

CALCAREOUS MARINE ALGAE FROM THE CARBONIFEROUS (MOSCOVIAN-GZHELIAN) OF THE CANTABRIAN ZONE (NW SPAIN)

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ABSTRACT

A taxonomic revision of shallow-water Carboniferous (Pennsylvanian) red and green algae observed in Ponga, Picos de Europa and Pisuerga-Carrión Units in NW Spain is presented. Some microproblematics are included. Thirty-two genera are described; three genera and four species are new: *Anatolipora cantabriensis* n. sp., *Pelayella multiporosa* n. gen., n. sp., *Kasimophyllum demuesensis* n. gen., n. sp. and *Penella pongaensis* n. gen., n. sp. The microflora is typically Western Paleotethyan and remarkably similar to that observed in the Carnic Alps and Central Urals.

Keywords: Carboniferous microflora, taxonomy, green algae, red algae.

RESUMEN

Se realiza una revisión de las algas verdes y rojas de ambientes someros registrados en los depósitos del Carbonífero superior de las unidades del Ponga, Picos de Europa y Pisuerga-Carrión en el NO de España, incluyendo algunos grupos problemáticos. Se describen formas pertenecientes a treinta y dos géneros, entre las que se encuentran tres nuevos géneros y cuatro nuevas especies: *Anatolipora cantabriensis* n. sp., *Pelayella multiporosa* n. gen., n. sp., *Kasimophyllum demuesensis* n. gen., n. sp. and *Penella pongaensis* n. gen., n. sp. La microflora estudiada es típica del Paleotethys occidental, presentando grandes semejanzas con la que se ha descrito en los Alpes Cárnicos y en los Urales Centrales.

Palabras clave: Microflora carbonífera, taxonomía, algas verdes, algas rojas.

INTRODUCTION

The abundance of algae in the Carboniferous of northern Spain is well documented since the pioneering work of Rácz (1966 a, b) who reported their morphology with great taxonomic accuracy. These two papers by Rácz, as well as other studies on algae (or containing information related to algae) developed subsequently in the Cantabrian Zone (Riding, 1979; Bowman, 1979; Eichmüller and Seibert, 1984; Eichmüller, 1985; Rácz, 1984; Dingle *et al.*, 1993; Hensen *et al.*, 1995; Barba Regidor, 1998; Samankassou, 2001; Della Porta *et al.*, 2002; Della Porta, 2003), dealt mostly

with Bashkirian and (especially) Moscovian materials. Algae from the final part of the Carboniferous succession, e. g., that embracing from the uppermost Moscovian to the lower Gzhelian, have remained rather unknown until recently as a result of the fact that the stratigraphy of this final part of the Carboniferous succession has not been so deeply investigated in the Cantabrian Zone until much later than the older Carboniferous. Among the few papers containing information on latest Carboniferous algae, we can mention studies on Kasimovian algae by Rodríguez and Moreno-Eiris (1986) and Minwegen (2001), the latter also studying numerous Moscovian localities.

During the late 1980's and 1990's, the SCCS program for establishing levels of correlation in the upper part of the Carboniferous system has led to an intensive biostratigraphic study of successions of this age through the Cantabrian Zone and, particularly, of those outcropping in the Picos de Europa structural unit (Figs. 1-2). In parallel with these studies, several investigations on the regional geology of the eastern part of the Cantabrian Zone, the area where younger Carboniferous successions of this zone exist, were carried out, leading to a better knowledge of its stratigraphy (Villa and Martínez García, 1989; Martínez García and Villa, 1998, 1999; Venturini *et al.*, 1998; Sánchez de Posada *et al.*, 1999). Especially significant is the study on the stratigraphy and sedimentology of the latest Carboniferous successions of the northern part of the Picos de Europa massifs carried out by Merino-Tomé *et al.* (2001).

