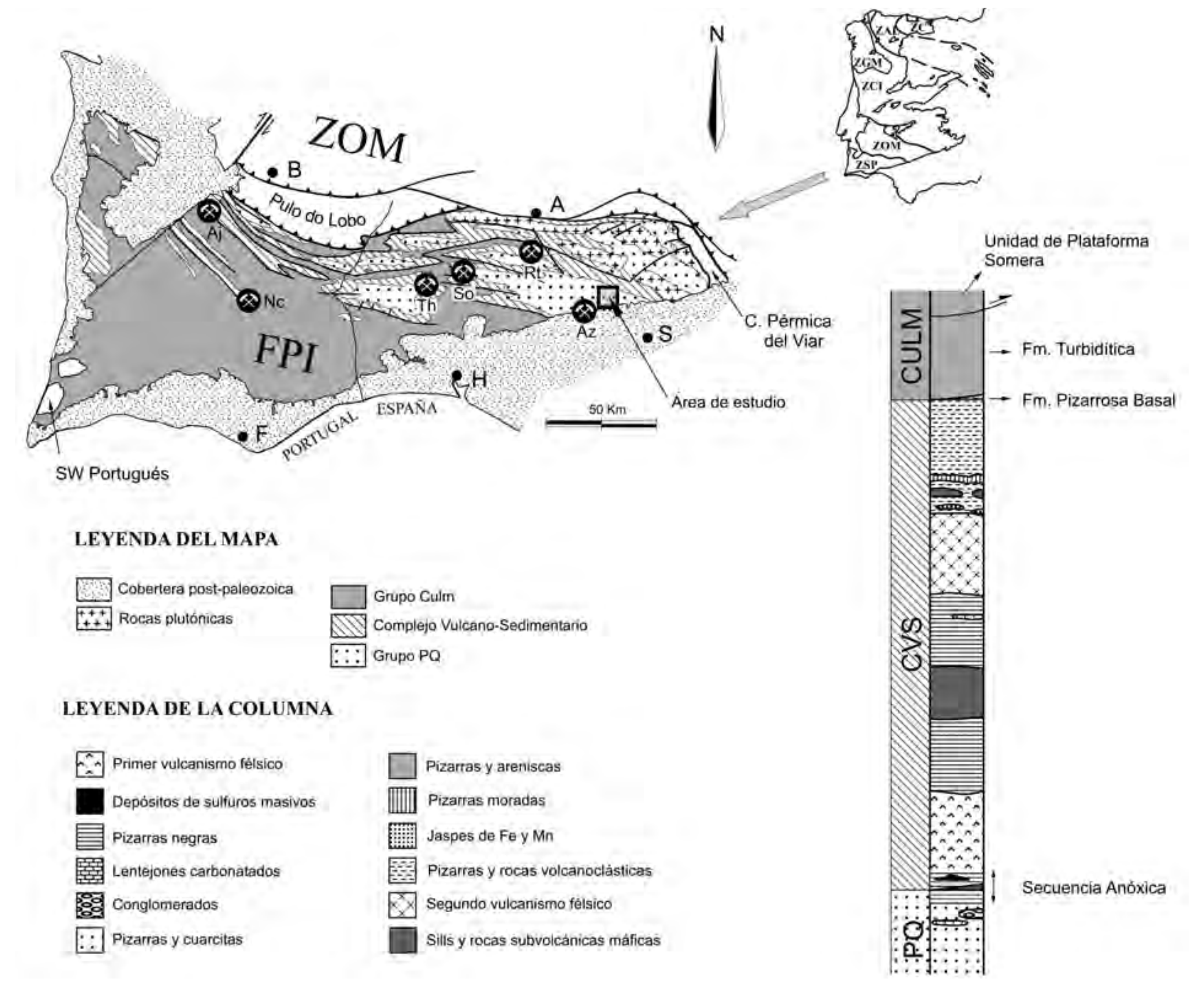

FIGURA 1–Mapa geológico y columna estratigráfica regional de la Faja Pirítica Ibérica. Zonación del Macizo Ibérico (esquina superior derecha). Abreviaturas geologicas: FPI) Faja Pirítica Ibérica; ZC) Zona Cantábrica; ZAL) Zona Asturoccidental Leonesa; ZGM) Zona Galicia Trás-os-Montes; ZCI) Zona Centro-Ibérica; ZOM) Zona Ossa Morena; ZSP) Zona Sur Portuguesa; PQ) Grupo Pizarroso Cuarcítico; CVS) Complejo Vulcano Sedimentario. Distritos mineros: Aj) Aljustrel; Az) Aznalcóllar; Nc) Neves-Corvo; Rt) Riotinto; So) Sotiel-Coronada; Th) Tharsis. Poblaciones: A) Aracena; B) Beja; F) Faro; H) Huelva; S) Sevilla.

FIGURE 1–Geological map and regional stratigraphical log of the Iberian Pyrite Belt. Iberian Massif Zonation (upper right corner). Geological abbreviations: FPI) Iberian Pyrite Belt; ZC) Cantabrian Zone; ZAL) West Asturian Leonese Zone; ZGM) Galicia Trás-os-Montes Zone; ZCI) Central Iberian Zone; ZOM) Ossa Morena Zone; ZSP) South Portuguese Zone; PQ) Phyllite Quartzite Group; CVS) Volcano Sedimentary Complex. Mining districts: Aj) Aljustrel; Az) Aznalcóllar; Nc) Neves-Corvo; Rt) Riotinto; So) Sotiel-Coronada; Th) Tharsis. Populations: A) Aracena; B) Beja; F) Faro; H) Huelva; S) Sevilla.

El origen de las mineralizaciones de sulfuros, y su localización espacio/temporal, parece haber estado fuertemente influenciado por las características paleoambientales y paleogeográficas de la cuenca en la que se formaron (Sáez *et al.*, 1999). El análisis estratigráfico, sedimentológico y paleontológico preciso de las rocas que representaron el relleno de la cuenca devono-carbonífera de la FPI es una tarea a medio hacer y un objetivo de primera categoría en el conocimiento geológico de la región. En este trabajo se presenta el análisis palinoestratigráfico de los materiales que forman el muro de la serie estratigráfica regional, se proporcionan datos cronoestratigráficos y se profundiza en el conocimiento de las características paleoambientales de la cuenca sedimentaria.

CARACTERÍSTICAS GENERALES DE LA FPI

Cartográficamente, la FPI dibuja una banda de 200 km de largo y 40 km de anchura que, siguiendo las directrices hercínicas, se extiende desde el sur de Lisboa en Portugal, hasta las proximidades de la ciudad de Sevilla en España (Fig. 1). Su registro estratigráfico está formado por rocas sedimentarias e ígneas de edad Devónica y Carbonífera que, tradicionalmente, han sido divididas en tres unidades litoestratigráficas (Schermerhorn, 1971). De muro a techo son: a) Grupo Pizarroso-Cuarcítico (PQ) constituido por una potente serie detrítica de pizarras y areniscas que hacia el techo incluye niveles conglomeráticos y lentejones carbonatados que contienen conodontos del Devónico Superior; b) Complejo Vulcano Sedimentario (CVS), de edad Devónico Superior-Carbonífero Inferior, formado por vulcanitas félsicas y máficas intercaladas en rocas sedimentarias de diverso origen, entre las que se incluyen los sulfuros masivos que caracterizan a la región, pizarras negras, areniscas, niveles de jaspes manganesíferos y lentejones carbonatados; y c) Grupo Culm, de edad Carbonífero, compuesto esencialmente por alternancias de pizarras, areniscas y algunos conglomerados constituyendo secuencias características de depósitos turbidíticos. Los límites de estas tres unidades están representados por dos niveles de pizarras negras, que aunque localmente discontinuos, son correlacionables a escala regional (Sáez y Moreno, 1997; Moreno *et al.,* 2003; Colmenero *et al.,* 2002). Los conodontos incluidos en el nivel pizarroso del límite PQ-CVS proporcionaron una edad Fameniense superior (Boogaard, 1963); esta edad fue posteriormente precisada como Struniense superior sobre la base de estudios palinológicos (ver apartado sobre antecedentes palinológicos). Las pizarras del límite CVS-Culm fueron consideradas como Tournaisiense tardío-Viseense inferior (Boogaard, 1963) o Viseense superior-Namuriense inferior (Schermerhorn, 1971).

Todos los materiales de la FPI están afectados por la fase Astúrica de la Orogenia Hercínica que dio lugar a una deformación de tipo *thin-skined* (Silva *et al.,* 1990) caracterizada por pliegues, cabalgamientos y mantos de corrimiento que producen un dispositivo geométrico en escamas y la repetición múltiple de la serie estratigráfica. Esta deformación junto con el basculamiento hacia el oeste que desde el Terciario sufre la Meseta Ibérica (Martín Serrano, 1991), producen una mayor denudación en la zona este de la Faja Pirítica, causando el afloramiento de los materiales más antiguos en los núcleos de los antiformes más orientales.

El contenido paleontológico de la FPI es pobre. La mayor parte de las dataciones realizadas han sido establecidas sobre la base de goniatites, generalmente asociados a concreciones diagenéticas incluidas en tramos pizarrosos (Oliveira y Wagner-Gentis, 1983), y al escaso número de conodontos contenidos en los también escasos lentejones carbonatados que aparecen “espolvoreados” por la región (Boogaard, 1963; Boogaard & Schermerhorn, 1975a, b, 1980, 1981). Algunas de estas dataciones fueron realizadas sobre ejemplares resedimentados que proporcionaron edades erróneas, más antiguas que las de los depósitos que los contienen (Moreno *et al.,* 2001). La macroflora se ciñe a briznas inclasificables, transportadas y depositadas en el techo del PQ, y a tallos de *Archeocalamites* sin valor cronoestratigráfico que también fueron transportados y acumulados en la base de determinados niveles turbidíticos del Culm (Moreno, 1987/1993).

El contenido en palinomorfos es irregular y escaso en comparación con otras regiones del hercínico europeo. Ocasionalmente, asociaciones de esporas y acritarcos pueden resultar abundantes y proporcionar dataciones precisas de manera que, a pesar de las dificultades expuestas, la Paleopalinología se presenta como la principal herramienta bioestratigráfica (ver apartado de antecedentes palinológicos).

UNIDAD OBJETO DE ESTUDIO: GRUPO PQ

El área de estudio se localiza en el extremo oriental de la FPI, en el núcleo del antiforme de Valverde de Camino, sobre materiales pizarrosos del Grupo PQ (Figs. 1 y 2).

El PQ constituye la base de la serie estratigráfica regional. Su potencia es desconocida, ya que el muro no aflora en ningún punto. Strauss (1970) le calcula un espesor mínimo de 2.000 m. La mayor parte de su columna estratigráfica está formada por pizarras negras con intercalaciones de niveles centimétricos de areniscas cuarzosas y cuarzovacas. Estos niveles a veces se agrupan y constituyen tramos lutítico-areniscosos de potencia métrica, con una relación arena/lutita igual a uno (a/l = 1) que aparecen intercalados entre las pizarras rompiendo la monotonía de la serie pizarrosa. Representan la sedimentación en una plataforma marina somera de baja energía, esporádicamente afectada por la acción de tormentas y oleaje (Moreno y Sáez, 1991; Moreno *et al.,* 1996).

Hacia techo de la unidad, y en respuesta a un proceso de somerización de la cuenca, aumenta la relación arena/lutita, produciendo secuencias dominantemente areniscosas que son interpretadas como depósitos de barras litorales (Moreno y Sáez, 1990). También en el techo de la unidad, ocupando posiciones estratigráficamente equivalentes, existen niveles discontinuos de con-

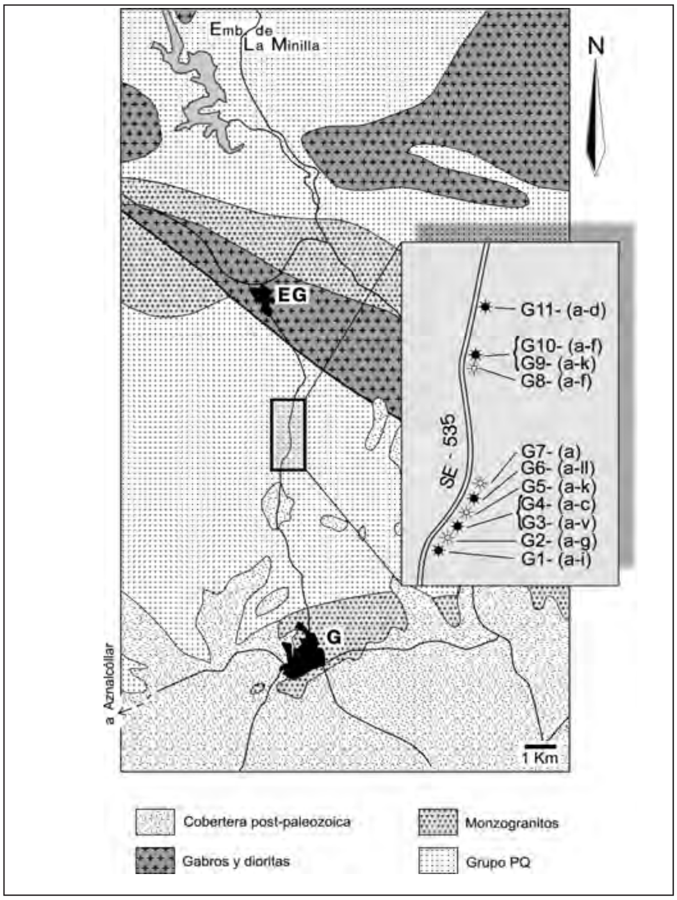

FIGURA 2–Esquema geológico del área de estudio mostrando la localización de las estaciones de muestreo. Los asteriscos negros corresponden a estaciones con muestras productivas. Los asteriscos blancos corresponden a estaciones con todas las muestras estériles. Poblaciones: EG) El Garrobo; G) Gerena.

FIGURE 2–Geological scheme of study area showing the location of sample localities. Full marks represent productive sample localities and open marks represent barren sample localities. Populations: EG) El Garrobo; G) Gerena.

glomerados de diversos tipos y lentejones carbonatados que se han interpretado como depósitos de avenidas efímeras asociadas a abanicos deltaicos, depósitos producidos por flujos de gravedad de gran envergadura y bioconstrucciones carbonatadas tipo *mound* (Moreno *et al.*, 1996/2001). Estos materiales, junto con la secuencia areniscosa, constituyen un mosaico de facies sin relación sedimentológica aparente que rompen la monotonía deposicional de la mayor parte de la serie estratigráfica del PQ. Indican el inicio de la variedad deposicional que a partir de ese momento va a caracterizar la cuenca de la FPI. Depósitos de alta energía insertos en un ambiente global más tranquilo de plataforma compartimentada en *horsts* y *grabens* en respuesta a las primeras manisfestaciones orogénicas regionales.

METODOLOGÍA

Las muestras de pizarra que constituyen la base de este trabajo fueron tomadas de afloramientos de campo del área de estudio (Figs. 1 y 2). Dada la suavidad del relieve y la espesa cobertera vegetal, tipo Matorral Mediterráneo, que tapiza la superficie del terreno, los mejores afloramientos son los que proporcionan los taludes de las carretras y otras vías de comunicación. La densidad de la red de muestreo y el número de muestras por estación son de carácter aleatorio, y han estado determinados por las características de los afloramientos. Las estaciones muestreadas se localizan en los taludes de la carretera comarcal SE-535, entre los pueblos de Gerena y El Garrobo (Figura 2), que discurre en dirección NS –perpendicular a las estructuras geológicas– y ocupando una posición centrada del área de estudio seleccionada.

Se analizaron un total de 23 muestras, de las cuales 11 fueron productivas. Las técnicas de extracción de palinomorfos empleadas se ajustan a las descritas por Wood *et al.* (1996). Éstas se basan en un ataque inicial en frío con HCl diluido al 36%, para eliminar los minerales carbonatados, seguido de un ataque en caliente con HF (48%) que elimine la fase silicatada, y por último un nuevo ataque con HCl (36%) en caliente para disolver los minerales carbonatados remanentes y fluoruros de neoformación. El residuo palinológico obtenido fue oxidado con Solución Schulze fumante, en tiempos variables, con el fin de aclarar los palinomorfos oscurecidos por el efecto de la maduración térmica y eliminar los fragmentos no orgánicos concentrados en el residuo. Tras la oxidación, los palinomorfos fueron neutralizados con agua destilada y concentrados con ayuda de un tamiz de 20 µm. Se montaron una media de dos láminas por muestra empleando Cellosize como agente dispersante y Elvacite como medio de montaje.

El estudio microscópico se llevó a cabo en el Departamento de Geología de la Universidad de Huelva con ayuda de un microscopio Nikon Labaphot-2. Las microfotografías fueron tomadas con una cámara Nikon Digital Coolpix 995; la localización de cada palinomorfo fotografiado en este trabajo se especifica en la Tabla 1 mediante los siguientes datos: especie del taxón, número de lámina/número de figura, código de la muestra de campo, código de la preparación de laboratorio, sistema de coordenadas x/y referidos al microscopio utilizado y, por último, número de registro que indica el código de referencia de cada espécimen en el registro del Laboratorio de Estratigrafía del Departamento de Geología de la Universidad de Huelva, donde se encuentran almacenados.

Especie	**Lámina/figura**	**Muestra**	**Preparación**	**Coordenadas x/y**	**Referencia**
Punctatisporites planus	1/1	G9-e	B-38 B	H620/0945	UHU.255
	1/2	G10-e	B-30 A	H436/0870	UHU.256
Punctatisporites scabratus	1/3	G9-e	B-38 B	H510/0970	UHU.257
	1/4	G10-e	B-30 A	H360/0931	UHU.258
	1/5	G9-e	B-38 B	H590/1010	UHU.259
Retusotriletes rotundus	1/6	G9-e	B-38 A	H650/1010	UHU.260
	1/7	G4-c	B-27 B	H435/0930	UHU.261
Retusotriletes rugulatus	1/8	G10-e	B-30 A	H474/1030	UHU.262
	1/9	G10-e	B-30 A	H515/0970	UHU.263
Verrucosisporites scurrus	1/10	G10-e	B-30 A	H551/1005	UHU.264
	1/11	G9-e	B-38 A	H475/0938	UHU.265
	1/12	G10-e	B-30 B	H648/1030	UHU.266
Convolutispora ampla	2/1	G10-e	B-30 A	H615/1000	UHU.267
	2/2	G9-e	B-38 B	H641/1003	UHU.268
Convolutispora sp. A	2/3	G10-e	B-30 A	H670/0980	UHU.269
	2/4	G10-e	B-30 A	H731/0964	UHU.270
Dictyotriletes sp. A	2/5	G9-e	B-38 A	H575/0981	UHU.271
Aneurospora greggsii	2/6	G9-i	B-44 C	H673/0935	UHU.272
	2/7	G10-e	B-30 A	H469/0972	UHU.273
	2/8	G10-e	B-30 A	H470/0965	UHU.274
Cristatisporites triangulatus	2/9	G4-c	B-27 A	H666/0931	UHU.275
Chelinospora concinna	2/10	G10-e	B-30 A	H620/1010	UHU.276
	2/11	G10-e	B-30 B	H370/0928	UHU.277
	2/12	G10-e	B-30 A	H585/0892	UHU.278
Cristatisporites sp. cf. *C. inusitatus*	3/1	G10-e	B-30 A	H430/0943	UHU.279
	3/2	G4-c	B-27 A	H470/1010	UHU.280
	3/3	G4-c	B-27 B	H535/1020	UHU.281
Cristatisporites triangulatus	3/4	G4-c	B-27 A	H450/0927	UHU.282
	3/5	G4-c	B-27 B	H630/0980	UHU.283
	3/6	G10-e	B-30 A	H601/1000	UHU.284
Diducites sp. A	3/7	G9-e	B-38 B	H501/0982	UHU.285
	3/8	G4-c	B-27 B	H426/0884	UHU.286
Geminospora lemurata	3/9	G4-c	B-27 B	H539/0850	UHU.287
	3/10	G9-e	B-38 B	H430/0960	UHU.288
	3/11	G9-e	B-38 B	H645/0955	UHU.289
Grandispora sp. A	3/12	G9-e	B-38 B	H570/0960	UHU.290
Leiosphaeridia sp.	4/1	G1-b	B-21 B	H521/0908	UHU.291
	4/2	G1-b	B-21 B	H395/0894	UHU.292
Tasmanites sp.	4/3	G1-b	B-21 B	H480/0898	UHU.293
Maranhites brasiliensis	4/4	G1-b	B-21 B	H555/0965	UHU.294
	4/5	G1-b	B-21 B	H520/0971	UHU.295
Maranhites britoii	4/6	G1-b	B-21 A	H340/0858	UHU.296
	4/7	G1-b	B-21 B	H480/0933	UHU.297
	4/8	G1-b	B-21 A	H470/0935	UHU.298
	4/9	G1-b	B-21 B	H662/0919	UHU.299
Maranhites mosesii	4/10	G11-b	B-24 A	H651/0980	UHU.300
Gorgonisphaeridium sp. cf. *G. disparatum*	4/11	G1-b	B-21 B	H431/0942	UHU.301
Gorgonisphaeridium sp. A	4/12	G10-e	B-30 A	H400/0861	UHU.302

TABLA 1–Registro de especímenes ilustrados.
TABLE 1–Inventory of illustrated specimens.

ANTECEDENTES PALINOLÓGICOS

Los estudios de naturaleza palinológica realizados hasta la fecha en la FPI son pocos, especialmente si los comparamos con los existentes en regiones análogas del Hercínico europeo. Probablemente la escasez de niveles productivos, su dificultad de localización, las desiguales condiciones de conservación de los palinomorfos y la oscilación en el grado de maduración térmica hayan contribuido a que el número de estudios de esta índole sea tan bajo. Entre ellos, la mayoría están dirigidos a datar los yacimientos de sulfuros que caracterizan la región. Éste es el caso de las dataciones cronoestratigráficas de las mineralizaciones de Aznalcóllar, Neves-Corvo y Tharsis realizadas por Pereira *et al*. (1996), Oliveira *et al*. (1997) y González *et al*. (2002), respectivamente. Otros niveles pizarrosos lateralmente correlacionables con los sulfuros han sido estudiados por Cunha y Oliveira (1989) en la región de Santo Domingo, y por Moreno *et al*. (2003) en el sector de Calañas.

El análisis palinológico del muro de la serie estratigráfica regional fue el objetivo del estudio realizado por Lake *et al*. (1988), trabajo palinológico pionero en la FPI. Estos autores muestran la existencia de palinoflora de edad Givetiense superior-Frasniense inferior en las pizarras del Grupo PQ aflorantes en el paraje denominado Ribera del Jarama (datos comparables a los que se proporcionan en el presente estudio). También Oliveira *et al.* (op. cit.) incluyen las pizarras del PQ del área de Neves-Corvo que aportaron individuos del Fameniense superior.

El contenido en palinomorfos de las pizarras del Grupo Culm (techo de la serie estratigráfica regional) tampoco ha sido suficientemente estudiado. Pereira (1999) realiza el análisis palinológico de los depósitos turbidíticos del SO de Portugal. Los trabajos de Oliveira *et al*. (op. cit.) del área de Neves-Corvo y Moreno *et al*. (2001) en los alrededores de Aznalcóllar tratan el tema de soslayo.

El análisis palinológico de las pizarras de la FPI también ha sido realizado con fines de índole más estrictamente sedimentológica y paleogeográfica; la existencia de secuencias condensadas y expandidas como consecuencia de la paleotopografía de la cuenca fue deducida por González *et al.* (2001) en el sector de Las Herrerías.

En ninguna de las publicaciones anteriormente mencionadas se proporciona la sistemática de los palinomorfos objeto de estudio. Los trabajos de González *et al*. (en prensa) y González *et al*. (en revisión) se basan en la clasificación sistemática de la asociación de palinomorfos de las pizarras negras del Fameniense superior de la FPI a escala regional (biozonas *Rugospora variabilis-Grandispora cornuta,* VCo, y *Retispora lepidophyta-Verrucosisporites nitidus,* LN, del esquema de Streel *et al.,* 1987).

En el presente estudio también se incluye la sistemática de la asociación de esporas, acritarcos y algas prasinofíceas de las pizarras del muro del Grupo PQ.

SISTEMÁTICA

Todos los palinomorfos recuperados en la FPI e incluidos en el presente apartado de sistemática son tratados como forma-géneros y forma-especies, bajo el auspicio del Código Internacional de Nomenclatura Botánica (Greuter *et al.*, 1994), con la excepción de los incluidos dentro de la clase Prasinophyceae Christensen, 1962. Cuando el deficiente estado de conservación ha impedido la correcta asignación a nivel específico, o bien no se han recuperado suficientes especímenes de un taxón presumiblemente nuevo, se ha utilizado una designación informal de letras (sp. A). Cuando uno o varios especímenes no han podido ser atribuidos con exactitud a una especie previamente instituida, se ha utilizado el epíteto “cf” antecediendo al binomio de la especie comparable.

Las clasificación supragenérica de las esporas ha seguido el esquema de Potonié & Kremp (1954), posteriormente modificado por Potonié (1966, 1970, 1975), Dettman (1963), Richardson (1965) y Smith & Butterworth (1967). La terminología adoptada corresponde a la descrita en los glosarios de Dettman (1963), Kremp (1965), Smith & Butterworth (1967) y Playford & Dettmann (1996).

Los palinomorfos marinos descritos han seguido diferentes esquemas clasificatorios. Los acritarcos se han organizado alfabéticamente, dado que no existe ningún esquema supragenérico ampliamente aceptado. Los géneros *Leiosphaeridia* Eisenack, 1958, *Tasmanites* Newton, 1875 y *Maranhites* Brito, 1965, han sido transferidos a la clase Prasinophyceae (algas prasinofíceas) de acuerdo con Tappan (1980), Norris (1980) y Colbath (1990, 1996). La terminología empleada corresponde a la descrita en los glosarios de Williams *et al*. (2000).

(a) Esporas

Anteturma PROXIMEGERMINANTES R. Potonié, 1970
Turma TRILETES Reinsch emend. Dettmann, 1963
Suprasubturma ACAVATITRILETES Dettmann, 1963
Subturma AZONOTRILETES Luber emend. Dettmann, 1963
Infraturma LAEVIGATI Bennie & Kidston emend. R. Potonié, 1956
Género *Punctatisporites* Ibrahim emend. R. Potonié & Kremp, 1954
Especie tipo: *Punctatisporites punctatus* (Ibrahim)

Ibrahim, 1933; por designación original.

Punctatisporites planus Hacquebard, 1957
(Lám. 1, Figs. 1, 2)

1957 *Punctatisporites planus* Hacquebard, p. 308; Pl. 1, Fig. 12.

Descripción.–Espora radial de tipo trilete, amb circular a subredondeado. Lesuras distinguibles, rectas, simples, ocupando 2/3 a 3/4 del radio de la espora. Exina simple, no cavada, de 1-3 µm de grosor. Superficie lisa a débilmente micropunteada. Suele presentar un pliegue de compresión de gran escala.

Dimensiones (8 especímenes).–Diámetro ecuatorial 39 (47) 51 µm.

Comparación.–Esta especie es comparable a *Punctatisporites debilis* Hacquebard, 1957 (p. 308; Pl. 1, Figs. 5-6), pero esta última difiere por el menor grosor de la exina (1 µm) y la presencia de un mayor número de pliegues de compresión de menor tamaño.

Distribución y comentarios.–Formas asignadas a *P. debilis* han sido ampliamente registradas durante el Devónico Superior (Fameniense superior)-Carbonífero Inferior (Turnaisiense) en gran parte del mundo: Islas Británicas e Irlanda (Phillips & Clayton, 1980; Clayton, Keegan & Sevastopulo, 1982; Clayton, 1986; Higgs, 1975; Higgs & Clayton, 1984; Higgs *et al*., 1988), Canadá (Hacquebard, 1957; Playford & McGregor, 1993), Alemania (Higgs & Streel, 1984), Portugal (Pereira, 1999), España (Moreno *et al*., 2003), Bélgica (Higgs, 1996), Estados Unidos (Clayton, Manger & Owens, 1998) y Arabia Saudita (Clayton, 1995). Aunque no existen registros de *P. planus* más abajo del Fameniense superior, el escaso valor cronoestratigráfico que posee el género *Punctatisporites* permite desestimar este taxón a la hora de dilucidar el rango de edad de la asociación recuperada.

Punctatisporites scabratus McGregor, 1960
(Lám. 1, Figs. 3-5)

1960 *Punctatisporites scabratus* McGregor, p. 29; Pl. 11, Fig. 6.

Descripción.–Espora radial de tipo trilete, amb circular. Lesuras distinguibles, rectas a ligeramente sinuosas, con finos labios de 1 µm de altura y grosor, ocupando 1/3 del radio de la espora. Exina simple, escabrada, de 1,5-2,5 µm de grosor.

Dimensiones (10 especímenes).–Diámetro ecuatorial 33 (46) 51 µm.

Comparación.–A pesar de presentar un diámetro ecuatorial algo menor que el específico descrito por McGregor para *Punctatisporites scabratus* (55-66 µm), los especímenes hallados en la FPI pueden ser asignados con seguridad a dicho taxón, basándose en el carácter escabrado de su exina. *P. irrasus* Hacquebard 1957 (p. 308; Pl. 1, Figs. 7-8) se asemeja a *P. scabratus*, pero difiere por el carácter microgranulado de la exina y la habitual presencia de pliegues de compresión de gran tamaño, que pueden llegar a modificar el amb de la espora.

Distribución.–Registrado en el Frasniense? de Canadá (McGregor, 1960).

Infraturma RETUSOTRILETI Streel en Becker, Bless, Streel & Thorez, 1974

Género *Retusotriletes* Naumova emend. Streel, 1964

Especie tipo: *Retusotriletes simplex* Naumova, 1953; por designación subsiguiente de Potonié (1958, p. 13).

Retusotriletes rotundus (Streel) Streel, 1967
(Lám. 1, Figs. 6, 7)

1964 *Phyllothecotriletes rotundus* Streel, p. 4; Pl. 1, Figs. 1, 2.
1967 *Retusotriletes rotundus* (Streel) Streel, p. 25; Pl. I, Fig. 11; Pl. II, Figs. 16, 17.
1967 *Retusotriletes triangulatus* (Streel) Streel, p. 24; Pl. II, Figs. 18-20.
1969 *Retusotriletes goensis* Lele & Streel, p. 93; Pl. I, Figs. 12-16.

Para sinonimia adicional ver McGregor (1973, p. 20) y McGregor & Camfield (1976, p. 26).

Descripción.–Espora radial de tipo trilete, amb circular a ligeramente subtriangular. Lesuras distinguibles, simples, rectas, ocupando 1/2 a 4/5 del radio de la espora. Exina no cavada, lisa, de 3-4 µm de grosor. Las lesuras se prolongan ecuatorialmente en forma de curvaturas perfectas distinguibles, de aproximadamente 1 µm de anchura, que pueden coincidir en parte con el contorno ecuatorial. Superficie proximal polumbrada; polumbra subtriangular o redondeada, ocupando aproximadamente 1/3 del radio de la espora y englobando a veces un área central subtriangular a subredondeada de color más claro.

Dimensiones (12 especímenes).–Diámetro ecuatorial 40 (65) 92 µm.

Observaciones.–Las formas halladas en la FPI presentan una alta variabilidad tanto en el tamaño total de la espora como en la morfología de la polumbra.

Distribución.–Ejemplares de esta especie han sido registrados en el Devónico Inferior-Medio de Bélgica (Streel, 1964, 1967) y Canadá (McGregor, 1973; McGregor & Camfield, 1976, 1982); Devónico Medio de Polonia (Turnau & Racki, 1999); Devónico Superior del

Oeste de Australia (Balme, 1988; Grey, 1992), Escocia (Marshall & Allen, 1982) e Irán (Hashemi & Playford, 1998); Devónico Superior-Carbonífero Inferior de Irlanda (Higgs & Russell, 1981; Higgs, Clayton & Keegan, 1988) y Sur de España (González *et al.*, 2002; Moreno *et al.*, 2003); y Carbonífero Inferior de Estados Unidos (Clayton *et al.*, 1998).

Retusotriletes rugulatus Riegel, 1973
(Lám. 1, Figs. 8, 9)

1965 *Retusotriletes dubius* (Eisenack) Richardson, p. 564; Pl. 88, Fig. 6.
1966 *Retusotriletes* sp. McGregor & Owens, Pl. 9, Fig. 2.
1967 *Retusotriletes* sp. 1 Hemer & Nygreen, Pl. 2, Fig. 6.
1973 *Retusotriletes rugulatus* Riegel, p. 82; Pl. 10, Figs. 2-5.
1974 *Stenozonotriletes extensus* Naumova; Hamid, Pl. 10, Fig. 3.
1982 *Retusotriletes rugulatus* Riegel; McGregor & Camfield, pp. 58-59; Pl. 17, Figs. 1-5.

Descripción.–Espora radial de tipo trilete, amb circular a ligeramente subtriangular. Lesuras perceptibles, simples y rectas, ocupando 4/5 del radio de la espora. Exina no cavada, de 2 µm de grosor. Curvaturas perfectas distinguibles, de aprox. 1 µm de anchura, que pueden coincidir en parte con el contorno ecuatorial. Las áreas de contacto presentan numerosos rugulae delgados (<1 µm de altura y anchura) mostrando a veces una estructura pseudoreticulada. El resto de la exina es escabrada.

Dimensiones (4 especímenes).–Diámetro ecuatorial 52-62 µm.

Comparación.–*Retusotriletes phillipsii* Clendening, Eames & Wood 1980 (pp. 15-20; Pl. 1, Figs. 1-9) puede ser comparada con *R. rugulatus* Riegel, 1973, pero difiere por la presencia de unas áreas de contacto visiblemente más delgadas, que presentan pequeños granos y finas estrías dispuestas de forma radial.

Distribución.–Registrado en el Eifeliense-Frasniense superior de Canadá (McGregor, 1981; McGregor & Camfield, 1982); Givetiense inferior de Alemania (Riegel, 1973); y Givetiense superior-Frasniense inferior de Francia (Loboziak & Streel, 1980).

