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A new Mississippian dasyclad alga (Chlorophyta) from SW Spain: Implications for the reproductive evolution of the dasyclads during the Late Palaeozoic

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Key words: Dasyclads, algae, taxonomy, reproductive evolution, Visean, Mississippian, SW Spain

ABSTRACT

Analysis of the microflora from the Mississippian deposits of southwest Spain has revealed the presence of a new species: *Palaepimastoporella espielensis* new gen. new sp. It is assigned to the family Seletonellaceae comprising of primitive (i.e., aspondyl) dasyclads. *Palaepimastoporella* is one of the earliest representative of the epimastoporid-lineage, an important group of cladospore algae, widespread during the Pennsylvanian and Cisuralian (= Early Permian). Following the erection of *Palaepimastoporella*, the genera *Epimastopora* Pia and *Epimastoporella* Roux are briefly revised. The epimastoporid-lineage is regrouped in the subtribe Epimastoporellinae n. subtrib., separated here from the true Gyroporelleae (aspondyl, cylindrical, exclusively vesicular dasyclads). This lineage is also compared to some euspondyl vesicular cladospore Cyclocrinaceae: Cyclocrineae and Mastoporeae.

RESUME

L' analyse de la microflore des dépôts mississippiens du Sud-Quest de l'Espagne est complétée par la description d'une nouvelle espèce: *Palaepimastoporella espielensis* n. gen. n. sp. Le genre est attribué à la famille Seletonellaceae qui réunit les dasycladales primitives, c'est-à-dire aspondyles. *Palaepimastoporella* est le plus ancien représentant de la lignée des Epimastopores, un important groupe d'algues cladospores, qui domine la flore algale du Pennsylvanien au Cisuralien (= Permien inférieur). La création de *Palaepimastoporella* oblige à redéfinir brièvement les genres *Epimastopora* Pia et *Epimastoporella* Roux, puis à regrouper la lignée des Epimastopores en une nouvelle sous-tribu Epimastoporellinae n. subtrib. Celle-ci était jusqu'ici rattachée aux Gyroporelleae, qui se distinguent en fait parce qu'elles sont aspondyles, cylindriques et exclusivement vesiculifères. Ces Epimastoporellinae ont parfois été attribuées aux dasycladales euspondyles vesiculifères cladospores de la famille Cyclocrinaceae, spécialement aux tribus Cyclocrineae et Mastoporeae.

1. Introduction

The Guadiato area, SW Spain, exhibits upper Visean – lower Serpukhovian carbonate platform rocks (see Cózar & Rodríguez 1999a) (Fig. 1), from which a new green alga important for the knowledge of the reproductive patterns of the dasyclads, has been discovered. This alga, *Palaepimastoporella* n. gen., allows us to discuss an important problem concerning this order of green algae during the Palaeozoic: the question of the origin of the cladospore "epimastoporids", widespread during the Pennsylvanian – Cisuralian (= Early Permian). This taxon occurs close to the Asbian/Brigantian boundary, so its local potential utility as biomarker can be highlighted. It seems to be one of the most ancient representative of the epimastoporid-lineage, considered herein as Epimastoporellinae n. subtrib.

Systematics

The nomenclature and classification are adopted from Bassoullet et al. (1979), Chuvashov et al. (1987), Deloffre (1988) and De Castro (1997), in particular, from the latter publication "laterals" are used here to replace the ambiguous terms: branchlets, ramifications, pores, or "rameaux" in French.