UPPERMOST CARBONIFEROUS FROM THE EASTERN CANTABRIAN ZONE

The Cantabrian Zone (Lotze, 1945), situated in the northwestern part of the Iberian Peninsula, constitutes a foreland basin, deformed by thin-skinned tectonics into an arcuate fold belt. Stratigraphic and structural characters have been used by Julivert (1971) and Pérez Estaún *et al.* (1988) to distinguish within the Cantabrian Zone several major geological provinces (or structural units; Fig. 1).

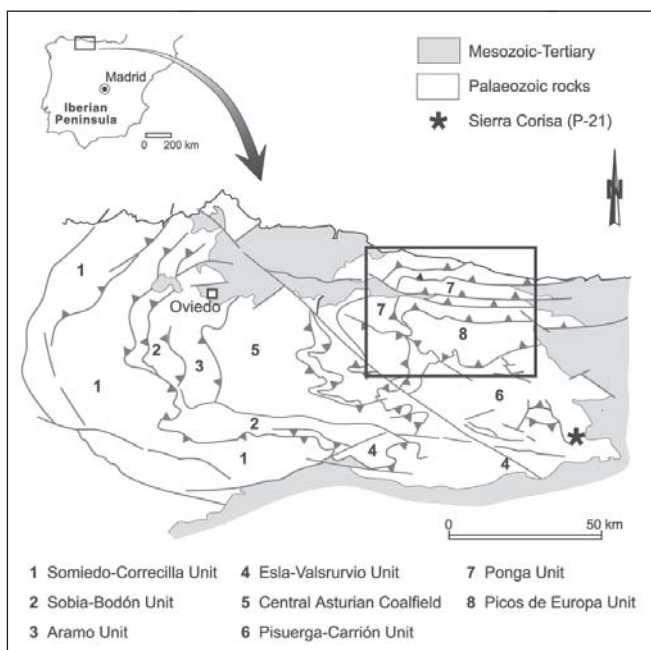


Figure 1. Sketch showing the main structural units of the Cantabrian Zone. Box shows the area enlarged in figure 2.

These units spread along the provinces of Asturias, Cantabria, León and Palencia, in northern Spain.

The most complete Carboniferous successions of the Cantabrian Zone are present in the eastern units (Central Asturian Coalfield, Ponga Unit, Picos de Europa Unit, and Pisuerga-Carrión Unit). A remarkable feature in these successions is that, during late Carboniferous, the sedimentation was strongly influenced by tectonics, resulting in synorogenic deposits with important facies and thickness variations. As a result of the west-eastern progression of deformation, the top of the Carboniferous succession becomes younger in an eastern direction. The Picos de Europa Unit is the only region where sedimentation in a shallow carbonate platform lasted until Gzhelian.

Materials analyzed in this work come from sections and localities situated in the Ponga Unit (Pen section), Picos de Europa Unit (Las Llacierias, Demués, Berodia-I, Berodia-II sections, and Inguanzo locality), and Pisuerga-Carrión Unit (Sierra Corisa locality). The location of sections is shown in figures 1-2, the correlation in figure 3, and the stratigraphic position of samples studied in tables 1-2. The list of species, as well as their range in the sections and localities studied in this paper are given in table 3.

Pen section

This section (Figs. 2-3, Table 2) exposes an unconformable marine succession consisting of a thin calcareous band at the base, which is overlain by siliciclastics. The calcareous band yields fusulinaceans belonging to the *Protriticites* Zone and algae at closely situated various levels (samples BM-78, BM-79, BM-85). Further stratigraphic information on these deposits is given in Martínez García *et al.* (1985) and Villa (1995).

Las Llacierias section

This section outcrops in the vicinity of Covadonga, Asturias (Figs. 2-3, Table 1). The upper part of this section (the one studied in this paper) is the most extensively studied succession of the Cantabrian Zone embracing the Moscovian/Kasimovian transition. This part corresponds to the Picos de Europa (part) and Las Llacierias formations (Fig. 3). Diverse fossil groups (brachiopods, corals, conodonts, fusulinaceans, spores and algae) have been collected from these strata (Marquínez *et al.*, 1982; Villa *et al.*, 1993, 1997; Coquel and Rodríguez, 1994; Méndez, 2002). Their age has been mainly established on the base of the fusulinoid faunas and it ranges from upper Krevyakinian to upper Khamovnikian (van Ginkel and Villa, 1999; Villa and van Ginkel, 2000). The upper part of the Picos de Europa Formation represents sedimentation in a platform-lagoonal environment which evolved towards more open marine conditions. Towards the top of the formation organic build-ups are found. According to Bahamonde *et al.* (2000), the uppermost part of the Picos