Infraturma APICULATI Bennie & Kidston emend. R. Potonié, 1956
Subinfraturma VERRUCATI Dybová & Jachowicz, 1957
Género *Verrucosisporites* Ibrahim emend. Smith & Butterworth, 1967
Especie tipo: *Verrucosisporites verrucosus* (Ibrahim) Ibrahim 1933; por designación original.
Verrucosisporites scurrus (Naumova) McGregor & Camfield, 1982
(Lám. 1, Figs. 10-12)

1953 *Lophozonotriletes scurrus* Naumova, p. 38; Pl. III, Figs. 22, 23.
1982 *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, pp. 61-62; Pl. 18, Figs. 10-17, 22; text-fig. 96.

Para sinonimia adicional ver McGregor & Camfield (1982; pp. 61-62).

Descripción.–Espora radial de tipo trilete, amb subcircular. Lesuras apreciables a distinguibles, simples y rectas, ocupando 3/4 partes del radio de la espora. Exina no cavada de 3-5 µm de espesor, ornamentada distal y ecuatorialmente con elementos frecuentemente truncados de tipo verruga, báculo y rara vez de tipo espátula. El tamaño de los elementos esculturales varía entre 2-8 µm (normalmente 3-4 µm) tanto en altura como en sección basal, y su separación oscila entre 1-7 µm, hallándose frecuentemente unidos para formar rugulae cortos e irregulares.

Dimensiones (3 especímenes).–Diámetro ecuatorial 42-50 µm.

Comparación.–Esta especie es comparable a *Raistrickia aratra* Allen, 1965 (pp. 701-702; Pl. 96, Figs. 3, 4), sin embargo su ornamentación, basada principalmente en elementos esculturales redondeados tipo cono o verruga, posee un tamaño claramente mayor (6-14 µm de altura). Otra especie comparable es *Verrucosisporites gobbettii* Playford, 1962 (pp. 586–587, Pl. 80; Figs. 1-4), pero esta presenta elementos esculturales de mayor diámetro basal (hasta 8 µm) y menor altura (2-3 µm).

Distribución.–*V. scurrus* ha sido registrado en el Eifeliense-Givetiense inferior de Canadá (McGegor & Camfield, 1982); Givetiense de Polonia (Turnau & Racki, 1999); Givetiense superior de Rusia (Naumova, 1953); Givetiense-Frasniense de Brasil (Loboziak *et al.*, 2000); y Fameniense superior-Turnaisiense inferior de Irlanda (Higgs *et al.*, 1988).

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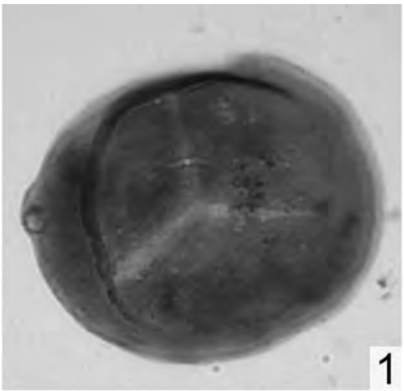
LÁMINA 1–*1, 2, Punctatisporites planus* Hacquebard, 1957, enfoque medio, x 1.000. *3-5, Punctatisporites scabratus* McGregor, 1960, enfoque proximal, x 1.250. *6, 7, Retusotriletes rotundus* (Streel) Streel, 1967, enfoque proximal; *6,* x 1.000; 7, x 700. *8, 9, Retusotriletes rugulatus* Riegel, 1973, enfoque proximal; 8, x 1.000; 9, x 600. *10-12, Verrucosisporites scurrus* (Naumova) McGregor & Camfield, 1982, enfoque distal, x 1.000.

LÁMINA 1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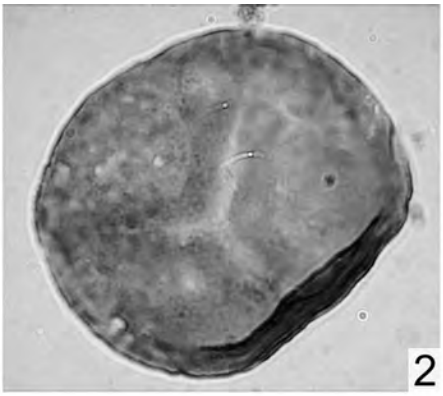
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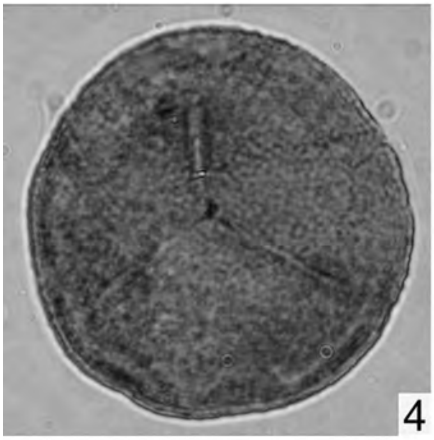
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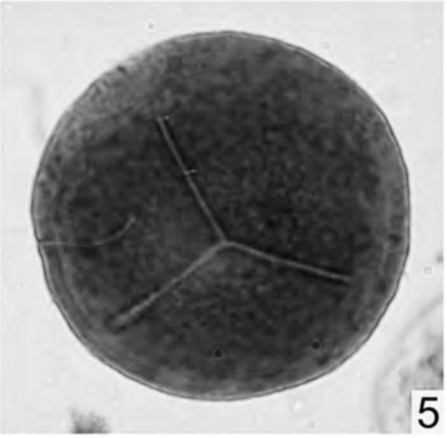
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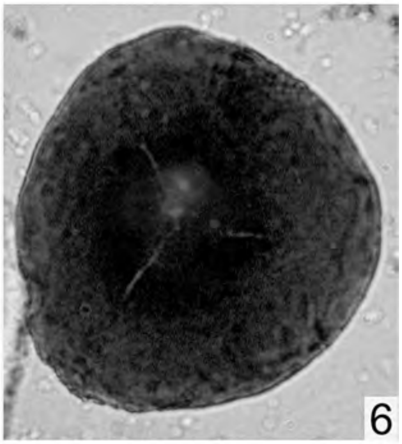
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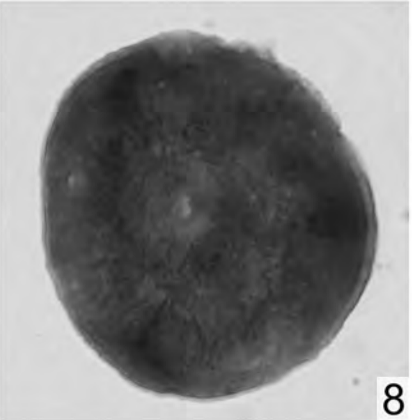
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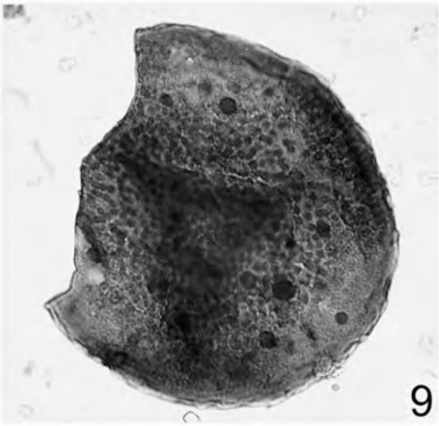
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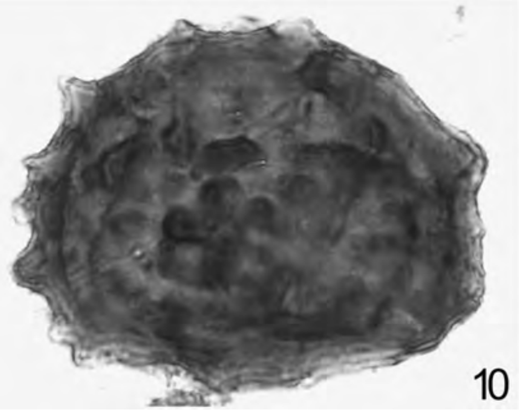
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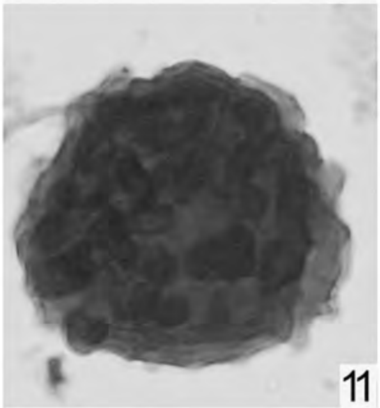
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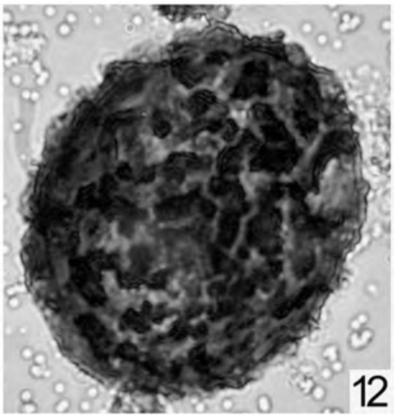
12

Infraturma MURORNATI R. Potonié & Kremp, 1954
Género *Convolutispora* Hoffmeister, Staplin & Malloy, 1955
Especie tipo: *Convolutispora florida* Hoffmeister, Staplin & Malloy, 1955; por designación original.

Convolutispora ampla Hoffmeister, Staplin & Malloy, 1955
(Lám. 2, Figs. 1, 2)

1955 *Convolutispora ampla* Hoffmeister, Staplin & Malloy, p. 384; Pl. 38, Fig. 12.

Descripción.–Espora radial de tipo trilete, amb circular a subcircular, originalmente esférica. Lesuras apreciables a indistinguibles, simples y rectas, ocupando 1/2 a 2/3 del radio de la espora. Exina no cavada, de 3-5 µm de grosor (incluidos rugulae). Ornamentación reducida a inexistente en las áreas de contacto, y bien desarrollada en las regiones próximo-ecuatorial y distal. Ornamentación basada en una alta densidad de rugulae libres o anastomosados, de crestas redondeadas y dimensiones en torno a 1-1,5 µm de anchura y hasta 2 µm altura, que generan lumina pequeñas y generalmente alargadas, de 0,5-1 µm de anchura y aprox. 3 µm de longitud.

Dimensiones (4 especímenes).–Diámetro ecuatorial 43-62 µm.

Observaciones.–Las características específicas de este taxón: gran densidad de finos rugulae delimitados por lumina alargadas, exoexina relativamente gruesa, y lesuras simples parcialmente encubiertas por la ornamentación, se ajustan perfectamente a la descripción de *Convolutispora ampla* Hoffmeister, Staplin & Malloy, 1955.

Distribución y comentarios.–Ampliamente descrita durante el Turnaisiense-Namuriense (ver, por ejemplo, Hoffmeister, Staplin & Malloy, 1955; Love, 1960; Smith & Butterworth, 1967; Barss, 1967; Urban, 1971; Braman & Hills, 1992; Playford, 1971, 1976, 1978; Playford & Satterthwait, 1985), no existen registros pre-Carboníferos de este taxón. La posición estratigráfica de las muestras analizadas en este trabajo, junto al rango de distribución del resto de la asociación de palinomorfos identificados, desaconsejan la utilización de *C. ampla* como indicador biostratigráfico. Más bien permite plantear la posibilidad de ampliar su rango estratigráfico, al menos en la FPI, haciéndolo descender hasta el Devónico Medio.

Convolutispora sp. A
(Lám. 2, Figs. 3, 4)

Descripción.–Espora radial de tipo trilete, originalmente esférica, amb circular a subcircular. Lesuras apreciables a indistinguibles, simples y rectas, ocupando 1/5 a 2/3 del radio de la espora. Exina no cavada de 3-5 µm de grosor (rugulae incluidos). Ornamentación reducida a inexistente en el área de contacto y bien desarrollada distal y ecuatorialmente, con rugulae de 1-4 µm de grosor y altura, y lumina alargadas de 1-6 µm de longitud y 1-2 µm de anchura.

Dimensiones (5 especímenes).–Diámetro ecuatorial 39-58 µm.

Comparación.–Atendiendo a la clave dicotómica que Playford & Satterthwait (1985, p. 150; Apéndice 1) aplican al género *Convolutispora* (basada en el índice de rugulae "RgI" junto a otras características morfológicas definitorias a nivel específico, tales como tamaño de la espora, tipo y distribución de los rugulae y características de las lesuras), esta especie podría ser asignada a *Convolutispora fromensis* Balme & Hassell, 1962 (p. 8; Pl. 1, Figs. 14-16) pero el mayor grosor de la exina (3-5 µm frente a 2-3 µm en *C*. sp. A) y el carácter envolvente de su ornamentación desaconseja dicha asignación.

Género *Dictyotriletes* Naumova emend. R. Potonié & Kremp, 1954
Especie tipo: *Dictyotriletes bireticulatus* (Ibrahim) R. Potonié & Kremp, 1955; por designación original.

Dictyotriletes sp. A
(Lám. 2, Fig. 5)

Descripción.–Espora radial de tipo trilete, originalmente esférica, amb circular a subcircular. Lesuras apreciables a indistinguibles, simples, rectas a ligeramente sinuosas, ocupando 1/2 a 2/3 del radio de la espora. Exina no cavada, de 4-5 µm de grosor (muros incluidos). Ornamentación reducida a inexistente en las áreas de contacto y bien desarrollada ecuatorial y distalmente. Ornamentación basada en muros de 1-2 µm de grosor y altura que encierran lumina poligonales irregulares de 1-7 µm (normalmente en torno a 3 µm) de máxima dimensión.

Dimensiones (3 especímenes).–Diámetro ecuatorial 46, 48, 51 µm.

Comparación.–Estos especímemes se asemejan a *Dictyotriletes cuniculosus* Playford & Satterthwait, 1985 (p. 139; Pl. 3, Figs. 7-9) pero difieren por su menor tamaño y la presencia de muros más bajos y cortos, de sección redondeada. *D. migratus* Naumova, 1953 (p. 18; Pl. II, Fig. 8), posee características semejantes a *D*. sp. A, pero la brevedad de su descripción y su deficiente representación grafica (representada únicamente por un dibujo a mano alzada) imposibilita una comparación más fidedigna.

Subturma ZONOTRILETES Waltz, 1935
Infraturma CINGULATI R. Potonié & Klaus emend. Dettmann, 1963

Género *Aneurospora* Streel, 1964
Especie tipo: *Aneurospora goensis* Streel, 1964; por designación original.
Aneurospora greggsii (McGregor) Streel en Becker, Bless, Streel & Thorez, 1974
(Lám. 2, Figs. 6-8)

1964 *Retusotriletes greggsii* McGregor, p. 10; Pl. 1, Figs. 1-12.
1974 *Aneurospora greggsii* (McGregor) Streel en Becker, Bless, Streel & Thorez, p. 24; Pl. 16, Figs. 6-15.

Descripción.–Espora radial de tipo trilete, amb triangular subredondeado. Superficie distal ligeramente más redondeada que la proximal. Lesuras distinguibles, simples y rectas, ocupando 4/5 del radio de la espora y terminando en curvaturas perfectas acompañadas por un engrosamiento ecuatorial a ligeramente proximal de 1,5-4 µm de anchura. Exina no cavada de 1,5 µm de grosor, densamente ornamentada distal y ecuatorialmente con conos inferiores a 1 µm de altura y sección basal. Áreas de contacto lisas.

Dimensiones (13 especímenes).–Diámetro ecuatorial 40 (46) 56 µm.

Comparación.–*Aneurospora greggsii* (McGregor) Streel en Becker *et al.*, 1974 puede ser comparada con *Geminospora lemurata* Balme emend. Playford 1983 (descrita a continuación), sin embargo esta última especie posee un amb algo más redondeado, carece de engrosamiento ecuatorial y es claramente cavada.

Distribución.–Especie ampliamente registrada en el Hemisferio Norte desde el Givetiense al Fameniense Superior: Polonia (Turnau, 1996; Turnau & Racki, 1999), Bélgica (Becker *et al.,* 1974; Streel, 1967, 1999), Francia (Loboziak & Streel, 1980), Alemania (Higgs & Streel, 1984), Portugal (Cunha & Oliveira, 1989; Oliveira *et al*., 1986), Escocia (Marshall & Allen, 1982), Canadá (McGregor, 1964) y Estados Unidos (Streel & Traverse, 1978).

Infraturma PATINATI Butterworth & Williams, 1958
Género *Chelinospora* Allen, 1965
Especie tipo: *Chelinospora concinna* Allen, 1965; por designación original.
Chelinospora concinna Allen, 1965
(Lám. 2, Figs. 10-12)

1965 *Chelinospora concinna* Allen, pp. 728-729; Pl. 101, Figs. 12-20.

Descripción.–Espora radial de tipo trilete, amb circular a subcicular. Lesuras distinguibles a perceptibles, rectas, simples o con labios delgados (inferiores a 1 µm), que se extienden prácticamente hasta la zona ecuatorial. Exina no cavada, escabrada, distalmente cubierta por una pátina de 2-13 µm de grosor, que se adelgaza en la superficie proximal. En las áreas de contacto de algunos ejemplares se puede observar una débil ornamentación con verrugas de hasta 2 µm de altura y grosor. La pátina está groseramente reticulada con muros de 1-6 µm de altura y 1-2 µm de anchura que encierran grandes lumina poligonales a irregulares de 5-14 µm de dimensión máxima. Esta ornamentación tiende a modificar ligeramente el amb de la espora.

Dimensiones (4 especímenes).–Diámetro ecuatorial 47-56 µm.

Observaciones.–Los especímenes estudiados presentan una gran variabilidad en el grosor de la pátina, en la altura de los muros y en las dimensiones de las lumina. Además, el deficiente estado de conservación se traduce en fenómenos de corrosión tanto en la pátina como en el retículo.

Distribución.–Espora prácticamente cosmopolita registrada por diversos autores durante el Givetiense superior-Frasniense, especialmente en el Hemisferio Norte; ver, por ejemplo, Vigran, 1964; Allen, 1965, 1967, 1973; Loboziak & Streel, 1980; McGregor, 1981; Marshall & Allen, 1982 y Richardson & McGregor, 1986.

Suprasubturma LAMINATITRILETES Smith & Butterworth, 1967
Subturma ZONOLAMINATITRILETES Smith & Butterworth, 1967
Infraturma CINGULICAVATI Smith & Butterworth, 1967
Género *Cristatisporites* R. Potonié & Kremp emend. Butterworth *et al*. en Staplin & Jansonius, 1964.
Especie tipo: *Cristatisporites indignabundus* (Loose) Potonié & Kremp, 1954; por designación original.
Cristatisporites sp. cf. *Cristatisporites inusitatus* (Allen) McGregor & Camfield, 1982
(Lám. 3, Figs. 1-3)

cf. 1965 *Samarisporites inusitatus* Allen, p. 717; Pl. 99, Figs. 7–9.
cf. 1982 *Cristatisporites inusitatus* (Allen) McGregor & Camfield, p. 29.

Descripción.–Espora radial de tipo trilete, amb triangular subredondeado a subredondeado conforme a la cavidad de la espora. Lesuras apreciables a indistinguibles debido a la ornamentación, con labios de hasta 2 µm de anchura cada uno, que se extienden hasta el margen externo de la zona. Exina cavada; exoexina extendida ecuatorialmente hasta formar una zona de contorno irregular (¿efecto de la corrosión?), de 8 µm de anchura máxima; exoexina proximal lisa a escabrada; exoexina distal cubierta por una densa ornamentación de cristas de 1-1.5 µm de grosor, hasta 7 µm de altura y 7-20 µm de longitud; cristas aisladas, formadas por la coalescencia de varias espinas aplanadas, dispuestas generalmente de forma concéntrica; las cristas se prolongan aprox. hasta la mitad de la zona. Intexina delgada (0,5 µm de grosor), de ornamentación indistinguible, poco separada de la exoexina, ocupando 4/5 del diámetro total de la espora.

Dimensiones (14 especímenes).–Diámetro ecuatorial 42 (56) 70 µm.; diámetro de la cavidad de la espora 35 (42) 57 µm.

Observaciones.–Los especímenes hallados en la FPI no presentan un óptimo estado de preservación, hallándose con facilidad individuos cuya zona ha sido total o parcialmente eliminada. Este hecho imposibilita el análisis del patrón estructural de dicha zona, por lo que no es posible una completa asignación a *Cristatisporites inusitatus* (Allen) McGregor & Camfield, 1982.

Cristatisporites triangulatus (Allen) McGregor & Camfield, 1982
(Lám. 2, Fig. 9; Lám. 3, Figs. 4-6)

1965 *Samarisporites triangulatus* Allen, p. 716; Pl. 99, Figs. 1-6.
1982 *Cristatisporites triangulatus* (Allen) McGregor & Camfield, p. 29.

Para sinonimia adicional ver Allen (1982, pp. 158-159) y Balme (1988, p. 136).

Descripción.–Espora radial de tipo trilete, amb triangular a triangular subredondeado, contorno de la cavidad de la espora redondeado. Lesuras perceptibles a claramente distinguibles, rectas a ligeramente sinuosas, con labios elevados de 1,5-2 µm de anchura cada uno, extendiéndose más allá de la zona, frecuentemente hasta el margen ecuatorial. La zona presenta una anchura variable de 2-10 µm, adelgazándose hasta desaparecer en posiciones interradiales, y alcanzando su máxima extensión en zonas apicales; suele presentar espinas delgadas y galeae aisladas o rara vez unidas por sus bases, de hasta 3 µm de sección basal y 2 µm de altura. Exina cavada; intexina muy cerca de la exoexina, indiferenciable. Exoexina proximal lisa; exoexina distal ornamentada con espinas, galeae y conos unidos entre sí en su parte basal para formar cristas de hasta 1 µm de grosor y 3 µm de altura, dispuestas a veces de forma aleatoria y a veces de forma concéntrica, paralelamente al margen interno de la zona.

Dimensiones (10 especímenes).–Diámetro ecuatorial 36 (50) 60 µm; diámetro de la cavidad de la espora (en vista polar) 30 (38) 54 µm.

Observaciones.–A pesar del escaso número de ejemplares estudiados, éstos muestran una alta variabilidad ornamental de la exoexina distal, similar a la descrita por Allen (1982, p. 159) y Balme (1988, p. 137). Se observa una gradación completa entre individuos ornamentados con espinas, conos y galeae raramente unidos por su base, formando cristas aisladas de escasa dimensión, y especímenes ornamentados principalmente con cristas más alargadas dispuestas de forma aprox. concéntrica junto a elementos apiculares aislados.

Distribución y comentarios.–Especie virtualmente cosmopolita y ampliamente registrada durante el Givetiense-Frasniense medio (ver Allen, 1982; Richardson & McGregor, 1986 y Balme, 1988). Recientemente han sido recuperados especímenes de *C. triangulatus* en el Fameniense superior de la Faja Pirítica Ibérica (González *et al.*, en prensa). El carácter sinsedimentario que González *et al*. confieren a estos especímemes, plantea la necesidad de ampliar el rango de distribución de este taxón, al menos en la FPI, hasta prácticamente el límite Devono-Carbonífero. Hasta la fecha, la presencia de *C. triangulatus* en el Fameniense superior en esta región había sido relacionada con fenómenos de removilización sedimentaria (Pereira *et al*., 1994).

Suprasubturma PSEUDOSACCITITRILETES
Richardson, 1965
Infraturma MONOPSEUDOSACCITI Smith &
Butterworth, 1967
Género *Diducites* Van Veen, 1981
Especie tipo: *Diducites plicabilis* Van Veen, 1981;
por designación original
Diducites sp. A
(Lám. 3, Figs. 7, 8)

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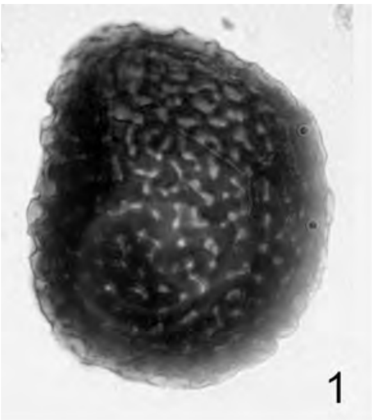
LÁMINA 2–*1, 2, Convolutispora ampla* Hoffmeister, Staplin & Malloy, 1955, enfoque distal, x 1.000. *3, 4, Convolutispora* sp. A; *3*, enfoque proximal, x 750; *4*, enfoque distal, x 800. 5, *Dictyotriletes* sp. A, enfoque distal, x 1.000. *6-8, Aneurospora greggsii* (McGregor) Streel en Becker, Bless, Streel & Thorez, 1974, enfoque proximal, x 1.000. *9, Cristatisporites triangulatus* (Allen) McGregor & Camfield, 1982, vista transversal, x 600. *10-12, Chelinospora concinna* Allen, 1965; *10, 12*, enfoque medio, x 1.000; 11, enfoque distal, x 1.000.

LÁMINA 2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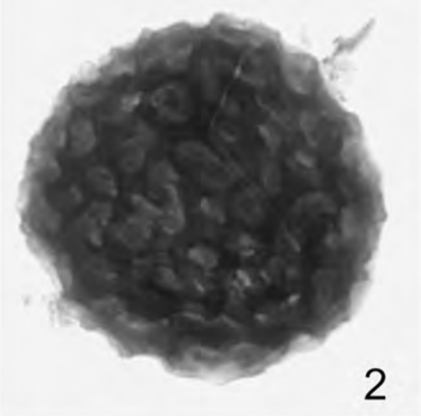
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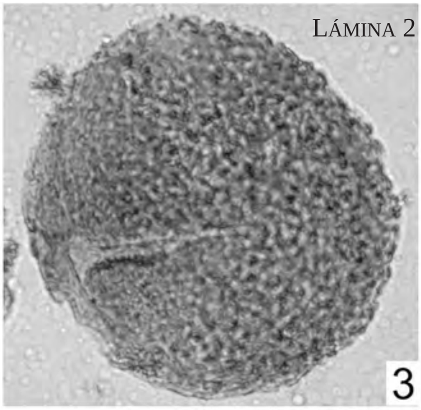
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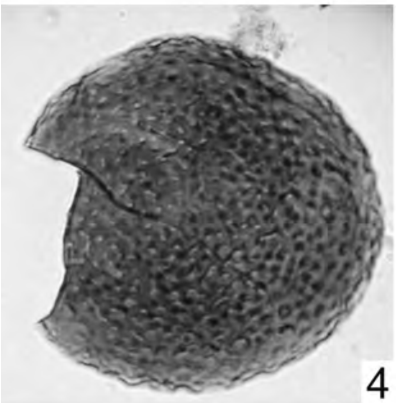
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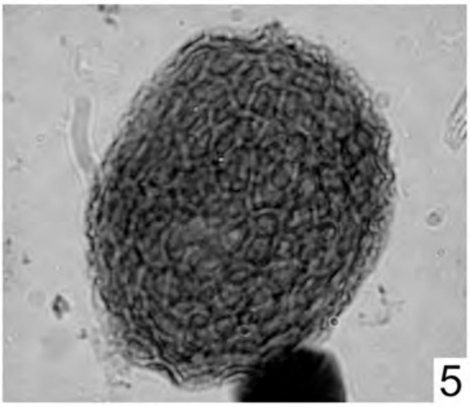
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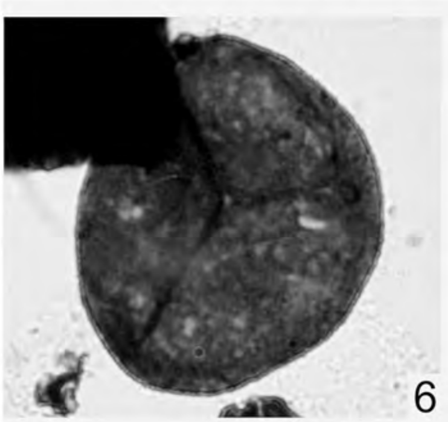
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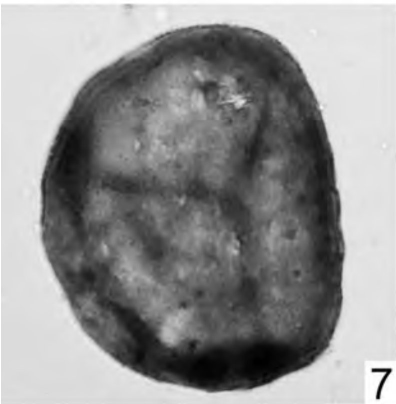
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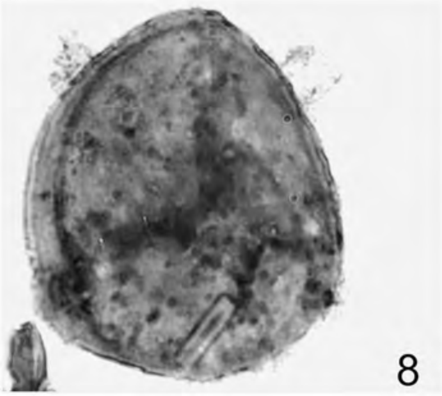
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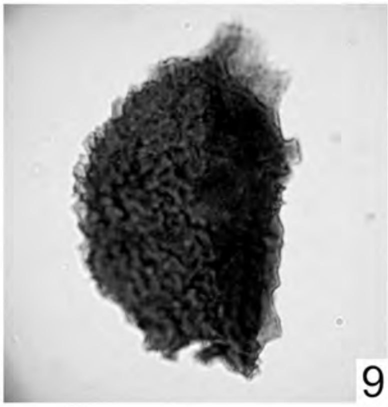
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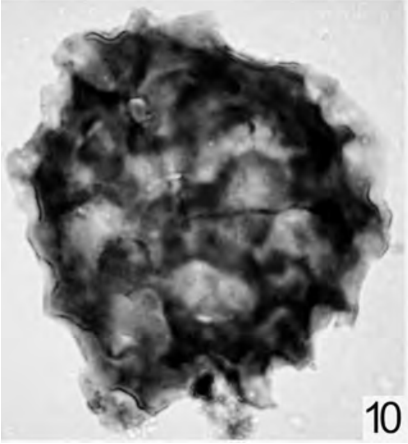
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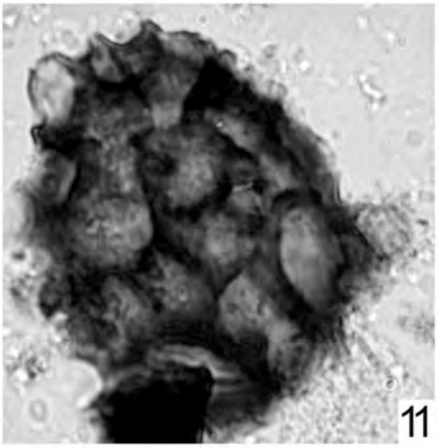
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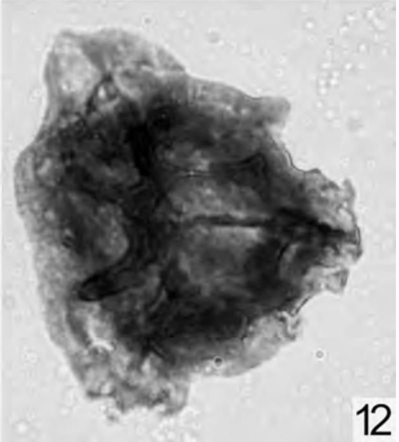
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Descripción.–Espora radial de tipo trilete, amb triangular subredondeado. Lesuras distinguibles, simples, rectas, extendiéndose desde los 4/5 del radio de la espora hasta las inmediaciones del margen ecuatorial. Exina cavada; exoexina dividida en dos capas: una interna conforme al contorno de la intexina, de 0,7 µm de grosor, ornamentación indistinguible y plegada ecuatorialmente; y otra externa, mucho más delgada, de 0,1-0,2 µm de grosor, microrrugulada, totalmente unida a la capa interna y reconocible por su aspecto traslúcido. Intexina lisa, de 0,5 µm de grosor, conforme al amb de la espora, y plegada ocasionalmente en su margen ecuatorial.

Dimensiones (3 especímenes).–Diámetro ecuatorial 50, 51, 51 µm; diámetro de la intexina 38, 38, 40 µm.

Comparación.–Los especímenes descritos son comparables a *Diducites mucronatus* (Kedo) Van Veen, 1981 (pp. 275, 277-280; Pl. III, fig. 8; Pl. IV, Figs. 57; Pl. V, Figs. 1-6) pero difieren por un mayor grado de triangularidad y por la existencia de pliegues ecuatoriales en la capa interna de la exoexina. Además, *D. mucronatus* posee una intexina rígida de mayor grosor que la descrita para los especímenes estudiados en la FPI.

Género *Geminospora* Balme emend. Owens, 1971

Especie tipo: *Geminospora lemurata* Balme emend. Playford, 1983; por designación original.

Geminospora lemurata Balme emend. Playford, 1983
(Lám. 3, Figs. 9-11)

1962 *Geminospora lemurata* Balme, p.5; Pl. 1, Figs. 5-10.
1983 *Geminospora lemurata* Balme emend. Playford, pp. 316-321; Figs. 1-9.

Para sinonimia adicional ver Playford (1983, p. 320).

Descripción.–Espora radial de tipo trilete, amb circular ligeramente subtriangular. Lesuras claramente distinguibles, rectas, ocupando aprox. 3/4 del radio de la espora. Curvaturas perfectas distinguibles a indistinguibles. Exina cavada; exoexina de 2 µm de grosor, marcadamente convexa en la superficie distal y plana a piramidal en la superficie proximal. Áreas de contacto escabradas a punctadas, ligeramente deprimidas. Ecuatorial y distalmente presenta diminutos conos y espinas (de sección basal y altura inferior a 1µm) densamente distribuidos. Intexina lisa, de 0,4 µm de grosor, con frecuencia plegada ecuatorialmente.

Dimensiones (21 especímenes).–Diámetro ecuatorial 39 (46) 57 µm; diámetro de la intexina 30 (40) 46 µm.