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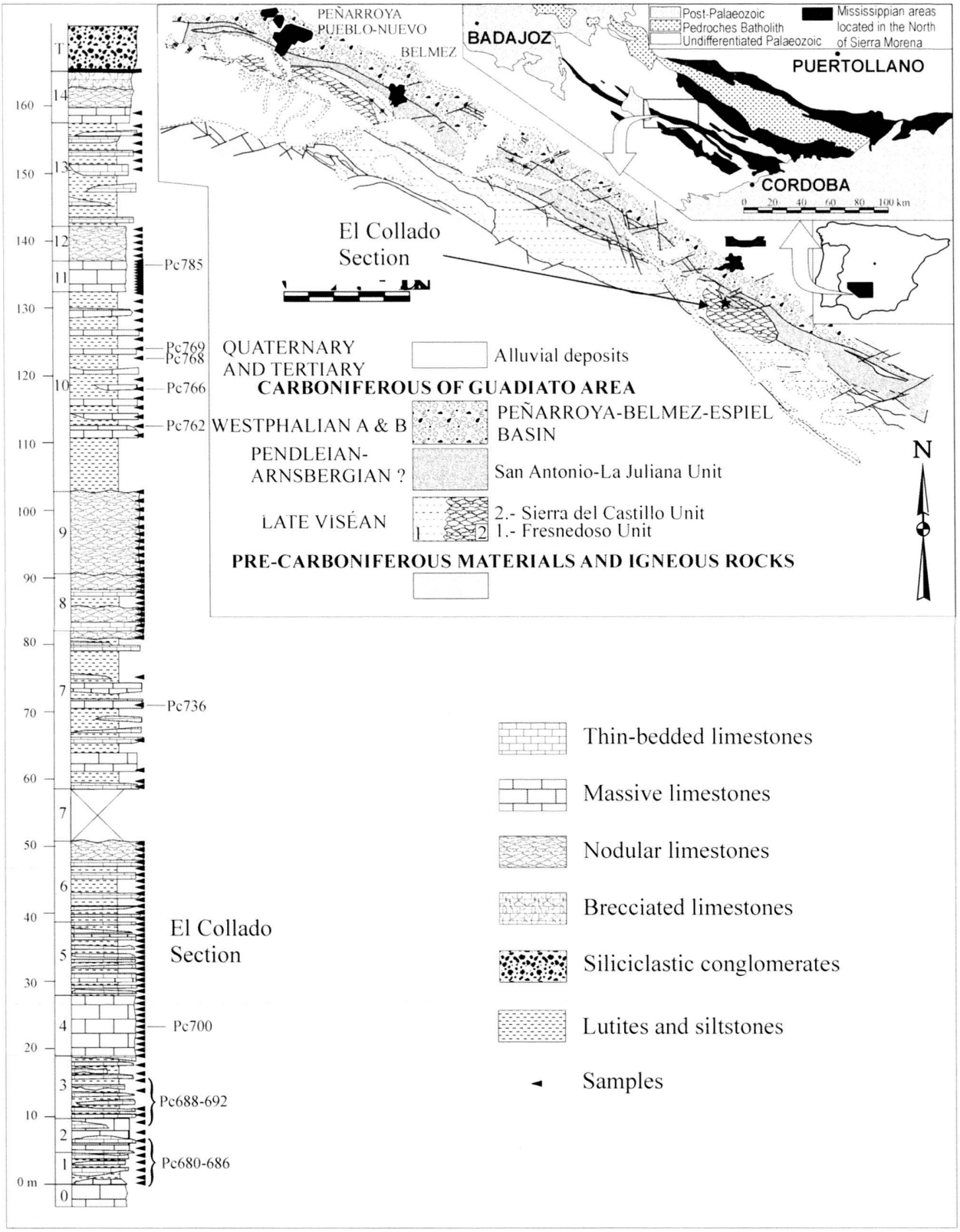

Fig. 1. Location of the Guadiato area (modified from Cózar & Rodríguez 1999a). Stratigraphic section of El Collado (see detailed location and description of the sections in Cózar 1996). Horizons with *Palaepimatoporella espielensis* new gen. new sp. are arrowed.