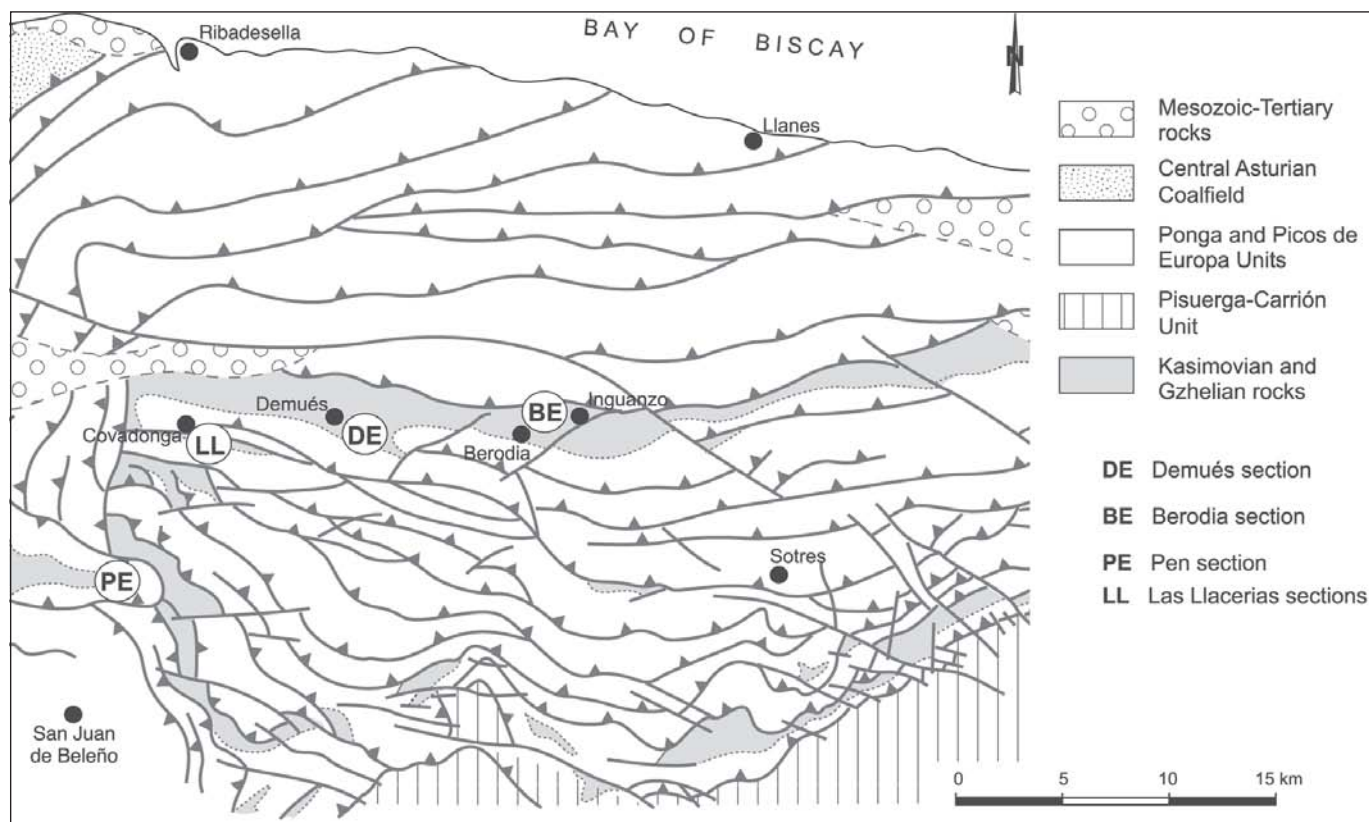


Figure 2. Geological sketch of the area around the sections studied in the Ponga and Picos de Europa structural units.