Distribución.–Especie prácticamente cosmopolita durante el Givetiense-Frasniense superior, especialmente abundante durante el límite Givetiense-Frasniense (límite Devónico Medio-Devónico Superior). Para más referencias ver Playford, 1983 (pp. 321-322).

Género *Grandispora* Hoffmeister, Staplin & Malloy emend. Neves & Owens, 1966

Especie tipo: *Grandispora spinosa* Hoffmeister, Staplin & Malloy, 1955; por designación original.

Grandispora sp. A
(Lám. 3, Fig. 12)

Descripción.–Espora radial de tipo trilete; amb triangular subredondeado. Lesuras distinguibles, simples, rectas a ligeramente sinuosas, ocupando 4/5 del radio de la espora. Exina cavada; exoexina de 2 µm de grosor, distal y ecuatorialmente ornamentada con galeae y conos de 0,5-2 µm de altura, 2-7 µm de sección basal y 4-11 µm de separación; Exoexina proximal y distal (excluida la ornamentación) escabrada. Intexina lisa de aprox. 0,3 µm de grosor, distinguible, ocupando 4/5 del tamaño total de la espora.

Dimensiones (1 espécimen).–Diámetro ecuatorial 52 µm; diámetro de la intexina 44 µm.

Observaciones y comparación.–El estado de conservación del único espécimen observado en las muestras analizadas no es el adecuado para una correcta asignación específica. Sin embargo, puede ser comparable a *Grandispora echinata* Hacquebard, 1957 (p. 317; Pl. 3, Fig. 17), aunque esta última especie presenta labios bien definidos en las lesuras, carece de conos y galeae en la ornamentación de la exoexina distal y posee en general un mayor tamaño de los elementos esculturales. *G. fameniensis* (Naumova) Streel var. *fameniensis* Nekriata (sic) en Higgs, Avkhimovitch, Loboziak, Maziane-Serraj, Stempien-Salek & Streel, 2000 (p. 221; Pl. 4, Figs. 3-6), presenta una exoexina más delgada, curvaturas perfectas distinguibles y elementos esculturales, basados únicamente en espinas y galeae, de mayor tamaño.

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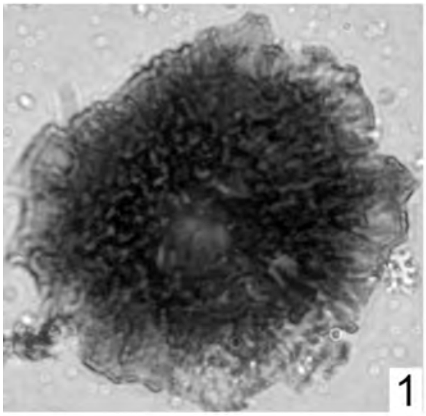
LÁMINA 3–*1-3*, *Cristatisporites* sp. cf. *C. inusitatus* (Allen) McGregor & Camfield, 1982, enfoque distal, x 1.000. *4-6*, *Cristatisporites triangulatus* (Allen) McGregor & Camfield, 1982; *4*, enfoque proximal, x 1.000; *5*, enfoque proximal, x 900; *6*, vista transversal, x 850. 7, 8, *Diducites* sp. A, enfoque medio; *7*, x 900; 8, x 1.000. *9-11*, *Geminospora lemurata* Balme emend. Playford, 1983; *9*, *10*, vista no polar, x 1.000; *11*, enfoque medio, x 1.000. 12, *Grandispora* sp. A, enfoque medio, x 1.000.

LÁMINA 3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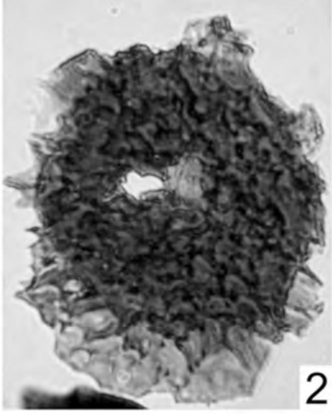
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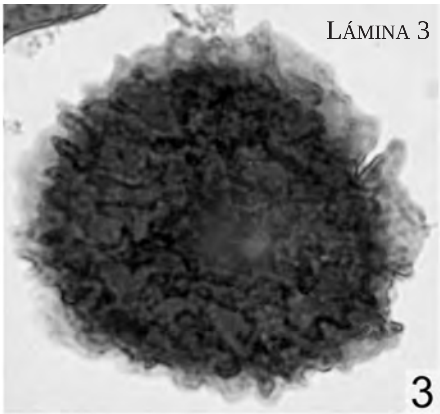
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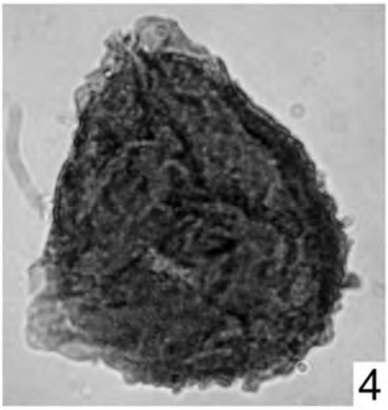
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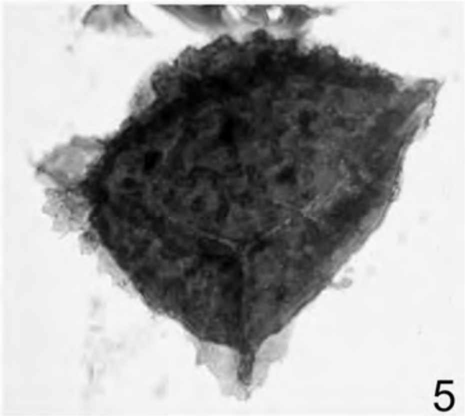
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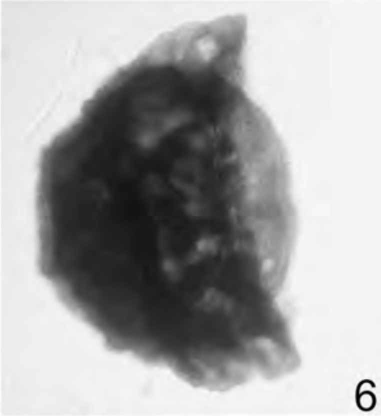
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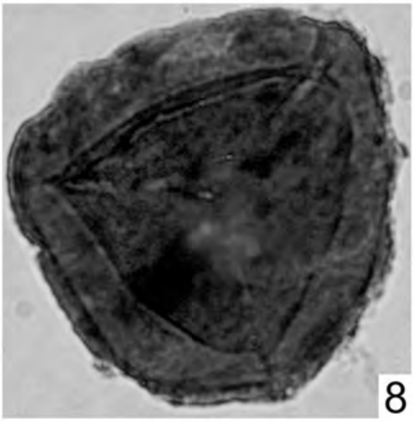
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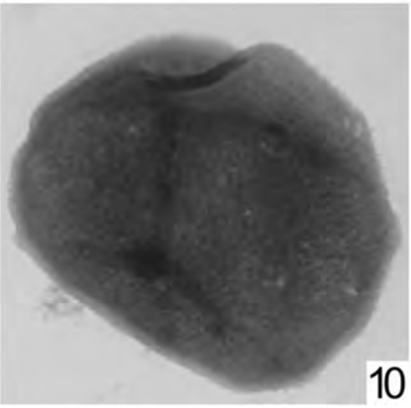
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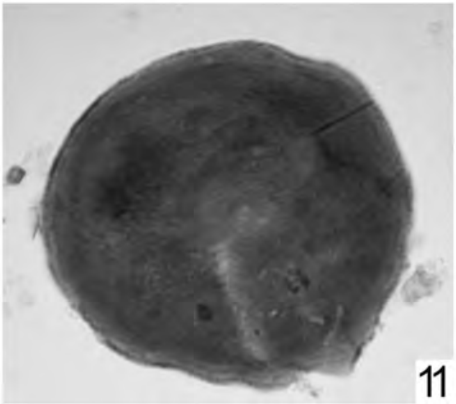
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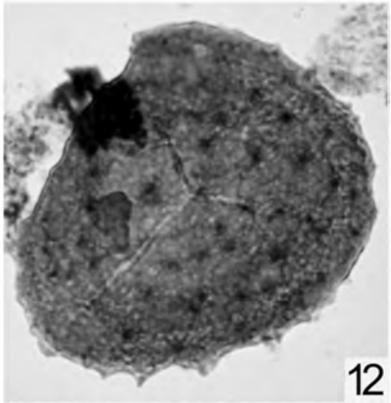
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(b) Algas Prasinofíceas

División CHLOROPHYTA Pascher, 1914
Clase PRASINOPHYCEAE Christensen, 1962
Familia LEIOSPHAERIDIACEAE Timofeev, 1956 nom. corr. MÄDLER, 1963
Género *Leiosphaeridia* Eisenack, 1958
Especie tipo: *Leiosphaeridia baltica* Eisenack, 1958; por designación original.
Leiosphaeridia spp.
(Lám. 4, Figs. 1, 2)

Observaciones.–Se han obtenido diversos especímenes atribuibles a *Leiosphaeridia* Eisenack, 1958. Dichas formas presentan una vesícula esférica simple, de contorno circular/subcircular (de 19-49 µm de diámetro) y eilyma delgada (de 0,7-1 µm de grosor), modificada por pliegues de compresión de gran escala. El valor biostratigráfico de este taxón no es significativo, por lo que no se ha llevado a cabo su clasificación a nivel específico.

Género *Tasmanites* Newton, 1875
Especie tipo: *Tasmanites punctatus* Newton, 1875; por designación original.
Tasmanites spp.
(Lám. 4, Fig. 3)

Observaciones.–Se han hallado diversos especímenes de vesícula simple, redondeada/subredondeda, de 33-75 µm de diámetro y eilyma gruesa (2,5-4 µm), lisa o microgranulada asignables a *Tasmanites* Newton, 1875. Dado el escaso valor biostratigráfico de este género, no se ha llevado a cabo su clasificación a nivel específico.

Familia PTEROSPERMELLACEAE Eisenack, 1972
Género *Maranhites* Brito emend. Burjack & Oliveira, 1989.
Especie tipo: *Maranhites brasiliensis* Brito, 1965 emend. Burjack & Oliveira, 1989; por designación original.
Maranhites brasiliensis Brito emend. Burjack & Oliveira, 1989
(Lám. 4, Figs. 4, 5)

1965 *Maranhites brasiliensis* Brito, p. 2; Est. I, Fig. 1. (1965a).
1989 *Maranhites brasiliensis* Brito emend. Burjack & Oliveira, pp. 49-51; Est. I, Figs. 1, 2, 4, 5, 8, 9.

Para sinonimia adicional ver Eisenack (1979, p. 367).

Descripción.–Vesícula originalmente discoidal, de contorno circular y margen ondulado. Eilyma dividida en dos paredes; endeilyma lisa de 2,5-3 µm de espesor, ornamentada ecuatorialmente con engrosamientos de contorno subcircular a elíptico, de 3-4 µm de dimensión mayor, unidos entre sí mediante arcos de 1-3 µm de anchura y hasta 4 µm de longitud. Uno de los engrosamientos posee una morfología alargada, ligeramente cóncava, de 11-14 µm de longitud y 6-7,5 µm de anchura. Perieilyma visiblemente más delgada, escabrada. No se observan estructuras de enquistamiento.

Dimensiones (4 especímenes).–Diámetro ecuatorial 80-105 µm.

Comparación.–Esta especie difiere de *Maranhites gallicus* Taugourdeau-Lantz, 1968 (p. 162; Pl. XIII, Fig. 9; Pl. XIV, Figs. 1-3) únicamente por la falta de conexión entre sus engrosamientos ecuatoriales.

Distribución.–Descrita en el Frasniense-Estruniense inferior de Brasil (Brito, 1965a, b, 1967a, b, 1976, 1978; Daemon *et al*, 1967; Daemon & Contreiras, 1971; Burjack & Oliveira, 1989) Emsiense-Frasniense inferior de Francia (Moreau-Benoit, 1974; Taugourdeau-Lantz, 1968); Emsiense-Frasniense de Ghana (Anan-Yorke, 1974); Givetiense-Frasniense de Australia (Colbath, 1990); Fameniense de Norteamérica (Wood, 1984; Playford & McGregor, 1993); y Fameniense de España y Portugal (Moreno *et al.*, 2003; Cunha & Oliveira, 1989; Pereira, 1999).

Maranhites britoii Stockmans & Willière, 1969
(Lám. 4, Figs. 6-9)

1969 *Maranhites britoii* Stockmans & Willière, p. 44; Pl. 2, Figs. 4, 7.
1980 *Maranhites* sp. Attar, Candilier, Fournier & Coquel, p. 594; Pl. 5, Fig. 6.

Descripción.–Vesícula originalmente discoidal, de contorno circular a subcircular y borde ondulado; Eilyma dividida en dos paredes; endeilyma lisa, de 1.5-2 µm de grosor. Las concavidades ecuatoriales están ocupadas por proyecciones traslúcidas subredondeadas, subrectangulares u ovales de 5-19 µm de diámetro máximo, proyectadas más allá del margen de la vesícula, confiriendo a ésta un aspecto lobulado. Perieilyma mucho más delgada, lisa o ligeramente rugulada/reticulada. No presenta estructura de enquistamiento.

Dimensiones (8 especímenes).–Diámetro ecuatorial 40 (57) 79 µm.

Observaciones.–La deficiente calidad de preservación de los especímenes estudiados se traduce en la pérdida parcial o total de las estructuras vesiculares ecuatoriales, modificando visiblemente el contorno de la vesícula.

Distribución.–Registrada en el Frasniense de Francia (Le Hérissé & Deunff, 1988); Frasniense superior y Fameniense de Belgica (Stockmans & Willière, 1969; Martin, 1981, 1985); Devónico Superior-Carbonífero Inferior de Algelia (Moreau-Benoit *et al.*, 1993; Latreche & Coquel, 1996); y Frasniense de Irán (Hashemi & Playford, 1998).

Maranhites mosesii (Sommer) Brito, 1967
(Lám. 4, Fig. 10)

1956 *Tasmanites mosesii* Sommer, p.458; Pl, 1, Figs. 6-8.
1963 *Tapajonites mosesii* Sommer & Van Boekel, p. 35; Pl. 2, Figs. 1-3.
1965 *Tapajonites mosesii* Brito, pp. 2, 4; Pl. 3, Figs. 1-3, 5. (1965b).
1966 *Tapajonites mosesi* Benoit, p. 226; Pl. 3, Fig. 57.
1967 *Maranhites mosesii* (Sommer) Brito, Pl. 2, Fig. 12. (1967a).
1967 *Maranhites mosesii* (Sommer) Brito, pp. 164-165; Pl. 2, Figs. 3-6. (1967b).

Para más sinonimia ver Eisenack *et al*. (1979, p. 372) y Burjack & Oliveira (1989, pp. 51, 53).

Descripción.–Vesícula originalmente discoidal, de contorno circular. Eilyma dividida en dos paredes; endeilyma lisa, de 1,5-2,5 µm de grosor, ornamentada ecuatorialmente con 3-7 engrosamientos subcirculares a elípticos, no equidistantes de 10-18 µm de diámetro máximo. Perieilyma mucho más delgada, lisa o microrugulada/microreticulada. No se observa estructura de enquistamiento.

Dimensiones (4 especímenes).–Diámetro ecuatorial 56-62 µm.

Observaciones.–Burjack & Oliveira, 1989 (pp. 51-54), proponen la disociación de Maranhites mosesii (Somer) Brito, 1967 en M. mosesii (Somer) Brito emend. Burjack & Oliveira, 1989 y M. insulatus Burjack & Oliveira, 1989. El análisis palinológico realizado en materiales devónicos de la FPI (González *et al.*, b, en revisión), pone de manifiesto la gran variabilidad morfológica de *M. mosesii* y la dificultad de sostener la propuesta de segregación de estos autores.

Distribución.–Descrito en el Devónico de Francia (Moreau-Benoit, 1966); Devónico Medio y Superior de Brasil (Sommer, 1956; Sommer & Van Boekel, 1966; Brito, 1965b, 1967a, b, 1976, Brito & Quadros, 1984; Ludwig & Müller, 1968; Burjack & Oliveira, 1989); Devónico Superior de España y Portugal (Pereira *et al.*, 1994; Pereira, 1999; Moreno *et al.*, 2003); Devónico Superior de Norteamérica (Molyneux *et al.*, 1984; Playford & McGregor, 1993); y Devónico Superior-Carbonífero Inferior de Algelia (Attar *et al.*, 1980) y Sahara (Coquel & Latreche, 1989).

(c) Acritarcos

Grupo ACRITARCHA Evitt, 1963
Género *Gorgonisphaeridium* Staplin, Jansonius & Pocock, 1965
Especie tipo: *Gorgonisphaeridium winslowiae* Staplin, Jansonius & Pocock, 1965; por designación original.
Gorgonisphaeridium sp. cf. *Gorgonisphaeridium disparatum* Playford, 1977
(Lám. 4, Fig. 11)

cf. 1977 *Gorgonisphaeridium disparatum* Playford, p. 23; Pl. 9, Figs. 8-16.

Descripción.–Vesícula originalmente esférica, contorno circular a subcircular y procesos claramente distinguibles. Eilyma en torno a 1 µm de grosor, escabrada, con numerosos procesos (en torno a 100), sólidos, lisos, de base subredondeada, 1,5 µm de sección basal, 2-7 µm de longitud, y 2-9 µm de separación. La mayoría de los procesos presenta bifurcaciones y algunas trifurcaciones apicales de segundo orden, produciendo pinnae de terminaciones redondeadas. Existen, además, escasos procesos simples, no furcados, con terminaciones igualmente redondeadas. No se observa estructura de enquistamiento, sí diversos pliegues de compresión paralelos al contorno de la vesícula.

Dimensiones (1 espécimen).–Diámetro de la vesícula 35 µm; diámetro total 42 µm.

Observaciones.–Se desestima la completa asignación a *Gorgonisphaeridium disparatum* Playford, 1977 en base al deficiente estado de preservación del único espécimen registrado.

Distribución.–Registrado previamente en el Emsiense de Canadá (Playford, 1977).

Gorgonisphaeridium sp. A
(Lám. 4, Fig. 12)

Descripción.–Vesícula esférica originalmente redondeada, de contorno circular y procesos claramente distinguibles. Eilyma 1-1,5 µm de grosor, lisa; densamente ornamentada con numerosos procesos sólidos, homomórficos, lisos, de ápices afinados, base circular, 0,5-1,2 µm de sección basal, 1-3 µm de longitud y 1-2 µm de separación. No se observa estructura de enquistamiento, sí algunos pliegues de compresión de gran escala.

Dimensiones (3 especímenes).–Diámetro de la vesícula 28, 29, 31 µm.

Comparación.–Existe cierta semejanza entre *Gorgonisphaeridium* sp. A y *G. carnarvonense* Playford, 1981, pero la especie del Frasniense australiano presenta una mayor densidad de procesos más cortos y delgados.

COMPOSICIÓN, EDAD Y CARACTERÍSTICAS AMBIENTALES DE LA PALINOFLORA

El análisis palinoestratigráfico de las pizarras negras que afloran en el núcleo del antiforme de Valverde del Camino proporciona datos cronoestratigráficos y paleoambientales que permiten profundizar en el conocimiento de la cuenca devónica de la FPI. La mayoría de las muestras analizadas contienen una asociación de palinomorfos compuesta fundamentalmente por miosporas de tipo trilete y en menor medida microflora de origen marino o microfitoplancton (algas prasinofíceas y acritarcos). De forma minoritaria, también se recuperaron partículas peculiares de procedencia continental, tales como fitoclastos y tétradas de esporas tipo trilete.

De un total de 11 muestras, han sido identificadas 16 especies de esporas, 4 de algas prasinofíceas y 2 de acritarcos. Once de las especies de esporas y 3 de las de microfitoplancton han sido asignadas a especies previamente descritas. Tres especies, una por cada grupo de palinomorfos diferenciado, han sido comparadas con taxones ya instituidos y 5 especies no registradas con anterioridad (4 de esporas y 1 de acritarcos), han sido descritas bajo nomenclatura abierta (sp. A), dado el escaso número de especímenes disponibles. Con carácter general, la productividad palinológica de las pizarras ha sido baja, exceptuando las muestras G9-e y G10-e, y su estado de conservación deficiente, lo cual se traduce en una desigual distribución del contenido palinológico a lo largo del perfil estudiado, como se observa en la Tabla 2.

La asociación de miosporas de las pizarras del PQ del área de estudio esta compuesta mayoritariamente por taxones representativos del Devónico Medio-Superior. Entre las especies con mayor valor bioestratigráfico destacan *Chelinospora concinna* Allen, 1965, *Cristatisporites triangulatus* (Allen) McGregor & Camfield, 1982, *Geminospora lemurata* Balme emend. Playford, 1983, *Retusotriletes rugulatus* Riegel, 1973, *Aneurospora greggsii* (McGregor) Streel en Becker, Bless, Streel & Thorez, 1974 y *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, 1982.

G01b	G04c	G06i	G09b	G09e	G09g	G09i	G10a	G10e	G11a	G11b	Muestra / Especie
											MIOSPORAS
				●				●			*Punctatisporites planus*
				●		●		●			*P. scabratus*
	●			●						●	*Retusotriletes rotundus*
						●		●		●	*R. rugulatus*
								●			*Verrucosisporites scurrus*
				●				●			*Convolutispora ampla*
				●				●			*C.* sp. A
				●							*Dictyotriletes* sp. A
						●		●			*Aneurospora greggsii*
		●						●			*Chelinospora concinna*
	●			●	●	●		●			*Cristatisporites* sp. cf. *C. inusitatus*
	●			●		●		●			*C. triangulatus*
	●				●			●			*Diducites* sp. A
	●			●	●	●		●		●	*Geminospora lemurata*
					●						*Grandispora* sp. A
											ALGAS PRASINOFÍCEAS
●									●		*Leiosphaeridia* spp.
●	●			●		●	●	●		●	*Tasmanites* spp.
●											*Maranhites brasiliensis*
●	●										*M. britoii*
										●	*M. mosesii*
											ACRITARCOS
	●										*Gorgonisphaeridium* sp. cf. *G. disparatum*
			●					●		●	*G.* sp. A

TABLA 2–Composición de la asociación de palinomorfos recuperada de las pizarras del Grupo PQ analizadas.

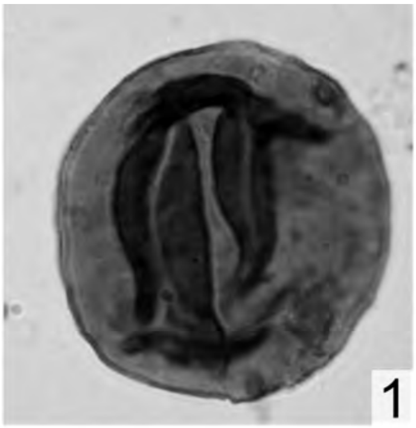
TABLE 2–Composition of the palynomorph assemblage obatained from the PQ Group shales.

La presencia de las miosporas *C. triangulatus* y *C. concinna* permite la asignación directa de la asociación recuperada a la Biozona TCo (*C. triangulatus-C. concinna*) del esquema de Streel *et al*. (1987), asignable al Givetiense superior-Frasniense inferior (Tabla 3). Biozona que está definida por la presencia de *C. triangulatus*, que

→

LÁMINA 4–*1, 2, Leiosphaeridia* spp.; *1,* x 1.000; *2,* x 800. *3, Tasmanites* sp., x 800. *4, 5, Maranhites brasiliensis* Brito emend. Burjack & Oliveira, 1989; *4,* x 450; *5,* x 600. *6-9, Maranhites britoii* Stockmans & Willière, 1969; *6,* x 700; *7, 9,* x 800; *8,* x 1.000. *10, Maranhites mosesii* (Sommer) Brito, 1967, x 800. 11, *Gorgonisphaeridium* sp. cf. *Gorgonisphaeridium disparatum* Playford, 1977, x 1.250. *12, Gorgonisphaeridium* sp. A, x 1.800.

LÁMINA 4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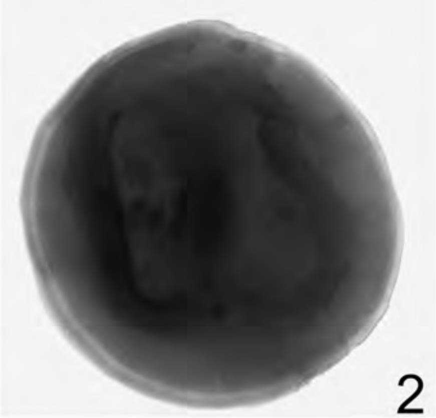
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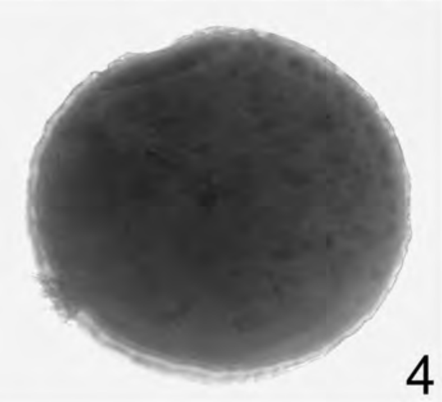
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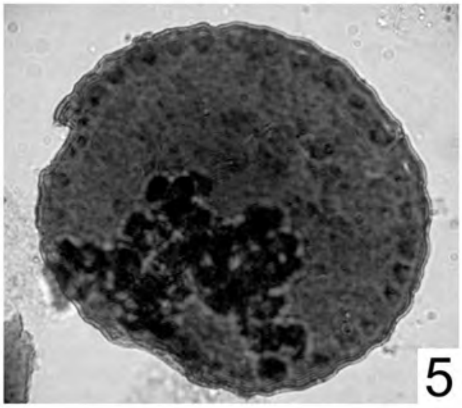
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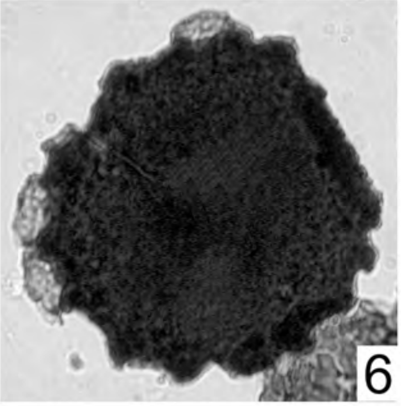
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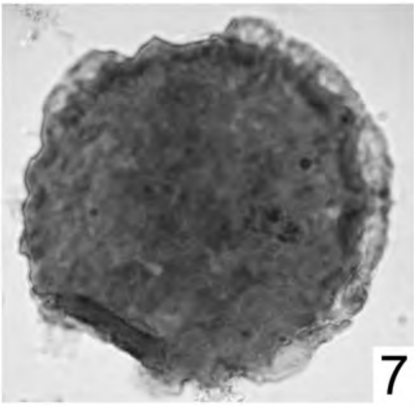
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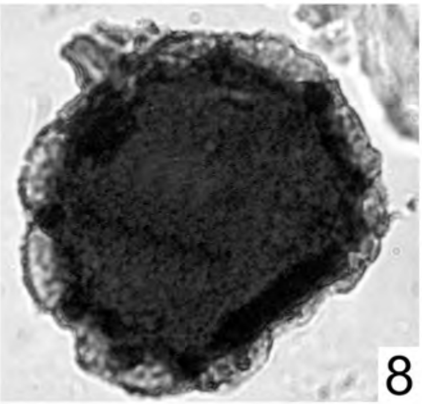
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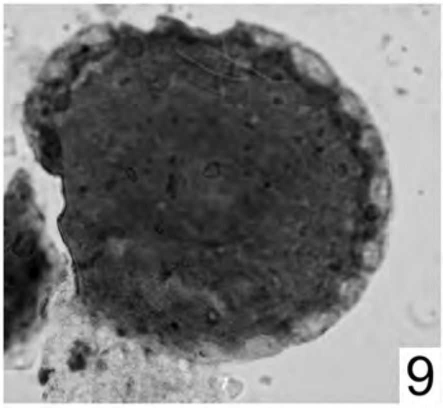
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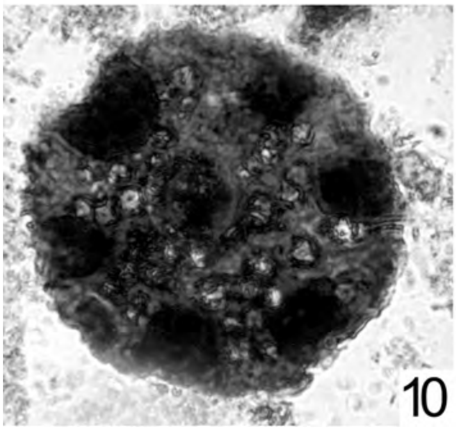
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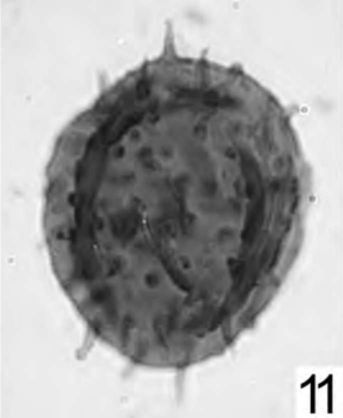
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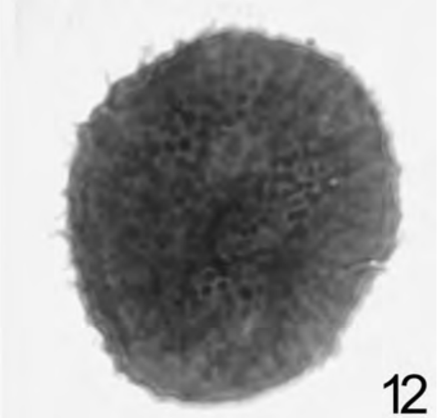
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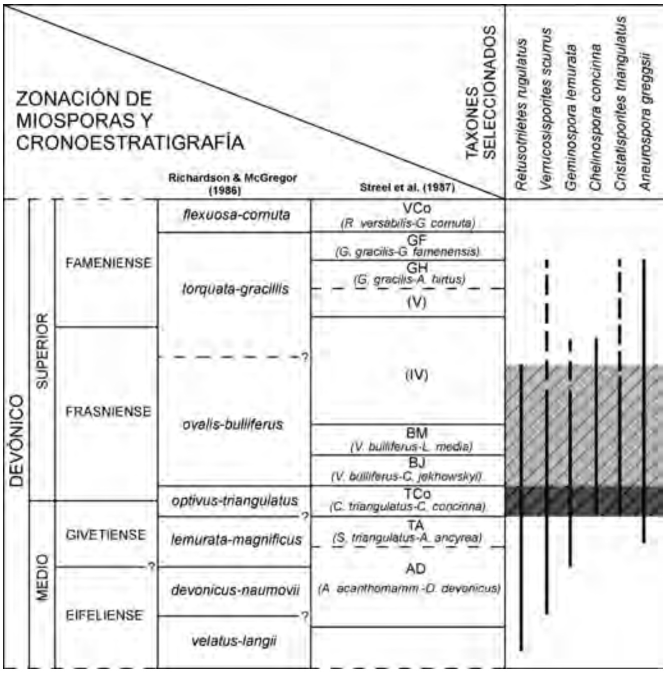

TABLA 3–Rango estratigráfico propuesto (gris oscuro) y máximo (gris claro) de la asociación de esporas seleccionadas de las pizarras del Grupo PQ. Comparación con los esquemas de biozonación de Richardson & McGregor (1986) y Streel *et al*. (1987).

TABLE 3–Suggested (dark colour) and maximum (light colour) stratigraphical range of a selected spore assemblage from the PQ Group shales. Richardson & McGregor (1986) and Streel *et al*. (1987) biozonation schemes are included.

aparece por primera vez en la Biozona TA (*C. triangulatus-A. ancyrea*), y por la aparición conjunta de *C. concinna y Cirratriradiates jekhowinski* Taugourdeau-Lantz, 1967. La asociación estudiada no contiene ningún ejemplar de *C. jekhowinski*, aunque el resto de miosporas son características y comunes en este intervalo de edad. Esta asignación se ve además reforzada por la ausencia de especies características de la Biozona inmediatamente superior, BJ *(V. bulliferus-C. jekhowinski)*, tales como *Archeoperisaccus opiparus* Owens, 1971, *A. ovalis* Naumova, 1953, *Lophozonotriletes media* Taugourdeau-Lantz, 1967 y *Verrucosisporites bulliferus* Richadson & McGregor, 1986. Cabe la posibilidad de que la ausencia de estos taxones se deba al carácter empobrecido de la asociación en relación con su deficiente estado de conservación. En tal caso, el rango de edad debería ampliarse hasta el Frasniense superior según criterios de distribución estratigráfica de los especímenes (Tabla 3). Teniendo en cuenta esta posibilidad, consideramos que la edad proporcionada por la asociación de palinomorfos de las pizarras del PQ de la parte más oriental de la FPI es Givetiense superior-Frasniense inferior?, donde el signo de interrogación hace referencia a la posibilidad de ampliación indicada anteriormente.

En cuanto al contenido en microflora marina, lo más reseñable es la presencia de diversas especies de algas prasinofíceas del género *Maranhites* Brito emend. Burjack & Oliveira, 1989, tales como *M. mosesii* (Sommer) Brito, 1967, *M. brasiliensis* Brito emend. Burjack & Oliveira, 1989 y *M. britoii* Stockmans & Willière, 1969, cuyo rango bioestratigráfico abarca gran parte del Devónico Medio y Superior. La escasa representación de acritarcos se ciñe a algunos especímenes asignables al género *Gorgonisphaeridium* Staplin, Jansonius & Pocock, 1965, recuperados de forma errática.