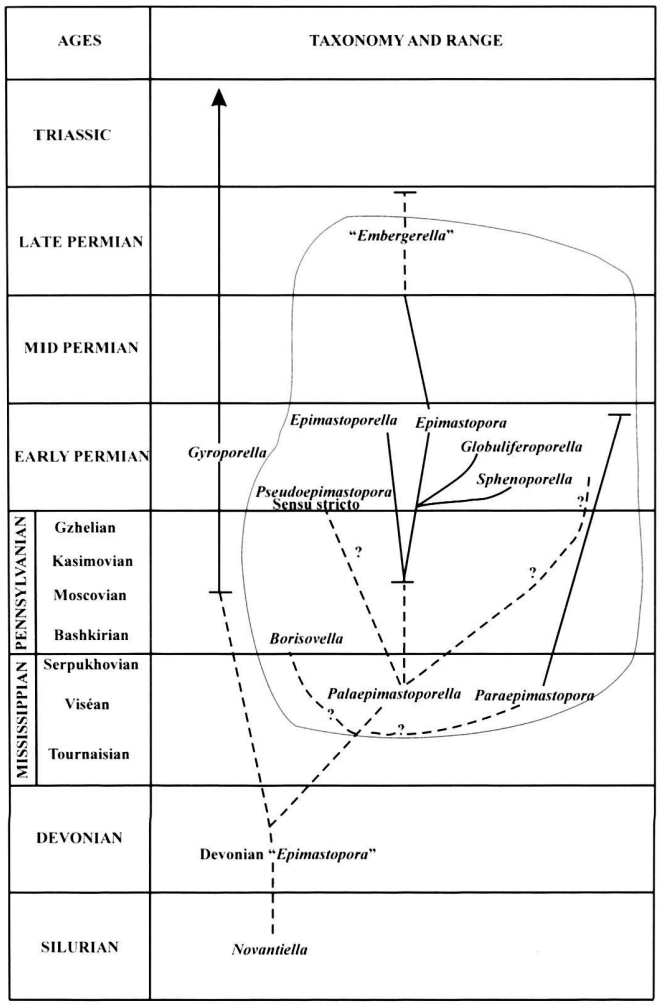

Fig. 2. Composition and stratigraphic range of the Epimastoporellinae n. subtrib. compared with some other Gyroporelleae.

Class Chlorophyta

Order Dasycladales

Family Seletonellaceae (Korde) Bassoullet et al. 1979

Tribe Gyroporelleae (Pal) Bassoullet et al. 1979

Subtribe Epimastoporellinae n. subtrib.

Synonyms. – Gyroporelleae (pars), Cyclocrineae (pars), Cyclocrininae (pars), Mastoporeae (pars), Mastoporinae (pars).
Diagnosis. – Thallus aspondyl, cylindrical, club-shaped or spherical, generally broken in large ribbons. Wall microsparitic, white, probably originally aragonitic. Fertile cladospore laterals, probably not completely calcified, inflated vesicular to prismatic, differing in form according to the genera.
Composition (Fig. 2). – (1) *Epimastoporella* Roux 1979 (= *Epimastopora* Pia 1922 of the authors, non Johnson 1946, nec Korde 1951; for discussion see Gortani 1906; Elliott 1956; Kochansky-Devide & Herak 1960; Perret & Vachard 1977; Roux 1979; Flügel & Flügel-Kahler 1980; Mamet et al. 1987; Greuter et al. 1994; Granier & Deloffre 1994; Granier & Grgasovic 2000; = *Pseudoepimastopora* of the authors, non *Pseudoepimastopora* Endo 1960 as defined by its type species; = ? "*Embergerella*" Güvenç 1972, preoccupied, see Granier & Grgasovic 2000), (2) Epimastopora Pia ex Korde 1951 emend. Roux 1979 (= *Globuliferoporella* Chuvashov 1974), (3) *Palaepimastoporella* n. gen., (4) *Pseudoepimastopora* Endo 1960 (reduced to its type species), (5) *Paraepimastopora* Roux 1979 (= *Epimastopora* sensu Johnson 1946), (6) *Sphenoporella* Chuvashov in Chuvashov & Anfimov 1988, (7) *Borisovella* Ivanova 1988 [including *Epimastopora macropora* (Maslov) sensu Vachard in Perret & Vachard 1977].
Comparison. – Epimastoporellinae n. subtrib. differs from the other Gyroporelleae (i.e., the Gyroporellinae nomen translat. Berchenko in Chuvashov et al. 1987) by the shape of the laterals, especially by the joint presence of vesicular ovoid and polygonal laterals. Epimastoporellinae belong to the Selotenellaceae since they are aspondyl, but they are convergent (due to the great number of vesicular laterals) with some euspondyl Cyclocrinaceae Pia 1920 nomen translat. Chuvashov et al. (1987), a family (Ordovician to Recent), which is composed of the tribes Bornetelleae, Coniporelleae and Cyclocrineae (including the subtribe Mastoporinae). Although fundamentally differentiated by their aspondility and euspondility, some similarities exist between Epimastoporellinae and both tribes of Cyclocrinaceae: Cyclocrineae Pia 1920 and Mastoporeae Pia 1920 nomen translat. Deloffre 1988. Nevertheless, Epimastoporellinae n. subtrib. differ also from Cyclocrineae, by the shape of the laterals and the absence of a perforated calcareous skeleton, and differ from Mastoporeae, by the absence of the second order of laterals (suggested by Pia 1920 and demonstrated by Elliott 1972).
Remarks. – *Palaepimastoporella* and *Paraepimastopora* are the first typical representative of the subtribe Epimastoporellinae (late Visean). Their ancestors may be several taxa from the Late Silurian such as *Novantiella* Elliott (Elliott 1972; Poncet 1986) or Devonian such as "*Epimastopora*" *faveolata* Shuysky in Shuysky & Patrunov 1991 and "*E.*" *oblonga* Shuysky in Shuysky & Patrunov 1991 or "*Epimastoporella*" *trelonensis* Poncet 1981 (Fig. 2).
Range. – Upper Visean (this work) to Upper Permian (Korde 1965) (Fig. 2).