de Europa Formation represents the evolution from a shallow to a drowned platform, which was finally replaced by a mixed ramp represented by Las Llacierias strata. The latter consists of packstones and wackestones alternating with grainstones and marls. Its upper part corresponds to a megasequence of tempestites made up of grainstone to mudstone. On the whole, the materials of the Las Llacierias Formation are deposits that accumulated on a storm-dominated monoclinical platform-slope (ramp), under conditions of high sedimentation rate (Leyva *in Villa et al.*, 1993).

Demués section

This section (Figs. 2-3, Table 2) exposes strata belonging to the Demués Formation along the trail leading from the village of Demués to the pastures in the northern slope of the Picos de Europa mountains. Different studies on the stratigraphical, sedimentological and paleontological characteristics of this section have been carried out by Bruner *et al.* (1998), Martínez García and Villa (1998), and Sánchez de Posada *et al.* (1999, 2002). The Demués Formation is composed of an alternation of limestones, marls, shales, carbonaceous shales, sandstones and calcareous conglomerates, and a thin coal-seam. Marine beds yield fossils belonging to many benthic groups (especially brachiopods, porifera, molluscs, foraminifers, ostracods, and algae), all of them reflecting shallow-marine environments. Spores have been recovered from beds at differ-

ent levels throughout the entire succession. Fusulinaceans and spores allowed dating these rocks in terms of both the West-European and the Russian stratigraphical scales. The succession at Demués section ranges in age from uppermost Moscovian or basal Kasimovian to the middle part of the Kasimovian (upper Khamovnikian) in the Russian stratigraphic scale, and probably from Cantabrian (lower?) to a level near the Barruelian/Stephanian B boundary in the West European stratigraphic scale (Sánchez de Posada *et al.* 1999, 2002).

Berodía sections

The name Berodía-I and Berodía-II refer to Puentellés Formation outcrops located along the road leading from the Casaño River valley to the small village of Berodía (Figs. 2-3, Table 2). The Puentellés Formation outcrops in this area splitted in two structural units, which are separated by a thrust fault (Martínez García and Villa, 1998). Berodía-I is the section located closest to the village of Berodía.

The Puentellés Formation is a thick calcareous succession ranging from upper Kasimovian to lower Gzhelian within which two different members can be recognized: a lower member consisting of reworked and resedimented carbonates, and an upper member, made up of autochthonous limestones (Merino-Tomé *et al.*, 2001). Lower member strata are bedded alternations of calcareous breccias

Sample	Stratigraphic position with respect to samples in Villa et al, 1997, and Villa & van Ginkel, 2000	Age	Fusulinid zone
BM-11	Picos de Europa Fm. (upper part of the upper member), 4 m below LL-9001	Late Moscovian (Myachkovian)	<i>Fusulinella</i> Zone (upper part)
BM-12	idem	idem	idem
BM-13	idem, 0.5 m above LL-9001	idem	idem
BM-14	idem, 4 m above LL-9001	idem	idem
BM-16	idem, 0.5 m below LL-9003	idem	idem
BM-17	idem, equivalent to LL-9003	late Myachkovian	idem
BM-18	idem, 0.4 m below LL-9004	idem	idem
BM-19	idem, equivalent to LL-9005	idem	idem
BM-25	idem, 0.8 m above LL-9008	idem	idem
BM-28	idem, equivalent to LL-9009	idem	idem
BM-31	idem, 4.8 m above LL-9009	idem	idem
BM-38	idem, equivalent to LL-9011	Moscovian/Kasimovian transition interval	<i>Protriticites</i> Zone
BM-39	idem, 2 m above LL-9011	idem	idem
BM-40	idem, 4 m above LL-9011	idem	idem
BM-46	idem, 4 m below LL-9014	earliest Kasimovian (early Kreviakianian)	idem
BM-47	idem, equivalent to LL-9014	idem	idem
BM-52	idem, equivalent to LL-9016	early Kasimovian (Kreviakianian)	idem
BM-63	idem, equivalent to LL-9024	idem	idem
BM-69	Las Llacierias Fm., equivalent to LL-9031	idem	idem
BM-70	idem, equivalent to S-236	idem	idem
BM-72	idem, equivalent to LL-9034	idem	idem
BM-74	idem, equivalent to LL-9037	Kasimovian (early Khamovnikian)	<i>Montiparus</i> Zone
BM-74B	idem, equivalent to LL-9038	idem	idem
BM-76	idem, equivalent to LL-9044	late Khamovnikian	idem
BM-76B	idem, slightly above LL-9044	idem	idem
BM-77B	idem, equivalent to LL-9047	idem	idem