Las muestras analizadas presentan un elevado porcentaje de miosporas de origen continental y una proporción menor de microflora marina, constituida mayoritariamente por algas prasinofíceas y escasos acritarcos. El deficiente estado de conservación parece haber influido en el porcentaje final de cada uno de estos grupos palinológicos y plantea la sospecha que estas proporciones pudieran ser de origen secundario. La relación inicial entre los diferentes grupos de palinomorfos pudiera haberse modificado durante la tafocenosis. Posiblemente haya existido una disminución en el contenido de palinomorfos de pared delgada (fundamentalmente esporas simples, no ornamentadas de pared fina y acritarcos) a favor de un aumento en la proporción de palinomorfos de pared gruesa (esporas de exina gruesa y algas prasinofíceas). Aunque este hecho dificulte las interpretaciónes de tipo paleoambiental, hay algunos datos fundamentales a destacar: 1) presencia de microfitoplancton, 2) elevada proporción y variedad de miosporas y 3) presencia relativamente común de tétradas y microfitoclastos. Datos que indican medio marino, proximidad al área fuente y escaso transporte respectivamente. Por lo tanto, y como había sido propuesto anteriormente por Moreno y Sáez (1991) y Moreno *et al*. (1996), la parte inferior del Grupo PQ se debió depositar en un medio sedimentario marino, somero y cercano a tierra emergida.

CONCLUSIONES

El análisis palinoestratigráfico de las pizarras de la parte inferior del Grupo PQ del sector más oriental de la Faja Pirítica Ibérica permite extraer las siguientes conclusiones:

1) La pizarras estudiadas contienen palinomorfos del Devónico Medio-Superior.
2) Se han identificado 16 especies de esporas de tipo trilete, 4 de algas prasinofíceas y 2 de acritarcos.
3) El estado de conservación de los palinomorfos es deficiente para la mayoría de los taxones, de manera que la proporción inicial de los grupos de palinomorfos parece haber sido modificada durante la tafocenosis.
4) La distribución de los taxones en el perfil estudiado es irregular y no parece seguir patrón alguno.
5) Los palinomorfos de mayor valor bioestratigráfico de la asociación recuperada son las esporas *Chelinospora concinna* Allen, 1965, *Cristatisporites triangulatus* (Allen) McGregor & Camfield, 1982, *Geminospora lemurata* Balme emend. Playford, 1983, *Retusotriletes rugulatus* Riegel, 1973, *Aneurospora greggsii* (McGregor) Streel en Becker, Bless, Streel & Thorez, 1974 y *Verrucosisporites scurrus* (Naumova) McGregor & Camfield, 1982.
6) La asociación de miosporas obtenida es asignable a la Biozona TCo (*C. triangulatus*-*C. concinna*) del esquema de Streel *et al*. (1987).
7) La edad que proporcionan los datos anteriores es Givetiense superior-Frasniense inferior? (el signo de interrogación hace referencia a la posibilidad ampliación del rango de edad hasta el Frasniense superior). Esta edad es, junto a la proporcionada por Lake *et al*. (1988), la más antigua reconocida para las rocas de la FPI.
8) El análisis de la asociación de palinomorfos indica un medio sedimentario marino y próximo al continente que corrobora el medio de plataforma marina somera propuesto por Moreno y Sáez (1991) para los materiales del grupo PQ.

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CAMPANIAN TO PALEOCENE DINOFLAGELLATE CYST BIOSTRATIGRAPHY FROM OFFSHORE SEDIMENTS IN THE TANO BASIN, SOUTHWESTERN GHANA

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Abstract

Dinoflagellate cysts have been recovered and studied from sediments between intervals 6,440 ft (1,932 m)-600 ft (180 m) in well 1S-3AX, offshore Tano basin. The dinoflagellate assemblage is abundant, diverse and well preserved. Three biozones *(Trichodinium castanea, Cordosphaeridium 'complex'*, and *Carpatella cornuta Zones)* have been identified based on the First Appearance Datum (FAD) and Last Appearance Datum (LAD) of important species. Biostratigraphically significant taxa found in the assemblages allowed the identification of Early to Late Campanian, Early to Late Maastrichtian and Early Paleocene age for the biozones respectively. Vertical distribution of dinoflagellate assemblages upwards in the well suggests a near shore or brackish environment of deposition for the Campanian sediments, and an open marine environment for the Maastrichtian and Paleocene sediments. The peridiniacean assemblage *(Andalusiella, Cerodinium, Phelodinium, Senegalinium)* is assigned to the tropical-subtropical Malloy suite of Lentin and Williams (1980).

Key words: Biostratigraphy, dinoflagellate, Campanian, Maastrichtian, Paleocene, Ghana.

Resumen

Se han estudiado los quistes de dinoflagelados de los sedimentos litorales en el intervalo entre 6.440 pies (1.932 m) y 600 pies (180 m) del sondeo 1S-3AX, de la cuenca de Tano. Las asociaciones de dinoflagelados son abundantes, diversas y están bien conservadas. Se han identificado tres biozonas (Zonas *Trichodinium castanea, Cordosphaeridium* complex y *Carpatella cornuta*) empleando los datos del registro de Primera Aparición y del registro de Última Aparición de las especies más representativas. Bioestratigráficamente, los taxones más significativos encontrados en las asociaciones nos permite datar las biozonas descritas en una edad de Campaniense inicial a Campaniense terminal, Maastrichtiense inicial a Maastrichtiense terminal y Paleoceno inicial, respectivamente. La distribución vertical de las asociaciones de dinoflagelados hacia techo del sondeo, nos sugiere un ambiente costero o mareal de deposición para los sedimentos de edad Campaniense y medio marino abierto para los sedimentos del Maastrichtiense y Paleoceno. La asociación de peridináceos *(Andalusiella, Cerodinium, Phelodinium* y *Senegalinium)* es asignada al grupo Malloy tropical-subtropical de Lentin & Williams (1980).

Palabras clave: Bioestratigrafía, dinoflagelados, Campaniense, Maastrichtiense, Paleoceno, Ghana.

INTRODUCTION

Well 1S-3AX is located at latitude 4° 43' 22.03"N and longitude 2° 58' 44.30"W offshore in the Tano Basin, in the southwestern part of Ghana (Fig. 1). Onshore, the rocks (Mesozoic-Tertiary) occur on the eastern side of a crescent-shaped basin which is located in approximately 200 m water depth, offshore southwestern Ghana. The basin lies between the mouths of the River Ankobra to the east and River Tano to the west, a distance of about 96 km and continues offshore into the Gulf of Guinea. The basin extends to the southeast corners of Côte d'Ivoire and occupies a total area of about 1165.50 sq. km. The sedimentary rocks of the basin are alternating sands, clays and limestones with a general dip direction of south southwest and dip angles between 2°-5°. The rocks overlie the Precambrian Birimian basement rocks. Both the limestone and clays have yielded fauna of mollusca, ostracoda and foraminifera. Khan (1970) and Cox (1952) have assigned Cenomanian-Maastrichtian to these rocks. Recent drilling reports indicate Aptian-Oligocene ages.

Offshore, information about the structure and sediment accumulation of the basin has been obtained from seismic, Ocean Drilling Programme (ODP) Leg 159 and Submersible Deep Dives (Equanaute Survey). Mascle *et al.* (1988) have indicated that the Côte d'Ivoire-Ghana (CIG) transform margin is the result of the continental break up due to transform motion and subsequent opening of the south Atlantic Ocean during Early Cretaceous times and suggest the morphological feature of this margin is a NE–SW trending 103 km long marginal ridge. Lamarche *et al*. (1997) indicated that the ridge comprises a sedimentary sequence continuous with the synrift sediments of the Ivorian Basin. Guiraud *et al*. (1997a) identified three lithofacies within the synrift to syntransform basal sequence which constitute the main component of the CIG sedimentary wedge. These are dark clays, yellowish siltstones and interbedded greenish fine sandstone, and grey coarse sandstones and microconglomerates. These lithologic sequences have been observed in boreholes drilled in the study area (i. e Tano Basin). Guiraud *et al*. (1997a) also interpreted a shallow marine deltaic environment for the synrift deposit of CIG ridge which is probably of Early Cretaceous age. Oboh-Ikuenobe *et al.* (1998) and Masure *et al.* (1998) have assigned an age range of Late Albian-Pleistocene to the sedimentary sequence that was drilled at sites 959 to 962 along the CIG transform passive margin from ODP Leg 159. These ages corroborate those obtained from boreholes drilled in the Tano Basin.

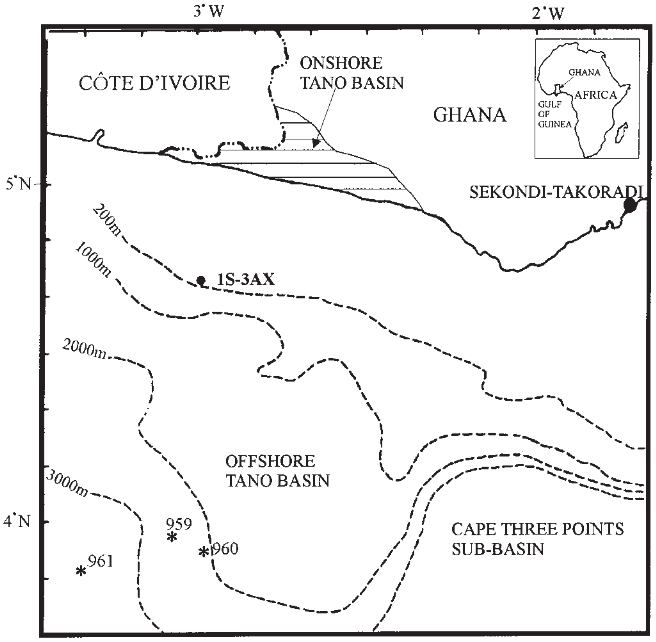

FIGURE 1–Location map of well 1S-3AX and location sites of ODP Leg 159 (959 through 961 in the CIG transform margin in offshore Tano basin (modified after Offshore Activity Map of GNPC, 1994).

MATERIALS AND METHODS OF STUDY

Thirty-six (36) cutting samples obtained from well 1S-3AX were used for this study. The lithologies of the samples are sandstones, sandy shales, shales and calcareous shales. The samples were processed for palynomorphs according to the standard techniques of maceration used for concentrating acid insoluble microfossils, by using commercial grades hydrochloric (35-38%), and hydrofluoric (40%) acids to digest the carbonates and silica-silicates of the rocks respectively. Oxidation was avoided because most of the organic matter was translucent and details could be seen under transmitted light. The residue was subjected to ultrasonication, and heavy liquid separation was in Zinc Bromide ($Zn\ B_2$) with specific gravity 2.0. The palynomorphs were prepared for light microscopy by strew mounting them in Polyvinyl alcohol (PVA) and curing them in ultra violet (UV) light for about two minutes.

SYSTEMATICS

Descriptive terminologies used in the systematic descriptions of the dinoflagellate cysts are those proposed by Williams *et al.* (1973), Evitt *et al.* (1977), Stover and Evitt (1978) and Norris (1978). The classification of the dinoflagellates employed is based on the "Cyst Genus" concept of Stover and Evitt (1978), and is put into three (3) morphological groups: a) Spiniferate/Gonyaulacoid, b) Peridinioid, and c) Dinogymnoid. They are listed as cyst genera under the above morphological groupings and their stratigraphic significance in relation to the present study stressed where appropriate.

Division PYRRHOPHYTA Pascher, 1914
Class DINOPHYCEAE Fritsch, 1935
SPINIFERATE/GONYAULACOID
Cyst Genus *Spiniferites* Mantell emend. Sarjeant, 1970
Spiniferites ramosus Loeblich Jr. and Loeblich III, 1966
(Pl. 3, Figs. 17, 19, 20)

Remarks.–Specimens observed exhibited considerable range of variation in process length, surface ornamentation and development of membrane between processes.

Spiniferites bear spine-like processes that are similar in structure and distribution to *Achomosphaera* Evitt, 1963 but differ by possessing sutural ridges that connect their bases.

Spiniferites septatus (Cookson and Eisenack) McLean, 1971
(Pl. 3, Figs. 14, 18)

Remarks.–The specimen is distinguished from other forms of *Spiniferites* by its septate processes and dense body. This specimen has been observed from the Maastrichtian of the present study. Costa and Manum (1988) indicate that the species appear for the first time at the base of the Paleocene. For the purposes of this study it would be suggested that the presence of this species is due to reworking, until further work from other wells in the area prove otherwise.

Cyst Genus *Cordosphaeridium* Eisenack, 1963b emend. Morgenroth, 1968
Cordosphaeridium inodes (Klumpp) Eisenack, 1963b
(Pl. 4, Figs. 14, 15)

Remarks.–The endophragm and periphragm are appressed between processes that are intratabular, fibrous, hollow, branched and expanded distally. The terminally flared funnel shaped processes are characteristic of this species.

Cordosphaeridium fibrospinosum Davey and Williams, 1966
(Pl. 4, Figs. 9, 10)

Remarks.–Dense fibrous, intratabular processes characterise this species. Processes are short and perforate; whole or in some cases bifurcated. Apical and antapical processes are indistinct.

Cordosphaeridium multispinosum Davey and Williams, 1966
(Pl. 4, Fig. 16)

Remarks.–This species has numerous, generally simple, short, parallel-sided fibrous processes with delicate appearance, single or branched with slight expansion distally.

Cordosphaeridium exilimurum Davey and Williams, 1966
(Pl. 4, Fig. 8)

Remarks.–The processes are frequently broad and fenestrate or perforate. Davey and Williams (1966), described this species as having an apical archeopyle. Eaton (1976), however, has indicated that the archeopyle in this species is in the precingular position and not apical as purported by Davey and Williams. Examination of some specimens studied here, supports Eaton's assertion.

Cyst Genus *Fibrocysta* Stover and Evitt, 1978
Fibrocysta bipolaris (Cookson and Eisenack) Stover and Evitt, 1978
(Pl. 3, Figs. 15, 22)

Remarks.–Specimens are characterized by their medium to long apical and antapical horns as well as distinct numerous solid, hollow and fibrous non-tabular processes.

Cyst Genus *Kenleyia* Cookson and Eisenack, 1965
Kenleyia pachycerata Cookson and Eisenack, 1965
(Pl. 3, Figs. 16, 21)

Remarks.–The low poorly delimited tuft-like, fibrous projections or lamella structures which enclose the cyst of *Kenleyia* in a sheath, differentiates it from the more or less distinct and long, fibrous processes of *Cordosphaeridium* and *Fibrocysta.*

Cyst Genus *Achilleodinium* Eaton, 1976
Achilleodinium sp.
(Pl. 3, Figs. 7, 8)

Description.–Cyst body subspherical to ellipsoidal with intratabular processes of variable size and shape, opened distally. Paracingulum and apical processes are narrower than those in the precingular and postcingular areas. Periphragm smooth, paratabulation indicated by intratabular and peritabular processes; paracingulum indicated by approximately six processes. Archeopyle is precingular with operculum free.

Dimensions.–Diameter of cyst body 42-55 µm, mean 50 µm. (6 specimens measured).

Length of processes.–12-20 µm, mean 16 µm.

Width of processes at base.–12-18 µm, mean 15 µm.

Remarks.–Specimens bear processes of variable sizes and shape which are opened distally. Paracingulum and apical processes are narrower than those in the precingular and postcingular areas.

Genus *Areoligera* Lejeune-Carpentier, 1938
Areoligera sp.
(Pl. 3, Figs. 12, 13)

Description.–Cyst body lenticular to ellipsoidal in shape; periphragm, endophragm not discernible. No parasutural elements observed. Processes peritabular, branched, forming arcuate distally branched process groups; tips of adjacent processes not connected by network of trabeculae. Autophragm or surface between processes smooth to scabrate. Paratabulation indicated by peritabular processes; archeopyle apical with operculum free. Paracingulum not discernible.

Dimensions.–Diameter of cyst body 60-75 µm, mean 68 µm. (8 specimens measured).

Length of processes.–12-18 µm, mean 15 µm.

Remarks.–The broad and membranous frequently fenestrate and digitate distal margins of this species are comparable to that of *A. coronata* (Wetzel) Lejeune-Carpentier, 1938. *Areoligera* differs from *Glaphyrocysta* in lacking intricate network of trabeculae between processes tips although a few adjacent processes tips may be joined occasionally by trabeculae.

Cyst Genus *Glaphyrocysta* Stover and Evitt, 1978
Glaphyrocysta sp.
(Pl. 4, Figs. 2, 6)

Description.–Cyst body lenticular to ellipsoidal in shape. No parasutural elements observed. Processes complex, formed by autophragm which is smooth to scabrate; processes complex, joined distally by a simple to intricate system of trabeculae; isolated processes are however, present. Mid-ventral and mid-dorsal areas are free of processes. Paratabulation indicated by archeopyle which is apical with free operculum. Paracingulum not easily discernible.

Dimensions.–Diameter of cyst body 60-100 µm, mean 72 µm. (15 specimens measured).

Length of processes.–12-36 µm, mean 26 µm.

Cyst Genus *Adnatosphaeridium* Williams
and Downie in Davey *et al.*, 1966
Adnatosphaeridium multispinosum Williams
and Downie, 1966
(Pl. 4, Figs. 1, 4)

Remarks.–A. multispinosum has numerous typical slender processes which rarely exceed half the mean diameter of the body in length. Generally *Adnatosphaeridium* differs from *Glaphyrocysta* in having spherical rather than a lenticular body and generally lacks the processes free areas normally present on *Glaphyrocysta.*

Cyst Genus *Trichodinium* Eisenack and Cookson, 1960
Trichodinium castanea (Deflandre) Clarke
and Verdier, 1967
(Pl. 3, Figs. 1, 2, 3)

Remarks.–This species is characterized by a short apical horn, and numerous relatively dense short solid

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PLATE 1–All figures x 660. *1, 2, 3. Cerodinium boloniense* (Riegel) Lentin and Williams, 1989. *4, 6, 7. Cerodinium obliquipes* (Deflandre and Cookson) Lentin and Williams, 1989. *5, 8. Cerodinium diebelli* (Alberti) Lentin and Williams, 1989. *9, 10, 11. Paleocystodinium australinium* (Cookson) Lentin and Williams, 1976. *12, 13. Paleocystodinium golzowense* Alberti, 1961. *14. Andalusiella gabonensis* (Stover and Evitt) Wrenn and Hart, 1988. *15, 16. Senegalinium laevigatum* (Malloy) Bujak and Davies, 1983. *17. Spinidinium* sp. *18, 19. Senegalinium bicavatum* Jain and Millepied, 1973.

Plate 1


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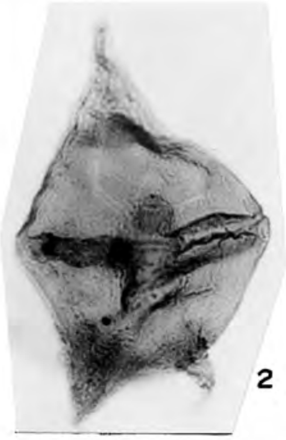
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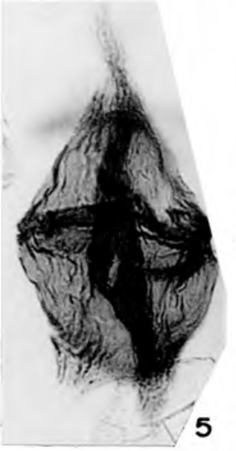
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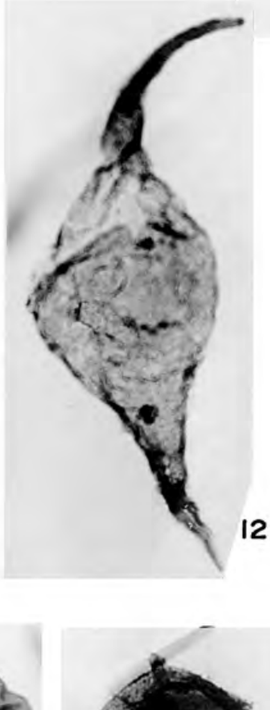
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spinae. Paratabulation is indicated by precingular archeopyle and paracingulum which is indicated by transverse equatorial alignment of spinae. From documented records this species appears to be restricted to the Campanian.

Cyst Genus *Carpatella* Grigorovich, 1969
Carpatella cornuta Grigorovich, 1969
(Pl. 3, Figs. 4, 6)

Remarks.–Horns present at both apical and antapical areas though not easily discernible in some specimens. Faint low parallel transverse equatorial ridges indicate paracingulum. From published data (Firth, 1987; Powell, 1999), this species is restricted to the Paleocene and has not been reported below the Maastrichtian/Danian boundary.

Cyst Genus *Xenascus* Cookson and Eisenack, 1969
Xenascus ceratioides (Deflandre) Lentin and
Williams, 1973
(Pl. 4, Figs. 5, 7)

Remarks.–Masure *et al.* (1998) described *X. ghanaensis* from CIG transform margin. This species has not been observed in the present study. *X. ghanaensis* Masure *et al.*, 1998 differs from *X. ceratioides* by having large pericoel around the margin of the central body and prominent truncated horns.

Genus *Odontochitina* Deflandre, 1935
Odontochitina operculata (Wetzel) Deflandre
and Cookson, 1955
(Pl. 2, Figs. 16, 17, 23)

Remarks.–*O. operculata* has a ceratoid shape with three long horns; one at apical antapical and a third probably in the paracingular area. *O. operculata* differs from *O. porifera* Cookson, 1956 by its smooth to scabrate surface of horn which is in contrast to perforate horns of *O. porifera* (Plate 2, Figures 17, 21).

Cyst Genus *Oligosphaeridium* Davey and Williams in
Davey *et al.*, 1966
Oligosphaeridium complex (White) Davey and
Williams, 1966
(Pl. 4, Figs. 12, 13)

Remarks.–Processes on these specimens are intratabular, open, expanded, serrated to sometimes branched distally. The rims of these processes bear long pointed to irregular bifurcate spinae. *Oligosphaeridium* differs from *Hystricosphaeridium* in lacking paracingular processes.

Cyst Genus *Diphyes* Cookson, 1965 emend. Davey
and Williams in Davey *et al*., 1966
Diphyes colligerum (Deflandre and Cookson)
Cookson, 1965
(Pl. 3, Figs. 10, 11)

Remarks.–The distinctive large antapical process which is diagnostic of this species enables easy orientation of the specimens. The genus *Coronifera* also possesses a large antapical and nontabular processes but however, differs from *Diphyes* by having a precingular archeopyle rather than an apical archeopyle which is observed in *Diphyes.*

PERIDINOID CYST
Cyst Genus *Andalusiella* Riegel, 1974
Andalusiella mauthei (Riegel) Riegel and Sarjeant,
1982
(Pl. 2, Figs. 1, 2)

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PLATE 2–All figures x 660. *1, 2. Andalusiella mauthei* (Riegel) Riegel and Sarjeant, 1982. *3, 5. Andalusiella polymorpha* (Malloy) Lentin and Williams, 1977. *4. Andalusiella rhomboides* (Boltenhagen) Lentin and Williams, 1980. *6, 12. Phelodinium tricuspis* (Wetzel) Stover and Evitt, 1978. *7, 11. Phelodinium magnificum* (Stanley) Stover and Evitt, 1978. *8. Dinogymnium digitus* (Deflandre) Evitt, Clarke and Verdier, 1967. *9. Andalusiella gabonensis* (Stover and Evitt) Wrenn and Hart, 1988. *10, 20. Dinogymnium undulosum* Cookson and Eisenack, 1970. *13. Andalusiella dubia* (Jain and Millepied) Lentin and Williams, 1980. *14, 15. Dinogymnium acuminatum* Clarke and Verdier, 1967. *16, 22, 23. Odontochitina operculatus* (Wetzel) Deflandre and Cookson, 1955. *17, 21. Odontochitina porifera* Cookson, 1956. *18. Dinogymnium* sp. 2. *19. Dinogymnium* sp. 1.

PLATE 2


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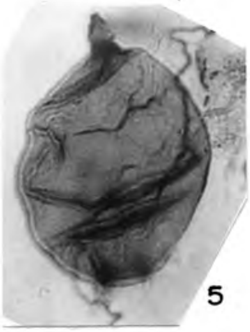
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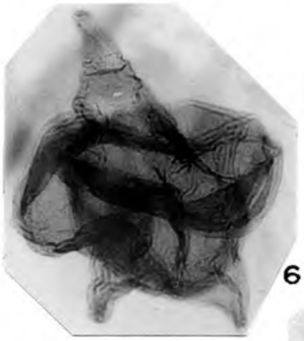
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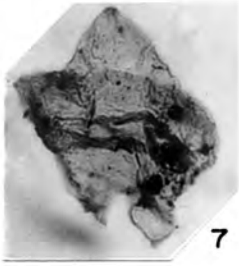
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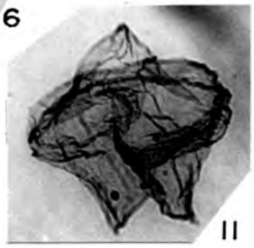
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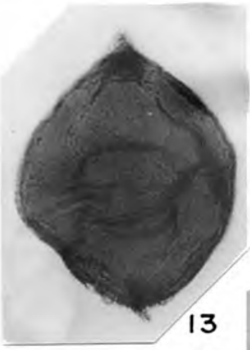
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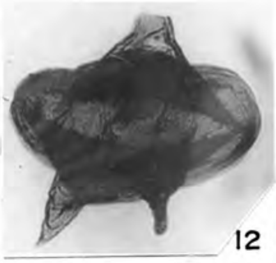
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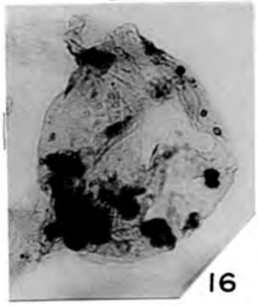
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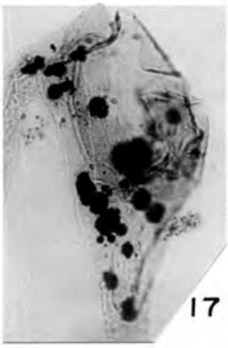
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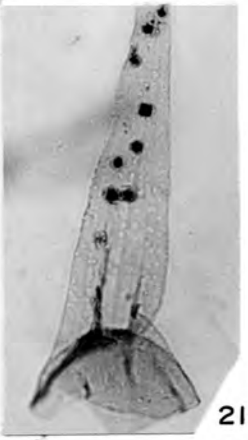
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Remarks.–The cyst is rhomboidal with a prominent apical and two antapical horns fused at base. Riegel (1974) and Riegel and Sarjeant (1982) in their emended diagnosis stated that the left antapical horn is short and sometimes marked by an angularity in the cyst wall with the right horn markedly longer. Masure *et al.* (1996) however, have shown from SEM micrographs of this species and diagramatic reconstruction that the left antapical horn is long with a short right antapical horn.

Andalusiella polymorpha (Malloy) Lentin and Williams, 1977
(Pl. 2, Figs. 3, 5)

Remarks.–*A. polymorpha* is differentiated from *A. mauthei* by having its antapical horns dissociated from adjacent bases close to the central body.

Andalusiella rhomboides (Boltenhagen) Lentin and Williams, 1980
(Pl. 2, Fig. 4)

Remarks.–This species differs from *A. dubia* (Jain and Millepied) Lentin and Williams, 1980, by its rhomboid shape and a single long apical and antapical horns. *A. dubia* (Plate 2, Figure 13) is ovoid to spherical in shape with very short horns.

Andalusiella gabonensis (Stover and Evitt) Wrenn and Hart, 1988
(Pl. 1, Fig. 14; Pl. 2, Fig. 9)

Remarks.–*A. gabonensis* is morphologically similar to *Paleocystodinium australinium* (Cookson) Lentin and Williams, 1976. However, *A. gabonensis* differs from the latter by having its antapical horn much closer to the base of the cyst body rather than being a spine-like projection emanating from about 2/3 to 3/4 the length of the primary antapical horn, as is the case in *P. australinium*.

Cyst Genus *Paleocystodinium* Alberti, 1961
Paleocystodinium golzowense Alberti, 1960
(Pl. 1, Figs. 12, 13)

Remarks.–*P. golzowense* appears strongly similar to *P. australinium*. It differs only in lacking the antapical's accessory spur or spine-like projection of *P. australinium* (Plate 1, Figures 9, 10, 11).

Cyst Genus *Spinidinium* Cookson and Eisenack, 1926
Spinidinium sp.
(Pl. 1, Fig. 17)

Description.–Cyst cornucavate with apical horn and two short antapical horns. Periphragm ornamented with widely to closely spaced spinae arranged in peritabular rows or intratabular clusters; endophragm smooth. Paratabulation indicated by peritabular and intratabular features. Archeopyle intercalary. Paracingulum indicated by the parallel alignment of ornaments.

Dimensions.–Length of cyst body 38-57 µm, mean 48 µm. (2 specimens measured). Width of cyst body 54-62 µm, mean 55 µm.

Remarks.–The short spinose ornamentation of the periphragm is characteristic of this species.

Cyst Genus *Wetzeliella* Eisenack 1938 emend. Lentin and Williams, 1976
Wetzeliella homomorpha Deflandre and Cookson, 1955
(Pl. 3, Figs. 5, 9)

Remarks.–Specimen possesses non-tabular processes, simple, branched, isolated with acuminate, blunt

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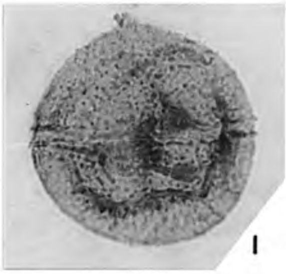
PLATE 3–All figures x 660, unless otherwise stated. *1, 2, 3. Trichodinium castanea* (Deflandre) Clarke and Verdier, 1967. *4, 6. Cornuta carpatella* Grigorovich, 1969. *5, 9. Wetzeliella homomorpha* Deflandre and Cookson, 1955. *7, 8. Achilleodinium* sp. *10, 11. Diphyes colligerum* (Deflandre and Cookson) Cookson, 1965. *12, 13. Areoligera* sp. *14, 18. Spiniferites septatus* (Cookson and Eisenack) McLean, 1971. *17, 19, 20. Spiniferites ramosus* Loeblich Jr. and Loeblich III, 1966. *15, 22. Fibrocysta bipolaris* (Cookson and Eisenack) Stover and Evitt, 1978. *16, 21. Kenleyia pachycerata* Cookson and Eisenack, 1965.

Plate 3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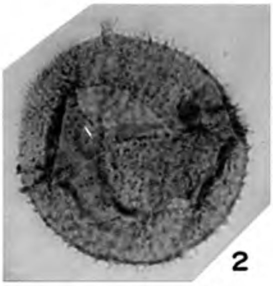
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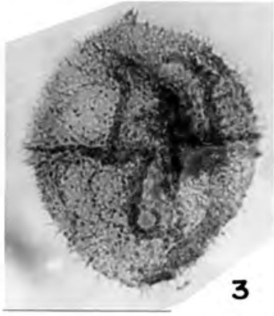
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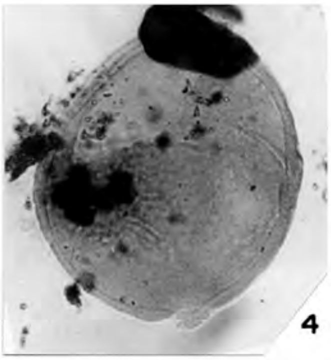
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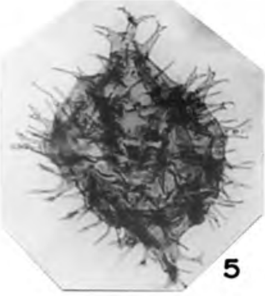
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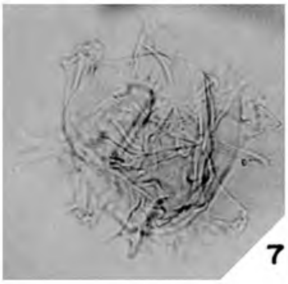
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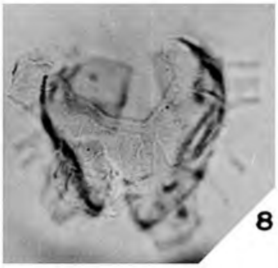
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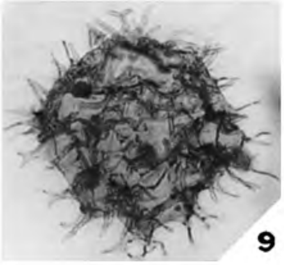
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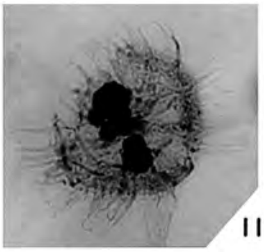
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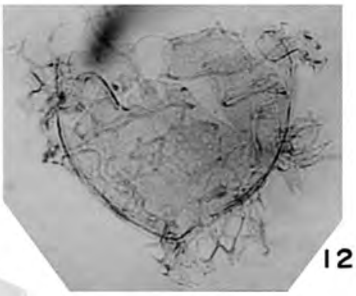
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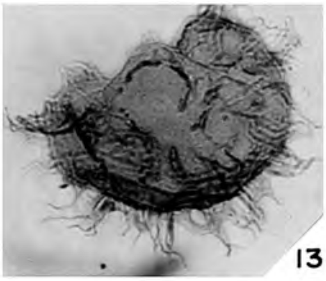
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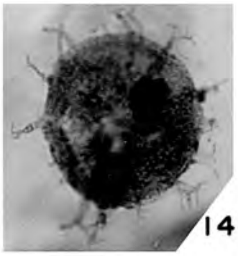
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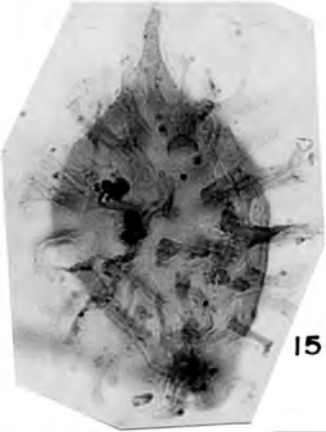
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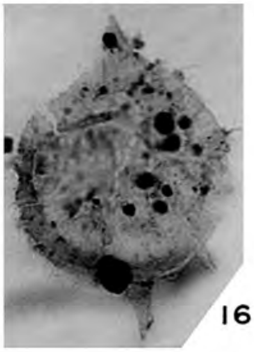
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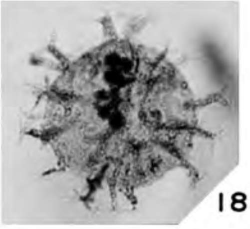
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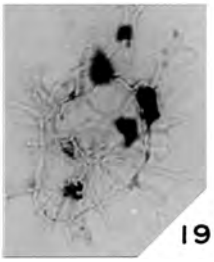
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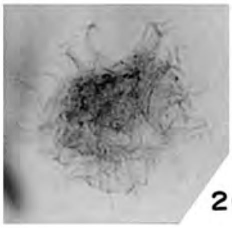
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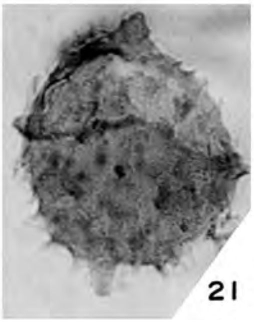
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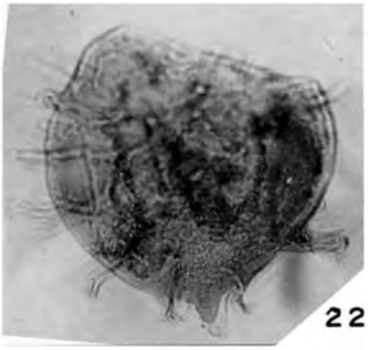
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or bifid tips and not connected distally. It is characterised by lack of well-developed horns and the endophragm is in contact with and not separated from the periphragm as is the case in other species.