Genus *Palaepimastoporella* new gen.

Derivatio nominis. – From palaeo: old, and *Epimastoporella*, related genus.
Type species. – *Palaepimastoporella espielensis* new sp., designated herein.
Diagnosis. – Elongate partially calcified skeleton composed of polygonal and cladospore, vesicular, aspondyl laterals, i. e. arranged randomly throughout the wall. Laterals have a double pore, internal and external.

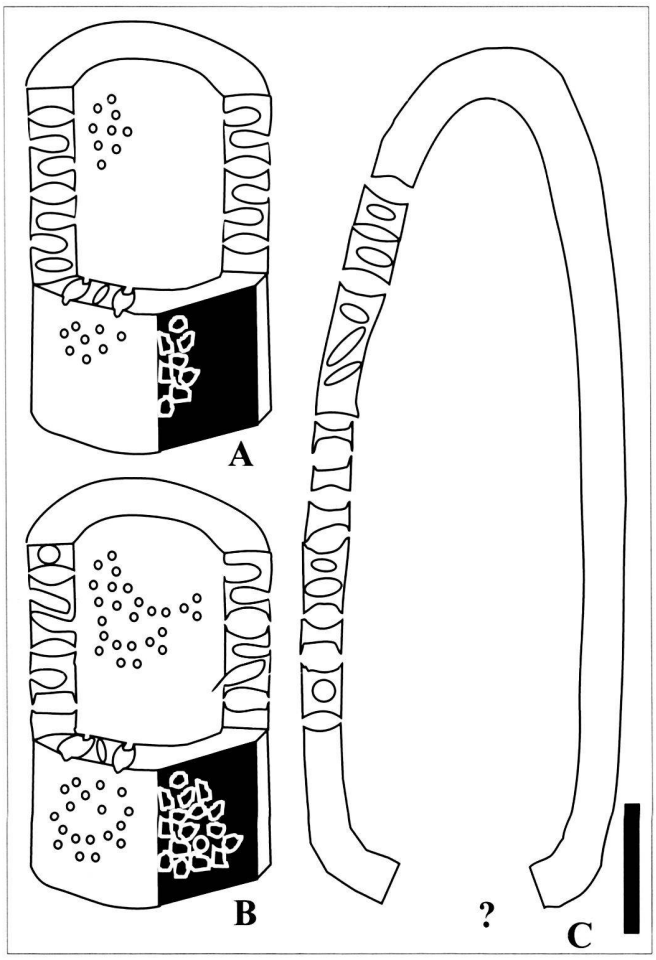

Fig. 3. Comparative cartoons between *Epimastoporella* (A, modified from Roux 1979) and *Palaepimastoporella* (B and C). (Scale bar in C = 1 mm, A and B not to scale).

Remarks. – The vesicular laterals are interpreted as reproductive organs (cladospores); the polygonal and irregular pores are interpreted as sterile laterals. The cladospore laterals are scarce and sparsely distributed, and no preferential arrangement has been observed. Round elements within the wall could be interpreted as tangential sections of the vesicular laterals. Elongate ovoid hollows have been interpreted as complete longitudinal sections in vesicular laterals because double apertures are observed. Some of the ovoid laterals are oblique to the calcareous skeleton and regrouped in pairs or trios (Figs. 3C, 4.3, 4.7). This pattern, not interpreted, seems to be very characteristic of *Palaepimastoporella*. Other laterals are quadratic or polygonal and the irregular wall is in some cases perpendicular to the calcareous skeleton or oblique. Double apertures are distinctive in the most polygonal laterals.

Tangential sections of the calcareous skeleton show polygonal cells in most sections. Circular tangential sections of the laterals are distinctly rare (Fig. 4.5, 4.9).

Comparison. – *Palaepimastoporella* differs from *Epimastoporella* Roux 1979 by the elongate thallus (Fig. 3), and the shape of the laterals: more rarely polygonal and more frequently ovoid.

Roux (1979) and Mamet (1991) considered the thallus of *Epimastoporella* as cylindrical and elongate, whereas other reconstructions of *Epimastopora* are elongate pyriform-, claviform- or ovoid-shaped thallus, perhaps slightly curved (Perret & Vachard 1977). As suggested by Pia (1922, 1937), some species are more probably large and spherical. Nevertheless, the large spherical or cylindrical thallus is always broken, and in the best cases of preservation, the shape of *Epimastoporella* may be flattened by lithostatic compaction (see Flügel & Flügel-Kahler 1980, pI. 5, fig. 1 or Mamet et aI. 1987, pI. 15, fig. 6). Finally, it can be assumed that the shape of Epimastoporellinae evolves from cylindrical *Palaepimastoporella* and converges with spherical *Mastopora*.

The laterals of the cylindrical *Pseudoepimastopora* Endo 1960 differs from *Palaepimastoporella* by their shape: proximally acrophore and distally more inflated than *Gyroporella* sensu Pia (1920). Similarly, *Epimastopora* (= *Globuliferoporella*) is distinct from the rest of the genera of the subtribe by the dumb-bell shape in axial section or paired branches in tangential section.

Few similarities are found with *Paraepimastopora*, which is distinguished by its thick and calcified skeleton and numerous simple, long, thin, isodiametric branches. *Paraepimastopora* first occurs in the Asbian-Brigantian from SW Spain (Sánchez-Chico et al. 1995, this work), and Ireland (Cózar & Somerville, unpublished data, see Fig. 4.11), thus, the first occurrence of *Paraepimastopora* and *Palaepimastoporella* is more or less synchronous (Fig. 2). It is not possible to define which of these two genera is the ancestral stock of the Epimastoporellinae.

Independent of the comparisons with the other Epimastoporellinae, some sections of *Palaepimastoporella* look like the Aciculellae *Coelosporella*. In *Palaepimastoporella* though, internal and external communication of the laterals are clear enough, and it does not show the same type of recrystallization as in *Coelosporella* (Perret & Vachard 1977). Moreover, although in most descriptions the thallus of *Coelosporella* is considered as cylindrical, actually it is unknown, and might be spherical.

Composition. – *Palaepimastoporella espielensis* new gen., new sp., the genus is considered monospecific.

Range. – Uppermost Asbian – lower Brigantian (upper Visean) of Spain and Ireland.

***Palaepimastoporella espielensis* new gen., new sp.**

Figs. 4.1–10

Derivatio nominis. – From Espiel, a town close to the stratum typicum.

Locus typicus. – EI Collado.

Stratum typicum. – Horizon Pc680, EI Collado Section, late Asbian (Cf6γ).

Holotype. – Specimen 2361/1 (Fig. 4.1).