Cyst Genus *Cerodinium* Vozzhennikova, 1963
Cerodinium boloniense (Riegel) Lentin and Williams, 1989
(Pl. 1, Figs. 1, 2, 3)

Remarks.–Cyst body is pentagonal with straight sides and well-developed short to medium apical and antapical horns. Riegel (1974) attributed variation in size to environmental conditions, with smaller size forms pointing to rapid reproduction rate in otherwise warm environment as opposed to larger sized forms in cool environment. It has been observed that there exist some larger forms in the assemblage. This may be due the movement of cold ocean currents, from the temperate zones carrying along with them these larger forms into tropical warm waters.

C. boloniensis is structurally similar to *Phelodinium magnificum* (Stanley) Stover and Evitt, 1978 (Plate 2, Figure 7, 11). However, the latter lacks the pentagonal outline of the cyst body and also has shorter and broader horns.

Cerodinium diebelli (Alberti) Lentin and Williams, 1987
(Pl. 1, Figs. 5, 8)

Remarks.–C. *diebelli* differs from *C. obliquipes* (Deflandre and Cookson) Lentin and Williams, 1989 (Plate 1, Figures 4, 6, 7) by having an elongate central body, with much longer apical and antapical horns. *C. diebelli* is the index species for the early-middle Maastrichtian Interval Zone of Roncaglia and Corradini (1997). This species been recorded from the Maastrichtian of the present study.

Cyst Genus *Phelodinium* Stover and Evitt, 1978
Phelodinium tricuspis (Wetzel) Stover and Evitt, 1978
(Pl. 2, Figs. 6, 12)

Remarks.–Phelodinium differs from *Cerodinium* and *Senegalinium* by its conspicous protrusion in the precingular area. Paracingulum is indicated at widest part of cyst by folds or transverse parallel ridges.

Cyst Genus *Senegalinium* Jain and Millepied, 1973
Senegalinium laevigatum (Malloy) Bujak and Davies, 1983
(Pl. 1, Figs. 15, 16)

Remarks.–Specimens show globose to spherical shapes with thin periphragm. The surfaces of periphragm and endophragm are smooth and often displaying folds and wrinkles. This species differs from *S. bicavatum* Jain and Millepied, 1973 (Plate 1, Figures 18, 19) by its extremely low apical and antapical horns which in some cases are inperceptible. The cyst genus *Senegalinium* also lacks the wide style of intercalary archeopyle exhibited by *Deflandrea.*

DINOGYMNOID CYST
Cyst Genus *Dinogymnium* Evitt, Clarke and Verdier, 1967
Dinogymnium acuminatum Clarke and Verdier, 1967
(Pl. 2, Figs. 14, 15)

Remarks.–Cyst body surface is ornamented with many straight, longitudinal ridges or ribs with pores. The pointed or acuminate nature of the extremity of the hypocyst characterizes this species. However, there are some specimens with a seemingly rounded hypocyst.

Dinogymnium sp. 1
(Pl. 2, Fig. 19)

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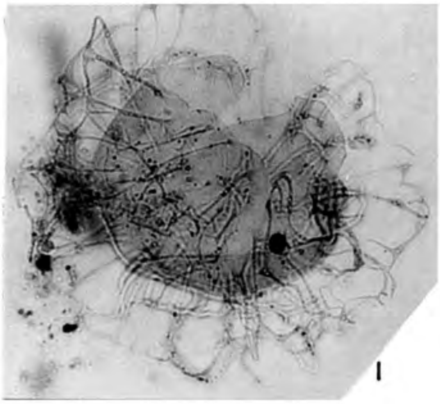
PLATE 4–All figures x 660, unless otherwise stated. *1, 4. Adnatosphaeridium multispinosum* Williams and Downie, 1966. *2, 6. Glaphyrocysta* sp. *3. Cordosphaeridium* sp. cf. *C. gracilis* (Eisenack) Davey and Williams, 1966b. *5, 7. Xenasus ceratioides* (Deflandre) Lentin and Williams, 1973. *8. Cordosphaeridium exilimurum* Davey and Williams, 1966. *9, 10. Cordosphaeridium fibrospinosum* Davey and Williams, 1966. *11. Spiniferites* sp. cf. *S. fluens* (Hansen) Stover and Williams, 1987. *12, 13. Oligosphaeridium complex* (White) Davey and Williams, 1966. *14, 15. Cordosphaeridium inodes* (Klumpp) Eisenack, 1963b. *16. Cordosphaeridium multispinosum* Davey and Williams, 1966.

PLATE 4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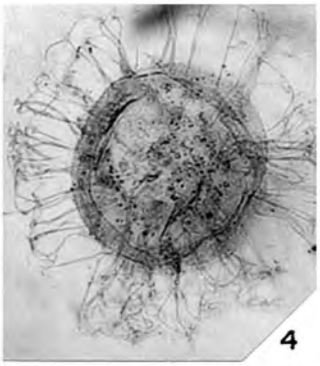
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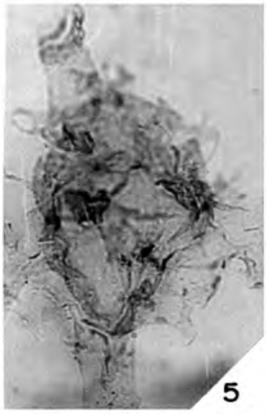
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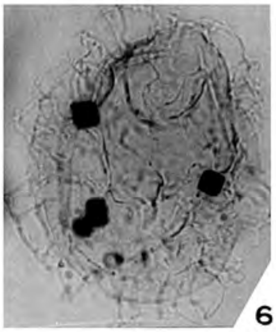
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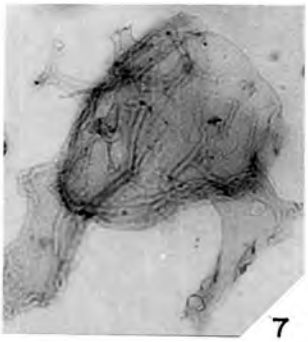
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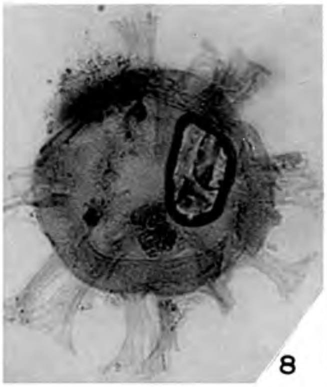
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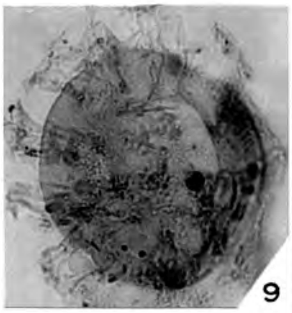
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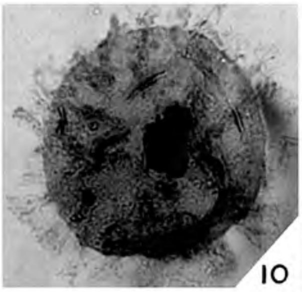
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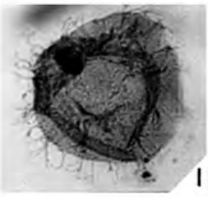
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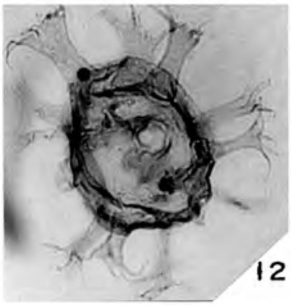
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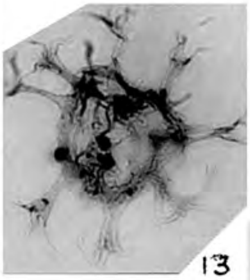
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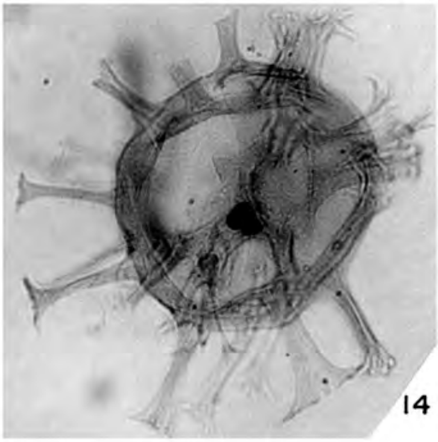
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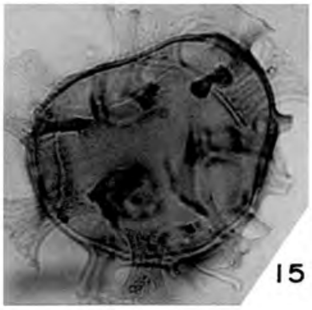
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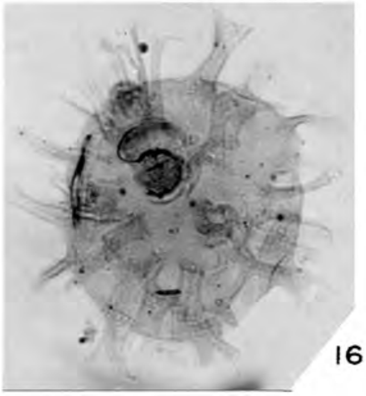
16

Description.–Proximate, biconical cyst with conical extremities. Parasutural elements absent. Hypocyst and epicyst ornamented with longitudinal ridges, straight, smooth to granulate with tiny pores converging at the extremities. Archeopyle is apical, small with free operculum. Paracingulum distinct, marked by folds, recurved and protruding from the precingular area.

Dimensions.–Length of cyst body 68 µm. (1 specimen measured). Width of cyst body: 55 µm.

Dinogymnium sp. 2
(Pl. 2, Fig. 18)

Description.–Proximate cyst with extended extremities closing up in a tight cone structure. Parasutural elements absent. Hypocyst and epicyst ormamented with longitudinal ridges which converge at the poles. Ridges undulose, straight, smooth to granulate with tiny pores. Archeopyle apical; operculum free. Paracingulum distinct, marked by a depression with folds.

Dimensions.–Length of cyst body 105 µm. (1 specimen measured). Width of cyst body: 50 µm.

Dinogymnium digitus (Deflandre) Evitt *et al.*, 1967
(Pl. 2, Fig. 8)

Remarks.–The hypocyst of this species is slightly larger than the epicyst. It is also ornamented with smooth and very few ridges.

PALYNOSTRATIGRAPHIC DISCUSSIONS

Three dinoflagellate zones have been identified based on the First appearance datum (FAD) and the Last Appearance Datum (LAD) of important species. These are *Trichodinium castanea* Zone, *Cordosphaeridium* 'complex' Zone and *Carpatella cornuta* Zone (Table 1).

AGE	DINOFAGELLATE ZONES	DEPTH (IN FEET)	DINOFLAGELLATES																																			
			Oligospaeridium complex	*Cerodinium bolonensis*	*C. diebelli*	*C. obliquipes*	*Andalusiella mauthei*	*A. polymorpha*	*A. gabonensis*	*Trichodinium castanea*	*Dinogymnium acuminatum*	*D. digitus*	*D. undulosum*	*Odontochitina operculata*	*O. porifera*	*Senegalinium laevigatum*	*Xenascus ceratoides*	*Polykrikos* sp.	*Glaphyrocysta* sp.	*Areoligera* sp.	*Paleocystodinium golzowense*	*P. australinum*	*Phelodinium tricuspis*	*P. magnificum*	*Spiniferites ramosus*	*S. septatus*	*Cordosphaeridium fibrospinosum*	*C. multispinosum*	*C. inodes*	*Diphyes colligerum*	*Florentina* sp.	*Fibrocysta bipolaris*	*Achilleodinium* sp.	*Kenleyia pachycerata*	*Achomosphaera* spp.	*Adnatosphaeridium multispinosum*	*Carpatella cornuta*	*Wetzeliella homomorpha*
EARLY PALEOCENE	*Carpatella cornuta* Zone	660																							+													
		950																			●						+	+	+			+						●
		1400	●		●																	●	●		+		+			+	+	+				+	●	
		1520	●		●	+	●												+	□	●	●	●	●	+	●	+	□	+			□		+	+		●	●
		3570	●	●	●		●		●										+	□	●			●	□					+	+	□		□		+		
		3720		●	●														□	+							□	□	+				+		+	+	●	
		3780				●													□	+	+	+	+		□	+	□	+	□		+	+		●				
		4220	×			●	●	●	●							●		●	□		□	●	●		+		+	●	+	+		●		+		+	●	
MAASTRICHTIAN	*Cordosphaeridium* 'complex' Zone	4280		●	+		●					●				●			+	□	×	+		×	●	+	●	+	+		●					+		
		4340	●	●		×			+		●					●			+	+	+	●	×		●	●	+	●	+	●		●	●	×	+	●		
		4400		●															+	+	×		×		+	+		+	●									
		4460	●															×	●		×			●									+			+		
		4540					●									×				+	●																	
		4660	+		●	●	+	●					●			●	●	□	●		●				□		×	●	+	●	●				+			
		4720		●	×		●				●							+	●		●		●		+	●					●							
		4840		+		●	●	●								●	×	+	+	●	●	●		●	+	+	+	+			□		×		+			
		4900	●	●			●		+		●					●		●	●			×									●							
		5060		+			●	×						●		●		+		●	×	×	●		●		+		+						●			
		5180	●	+		●	+			●						+		□	●	●	×				+													
CAMPANIAN	*Trichodinium castanea* Zone	5230		+		●	□		●	□		●			●	+					●			●	●								×		+			
		5280	+	●		+	+		●	□						+		×		●					+										●			
		5360		+		+	+			□	●		×			+								×	●													
		5460		+		+	□	+		●					×	+	×																					
		5600		+		+	●	+	+	+				●											●													
		5660				+				●																												
		5720				+	●	+		□	●	●		●	+		×	×													×							
		5780	●	□			□			●	×			+																								
		5840						+		●																												
		5900	□	□		●	+							+	+										●													
		6020	+	+										×											+													
		6060	●			×	+	●		●	×			×	●										●													
		6120	×				+				×			●											●										×			
		6180	●					●		+	×			×											●													
		6240		●		●	●			+				×			×								●													
		6300		●		●	●			●															●													
		6440	×				●		●	●															●													

×= 1-2 (Rare) ●=>2-5 (Few) + =>5-10 (Common) □=>10 (Abundant)

TABLE 1–Distribution of Campanian to Paleocene dinoflagellates cysts in Well 1S-3 AX.

Trichodinium castanea Zone

This zone is recognized in the lower section of the well 6,440 ft (1,932 m)-5,180 ft (1,554 m) and is characterized by the FAD of *Andalusiella* and *Trichodinium castanea*. It is dominated by peridinoid cysts especially those belonging to the subtropical-tropical Malloy suite of Lentin and Williams (1980). These include *Andalusiella, Senegalinium, Cerodinium* and *Phelodinium*. Other important taxa found along side this group are *Dinogymnium* spp., *Odontochitina* spp., *Glaphyrocysta/Areoligera* spp., *Spiniferites ramosus* and *Xenascus ceratioides*. The top of this zone is marked by the LAD of *Trichodinium castanea* and the FAD of *Areoligera*/*Glaphyrocysta*. Masure *et al.* (1998) reported that the FAD of *Andalusiella* and *Trichodinium castanea* suggests a Campanian age. *Andalusiella* has a reported FAD within the uppermost Early Campanian (Williams *et al.*, 1993). The LAD of *Trichodinium castanea* has been reported to occur in the Late Campanian (Williams *et al.*, 1993; Oboh-Ikuenobe *et al.*, 1998). Williams *et al.* (1993) have reported the FAD of *Senegalinium* and *Areoligera* in the Late Campanian. Most of the taxa mentioned above have been reported from Campanian-Maastrichtian sediments by various authors (Malloy, 1972; Riegel, 1974; Williams *et al.*, 1974; McIntyre, 1974; Shrank, 1987; Firth, 1987, 1993; El Beialy, 1995; Digbehi *et al.*, 1996; Mohr and Mao, 1997; Costa and Davey, 1999). As mentioned earlier, in comparing the stratigraphic ranges of the above-mentioned taxa, there is a significant overlap which points to a Campanian-Maastrichtian age for this zone. However, the FAD of *Andalusiella* at the base of the zone and the LAD of *Trichodinium castanea* and FAD of *Areoligera* at the top of the zone delimit the age of the zone to Early-Late Campanian.

Cordosphaeridium 'complex' Zone

The zone is recognized between 5,180 ft (1,554 m)-4,220 ft (1,266 m). It is characterized by the FAD of *Cordosphaeridium* spp. and the LAD of *Odontochitina operculata* at the base, and the LAD of *Dinogymnium* spp. at the top. Most of the taxa present in the preceding zone are present in this zone. The upper part of the zone sees the FAD of *Fibrocysta bipolaris* and *Kenleyia pachycerata* and the abundance of chorate or gonyaulacoid cysts including *Cordospaeridium, Areoligera*/*Glaphyrocysta* and *Spiniferites*. It has been reported from the northern hemisphere that *Cordosphaeridium fibrospinosum* has a FAD in the Early Maastrichtian, close to the boundary between the Early and Late Maastrichtian (Williams *et al.*, 1993).

The presence of *Paleocystodiunum australinum* and *Phelodiniun tricuspis* at the base of this zone is suggestive of a Early Maastrichtian age. *P. australinum* is considered to have its FAD in latest Campanian (May, 1980; Williams and Bujak, 1985; Edet, 1992). *P. tricuspis* has a Early Maastrichtian-Late Danian range (Williams *et al.*, 1999) and an Early Maastrichtian-early Late Paleocene range (Williams and Bujak, 1985).

The FAD of *C. diebelli* at the base of the zone also indicates early-middle Maastrichtian age. The FAD of this species occurs in the lowermost Maastrichtian in Israel (Hoek *et al.*, 1996), North America (Bujak and Williams, 1997; May, 1980), West Greenland (Nøhr-Hansen, 1996), Italy (Roncaglia and Corradini, 1997).

The LAD of *O. operculata* is a cosmopolitan 'event' which has often been reported in the proximity of the Campanian/Maastrichtian boundary (Wilson, 1971; May, 1980; Kirsch, 1991). However, the observed LAD of this species within the Early Maastrichtian has been reported by Williams and Bujak, (1985); Helby *et al.* (1987); Williams *et al.* (1993); Schrank and Ibrahim, (1995); Mohr and Mao, (1997); Costa and Davey, 1999; Roncaglia (2002). The LAD of *O. operculata* at the base of the zone thus supports an Early Maastrichtian age. The FAD of *Fibrocysta bipolaris* and *Kenleyia pachycerata* is in the upper part of the zone. They occur together with *Dinogymnium* spp., which disappears at the top of the zone. Brinkhuis and Zachariasse (1988, *in* Stover *et al.*, 1996) have mentioned that *Kenleyia* has a FAD which incidentally coincides with the LAD of *Dinogymnium acuminatum* in their older *Alisocysta circumtabulata* subzone (latest Maastrichtian) of the *Damassadinium californicum* Zone. The LAD of *Dinogymnium* in latest Maastrichtian rocks has also been reported by Stover and Evitt (1978), Stover *et al.* (1996) and Costa and Davey (1999). According to Oboh-Ikuenobe *et al.* (1998 in personal communication from H. Brinkhuis, 1996), the FAD of the lower latitude dinoflagellate *Kenleyia* has been reported in Late Maastrichtian sediments where they are not common. They also believed that the common co-occurrence of *Kenleyia* with the well known latest Maastrichtian dinoflagellate cysts *Dinogymnium* and *Pierceites pentagona* represents a condensed Maastrichtian-Danian section in sediments from the CIG transform margin. The upper part of this zone is thus Late Maastrichtian in age. This pre-Paleocene age is further supported by the LAD of the spore *Buttinia andreevi* in this zone. This spore is reported to be common in Maastrichtian sediments and do not range into the Paleocene. The age of the zone is thus Early-Late Maastrichtian.

Carpatella cornuta Zone

This zone is recognized between 4,220 ft (1,266 m)-660 ft (180 m). The FAD of *C. cornuta* and the absence of *Dinogymnium* spp characterize this zone. *Wetzeliella homomorpha* also makes it first appearance in this zone. Other important elements in this zone are similar to that of the preceding zone. Powell (1999) stated that the FAD of *C. cornuta* has been observed at the base of the *Carpatella cornuta* biozone and the LAD appears within the base of *Tectatodinium regulatum* (Tru) biozone of Hansen (1977) in the Danian Limestone Formation in Denmark with a chronostratigraphic age of Danian (Early Paleocene). Firth (1987) has also reported this species in the Danian of the Albany Core in Georgia. Firth (1987) and Powell (1999) reported that *C. cornuta* is one of the species restricted to the Paleocene and has not been reported below the Cretaceous/Tertiary boundary. Pocknall *et al.* (1997, *in* Yepes, 2001) reported the presence of *Fibrocysta bipolaris*, *Kenyelia lophophora and C. Cornuta* in the Danian of Venezuela. This observation is also the case in the present study. *Wetzeliella* is a characteristic Early Tertiary genus which has not been recorded from sediments older than the Paleocene. Various authors have recorded *Wetzeliella* from Paleocene to Oligocene sediments (Williams *et al.,* 1998; Eaton, 1976; Williams and Downie, 1966; Williams and Bujak, 1977). The presence especially of *C. cornuta* and *W. homomorpha* in this zone suggests an Early Paleocene (Danian) age.

PALEOECOLOGICAL NOTES

Dinoflagellate assemblage composition has been used in the study for paleoenvironmental recognition. This is because the relative abundance of species and morphotypes, which is the common method used to describe the dinoflagellate assemblage composition, is what most paleoecological modeling is based on.

Downie *et al.* (1971) recognized a variety of dinoflagellate-acritarch cyst associations in the Early Eocene of southeastern England which were named after the genus of which dominant species belong. Four associations were recognized. These are: (1) *Spiniferites* association, (2) *Micrhystridium* association (3) *Areoligera* association, and (4) *Wetzeliella* association. Islam (1984) expanded upon the concept of Downie *et al.* (1971) and recognized several other groups. Downie *et al.* (1971) and Islam (1984) indicated that the high percentage or count of peridiniacean forms *(Wetzeliella* association) implies near shore, estuarine or brackish condition, while the dominance of gonyaulacacean *(Spiniferites* and *Areoligera* associations) was interpreted as indicating open marine condition.

Harland (1973) defined gonyaulacacean ratio as the number of gonyaulacacean cysts species divided by the number of peridiniacean cysts species. He found that the gonyaulacacean ratio was higher in open marine environments and low in near shore (reduced-salinity) environment. Schrank (1987) has made similar observations.

The vertical distribution of dinoflagellate cysts shows that the *Trichodinium castanea* Zone is dominated by the peridiniacean cysts especially *Andalusiella*, *Cerodinium*, *Senegalinium*, *Phelodinium* as compared to the gonyaulacacean cysts. This suggests a lower gonyaulacacean ratio and is thus indicative of near shore, brackish environment. The high peridiniacean but low diversity of the cysts is probably indicative also of low salinity paleoenvironment (Sarjeant, 1970; Harland, 1973; Hultberg, 1986). This is supported by the general lack of foraminifera in the sediments.

The transition to the more open marine condition is reflected in the *Cordosphaeridium* 'complex' and *Carpatella cornuta* Zones by a replacement of the peridiniacean cysts with the more cosmopolitan gonyaulacacean cysts *(Cordosphaeridium*, *Spiniferites*, *Areoligera/Glaphyrocysta*, *Adnatosphaeridium)* which are equipped with distinct processes. The Campanian-Paleocene transgression that flooded most of Ghana resulted in marine sedimentation which provided favourable conditions for the development of marine phytoplankton-dominated palynofloras.

Lentin and Williams (1980) in a study of Late Cretaceous peridiniacean cysts distinguished three (3) assemblages or provincial suites which seem to show relationship to climatic belt. They defined the tropical-subtropical Malloy suite characterized by the occurrence of *Andalusiella*, *Cerodinium*, *Phelodinium* and *Senegalinium. Alterbidium*, *Spinidinium*, *Chatangiella* (smaller taxa) and *Isabelidium* which characterize the warm temperate Williams suite and the cool boreal McIntyre suite which is characterized by the occurrence of *Laciniadinium* and *Chatangiella* (larger taxa). Mao and Mohr (1992) identified a fourth suite (Helby suite) for cool temperate regions. This is characterized by the presence of *Amphidiadema*, *Nelsoniella*, *Satyrodinium*, *Xenikoon*, *Chatangiella* (larger taxa). The common occurrence of *Andalusiella*, *Cerodinium*, *Phelodinium* and *Senegalinium* in the Late Cretaceous sediments indicates that the Ghanaian peridiniacean cysts belong to the tropical-subtropical Malloy suite. Several species of the genera listed above in the Malloy Suite of the study range into the Maastrichtian. It is thus possible to suggest that the same suite identified by Lentin and Williams (1980) in Campanian sediments is present in the Maastrichtian as was reiterated by Yepes (2001).

Peridiniacean dinoflagellate cysts are presumably derived from heterotrophic dinoflagellate cysts (Harland, 1988; Schiøler *et al.*, 1997) and thus can be used as paleoproductivity indicators in upwelling systems with high concentration of nutrients (Powell *et al.*, 1990; Eshet *et al.*, 1994; Bujak, 1984) where cold and nutrient-rich marine waters are brought to the surface of the ocean. It stands to reason therefore, that the relative high abundance of peridiniacean cysts from the sediments especially in the *Trichodinium castanea* Zone are due to nutrient-rich waters leading to high productivity during the Campanian in the study area. The commonly presence of terrestrial organic matter in most of the samples and the absence of lithologies characteristic of upwelling systems (e. g. chert, phosphorites) suggest a continental source for the nutrients.

CONCLUSIONS

Abundant, diverse and well-preserved dinocysts recovered from the interval 6,440 ft (1,932 m)-600ft (180 m) in well 1S-3AX have been studied and discussed.

Three (3) dinoflagellate zones have been identified from this section of the well based on the FAD and LAD of important species. These are:

a) *Trichodinium castanea* Zone with an age range of Early to Late Campanian.
b) *Cordosphaeridium* ‘complex’ Zone with an age range of Early to Late Maastrichtian.
c) *Carpatella cornuta* Zone with an Early Paleocene (Danian) age.

From a paleoecological point of view, the vertical distribution upwards of the dinoflagellate cysts in the well indicate a near shore (brackish) environment for *Trichodinium castanea* Zone and an open marine environment for the *Cordosphaeridium* ‘complex’ and *Carpatella cornuta* Zones.

The occurrence of species of the genera *Andalusiella*, *Cerodinium*, *Phelodinium* and *Senegalinium* in the Late Cretaceous sediments, confirms the criteria used by Lentin and Williams (1980) to characterize a tropical-subtropical Malloy suite.

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TEST MORPHOLOGY AND ORGANIC LAYER OF *DISCORINOPSIS AGUAYOI* (BERMÚDEZ): RELATIONSHIPS WITH ENVIRONMENTAL CONDITIONS

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Abstract

A detailed study of the morphology of *Discorinopsis aguayoi* (Bermúdez) is carried out by analyzing four populations collected in Recent and Neogene brackish environments of Tuscany (Italy). The finding of fossil *D. aguayoi* is reported in this study for the first time. The modern populations lived in a thermal pool of Montecatini (Pistoia) and in the Lagoon of Orbetello (Grosseto), two brackish environments characterized by different salinities. The fossil specimens were found in Messinian and Pliocene sediments of two quarries near Leghorn and Florence respectively. The present investigation points out the invariant and the echophenotypic characters of *D. aguayoi*. Modern specimens exhibit morphological abnormalities, correlated to environmental conditions. In the modern populations, the organic layer, well preserved, has also been analyzed. SEM analysis shows "pore plugs" inside conical elevations beneath the pores. TEM investigation, points out the laminar fibrous nature of the organic layer, and microcavities in the organic thickenings and in the "pore plugs" of Montecatini individuals. The microcavities suggest that underlying structural differences between the two populations may be related to extreme conditions of the thermal pool.

Key words: Foraminifera, *Discorinopsis aguayoi*, morphology, ecology, organic layer, Italy.

Resumen

En este trabajo se realiza un estudio detallado de la morfología de *Discorinopsis aguayoi* (Bermúdez) analizando cuatro poblaciones actuales y del Neógeno recogidas en ambientes salobres de la región de Toscana (Italia). Se registra por vez primera el hallazgo de la especie fósil *D. aguayoi*. Las poblaciones recientes vivían en un estanque termal de Montecatini (Pistoia) y en la Laguna de Orbetello (Grosseto), dos ambientes salobres caracterizados por salinidades diferentes. Los ejemplares fósiles fueron encontrados en sedimentos del Messiniense y del Plioceno, en dos canteras ubicadas en las proximidades de Livorno y Florencia, respectivamente. El presente estudio pone en evidencia los caracteres tanto invariantes como ecofenotípicos de *D. aguayoi*. Los ejemplares recientes muestran anormalidades morfólogicas determinadas por la condiciones ambientales. En estas poblaciones recientes se ha analizado también la capa orgánica, que se presenta bien conservada. Los análisis al SEM han mostrado los "pore plugs" dentro de elevaciones cónicas presentes debajo de los poros. Por otro lado, el estudio al TEM ha puesto en evidencia la naturaleza fibrosa y laminar de la capa orgánica y la existencia de microcavidades tanto en los engrosamientos orgánicos bajo los poros como en los "pore plugs". Estas microcavidades sugieren que las diferencias estructurales entre las dos poblaciones podrían estar relacionadas con las condiciones ambientales extremas del estanque termal.

Palabras clave: Foraminíferos, *Discorinopsis aguayoi*, morfología, ecología, capa orgánica, Italia.

INTRODUCTION

Foraminiferal morphology is known to be related to genetic variability, life cycle (Nyholm, 1961; Sliter, 1965; Boltovskoy & Wright, 1976; Grell, 1988), ontogenetic stages (Boltovskoy & Wright, 1976; Zampi *et al.*, 1980) and environmental parameters (Bradshaw, 1957, 1961, 1968; Tufesco, 1968; Kurc, 1961; Seiglie, 1975; Seiglie, 1976; Boltovskoy & Wright, 1976; Vènec-Peyrè, 1981; Bernhard, 1986; Hallock *et al.*, 1986; Caralp, 1989; Bijma *et al.*, 1990; Alve, 1991; Yanko *et al.*, 1994; Alve, 1995; De Rijk, 1995; Toler & Hallock, 1998). As regards environment-related variability, the discrimination between ecophenotypic and invariant characteristics can be helpful in assessing the functional and taxonomic significance of foraminiferal morphological features, as suggested by Hemleben *et al*. (1977). Such investigation is however complex because the individual variability of each taxon in normal conditions should be known (Boltovskoy & Wright, 1976). Since the life cycle and behavior of foraminifera are not completely known, it is difficult to establish what are the normal conditions for each taxon (Boltovskoy & Wright, 1976). Even weak environmental variations undetected by standard measurements or analyses, can modify shell morphology (Boltovskoy & Wright, 1976). Chemical and biotic factors also influence living matter of the cell and therefore the structure of the test (Anderson & Bè, 1976).

A first approach to investigations on invariant and ecophenotypic foraminiferal features was carried out by one of the authors on a milioline species, *Triloculina rotunda* d'Orbigny (Zampi & D'Onofrio, 1986; Zampi & Benocci, 1995). For the present study, also realized with statistical methods, another benthic species, *Discorinopsis aguayoi* (Bermúdez) is selected. The selection of this rotalid is due to the availability of specimens which represented an interesting subject for our investigation. The study material consists of four populations collected in modern and Neogene brackish environments of Tuscany (Italy) such as a thermal pool of Montecatini (Pistoia), the Lagoon of Orbetello (Grosseto), the Messinian and Pliocene sediments of two quarries near Leghorn and Florence respectively. The four populations were referred to *Discorinopsis aguayoi* (Bermúdez) on the basis of morphological features and statistical analyses. Nevertheless, some of the diagnostic characters showed strong variability among the four populations, so to make our identification somewhat doubtful. In fact, Papi & Tavani (1959) and Zampi & D' Onofrio (1986) attribute the two modern populations to different species because of the not complete agreement with the morphological features of *D. aguayoi*. Both modern and fossil populations were found in sediments of hypohaline or strongly hypohaline environments, as indicated by the values of salinity or by micropaleontological and stratigraphic data. Thus they offered the opportunity for a detailed investigation of the relationship between their morphology and environment. Such analysis could also reveal the invariant traits of each population justifying their belonging to *D. aguayoi*. The data reported by Arnold (1954) on variations of *D. aguayoi* laboratory specimens may help to discriminate between invariant and ecophenotypic characters. Moreover, the availability of both Neogene and modern individuals enabled us to verify the stability of significant taxonomic features. Besides observations of the external morphology, we also have analyzed the well preserved organic layer of modern specimens, living in extreme conditions (an isolated thermal pool) or in a brackish lagoon. This last investigation has been carried out to test the possible influence of the environment on the organic layer.