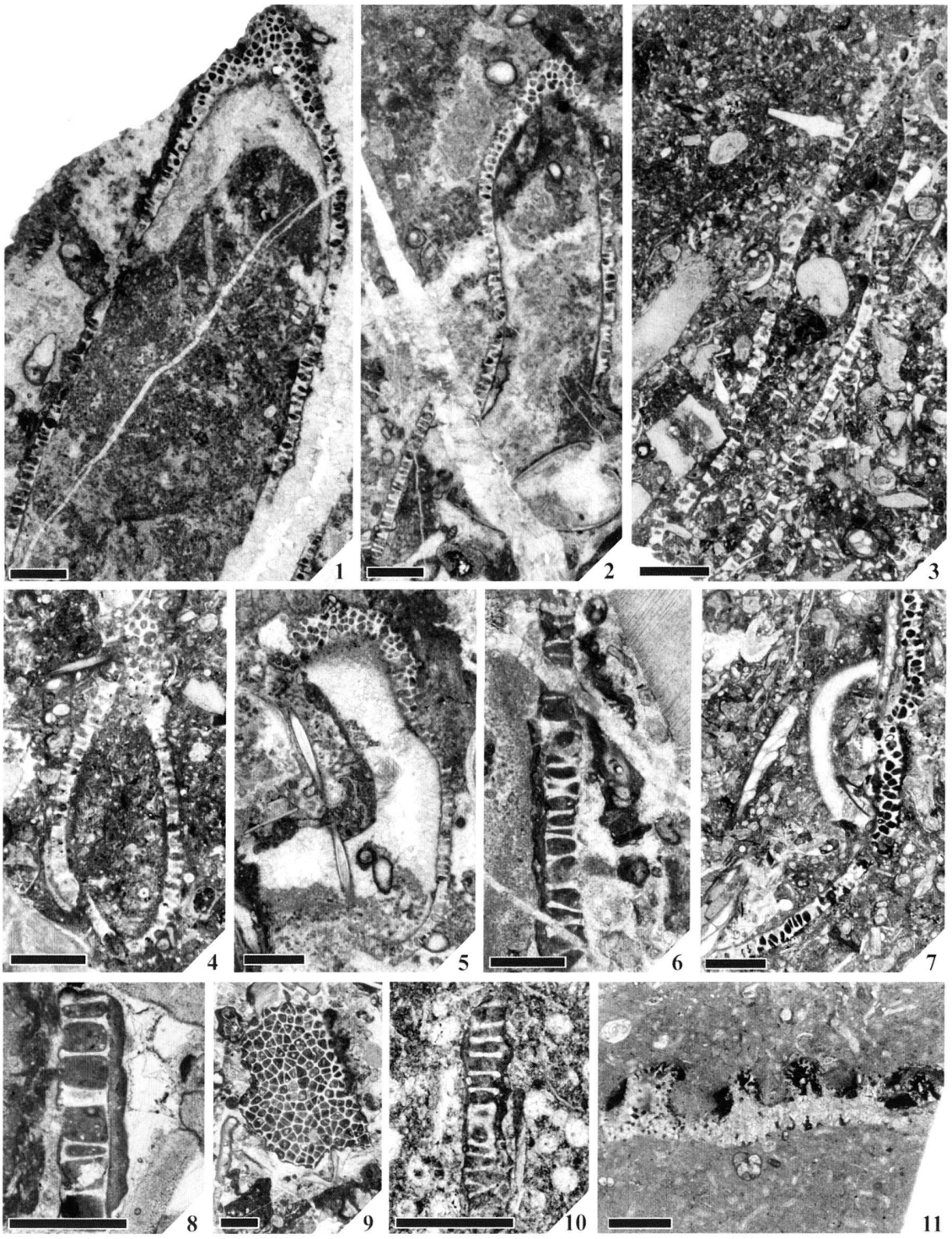

Fig. 4. 1–9. *Palaepimastoporella espielensis* new gen. new sp., base of El Collado Section, Asbian, except in 4.6, 8, 9 Brigantian (Seale bar = 1 mm). (1) Longitudinal section, specimen 2361/1, horizon Pc680, holotype. (2) Longitudinal section, specimen 2361/5, horizon Pc680. (3) Longitudinal section, specimen 2361/23, horizon Pc685. (4) Oblique section, specimen 2361/9, horizon Pc685. (5) Oblique fragment, specimen 2361/4, horizon Pc680. (6) Longitudinal fragment, specimen 2361/15, horizon Pc736. (7) Longitudinal fragment, specimen 2361/12, horizon Pc690. (8) Longitudinal fragment, specimen 2361/16, horizon Pc736. 9 Specimen 2361/13, horizon Pc736. (10) *Palaepimastoporella espielensis* new gen. new sp., longitudinal fragment, specimen 2361/24, horizon 20/8/14, Paulstown Quarry, Brigantian, Co. Carlow, Republic of Ireland (see Cózar & Somerville in press for location). (11) *Paraepimastopora* sp., Specimen 2361/29, horizon 18/3/8, Brigantian, Carganamuck Quarry, Co. Armagh, Republic of Ireland (see Somerville 1999 for location).

Type material. – The type material is abundant in El Collado, at horizons PC680-686, PC688-692 (more than 100 specimens), common at horizon PC700, reworked at horizon PC736, and sparsely distributed at horizons PC762, 766, 768, 769 and 785. Rare at the top of Sierra del Castillo section (3 specimens), at levels 12 and 13, and rare (2 specimens) at Peñarroya 2, level 2.

Repository of the types. – Department of Palaeontology, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid.

Diagnosis. – *Palaepimastoporella* with ovoid laterals oblique to the calcareous skeleton, regrouped in pairs or trios and randomly distributed in the skeleton.