METHODS

All samples were washed over a 63 µm sieve. Several specimens were examined under both the optical and electron microscope and photographed. The morphologic investigation, in light microscope and SEM, and the histochemistry of the organic layer (PAS reaction) were performed on individuals decalcified with 1% HCL solution (Arnold, 1954). Ultrastructural analysis of the organic layer, carried out only in some Montecatini and Orbetello specimens, was performed by fixing samples in 2.5% glutaraldehyde for 1.5 h in 0.1M phosphate buffer at pH 7.2 in which 1.8% saccharose had been added. Samples were rinsed in buffer and postfixed in 1% OsO_4 for 1 h. After further rinsing, foraminifera were decalcified with 2% EDTA for 15 min. Samples were then dehydrated in alcohol and embedded in Epon-Araldite. Ultra-thin sections were stained with an aqueous solution of uranyl acetate for 15 min and with an aqueous solution of lead citrate for 2 min, and then subjected to TEM (Philips CM10) analyses. Some semi-thin sections are taken for light microscopy and stained with an aqueous solution of methylene blue with dissolved 0.5 g of $CaCO_3$. Photos of the semi-thin sections were taken using a Leitz Ortolux photomicroscope system.

Biometric data

Five parameters were measured with an ocular micrometer: length (L), breadth (B), height of the test (H), length (l_2, l_3) and height (h_1, h_3) of the second and the third last chambers (Fig. 1). Length and height of the second and third last chambers were undoubtedly more difficult to measure in light microscopy because of their small size; the measures of those parameters that were most subjected to error were taken repeatedly in order to obtain an average value. Biometric data (Table 1) were collected on forty specimens randomly picked from each population. This number is suggested because few whole specimens were found in the Pliocene sample.

STATISTICAL ANALYSES

The biometric data are reported in natural logarithmic scale, which provides a more efficient discrimination of the statistical methods used. The statistical investigation did not involve all measured specimens, but only individuals (20 for each sample) with the same number of chambers in the last whorl to compare homogeneous samples. For any recorded variate (L/B:

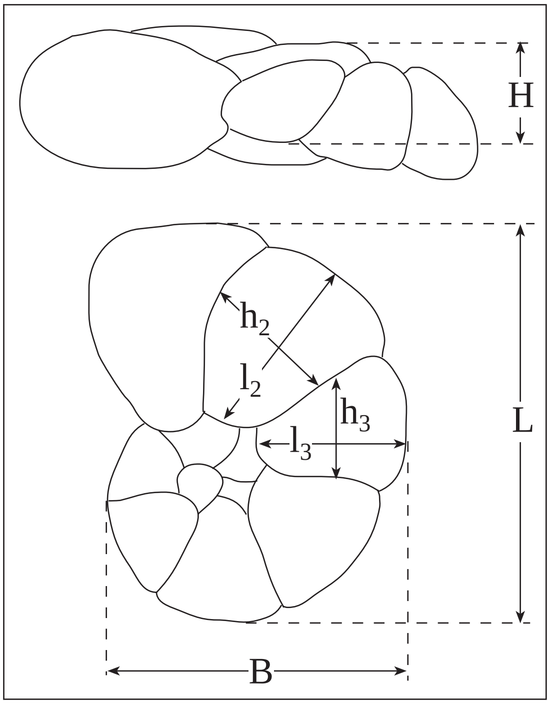


FIGURE 1–Biometrical parameters L: greatest spiral diameter; B: spiral diameter at the right angle of the greatest spiral diameter; H: height of the test; l_2, l_3, h_2, h_3: length and height of the second and third last chamber.

	Chambers of the last whorl	Specimens %	L min.	L max.	B min.	B max.	H min.	H max.	l2 min.	l2 max.	h2 min.	h2 max.	l3 min.	l3 max.	h3 min.	h3 max.
Messinian	7	7,50	240	360	200	260	140	180	130	150	70	100	110	140	70	90
	8	67,50	320	560	260	500	140	220	140	300	80	180	120	260	80	200
	9	22,50	440	540	340	440	180	260	180	240	90	180	140	220	100	190
	10	2,50	560	560	520	520	180	180	160	160	80	80	260	260	120	120
Pliocene	7	40,00	220	340	180	300	80	100	100	180	50	100	80	140	50	100
	8	20,00	240	380	190	330	60	140	120	200	60	100	100	180	60	120
	9	35,00	280	520	220	440	80	140	140	260	70	120	120	240	50	120
	10	5,00	460	520	380	400	100	160	200	200	100	100	180	180	80	80
Orbetello	6	5,00	280	340	240	260	100	140	140	140	100	120	100	120	60	100
	7	30,00	260	400	200	340	100	150	100	190	80	140	80	160	60	140
	8	50,00	300	520	240	400	110	180	100	260	80	150	100	220	80	150
	9	10,00	420	540	320	470	160	180	200	230	100	180	160	200	80	180
	10	5,00	460	500	340	440	160	170	220	220	110	130	220	220	80	90
Montecatini	7	35,00	180	420	160	390	120	160	80	160	60	140	80	140	60	120
	8	30,00	240	390	200	340	120	160	80	180	60	160	90	160	60	120
	9	32,50	300	460	240	380	140	201	100	200	50	130	100	180	60	120
	10	2,50	460	460	400	400	190	190	160	160	90	90	160	160	120	120

TABLE 1–Biometric measures (μm) of the four populations.

index of test curvature; L/H: index of test flatness; l_2/h_2; l_3/h_3: ratio between length and height of penultimate and third last chamber) the Scheffé test (Table 2) was performed to discriminate which particular couple of samples show significative differences in their mean values. Subsequently, a new variate P (L-B-H), proportional to the volume of the individuals, was added for computing Mahalanobis distances (Table 3) between pairs of samples and for performing canonical correlation analysis. Mahalanobis distances (Mahalanobis, 1936), are very effective in emphasizing differences between sample means and are utilized in taxonomical studies (e. g. Lovari & Scala, 1980). Moreover, the canonical correlation analysis attempts to reduce dimensionality by a parsimonious representation of the original variates. That allows a graphical display of sample data in such a way that visual and intuitive comparison of samples is possible (Fig. 2). This multivariate statistical method is frequently used to compare morphological groups of foraminifera on the basis of external morphology (Buzas, 1966; Painter & Spencer, 1984).

Log L/B

Sample	Pliocene	Orbetello	Montecatini
Messinian	0.970	0.340	0.105
Pliocene		0.611	0.034*
Orbetello			0.001*

Log l2/h2

Sample	Pliocene	Orbetello	Montecatini
Messinian	0.297	0.996	0.390
Pliocene		0.418	0.006*
Orbetello			0.274

Log l3/h3

Sample	Pliocene	Orbetello	Montecatini
Messinian	0.037*	0.753	0.945
Pliocene		0.320	0.007*
Orbetello			0.411

Log L/H

Sample	Pliocene	Orbetello	Montecatini
Messinian	0.000*	0.000*	0.980
Pliocene		0.073	0.000*
Orbetello			0.000*

TABLE 2–P-values of Scheffè test to investigate the significance of all the possible differences between the four samples for any variate (asterisk indicates significance lower than 0.05).

Sample	Pliocene	Orbetello	Montecatini
Messinian	22:61087	5:58546	4:52499
Pliocene		6:87878	14:12701
Orbetello			5:67337

TABLE 3–Values of the Mahalanobis distances between any pair of samples (distances computed on the five original variates).

These data and the morphological features described afterward confirm that all individuals belong to the same species: *Discorinopsis aguayoi* (Bermúdez). Mahalanobis distances (Table 3) and canonical analysis (Fig. 2) show affinity between modern and ancient specimens. The greatest affinity occurs between Messinian and Montecatini populations, although some affinities also exist between Pliocene and Orbetello populations. However it is not possible to exclude subspecific differentiation of the investigated populations. In fact, Montecatini specimens are differentiated enough from Orbetello individuals while Messinian and Montecatini populations are strongly differentiated from Pliocene specimens. Also Tufesco (1969) formulated the hypothesis of subspecific differentiation with regard to the individuals of *D. aguayoi* living in the Golovita Lagoon.

SYSTEMATICS AND ECOLOGY OF *D. AGUAYOI*

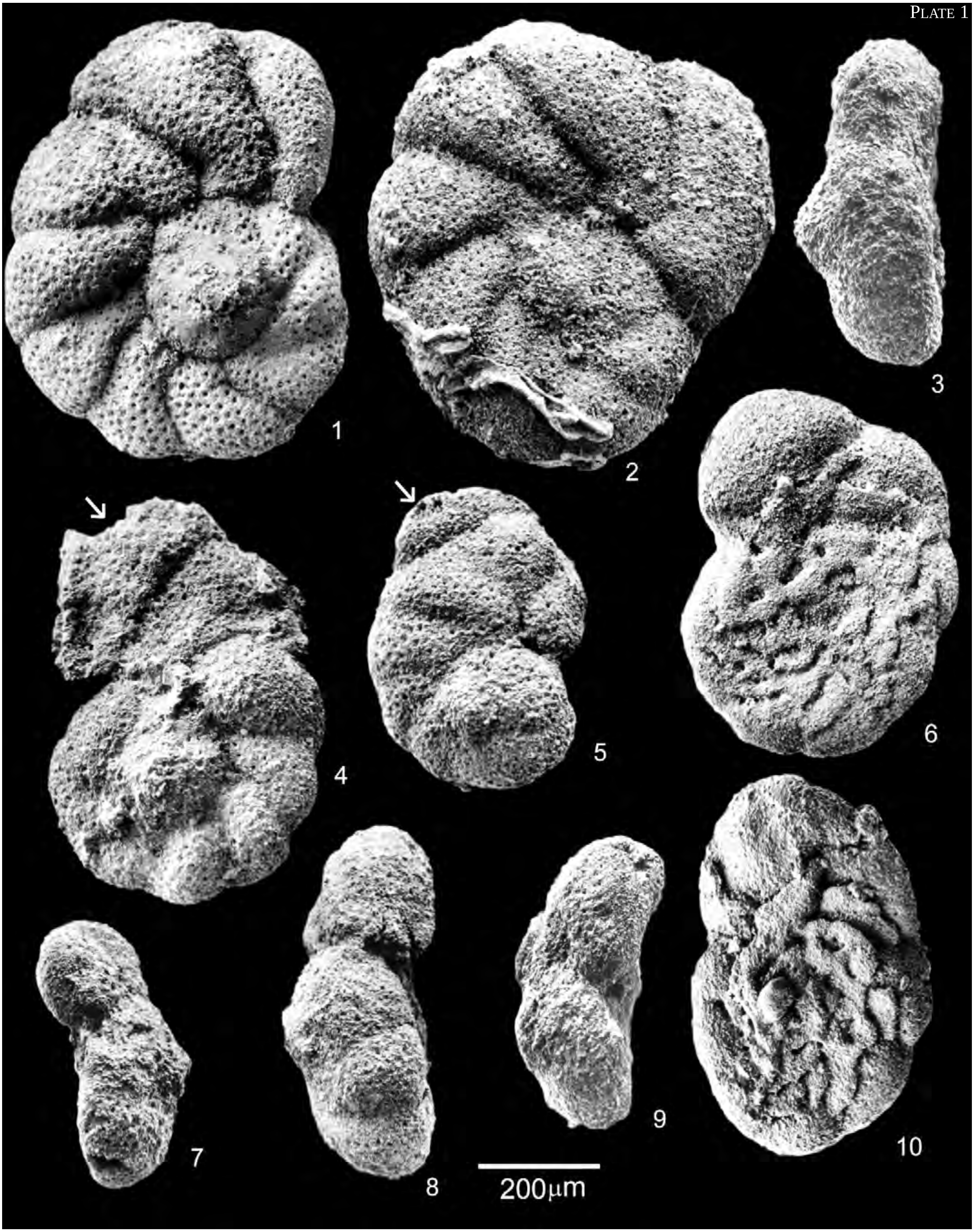
Order ROTALIIDA Delàge & Hérouard, 1896
Family DISCORBIDAE Ehrenberg, 1838
Genus *Discorinopsis* Cole, 1941
Discorinopsis aguayoi (Bermúdez, 1935)

1935 *Discorbis aguayoi* Bermúdez; Bermúdez: fide Ellis & Messina, 1940.

→

PLATE 1–*1-10*, Messinian specimens of *Discorinopsis aguayoi* (Bermúdez). *1-2*, *4-5*, dorsal view, note the adventitious chambers (arrows). *6*, *10*, ventral view. *3*, *7-9*, frontal view. The specimens show an abnormal inner whorl in dorsal and frontal view.

PLATE 1



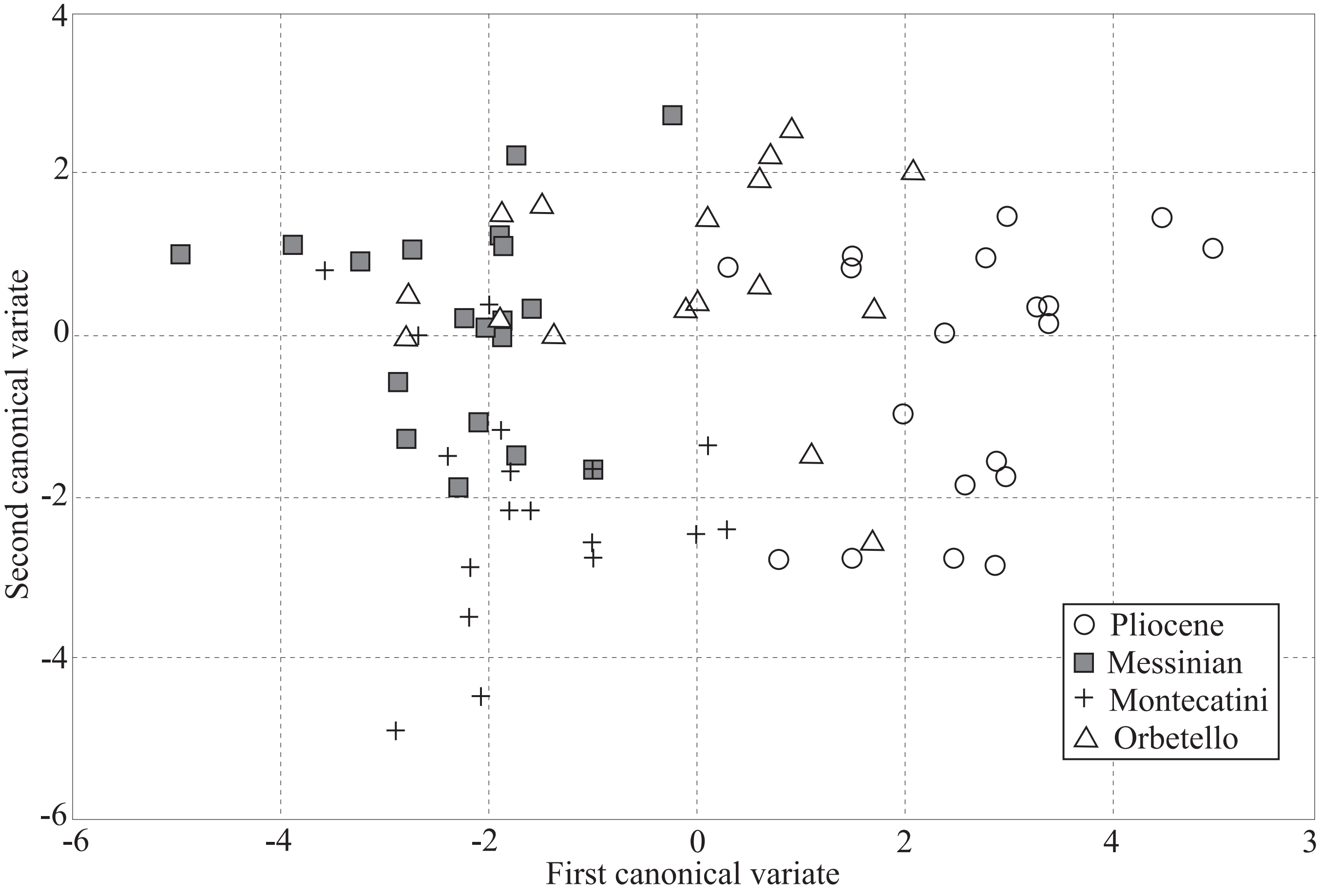


FIGURE 2–Plot of the first two canonical variates summarizing the five original variates to emphasize the differences between samples.

1948 *Discorinopsis vadescens* Cushman & Brönnimann: p. 20, Pl. 4, Figs. 9-10.
1950 *Discorbina lacunae* Silvestri: p. 80, Pl. 3, Figs. 22-23.
1953 *Discorinopsis aguayoi* (Bermúdez); Parker *et al.:* p. 7, Pl. 4, Figs. 23-24.
1954 *Discorinopsis aguayoi* (Bermúdez); Arnold: p. 4-13, Pl. 2, Figs. 1-17.
1957 *Discorbis*? *aguayoi* (Bermúdez); Todd & Brönnimann: p. 37, Pl. 9, Fig. 24.
1958 *Discorinopsis tropica* Collins: p. 406, Pl. 5, Fig. 7.
1959 *Rotalia beccarii* (Linneo); Papi & Tavani, p. 1-9.
1968 *Trichohyalus tropicus* (Collins); Albani, p. 117, Pl. 10, Figs. 13-14.
1969 *Trichohyalus aguayoi* (Bermúdez); Tufesco, p. 47, Figs. 2-4.
1974 *Lamellodiscorbis aguayoi* (Bermúdez); Resig, p. 70, Pl. 1, Figs. 15-16.
1981 *Trichohyalus tropicus* (Collins); Cann & De Deckker, p. 669, Fig. 1.
1983 *Discorinopsis aguayoi* (Bermúdez); Boltovskoy & Hincapiè de Martinez, p. 218, Pl. 2, Figs. 8-9.
1986 *Discorbis valvulatus* d'Orbigny; Zampi & D'Onofrio, p. 114.
1990 *Trichohyalus lacunae* (Silvestri); Albani & Serandrei Barbero, p. 327, Pl. 5, Figs. 19-20.
1991 *Trichohyalus lacunae* (Silvestri); Albani, *et al.*, p. 34, Pl. 1, Figs. 9-10.
1991 *Discorinopsis aguayoi* (Bermúdez); Scott *et al.*, p. 385, Pl. 2, Figs. 17-18.
1996 *Discorinopsis aguayoi* (Bermúdez); Zampi *et al.*, p. 17-25, Pl. 1, Figs. 11-18; Pl. 2, Figs.1-16a; Pl. 3, Figs. 1-4a.

The syntypes of *Discorinopsis aguayoi* are specimens from the northern coast of Cuba described by Bermúdez (1935) under the generic name of *Discorbis* (fide Ellis & Messina, 1940):

The diagnosis was.–Test vitreous, gently trochoid, outline circular, gently lobulate, periphery rounded; dorsal side consisting of several subglobular chambers; ten chambers in the last whorl, very coarsely perforate; sutures of the first whorl limbate, sutures of the last whorl depressed. In some specimens all sutures are limbate; proloculus recognizable on dorsal side; ventral side flat, almost completely filled with a broad vitreous thickening made by a layer of radial thin ribs and rugosities; aperture a slit at the basis of the last chamber, in contact with the ventral edge of the spire; on the ventral edge of the spire, broken specimens show a half-moon shape of the apertures of the inner chambers.

Dimension of the syntypes.–

Diameter 0.46 mm, height 0.2 mm (Pl. 15, Fig. 10).
Diameter 0.5 mm, height 0.2 mm (Pl. 15, Fig. 11).
Diameter 0.7 mm, height 0.34 mm (Pl. 15, Fig. 12).
Diameter 0.72 mm, height 0.23 mm (Pl. 15, Fig. 13).
Diameter 0.8 mm, height 0.22 mm (Pl. 15, Fig. 14).

About twenty specimens had been analyzed; and some individuals showed simple sutures, others thickened sutures.

In the following years, the species acquired various generic names *(Discorinopsis, Discorbina, Trichohyalus* and *Lamellodiscorbis)* as well as specific ones *(vadescens, tropica, valvulata, lacunae)*. Scott *et al.* (1991) confirmed the generic denomination of *Discorinopsis*, not justifying the attribution of *D. aguayoi* to the new genus *Trichohyalus* erected by Loeblich & Tappan (1953) for rotalids with secondary appositions of calcitic material in the umbilical area.

Discorinopsis aguayoi is recorded in littoral waters (Bermúdez, 1935; Arnold, 1954) and in several brackish environments (Cushman & Brönnimann, 1948; Parker *et al.,* 1953; Todd & Brönnimann, 1957; Collins, 1958; Albani, 1968; Tufesco, 1969; Boltovskoy & Hincapiè de Martinez, 1983; Zampi & D'Onofrio, 1986; Albani & Serandrei Barbero, 1990; Albani *et al.,* 1991; Scott *et al.,* 1991). This species tolerates a wide range of salinity and has been recorded also in nonmarine saline lakes (Resig, 1974; Cann & De Deckker, 1981) and in an inland pool (Papi & Tavani, 1959; Zampi *et al.,* 1996).

COLLECTION

Specimens of *D. aguayoi* living in modern (thermal waters of Montecatini and Laguna di Orbetello) and Neogene (Messinian and Pliocene) brackish environments were collected between 1958-1998 (Fig. 3).

Montecatini specimens

Sediments collected by Papi & Tavani (1959) in mineral waters of a Montecatini pool were used for studying the Montecatini specimens. The 0.65 m deep pool was long and narrow (17 m x 1.2 m-1.8 m) and dug out at the base of a travertine wall, from which water percolated into the pool. Salinity (8.6‰), temperature (13 °C-15 °C), pH (7), excess NaCl and $CaSO_4$, deficient $MgCl_2$ and $MgSO_4$ respect to sea water composition were measured by Papi and Tavani in February 1958 during sampling. Samples were collected from the bottom of the pool, covered by a thin layer of detritus, and from the travertine walls that were under water or moistened by the percolating

FIGURE 3–Location map: triangles indicate the sampling areas of *Discorinopsis aguayoi*.

water. An algal mat covered the walls of the pool. Foraminiferal assemblage included only *D. aguayoi* (mostly found on the walls of the pool) and *Miliammina fusca*. Because of the remarkable finding of foraminifera in mineral waters, further sampling would be useful, but the pool has dried out.

Orbetello specimens

Samples were collected in February 1984 (Zampi & D'Onofrio, 1986), using a Ross clamshell snapper, in an area of the Orbetello Lagoon located near a channel communicating with the sea. The bottom of this shallow area (1.2 m) consists of sand and silt covered by a mat of *Ruppia spiralis* (Cognetti, 1978). Lenzi & Angelini (1984) measured (February-July 1984) salinity (16-28‰), temperature (7-30 ºC), pH (7.5-8.4) and concentration of dissolved oxygen (saturated at 40%). The lower salinity detected in this part of the lagoon was due to the effect of small freshwater springs and to the Mulinaccio effluent in winter. The foraminiferal assemblage consists of *Ammonia beccarii tepida*, *Protelphidium anglicum*, miliolines (*Quinqueloculina aspera, Q. seminulum* and *Triloculina rotunda),* rare specimens of *Ammoscalaria runiana* and *Elphidium gunteri,* in addition to *D. aguayoi.*

Messinian specimens

The specimens were collected in a quarry (Pesciera Section: Bossio *et al.*, 1978), two km east of Rosignano Marittimo, Leghorn (Fig. 3). The quarry section is mostly composed of clastic gypsum and pelite. Ostracods *(Callistocythere, Cyprideis, Leptocythere, Loxoconcha* and *Xestoleberis),* few foraminifera (*Ammonia beccarii tepida*, *Cassidulinita prima, Bolivina* sp., *Elphidium* sp.) and vegetal remains including gyrogonites of *Characeae* are always present in the pelitic layers. In the succession, *D. aguayoi* occurs in the sample RMP 23, collected from a marly level. The organic fraction of this sample is composed of ostracods *(Cyprideis torosa* gr. and *Loxoconcha mulleri),* foraminifera *(Ammonia beccarii tepida* and *Discorinopsis aguayoi* associated to few specimens of *Bolivina variabilis)* and vegetal remains. Bossio *et al.* (1978, 1996) interpreted the depositional environment to be a brackish endoreic lake formed during the Messinian salinity crisis of the Mediterranean.

Pliocene specimens

Pliocene specimens of *D. aguayoi* were sampled from sediments of the S. Matteo quarry, near the village of Granaiolo, four km north of Castelfiorentino, Florence (Fig. 3). The Pliocene succession is composed of blue or dark clay and of fine sands with lignite layers that occasionally occur in the lower part of the succession. Few specimens of *D. aguayoi* are recorded only in the GRA 10 sample. The associated microfossils included several ostracods *(Aurila venilae*, *Cyprideis torosa* gr., *Leptocythere* sp., *Loxoconcha elliptica*, *L.* cf. *rhombovalis*, *Semicytherura* sp.), and foraminifers (miliolines, *Ammonia beccarii tepida*, *Cribrononion poeyanum* and *C. punctatum).* This association indicates that the depositional environment was a brackish lagoon.

MORPHOLOGY AND ECOPHENOTYPIC VARIATIONS

Number of chambers in the last whorl

The number of chambers in the last whorl ranges from 6 to 10 (Fig. 4), but the specimens mostly exhibit 7-9 chambers. The Messinian and Orbetello populations have the greatest number of specimens with 8 chambers in the last whorl, while Pliocene and Montecatini populations have a more uniform distribution (Fig. 4). Individuals with 10 chambers in the final whorl, as in the specimens of Bermúdez, have been recognized in the four populations. These data emphasize that the maximum number of chambers in the outer whorl is an invariant taxonomic trait, while the growth appears to be influenced by environmental parameters.

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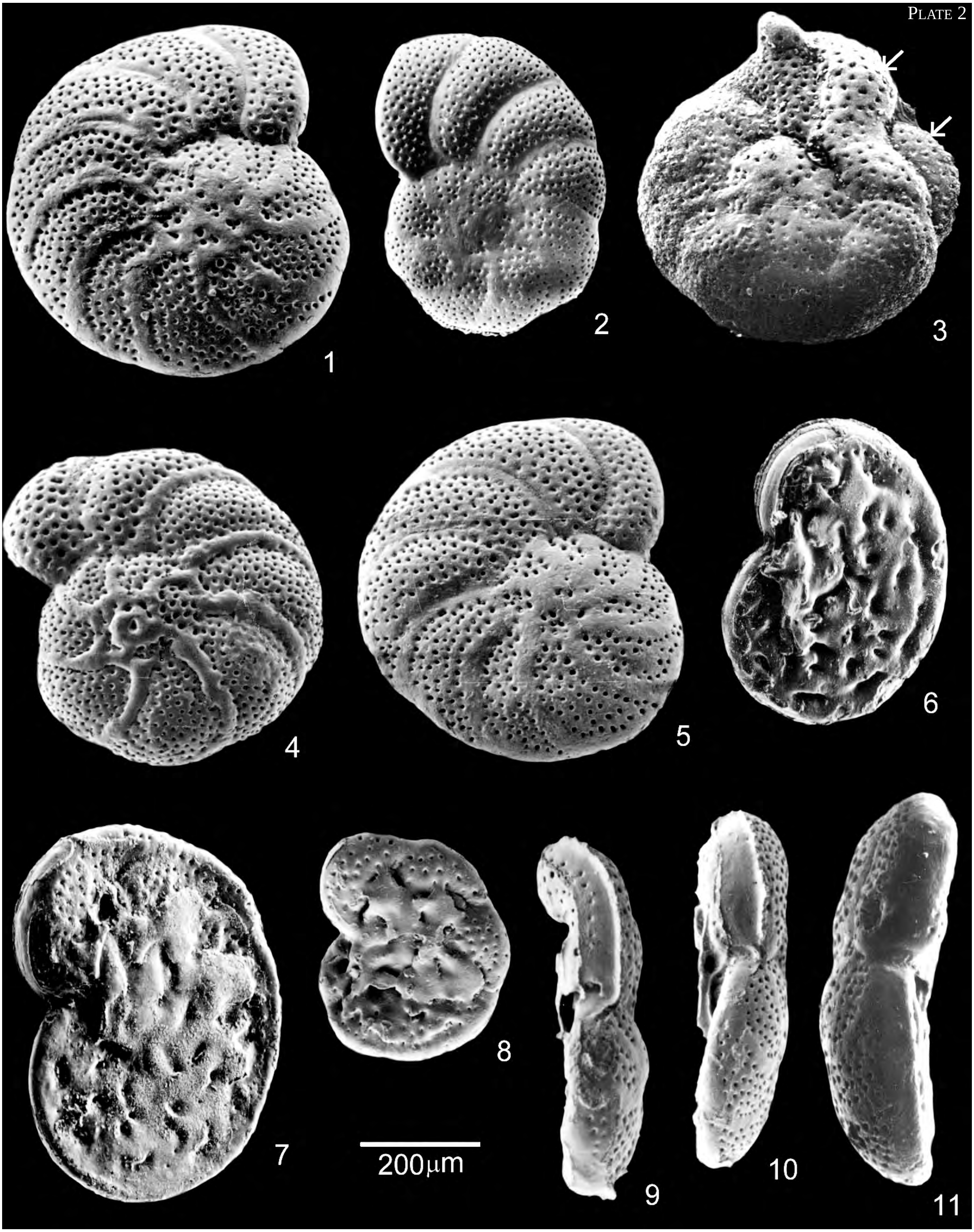
PLATE 2–*1-11,* Pliocene specimens of *Discorinopsis aguayoi* (Bermúdez). *1-5,* dorsal view, note the adventitious chambers (arrows), *1, 4-5,* specimens with strongly limbate sutures. *6-8,* ventral view, note the large calcitic encrustations. *9-11,* frontal view.

PLATE 2



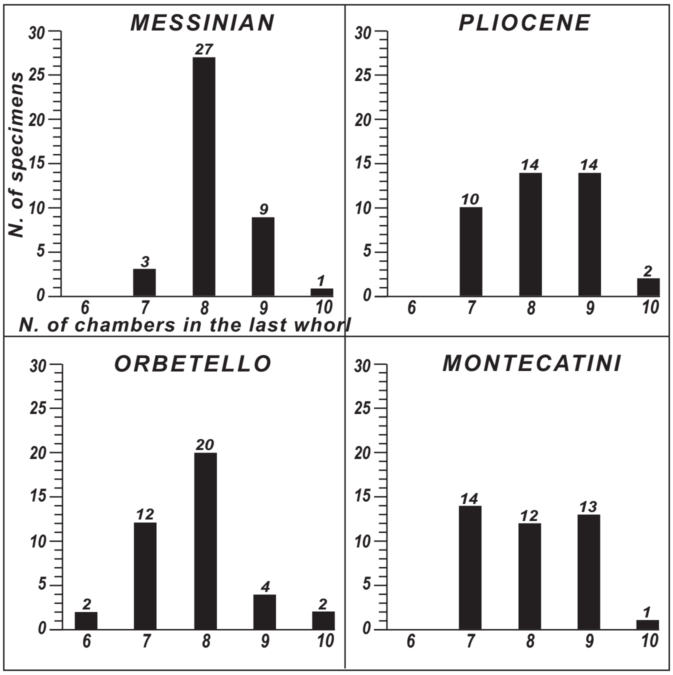


FIGURE 4–Chambers distribution in the last whorl.

Outline

The outline of the test shows a high degree of variability between the specimens of each population and between the four populations (Table 4). The outline can be elliptical (Pl. 1, Fig. 1; Pl. 2, Fig. 2; Pl. 3, Figs. 2-5, 9-10; Pl. 4, Fig. 4), subcircular (Pl. 1, Fig. 2; Pl. 2, Figs. 1, 9-10) or circular (Pl. 3, Fig. 1; Pl. 4, Figs. 1, 3, 5), weakly (Pl. 2, Figs. 1, 4-5) or strongly lobate in the last part of the outer whorl (Pl. 1, Figs. 1-2, 4-5; Pl. 3, Fig. 1). Particularly, the outline of several Montecatini specimens is almost circular, strongly lobate in the last part of the final whorl (Pl. 4, Figs. 1-2, 5), like the one of *D. aguayoi* living in the Lagoon of Golovita, Black sea (Tufesco, 1969), a strongly hypohaline environment quite similar to the pool of Montecatini.

The test of Scheffé, performed with the values of the index of curvature of the shell (Table 2), shows the greatest difference between the outline of Orbetello specimens and Montecatini individuals and, to a smaller extent, between the latter and Pliocene population. This morphological feature, then, may also vary as a consequence of environmental conditions.

Chamber morphology

The chambers of the inner whorl and the first chambers of the outer whorl show a fairly uniform shape and increase regularly in size (Pl. 1, Figs. 1-2, 4-5; Pl. 2, Figs. 1-2, 4-5; Pl. 3, Figs. 1-2, 4-9; Pl. 4, Figs. 1-5). Instead the last chambers are characterized by variable size and shape; these are inflated (Pl. 1, Figs. 1-2, 4-5; Pl. 3, Figs. 1-2, 4, 9) or subtrapezoidal and weakly inflated (Pl. 2, Fig. 2). Additionals chambers of irregular shape (adventitious chambers of Arnold, 1954) were observed on the edge of the outer whorl of few Messinian and Pliocene specimens (Pl. 1, Figs. 4-5; Pl. 2, Fig. 3). The test of Scheffé concerning the penultimate chamber (Table 2) shows a greater variability between Pliocene and Montecatini populations (mean value of l_2/h_2: Pliocene, 1.93; Montecatini, 1.45). With regard to the third last chamber, besides the Montecatini individuals also the Messinian specimens are distant from those of the Pliocene (mean value of l_3/h_3: Pliocene, 1.80; Montecatini, 1.32; Messinian, 1.36). Several Pliocene individuals show narrow and lengthened chambers (Pl. 2, Figs. 1, 4-5), while the Montecatini and Messinian specimens (particularly those of Montecatini) reveal rounded and prominently lobate chambers (Pl. 4, Figs. 1, 5). These data indicate that the variability of this character may be ascribed both to variation in heritable characteristics and to environmental parameters.