Description. – Several elongate sections of the thallus have been recorded, but usually, fragments of the calcareous skeleton are preserved as oblique and tangential sections. Fragments show a curved-shaped calcareous skeleton, probably close to the base or upper part of the thallus (Figs. 4.5, 4.7). Bifurcations of thallus have not been recognised. The skeleton occasionally contains very inflated vesicular laterals, similar to cysts of spherical morphology, in which apertures are not observed. More commonly, the calcareous skeleton contains polygonal or ovoid cavities more or less perpendicular to the skeleton, in which double apertures occur (Figs. 4.6, 4.8, 4.10). The size of the holotype is 10.5 mm, but fragments of the skeleton are from 1 mm to 6 mm. In tangential section the cavities show also a polygonal shape, slightly rounded, but totally spherical sections are rare. The inner diameter of the cavities is highly variable (Fig. 4.6). Occasionally, the cavities are not perpendicular to the skeleton, and are slightly oblique (around 20°–35°). This feature is shown by the wall between the cavities, which is always recrystallized and preserved as spar or microspar. Differentiation into layers or structures are not observed within the wall. The thickness of the calcareous skeleton varies from 200 µm to 300 µm and is uniform. The interpores, i. e. thickness of the wall in the skeleton is variable (from 20–30 µm up to 60 µm in ovoid laterals), and it seems to depend on the orientation of the section. No preferential arrangement of the laterals, and thin/thick wall is observed.

Association. – The association from the lower part of El Collado section (including the stratum typicum) is composed of common *Archaediscus* at *angulatus* stage (see Conil et al. 1980), *Palaeotextularia* (sensu stricto with two-layered wall), *Vissariotaxis*, *Saccamminopsis*, *Cribrospira*, *Mikhailovella*, *Nodasperodiscus* and *Endothyranopsis crassa* (Brady) emend. Cummings (N.B. The stratum typicum is the base of the section). This assemblage is typical of the late Asbian ("V3bγ" = "Zone 15"= Cf6γ).

Some sections of *Palaepimastoporella espielensis* could be confused with small specimens of *Coelosporella wetheredii* Wood 1940 emend. Perret & Vachard 1977, mainly due to the ovoid to lemon-shaped cavities. However, even these small fragments of *P. espielensis* always show more ovoid and some polygonal sections of laterals, that have been never observed in any type of section of *Coelosporella*.

Remarks. – The morphology observed in some specimens of *P. espielensis* is entire (see reconstruction in Fig. 3), but the base of the alga might correspond to a totally non-calcified structure.

Tangential sections of *P. espielensis* show some similarities with *Atractyliopsis* sp. 1 in Vachard & Montenat (1981), but this latter alga shows more round and distinctive coalescent cells and more regular wall thickness around the cysts. Strongly rounded and common spheres in *Atractyliopsis*? sp. 2 (Vachard & Montenat 1981) distinguish this alga from *P. espielensis*, although similar pairs of oblique laterals are observed.

P. espielensis differs from all the species of *Epimastoporella* by the joint occurrence of polygonal and ovoid laterals in the calcareous skeleton. The new genus is considered monospecific, however some species must be re-examined: especially *E. baschkirica* Kulik 1978 and *E. bodoniensis* Racz 1965.

Geographic and stratigraphic distribution. – *P. espielensis* occurs in the upper part of the Cantera del Castillo section (levels 12 and 13), base and middle part of El Collado section (Fig. 1) and base of Peñarroya 2 (level 2) (see Cózar 1996 and Cózar & Rodríguez 1999b for location). These sections correspond to the upper part of the Asbian ("V3bγ", upper "zone 15"). It also occurs in the upper part of El Collado, lower Brigantian ("V3c", "zone 16i"). In northeast Ireland, the species has been recorded mostly in the upper Asbian in the Mokeeran Quarry sections but also in the lower Brigantian (see Somerville 1999 for location). In the southeast Ireland, the species is recorded in the lower Brigantian in Co. Carlow (see Cózar & Somerville in press for location).

Conclusions

A new dasyclad alga has been identified and described: *Palaepimastoporella espielensis* new gen. new sp. It is one of the most primitive species of the subtribe Epimastoporellinae n. subtrib. (of the Gyroporelleae), together with *Paraepimastopora*, widely distributed in the Pennsylvanian, and rarely documented in the Mississippian.

Palaepimastoporella and the *Epimastoporellinae* are a possible case of co-existence of sterile polygonal laterals with vesicular fertile cladospore laterals, they are probably the most evolved reproductive pattern among the dasyclad Seletonellaceae.

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