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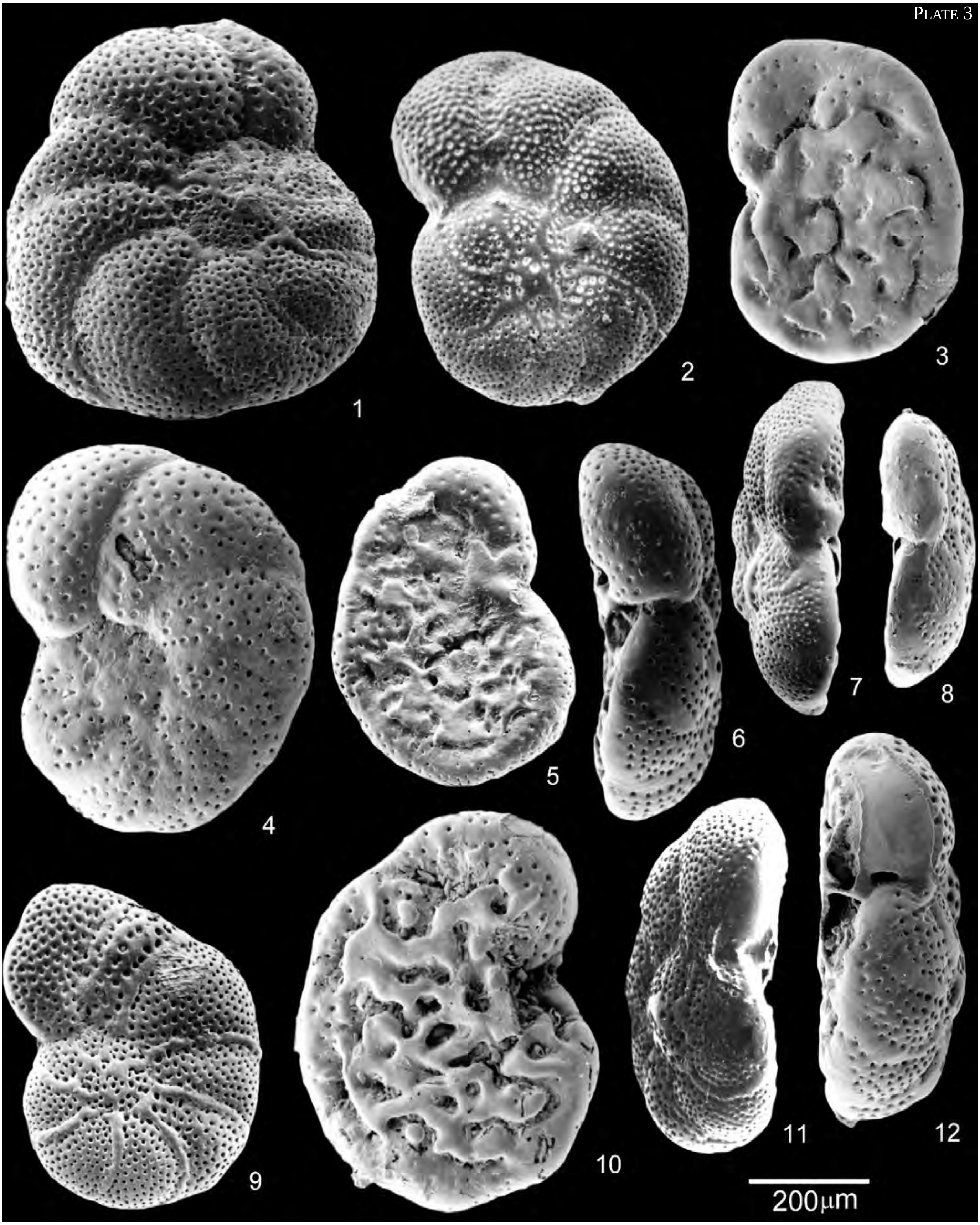
PLATE 3–*1-12*, Orbetello specimens of *Discorinopsis aguayoi* (Bermúdez). *1-2, 4, 9*, dorsal view, 1 specimen with weakly limbate sutures in the last whorl, *2-9*, specimens with strongly limbate sutures. *3, 5, 10*, ventral view, 3 specimen with large encrustations. *6-8, 11-12*, frontal view.

PLATE 3



	Ecophenotypic characters	**Messinian specimens**	**Pliocene specimens**	**Orbetello specimens**	**Montecatini specimens**
	Outline	Elliptical, subcircular, lobate	Elliptical, subcircular, mostly not lobate	Elliptical, mostly weakly lobate	Mostly circular, lobate, or strongly lobate
	Last chambers	Inflated	Mostly flattened	Mostly weakly inflated	Mostly inflated
	Test size	240-560 µm	220-520 µm	280-500 µm	180-460 µm
	Periphery	Rounded	Slightly rounded or subacute, buntly keeled	Rounded or subacute	Rounded
	Test height	140-180 µm	80-160 µm	100-170 µm	120-190 µm
Sutures	Morphology in the last whorl	Recurved or straight	Recurved	Recurved	Slightly recurved or radial
	Degree of limbation	Not identifiable	Strongly limbate	Mostly strongly limbate	Weakly limbate
	Pores size	4-6 µm	4-6 mm	2.4-5.6 mm	2.8-8 µm
	Ventral filling	Calcitic thickenings	Large and thick calcitic plates	Mostly large calcitic plates	Thin calcitic thickenings

The greatest number of chambers in the last whorl, the first and the secondary apertures, the pores large and prominent, the limbation of sutures, the depressed sutures of the last whorl, the contortion of the shell are the invariant characteristics of the four populations.

TABLE 4–Ecophenotypic and invariant morphological features of the four populations.

Morphological anomalies that confer to the shells an irregular outline were observed in the last chambers of several Montecatini specimens. Moreover abnormal early stages characterize the Messinian and Montecatini individuals (Pl. 1, Fig. 1-2, 4-5; Pl. 4, Figs. 1, 3-5). In fact, a protruding proloculus (Pl. 1, Fig. 3) and the swelling of the first or of the all chambers (Pl. 1, Figs. 1, 4-5) of the inner whorl characterize the Messinian individuals. In the Montecatini specimens, the small inner chambers are not recognizable and only a large (diameter: 80-100 µm) protruding chamber occupies the first whorl of the spire (Pl. 4, Figs. 1, 3-5). This feature of the Montecatini individuals is like the one described by Tufesco (1969) in specimens of *D. aguayoi* collected in a strongly hypohaline poorly oxygenated environment. A protruding proloculus has been observed in other benthic foraminifera *(Ammonia beccari tepida)* living in brackish environments with low values of dissolved O_2 (Zampi & D'Onofrio, 1984, 1986) or in infralittoral areas (ex. Bay of Guayanilla) with a high organic content *(Ammonia beccarii*, *Fursenkoina punctata:* Seiglie 1975, 1976). Therefore these anomalies may be due to locally low oxygen concentrations in the Montecatini pool and in the Messinian basin.

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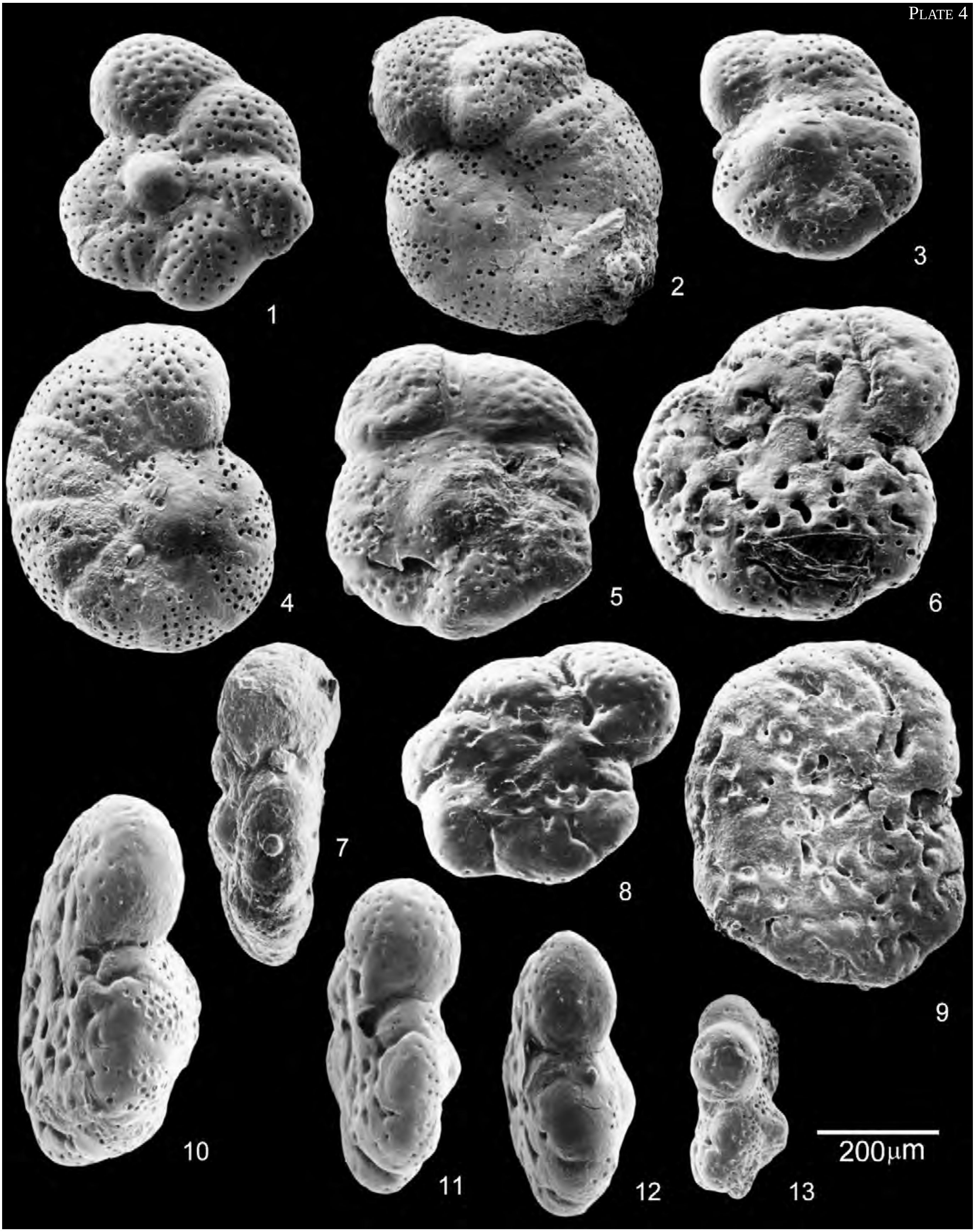
PLATE 4–*1-13*, Montecatini specimens of *Discorinopsis aguayoi* (Bermúdez). *1-5*, dorsal view. *6*, *8-9*, ventral view. *7*, *10-13*, frontal view. The specimens show a large protruding proloculus in dorsal and frontal view.

PLATE 4



Adventitious chambers

This morphological feature only characterizes a few Neogene specimens (Pl. 1, Figs. 4-5; Pl. 2, Fig. 3), that lived in a strongly (Messinian individuals) and in a weakly (Pliocene specimens) hypohaline environment. This character, previously observed in laboratory specimens (Arnold, 1954), has been described as a morphological variation with a hypothetical regenerative function. Our few observations does not clarify this hypothesis. Thus, we cannot establish any correlation of this character with the environment.

Test size

The measured specimens have a smaller size than both the specimens of Bermúdez (max. 800 µm) and the laboratory individuals of Arnold (max. 750 µm). The Messinian population and The Montecatini individuals show respectively the greatest (mean value of length: 427 µm) and the smallest size (mean value of length: 330 µm). The Orbetello and Pliocene specimens show a mean value of length of 347 and 395 µm, respectively. The mean size of Orbetello and Montecatini specimens is the most similar to that of *D. aguayoi* (357 µm) in the Golovita Lagoon (Tufesco, 1969). These measures reveal that, other environmental factors, other than salinity, may influence the test size of the four populations; in fact, the mean size of Orbetello and Pliocene individuals is smaller than the Messinian specimens. A comparison between the specimens of the four populations with the same number of chambers in the outer whorl (Table 1) shows that test size is related either to individual growth or to environmental conditions. This latter relation has been amply demonstrated by several investigations on foraminifera ecology (Boltovskoy & Wright, 1976; Yanko *et al.*, 1994; Hallock *et al.*, 1986; Caralp, 1989; Bijma *et al.*, 1990).

Periphery

The periphery can be slightly rounded (Pl. 2, Figs. 9-10; Pl. 3, Figs. 6, 12; Pl. 4, Figs. 9, 12-13), rounded (Pl. 1, Figs. 3, 7-9), or subacute (Pl. 2, Fig. 11; Pl. 3, Figs. 7-8, 11; Pl. 4, Fig. 11), weakly keeled only in the first part of the spire. The periphery of Pliocene population is buntly keeled (Pl. 2, Figs. 9-11); this thick keel, always associated to strongly limbate sutures, may be due to the high level of dissolved $CaCO_3$ in the waters of the Neogene basin. Therefore, we agree with the views of Hemleben *et al*. (1977) and we believe that the keel construction is a character genetically controlled, but also influenced by environmental factors when calcification occurs.

Test height

This character depends on the size of the specimens, but is also influenced by the morphology of the chambers of the outer whorl. Moreover, the swelling of the proloculus (Pl. 1, Fig. 2) or of the central area of the spire (Pl. 4, Figs. 1, 3-5) influence the height of test of Messinian and Montecatini populations. The test of Scheffé (Table 2) shows a significant difference in the index of shell flattening between Messinian-Pliocene, Messinian-Orbetello, Montecatini-Pliocene and Montecatini-Orbetello specimens. This morphological feature is influenced both by individual growth and by environmental conditions.

Sutures

The sutures of the last whorl are weakly (Pl. 2, Fig. 2; Pl. 3, Fig. 1, 4; Pl. 4, Fig. 4) or strongly limbate and prominent (Pl. 2, Figs. 1, 4-5; Pl. 3, Fig. 9), slightly curved (Pl. 4, Figs. 1, 3-4), curved (Pl. 1, Figs. 1-2, 4-5; Pl. 2, Figs. 1-2, 4-5; Pl. 3, Figs. 1-2, 4), at times almost straight (Pl. 1, Fig. 2) or radial (Pl. 3, Fig. 9; Pl. 4, Figs. 2, 5) in the last formed chambers, always depressed. In particular, the last suture is always weakly limbate and strongly depressed. This variability in the degree of limbation concerns particularly the sutures of the inner whorl of the Pliocene specimens. The strong limbation appears as a calcitic dorsal network (Pl. 2, Figs. 1, 4-5) masking the surface of the chambers. Since this morphological feature is unusual between Montecatini specimens, it may be correlated with the

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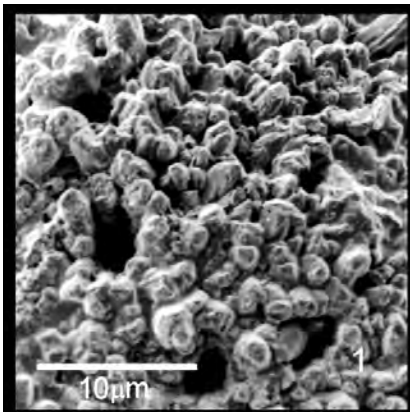
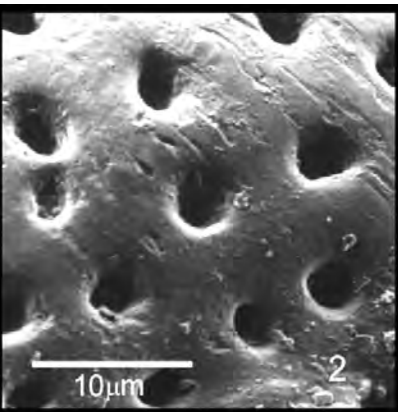
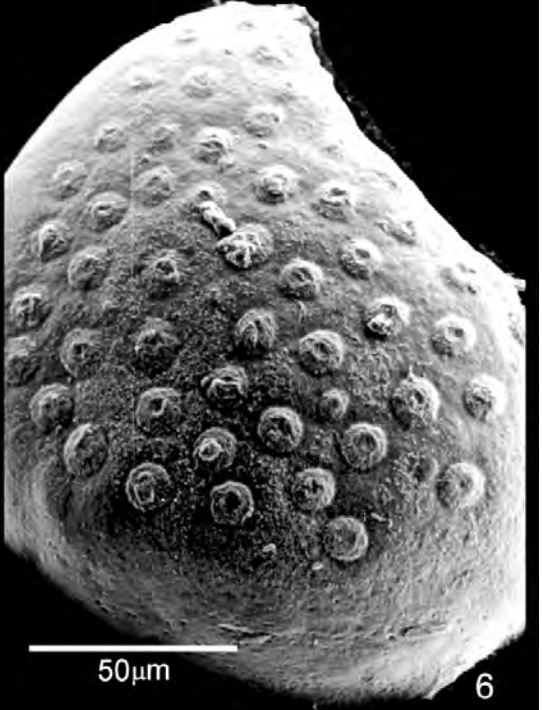
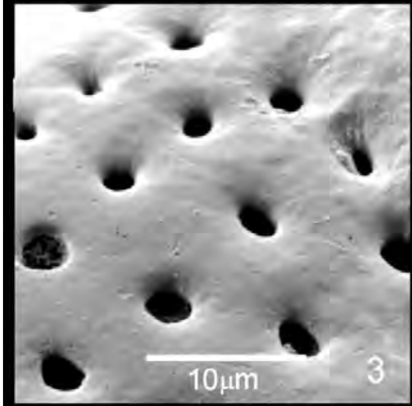
PLATE 5–*1-4,* Pores of penultimate chamber of the last whorl. *1,* Messinian specimen. *2,* Pliocene specimen. *3,* Orbetello specimen. *4,* Montecatini specimen. *5,* Organic layer of a decalcified Montecatini specimen. *6,* Organic layer of a decalcified penultimate chamber of a Montecatini specimen; outer surface is marked by conical elevations beneath the pores. *7,* pyritized organic layer of the last chamber of a Pliocene specimen. *8,* Orbetello specimen, “pore plugs” inside the conical elevation of the organic layer of the penultimate chamber. “Pore plugs” (arrow) are partially detached and collapsed during the SEM preparation.

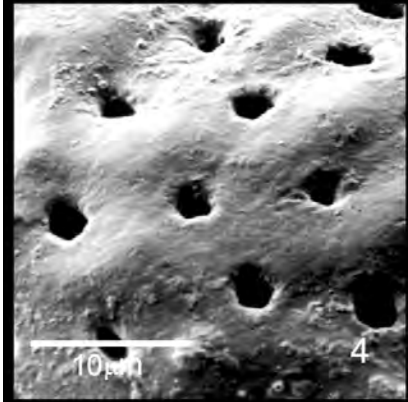
PLATE 5

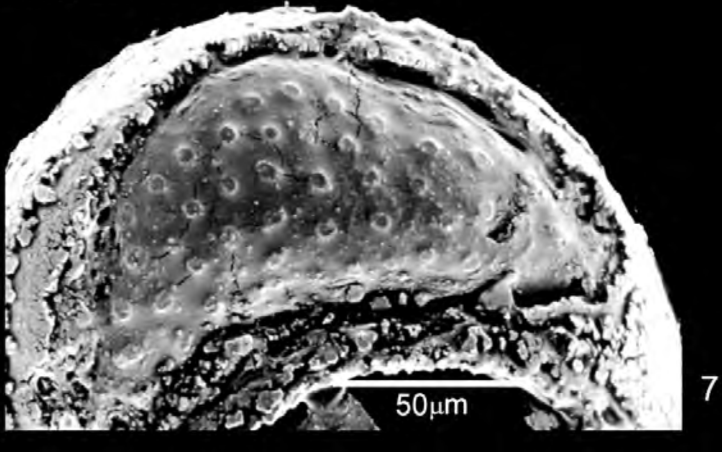












availability of $CaCO_3$. Arnold (1954) also observed this character, but he did not report salinity values of the laboratory cultures (ranging from 20 to 57‰) in which specimens with a strongly developed limbation of the early sutures lived. Also the morphology of the last sutures of the outer whorl appears as a variable character, as shown by the curved sutures of Pliocene specimens (Pl. 2, Figs. 1-2, 4-5) and by the straight (Pl. 1, Fig. 2) or radial (Pl. 4, Figs. 2, 5) sutures of Messinian and Montecatini specimens. This character, in fact, is strictly related to the morphology of the last chambers. Instead, the depression of the sutures described by Bermúdez (1935) and by Arnold (1954) is typical of the specimens of the four populations. Then, also this latter character appears, as the limbation, an invariant taxonomic trait.

Pores

The test wall is perforated; the pores large (Pl. 5, Figs. 1-4) and prominent, as described by Bermúdez (1935) and Arnold (1954), giving the examined tests a very distinctive appearance. Their size, as determined in the penultimate and in the third last chambers of the adult specimens, range from 2.4 to 8 µm. Nevertheless, the pore size is scarcely a significant taxonomic character, as affirmed by Boltovskoy & Wright (1976), because it may vary "in adjacent chambers of the same individual and in individuals of different age". The measures that we have pointed out are quite similar to those (1.5-7 µm) reported by Arnold (1954), but he cultered *D. aguayoi* under different values of salinity. Therefore, it is possible that the sizes of pores of our specimens could be influenced by salinity, or by other environmental parameters. According to Hemleben *et al*. (1977), in fact, the size of pores in foraminifera is "subject to ecological influence".

Aperture

The main aperture and the secondary perforations that open in the ventral filling show the shape described by Bermúdez (1935) and Arnold (1954). The main aperture consists of a low opening at the ventral edge of the last formed chamber (Pl. 1, Figs. 7-8; Pl. 3, Fig. 6; Pl. 4, Figs. 7, 10-12) with a thin lip in some adult specimen (Pl. 2, Figs. 9-10; Pl. 3, Fig. 12). Apertural characters appear as invariant traits of the investigated specimens. This observation emphasizes the specificity of the "reaction norm" (Dobzhansky, 1937) of foraminifera, since the shape of the aperture of another benthic porcellanaceous form, such as *Triloculina rotunda*, also varies in response to environmental conditions (Zampi & D'Onofrio, 1986).

Contortion

Several specimens of the four populations show the twisting of the test (Pl. 1, Figs. 7-9; Pl. 2, Fig. 11; Pl. 3, Figs. 6, 9). This character has not been reported by Bermúdez (1935), but a Cuban specimen, in apertural view, shows a contortion of the shell. According to our data, this morphological feature appears a genetic character of the examined specimens.

Ventral filling

The ventral side, slightly concave, is filled with a secondary calcitic growth, more or less complex, pierced by irregular openings. Its variability ranges from a loose network of thin, calcitic plates (Montecatini specimens, Pl. 4, Figs. 6, 8, 10) to the largest and more thick encrustations shown by the Orbetello (Pl. 3, Fig. 3) and Pliocene (Pl. 2, Fig. 8) individuals. We have never observed the large "cake" (Arnold, 1954) encrustations on the ventral filling of Montecatini specimens. Instead such morphological feature is fairly frequent among Pliocene morphotypes, and is associated with strongly limbate sutures and a keeled periphery. Therefore, the complexity of this calcitic growth may also be controlled by $CaCO_3$ availability.

THE ORGANIC LAYER OF THE MODERN TEST

The Organic layer is not preserved in the fossil populations, but several Pliocene specimens show this structure preserved as pyrite (Pl. 5, Fig. 7). The

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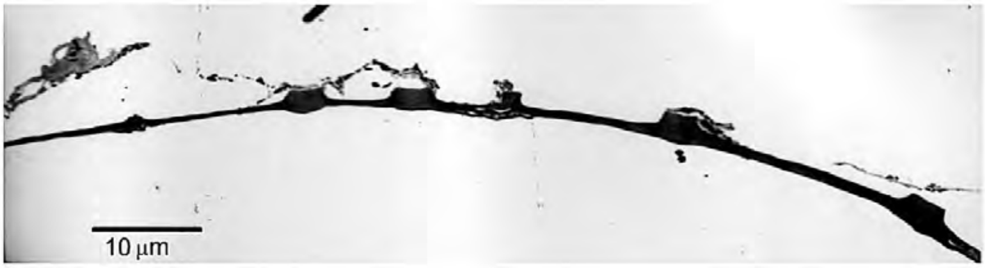
PLATE 6–*1-6*, Orbetello specimens. *1*, vertical cross section of the organic layer. *2-6*, vertical cross sections of the organic thickenings beneath the pores, note the laminated structure of the organic layer, the "pore plug" (arrow) and the remains of the outer membrane lining the pore process.

PLATE 6



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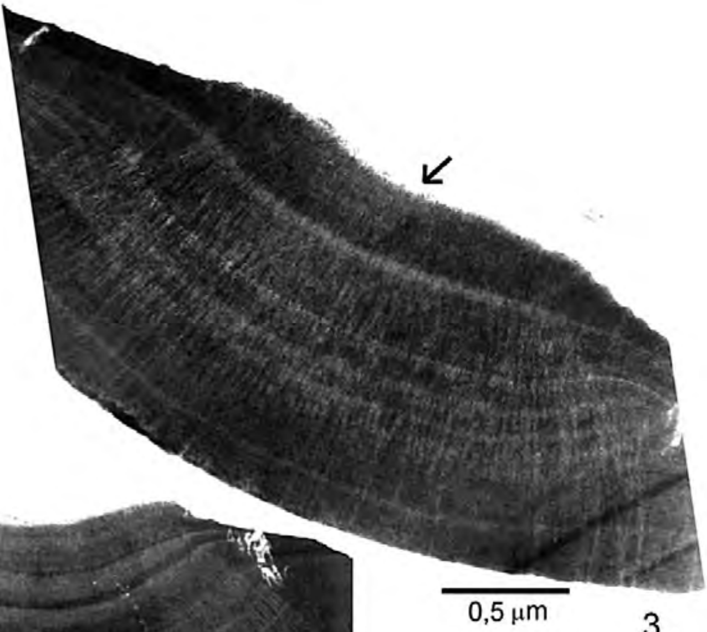

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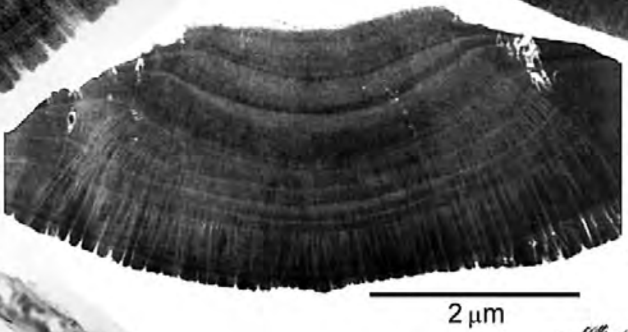

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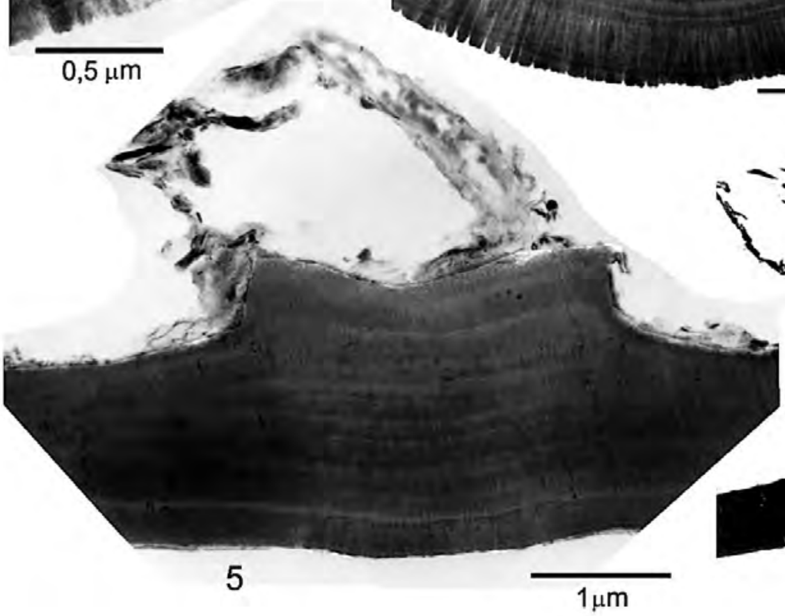

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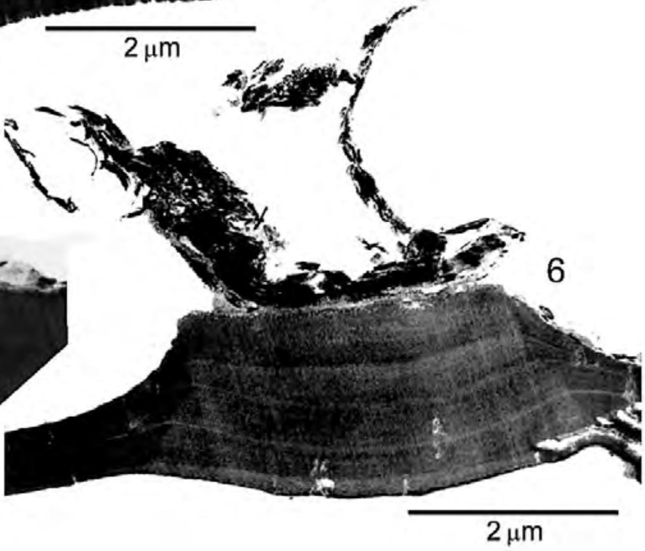

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organic layer of the Montecatini (Pl. 5, Fig. 5) and Orbetello specimens was examined in individuals in which the test wall was removed. Thin, transparent, yellowish-brown in Orbetello specimens, as observed by Arnold (1954) in cultured *D. aguayoi* individuals, the organic layer is strongly pigmented (red-brown), acid-resistant in the Montecatini individuals. It is clearly visible also in tests with a thin calcitic wall. The Organic layer in the Montecatini specimens is thick, while the organic layer in Orbetello individuals is highly fragile. The organic lining is positive with the PAS test. In OsO_4-fixed individuals, decalcified and embedded in epon-araldite, the organic layer is faintly visible or not visible at all in the last formed chambers (particularly in the Orbetello specimens). It is likely that the organic layer is thinner in younger chambers than in the older ones and damaged during TEM preparation. This structure becomes progressively thicker toward the prolocular region. In individual chambers, as observed in semi-thin sections (Pl. 8, Figs. 5-7), the organic layer is thicker on the distal edge of the chambers than on the proximal part where calcification is more active (Hemleben *et al.,* 1977). SEM observations show the structure of the organic layer, as described by Arnold (1954): "a surface pot-marked with truncated, conical elevations, with a crater-like depression within the minute cone". At the bottom of the depression lies a rounded structure designated by Arnold (1954) as a "pore plug". The semi-thin sections stained with methylene blue, also exhibit the "pore plugs" very well. In fact, as remarked by Arnold (1954), "pore plugs" are clearly differentiated from the underlying organic layer since they are more retentive of the stain (Pl. 8, Figs. 5-7). We cannot ascertain, whether the "pore plugs" are either firmly or faintly attached, but SEM shows this structure raised from the base of the funnel; furthermore, the "pore plugs" are also easily dislodged from the organic matrix during the process of grinding semi-thin sections of undecalcified tests, as already observed by Arnold (1954). Thus, even if "pore plugs" are permanently attached, the attachment is likely to be weak. In TEM the organic layer is seen to be a laminated sheet with dark and light bands of fibrous aspect (Pl. 6, Figs. 2-6; Pl. 7, Figs. 3-4, 6). The organic layer is closely pressed to the cytoplasm in the Montecatini specimens. In fact, protrusions of the organic layer penetrate the cytoplasm (Pl. 7, Fig. 6). The organic layer is thicker beneath the

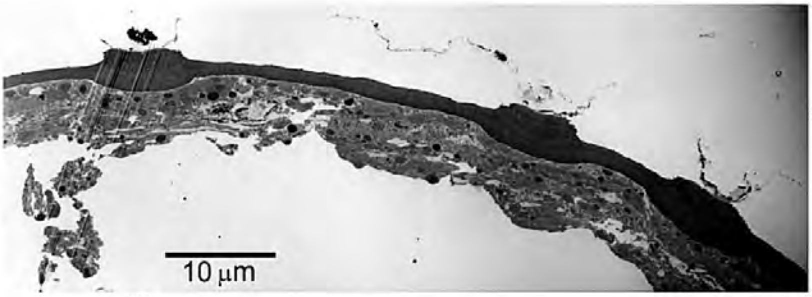
	Orbetello	**Montecatini**	**Arnold (54)**
Size of the "pore plugs"	1,97-3,42 µm	3,1-5,6 µm	2,5-6 µm
Thickness of the "pore plugs"	0,4-0,5 µm	0,63-1,2 µm	0,5-3 µm
Size of the organic thickening beneath the "pore plugs"	2,6-5 µm	5,3-7µm	–
Thickeness of the organic thickening beneath the "pore plugs"	1,33-1,79 µm	0,86-1,8 µm	–

TABLE 5–Measures of the "pore plugs" and of the underlying organic thickening in the Montecatini and Orbetello specimens. The size and thickness of the "pore plugs" are compared with the measures reported by Arnold (1954).

→

PLATE 7–*1-6,* Montecatini specimens. *1,* vertical cross section of the organic layer. *2-4,6,* organic thickenings beneath the pores and "pore plugs" (more elettron-dense) with a "deep-plate" shape, remains of the cytoplasm underlying the organic layer, osmiophilic granules (OG) and fragments of diatoms (arrow) are still recognizable; *3,* microcavities in an electron-dense layer in the "pore plug"; *4,* microcavities in an electron-dense layer at the base of the "pore plug"; remains of the outer organic membrane are recognizable over the "pore plugs"; *5,* higher magnification of an electron-dense organic sheet showing its fibrous nature and a band of microcavities; *6,* microcavities in an electron-dens layer at the boundary between the "pore plug" and the underlying organic thickening. In this picture is also visible a projection of organic layer penetrating into the cytoplasm.

PLATE 7



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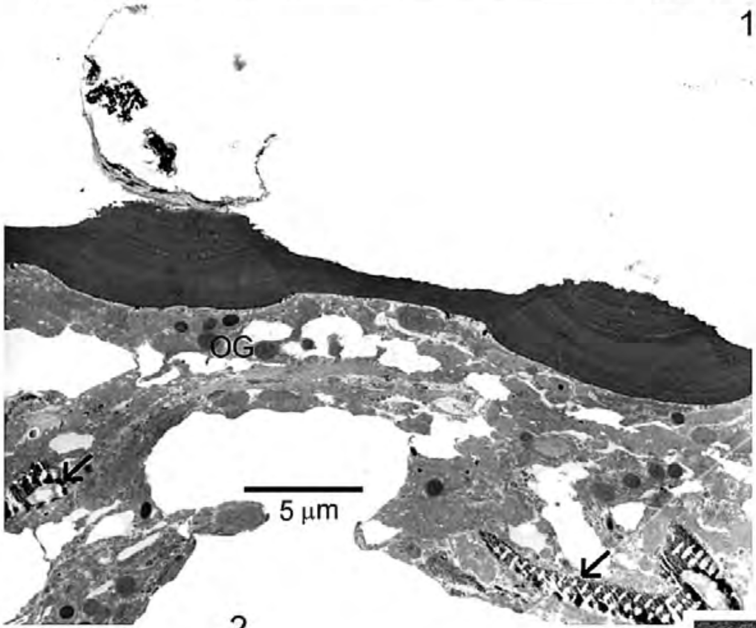

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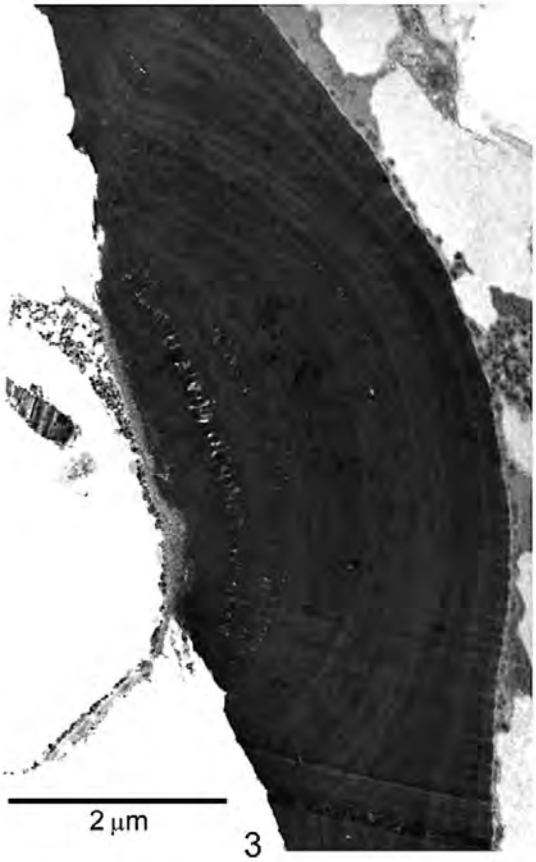

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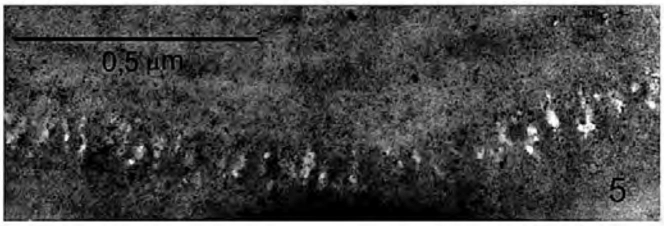

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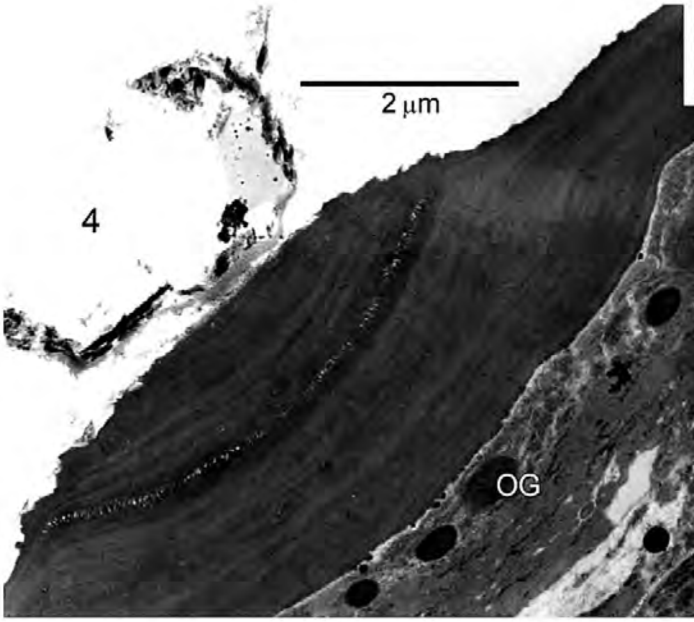

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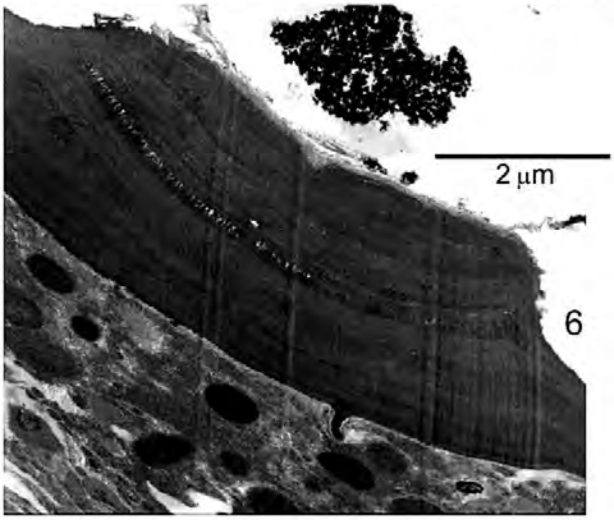

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pores, but in Montecatini specimens (Pl. 7) the thickenings are more concave, with a deep-plate shape, than in the Orbetello specimens (Pl. 6) and the "pore plugs", easily recognizable because they are more electron dense, show a greater size and thickness (Pl. 7, Figs. 1-4). The values of Montecatini "pore plugs" are more similar to measurements reported by Arnold (1954) than those of the Orbetello individuals (Table 5). The greatest thickness of the "pore plugs" of Montecatini specimens is revealed, besides micrographs, also by semi-thin sections stained with methylene blue (Pl. 8, Fig. 5). Micrographs of Montecatini specimens show bands of microcavities (size: 0.012-0.038 µm), irregular in shape and arrangement, at different levels of the organic thickenings beneath the pores and in the "pore plugs"; they are clearly visible in the more electron-dense laminar sheets (Pl. 7, Figs. 3-6). Since microcavities are not clearly identifiable in the Orbetello specimens, it could be supposed that they represent a structural difference between the two populations.

DISCUSSION

The present investigation identifies the ecophenotypic characters and the invariant traits of the examined specimens of *D. aguayoi*. In fact this study reveals several morphological features that are not invariant but that are determined by genetic characters influenced by environmental parameters ("reaction norm" of Dobzhansky, 1937). These include: the outline and the height of the test, the morphology of the chambers of the outer whorl and the morphology of the periphery, the size of the pores, the degree of limbation of the sutures and their greater or lesser bending, and the complexity of the ventral filling (Table 4). These traits have a limited taxonomic value because they are very variable. In contrast the invariant traits have high taxonomic value, since they have conserved a great stability over millions of years. These are the greatest number of chambers in the outer whorl, the limbate and depressed sutures (particularly, the last suture is always strongly depressed and weakly limbate), the apertural characters, the morphology of the pores, the contortion of the test. All analyzed specimens share these traits; they agree with the morphological features of *D. aguayoi*.

In addition to the morphological features, we have also examined the organic layer of the modern specimens. Under light microscope, the organic layer appears to be present in all chambers of the shell, as in *Rosalina floridana* (Angell, 1967a), *Ammonia beccarii* (Banner & Williams, 1973), *Patellina corrugata* (Berthold, 1976), *Heterostegina depressa* (Spindler, 1978), *Globigerinoides sacculifer* (Anderson & Bè, 1976), *Globorotalia menardii* (Hemleben *et al.*, 1977) and other planktonic foraminifera (Bè *et al.*, 1980). The organic lining is PAS-positive, confirming that the innermost coating is made up, mostly or partly, of polysaccharides as in some arenaceous foraminifera (Hedley, in Banner *et al.*, 1973), *Rosalina floridana* (Angell, 1967b; Lee, in Angell, 1967b), *Globigerinella aequilateralis*, *Globigerinoides ruber* and *G. sacculifer* (Moss, in Angell, 1967b) and as suggested for the strongly osmiophilic organic layer of an unnamed planktonic foraminifer (Towe, in Banner *et al.*, 1973) and *Globoratalia menardii* (Hemleben *et al.*, 1977). SEM analysis confirm the morphology of the organic layer of *D. aguayoi*, as described by optical microscope (Arnold, 1954). Therefore, it is an invariant character of the compared specimens. Instead, the greater thickening of this structure shown by the Montecatini specimens is due to environmental conditions: in fact it has been reported also in *Quinqueloculina fusca* (Schaudin, in Banner *et al.*, 1973), *Spiroloculina hyalina* (Schultz, in Banner *et al.*, 1973), and other benthic calcareous foraminifera with a thin calcitic wall living in waters with a very low value of salinity (Boltovskoy & Wright, 1976). This thickening supports the hypothesis of strengthening of the test and of the protective lining of the inner cytoplasm able to retard the biochemical process of cytoplasm decay (Boltvoskoy and Lena, in Banner *et al.*, 1973). In fact, the cytoplasm of the Montecatini individuals has been preserved over 40 years. TEM observations of the organic layer of *D. aguayoi* reveal features previously observed in other benthic and planktonic foraminifers such as *Rosalina floridana* (Angell, 1967b), *Ammonia beccarii* (Banner & Williams, 1973), *Globorotalia menardii* (Hemleben *et al.*, 1977), *Amphistegina lobifera* (Leutenegger, 1977), *Heterostegina depressa* (Spindler, 1978), *Globigerinoides ruber*, *G. sacculifer* and *Globigerinella aequilateralis* (Bè *et al.*, 1980). In fact, in the Montecatini and Orbetello specimens the last formed chambers are coated by a thin and easily damaged organic lining that thickens towards the prolocular region and that is very thick beneath the pores. Moreover, micrographs show a close resemblance between the multilamellar fibrous ultrastructure of the organic layer of Montecatini and Orbetello specimens and the laminar sheet of *Pelosphaera cornuta* (Hedley, in Banner *et al.*, 1973), *Rosalina floridana* (Angell, 1967b), and *Ammonia beccarii* (Banner & Williams,

PLATE 8

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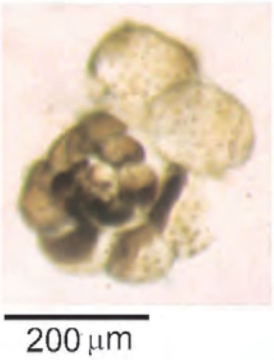

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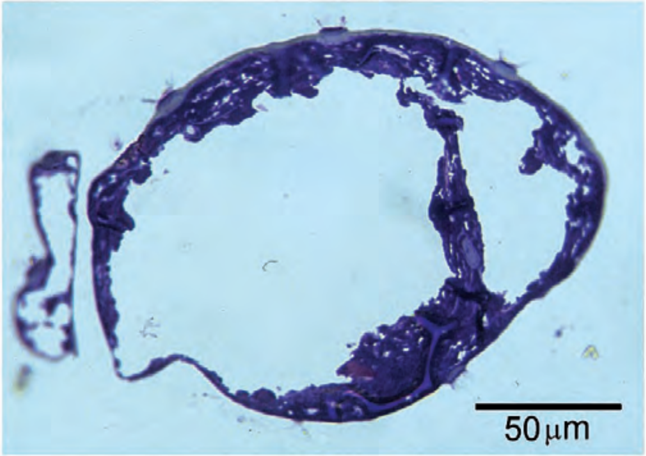

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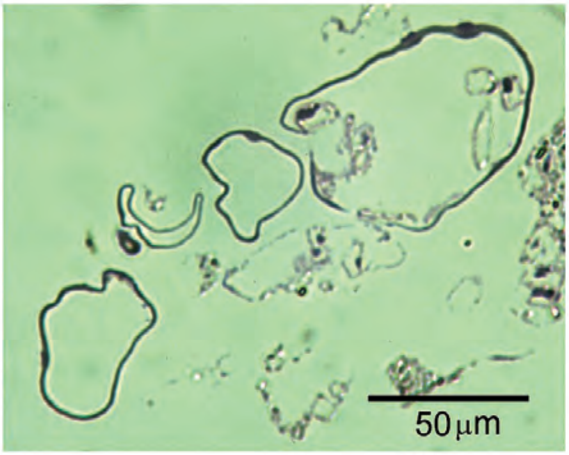

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PLATE 8–*1-2*, Organic layer of two Montecatini specimens decalcified with a EDTA and embedded in Epon-Araldite. Photographs show the thickening of the organic layer in the chambers of the inner whorl and in the older chambers of the eastern whorl. The thin organic layer of the youngest chambers of the final whorl was probably damaged by the chemical process for the TEM analysis. *3*, thin organic layer of an Orbetello specimen. *4*, a broken Montecatini specimen with a thick organic layer. *5-7*, semi-thin sections of Montecatini (5) and Orbetello (6-7) specimens stained with an aqueous solution of methylene blue and 0,5 g of $CaCO_3$. In both sections the "pore plugs" are the darkly stained elements. In Montecatini specimens remains of cytoplasm are recognizable.

1973). By contrast, the organic thickenings beneath the pores reveal structural differences between the Montecatini and Orbetello specimens. Variations concern the size of the "pore plugs" and the presence of microcavities in Montecatini specimens. As for the first feature, we cannot ascertain whether the measurements taken on Montecatini specimens are correlated with environmental conditions, because these are included in the range reported by Arnold (1954). The laboratory specimens were cultured in salinities ranging from 20 to 57‰, but Arnold did not specify in which salinity conditions he cultured the measured specimens. Therefore, we cannot exclude the possibility that a relationship exist between this character and the values of salinity. As concerns the microcavities, the available data do not allow us to establish their exact function. Nevertheless, their exclusive location in the organic thickenings beneath the pores and in the "pore plugs" suggest a possible implication in the osmotic function (already suggested by Arnold for the "pore plugs"), played in extreme environmental conditions. In fact, the Montecatini specimens lived in a strong hypohaline thermal pool, likely poorly oxygenated because of the decomposition of the algal matter covering the walls of the pool.

Fossil tests likely to belong to *D. aguayoi* are reported here for the first time. Papi & Tavani (1959) suggested that the Montecatini specimens may descend from Pliocene ancestors. Tufesco (1969) also indicated that the population of *D. aguayoi* recorded in the Pontic area may have been a Neogene faunistic relict. The finding of fossil specimens confirm the hypothesis formulated by previously mentioned authors.

An "unmistakable resemblance" between *Discorinopsis aguayoi* and *D. gunteri* was suggested by Scott *et al*. (1991). *D. gunteri,* the type species of *Discorinopsis,* is an Eocene species bearing a secondary ventral filling. Cushman & Brönnimann (1948) and Arnold (1954) carried out comparative studies on *D. gunteri* and *D. aguayoi*. According to Cushman and Brönnimann, these two species differ by their test size, the number of chambers in the last whorl and by the more complex umbilical filling in *D. aguayoi*. After examining *D. gunteri* topotypes received by Cole, Arnold (1954) established the difficulty in finding affinity between the two species since Cole's specimens were partially recrystallized (the reasons for which Loeblich & Tappan, 1953, discredited the validity of the genus *Discorinopsis* and assigned rotalids with umbilical filling to their new genus *Trichohyalus*). A detailed comparison between both the holotype and the specimens studied of *D. aguayoi* with *D. gunteri*, showed marked differences with regard to the number of chambers in the last whorl (seven for *D. gunteri*, ten for *D. aguayoi);* the greatest spiral diameter (2.89 mm for *D. gunteri,* quite large with respect to the drawing, reported by Cole rather than a maximum diameter of 0.8 mm for Cuban specimens of *D. aguayoi);* the morphology of the dorsal side (highly convex for *D. gunteri,* flat and depressed in the middle for *D. aguayoi);* the outline of the shell (weakly lobate for *D. gunteri,* lobate or strongly lobate for *D. aguayoi,* especially for the last chambers of the last whorl); the morphology of the chambers (flattened and sub-rectangular for *D. gunteri,* more inflated and generally sub-trapezoidal for *D. aguayoi);* the twisting of the test, which is lacking in *D. gunteri,* but frequent in *D. aguayoi* specimens; the limbation of sutures, lacking in *D. gunteri* (although this morphological feature may have been hidden by the subsequent recrystallization of the test); the morphology of sutures, depressed in both species, but very recurved in *D. gunteri*, slight recurved and at times almost radial in *D. aguayoi;* the umbilical filling, quite reduced for *D. gunteri,* structurally more complex for *D. aguayoi;* the depositional environment, the open sea for *D. gunteri,* as shown by associated benthic and planktonic foraminifera, a brackish environment for *D. aguayoi.* These differences in morphology and habitat indicate that specimens of *D. gunteri* and *D. aguayoi* are unlikely to belong to the same species.

CONCLUSIONS

1) Environmental conditions influence the test morphology of *D. aguayoi*. The morphological investigation, also supported by statistical methods (Mahalanobis distances and canonical analysis), show that the Messinian and Montecatini populations (living in lower salinity waters) substantially differ from Pliocene specimens, inhabiting environments with higher salinity values.

2) All analyzed specimens conform to the diagnostic morphological features of the syntypes of *D. aguayoi*. These last two results suggest the possible implications of this study on the taxonomy. In the past, species were established using exclusively morphological criteria. This taxonomical method led the "splitters" to interpret any morphological variation as a different species. Thus, the nomenclature of foraminifera is at present chaotic. Nowadays, the criteria used to classify species include, besides the morphology, ultrastructural, biochemical, cytological and ecological criteria. The first three are applied with difficulty to foraminifera, particularly if they are fossils or not

living specimens. With regard to the ecological criterion, a better knowledge of the degree of variability of foraminifera has invalidated many taxa, as shown also by the synonimic list of *D. aguayoi*.

3) Environmental conditions affect the morphology of the organic layer. This is testified by the greater thickness of the organic lining in the Montecatini specimens, with a thin calcitic wall, and by microcavities, revealed by TEM, in the organic thickenings beneath the pores and in the "pore plugs" of these individuals, living in a strongly hypohaline habitat, very likely oxygen-depleted. This feature is not recognizable in the Orbetello specimens, living in a brackish lagoon. We cannot ascertain if this character is a conservative inherited attribute (this hypothesis my be formulated because the Montecatini specimens are a relict fauna of Pliocene age, living in an isolated thermal pool) or, most likely, is an ecophenotypic adaptation. At present, our data are not sufficient to solve this problem. However, this ultrastructural variation is probably induced by extreme environmental conditions and may be related to a specific physiologic function.

4) The finding of fossil *Discorinopsis aguayoi* in Neogene sediments of Tuscany (Italy) indicate that since that time the species inhabited brackish environments of Mediterranean area.

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PLAGIARISM IN PALAEONTOLOGY. A NEW THREAT WITHIN THE SCIENTIFIC COMMUNITY

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When the editor of a journal, and then the reviewers, receive a manuscript, they always rely on the honesty of the author presenting the data. That is, it is always assumed that the data are correct. Somebody may disagree with the interpretations; this is part of the scientific debate and how science progresses. However, the data supporting the interpretations are assumed to be trustworthy. This is part of the moral/ethical responsibility of researchers in Science. Unfortunately, the frontier of this scientific ethical behaviour is sometimes transgressed. There are several well-known frauds in the history of the Palaeontology, for instance the Piltdown skull (Gould, 1994), maybe one of the most notorious cases of outright deceit. After reading a book on the history of the Palaeontology, it can be easily concluded that this dishonest practice is part of the history that does not correspond to the present-day scientific behaviour. Surprisingly, alarming cases of corrupt behaviour among palaeontologists have been recently highlithted, such as the peripatetic fossils from the Himalaya Mountains (Talent, 1989).

Here, a new case of scientific fraud, involving plagiarism of images and duplications of photos in different papers supposedly dealing with sediments and fossils from different areas and of different ages is reported. The person involved in this fraud is Mostafa M. Imam, from the Scientific Department of the College of Education for Girls in Saudi Arabia.

In the last two decades, Imam has published several papers, both by himself and in collaboration with other authors, on microfacies, foraminifers and coralline red algae from Eocene, Miocene and Pliocene sediments of several areas of Egypt and Libya. During these years, this author has repeatedly been plagiarising pictures of diverse organisms previously published by other authors. Additionally, Imam has been using the same pictures in the different papers that he has published concerning different areas and rocks of different ages.

The fraud came up looking at the pictures shown in a manuscript that Imam submitted for publication in *Revista Española de Micropaleontología*. The manuscript deals with the lower Miocene coralline red algae from Egypt and includes four plates, with eight pictures each. The alert started with the Figure 6 of the first plate. Imam identified the fossil illustrated in this figure as *Lithophyllum* spp. of the lower Miocene deposits of the Sadat Member (Gharra Formation) from Gabal Gharra (Cairo-Suez road, Egypt). Nevertheless, the image is actually the same photograph of a coralline alga, *Lithophyllum incrustans* Philippi, from the upper Pliocene deposits of Cabo Roche (Conil, SW Spain) (Aguirre *et al.*, 1993). The same specimen was later used in a review paper of the coralline species belonging to the subfamily Lithophylloideae from the Neogene basins of southern Spain (Braga and Aguirre, 1995).

But this is not the only image plagiarised in this manuscript that Imam tried to publish in *Revista Española de Micropaleontología*. There are at least 14 pictures in total copied from other papers published in different journals by different authors. Furthermore, Figures 2 and 5 (Plate 3) of this manuscript are exactly the same images. Nevertheless, Imam refers to them as different samples with different magnifications: the former is attributed to sample 103 (magnification x 80) and the latter is quoted as sample 100 (magnification x 60).

All these examples of plagiarism appear in one paper, which is not yet published (and fortunatelly may never be published). Thus, the next step is to go through the papers that Imam has already published to ascertain whether he used the same fraudulent practice in previous papers and, if so, for how long. Surprisingly, a quick look at the available papers reveals that Imam did the same in the past!! Below, some examples are provided.

1. Imam reported and illustrated the species *Archaeolithothamnium saipanense* Johnson in the middle Miocene (Langhian to Serravallian) sediments

of the Hammam Farum Member (Belayin Formation) at Gebel Gushia section, west-central Sinai (Egypt) [Fig. 3 (1)] (Imam, 1996). As the author explicitly states in the Introduction section of the paper, the mentioned section is located Lat. 29º 15'N and Long. 33º 10'E. No question about the source area of the material.

Later, Imam and Refaat (2000) quoted the same species [Fig. 7 (5)] in the Wadi Abura section (Lat. 22º 02'N, Long. 33º 34'E) and Gabal Hammam Sayidna Musa section (Lat. 28º 01'N, Long. 33º 34'E).

This species (as *Sporolithon saipanense)* is also cited in the lower Miocene (Burdigalian) deposits at Al Khums area of the Sirte Basin (NW Libya) (Fig. 1, Plate 3) (Imam, 2003). In this paper, Imam even proposed a total range biozone with this species, the *Sporolithon saipanense* Zone, that characterises the lower part of the Al Faidiyah Formation (Burdigalian in age) at Libya.

The reader soon discovers that this species of coralline alga is present in almost all the published papers by Imam. Nevertheless, the pictures shown in all these papers are exactly the same. Adding insult to injury, this picture actually belongs to a specimen first published by Johnson as *Archaeolithothamnium* sp. from the upper Eocene Matansa limestones of Saipan (Mariana Islands) (Fig. 10, Plate 37) (Johnson, 1957), latter published again in the seminal book on calcareous algae by Johnson (Fig. 1, Plate 2) (Johnoson, 1961).

2. In the paper dealing with the material from NW Libya, Imam (2003) identified *Lithothamnion macrosporangicum* Mastrorilli and *Lithothamnion libanum* Johnson. Imam shows these two species, respectively, in Figures 2 and 7 (Plate 3). However, these photographs are duplicated from Figures 2 and 5 (Plate II) of Aguirre *et al*. (1996), both of them representing conceptacles of *Lithothamnion ramossisimum* (Reuss) Piller from the Leitha Limestone (Middle Miocene –Badenian–) of the Vienna Basin.

3. In the same paper by Imam (2003), the Figure 3 (Plate 3) represents *Sporolithon* sp. from lower Miocene sediments of NW Libya. Notwithstanding, this picture is the one figured by Johnson as *Archaeolithothamnium nummuliticum* (Gümbel) Rothpletz (Fig. 2, Plate 2) from Eocene of Ryûkyû-rettô (Johnson, 1964).

4. The coralline algae from Libya illustrated by Imam (2003) in Figures 6, 7 and 8 of Plate 4, as well as the Figure 5 of Plate 5 are, respectively, identified by this author as *Sporolithon cyrenaicum* Raineri, *Mesophyllum guamense* Johnson, *Mesophyllum sancti-dionysi* Lemoine, and another specimen of *S. cyrenaicum*. Nevertheless, this photos are directly reproduced from a paper by Martín *et al*. (1993) dealing with the middle Miocene rhodoliths of Marion Plateau (NE Australia).

5. Figure 9 (Plate 4) reproduced by Imam (2003), which appears as *Lithothamnion disarmonicum* Conti, is really the picture of the holotype of *Lithothamnium luxurum* described by Johnson and Stewart from the Eocene deposits of Meganos Platform (California) (Johnson and Stewart, 1953).

6. Figure 10 (Plate 4) of Imam (2003) is presented as *Lithophyllum simplex* Lemoine and supposedly comes from the Al Khums Formation (Qabilat Ash Shurfah section at NW Libya). However, this picture corresponds to the microphotograph of a specimen of *Aethesolithon* dredged from middle Miocene deposits from Queensland Plateau (NE Australia) and published by Martín and Braga (1993) (Fig. 1, Plate 2). In this case, the specimen shown by Imam is rotated 180º with respect to the original picture.

7. Imam (2003) showed the basal part of a thallus of *Lithophyllum bonyense* Johnson (Fig. 2, Plate 5) and a conceptacle of *Lithophyllum kuglieri* Johnson (Fig. 4, Plate 5) in the material from Libya. However, these two pictures actually correspond to two photos of *Lithophyllum* from the Miocene deposits of Fiji studied and illustrated by Johnson (1961) (Figs. 1 and 2, respectively, of Plate 10). The same picture of the conceptacle attributed to *L. kuglieri* by Imam (2003) and supposedly coming from the NW of Libya, has been also published as *L. kuglieri* by Imam and Refaat (2000) [Fig. 7 (6)], but in this case the studied material theoretically belongs to the lower Miocene deposits of the Sinai (Egypt).

8. Figure 6 (Plate 5) of Imam (2003) shows a thallus with two conceptacles identified by this author as *Lithophyllum duplex* Maslov from the NW of Libya. However, this picture is originally figured by Piller and Rasser (1996) and Rasser and Piller (1997) as a recent specimen of *Lithophyllum kotchyanum* Unger dredged from the NW margin of the Safaga Island (Safaga Bay, Red Sea, Egypt).

9. Figure 7 (Plate 5) of the same paper (Imam, 2003) represents supperimposed thalli of *Lithoporella melobesioides* (Foslie) Foslie encrusting serpulid worm-tubes. However, the original source of this picture is Figure 6 of Aguirre *et al*. (1993), which shows laminar thalli of *Titanoderma* from the upper Pliocene deposits of Cabo Roche (Conil, SW Spain).

10. Martín *et al*. (1997) described and illustrated *Halimeda* plates from upper Miocene (Messinian) *Halimeda* mounds of the Sorbas Basin (Almería, SE

Spain). One of the picture that these authors figured (Fig. 7a) is exactly reproduced by Imam (2003) (Fig. 8, Plate 5) as *Halimeda* segments from the middle Miocene Al Khums Formation (NW Libya).

11. Imam (2003) illustrated *Spongites albanense* Johnson from the middle Miocene Ras Al Shaqqah section of NW Libya. This picture is copied from Figure 3 (Plate 26) figured by Johnson (1963) as *Archaeolithothamnium penicillum* Pfender.

Apart from these plagiarisms, Imam also duplicated images of coralline algae in different papers. Thus, he illustrated *Lithothamnion operculatum* Conti [Fig. 5 (Plate 3)] and *Mesophyllum lemoineae* Souaya [Fig. 8 (Plate 3)] from Libya (Imam, 2003). However, the same pictures are respectively cited by Imam and Refaat (2000) as *Mesophyllum vaughanii* Howe [Fig. 6 (8)] and *Lithophyllum densum* Lemoine [Fig. 6 (1)] in the material collected from southern Sinai (Egypt).

Figure 4 (Plate 4) of Imam (2003) and Figure 6 (6) of Imam and Refaat (2000) also represent duplicate pictures of supposedly different coralline algal species. The former corresponds to *Mesophyllum vaughani* (Howe) Lemoine from NW Libya, while the latter is quoted as *M. laffittei* Lemoine from the Sinai (Egypt). In this case, one picture is rotated 90º with respect to the other.

These are only some examples of the ingenuity of Imam. This behaviour is not limited to plagiarisms or duplications of pictures of coralline algae. Scrutiny of certain images published by Imam demonstrates that he also lifted pictures of microfacies and foraminifers. Regarding microfacies, Youssef *et al.* (1988) showed fragments of subangular cherts of a microcrystalline quartz (Fig. 6b) belonging to the phosphatic sandy biosparite facies described by these authors in the middle Miocene deposits of the Gebel Sarbut El Gamal section (west-central Sinai, Egypt). Surprisingly, the same picture, although turned upside-down, is also shown as representative microfacies of the Ras Al Shaqqah section, Al Khums Formation from NW Libya (Imam, 2003).

Figure 6 (Plate 6) and Figures 1 and 8 (Plate 7) of the microfacies illustrated by Imam (2003) from NW Libya are also repited by Youssef *et al*. (1988) as Figures 12A, 9B and 13C, respectively, in the paper dealing with middle Miocene deposits of the Sinai.

Additionally to the plagiarism and duplication of pictures of coralline algae and microfacies, Imam has also plagiarised pictures of dasyclads in other papers that he has already published, as confirmed by a study in progress carried out by other colleagues working on this group of green algae (Bruno Granier, Ioan Bucur, Baba Senowbary-Daryan, etc.).

Clearly, Imam has made an industry of copying other author’s work in his papers; it seems that no of the images he has used in his papers are originals. This fraudulent practice has important implications far beyond the only interest of scientists working on or interested in corallines or in dasyclads. It also affects researchers working on the regional geology of NW Africa. Imam has established the timing of sediments cropping-out in different places of NW Africa, and interpreted the palaeoenvironmental settings based on microfacies and calcareous algal assemblages. Yet, these results and conclusions are based on false and plagiarised data.

Beyond the only interest to Earth scientists, Imam’s unauthorized borrowing once again brings up the ever-lasting and recurrent issue of the scientific ethics. Nowadays, scientific literature is overwhelmed by papers, making it difficult task to discover fraudulent practices (untruthful data, plagiarism, duplications, and so on). Therefore, discovering these unusual practices and unethical behaviour of researchers is an issue that concerns to everybody within Science; the editors of journals, the reviewers involved in the revision and correction of manuscripts, and, of course, the scientists when reading papers. We all together are forced to struggle among fraudulent and dishonest practices in Science.

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CYTHEREIS TRIMINGHAMENSIS–A REPLACEMENT NAME FOR *CYTHEREIS ORNATISSIMA ICENICA* PYNE, WHATLEY AND WILKINSON, 2003

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It has been brought to the attention of the authors (recent email communication from Dr Ian Slipper, 11th February 2004) that *Cythereis ornatissima icenica* Pyne, Whatley and Wilkinson, 2003 is a junior homonym of *Cythereis icenica* Jones & Hinde, 1890. Since the latter has priority, it is necessary to propose a replacement name for the former species. The new name *Cythereis triminghamensis* reflects the fact that the species is restricted to the lower Maastrichtian Porosphaera beds of Sidestrand and the Grey Beds of Trimingham (the type locality), Norfolk, UK.

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INTERNATIONAL SCHOOL ON PLANKTONIC FORAMINIFERA

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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.

References in the text should be cited with the name of the author (in lowercases), followed by the year of publication. Use ampersand ('&') for two authors and '*et al.*' for more than two. References should be listed at the end of the text in alphabetical order of authors' names; journal and book titles are written out, not abbreviated. Examples:

Bengston, P. 1988. Open Nomenclature. *Palaeontology,* 31, 223-227.

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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Drawings, diagrams, photographic text-figures and plates should be compiled on separate sheets and numbered according to their sequence in the text. Good quality illustrations, ready for reproduction, should be not larger than double the final size. When reduced they must not exceed the type area of a page. Plates and photographic text-figures should be submitted at publication size. Typewriting is not acceptable on text-figures. Illustrations should be referred to in the text, and their placement should be indicated in the left-hand margin of the text.

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Manuscripts should be submitted in triplicate (original plus two copies) to the Editor. All copies should include high quality copies of all the figures. Submission of an article is understood to imply that the article is original and unpublished and is not being considered for publication elsewhere. After acceptance and last corrections of the manuscript, text should be sent as computer files with indication of name and version of the word processing program, the type of computer on which the text was prepared and the format of the files.

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