Table 1. Stratigraphic position and age of samples from Las Llacierias section mentioned in this paper.

and conglomerates, pebbly sandstones, graded and laminated silty and sandy limestones, skeletal grainstones and bioturbated marly limestones and marls. Accumulations of the fusulinoidean *Ferganites* occur in this member at several levels (Villa and Bahamonde, 2001). The upper member consists of dark pseudo-nodular mudstones and skeletal wackestones with intercalations of thick bedded algal bafflestones and isolated mud mounds. In contrast to the lower member, the upper one yielded more varied

fusulinacean assemblages, including *Rauserites*, *Jigulites*, *Quasifusulina* and *Ferganites*, which allowed accurate dating (Villa and van Ginkel, 1999; Villa and Ueno, 2002; Villa et al., 2003). Further data on the sedimentological characteristics of this formation are in Merino-Tomé et al. (2001), Villa and Bahamonde (2001), and Villa et al. (2003). With the exception of one taxon, all algal samples from the Puentellés Formation studied in this paper have been collected from the upper member.

Loc./Sect.	Sample	Stratigraphic position	Age	Fusulinid zone
Sierra Corisa	P21-39	Corisa Formation	late Moscovian (Myachkovian)	Fusulinella Zone (upper part)
	P21	idem	idem	idem
Pen	BM-78	Pen Limestone	early Kasimovian (late Krevyakinian)	<i>Protriticites</i> Zone
	BM-79	idem	idem	idem
	BM-85	idem	idem	idem
Demués	BM-276	Demués Formation, top of phylloid mound, 130 m above base of the section	Kasimovian	<i>Protriticites</i> Zone(?)
	BM-277	Demués Formation, upper part, 191 m above base of the section	Kasimovian (probably Khamovnikian)	<i>Montiparus</i> Zone(?)
	BM-281	Demués Formation, top of the section	Kasimovian (Khamovnikian)	<i>Montiparus</i> Zone
Berodia-I	BM-98	Puentellés Fm, 20 below top of the lower member	late Kasimovian (Dorogomilovian)	<i>Rauserites</i> Zone
	BM-101	Puentellés Fm., flanks of phylloid mound, 10 m above base of the upper member	probably early Gzhelian	<i>Rauserites</i> Zone
	BM-103	idem, but 2 m higher than BM-101	idem	idem
	BM-105	idem, but 5 m higher than BM-101	idem	idem
Berodia-II	BM-122	Puentellés Fm. (base of the upper member)	probably early Gzhelian	<i>Rauserites</i> Zone
	BM-123	idem, 7 m above base of the upper member, flank of phylloid mound	idem	idem
	BM-128	Puentellés Fm., upper part of the upper member	early Gzhelian	idem
Inguanzo	BM-251	Puentellés Fm.	either late Kasimovian or early Gzhelian	<i>Rauserites</i> Zone
	BM-257	idem	idem	idem

Table 2. Stratigraphic position and age of other samples, apart from those of the Las Llaceras section, mentioned in this paper.

Inguanzo locality

The two samples labeled "Inguanzo" have been collected from strata of the upper member of the Puentellés Formation exposed at the cut road leading to the Casaño River valley to the village of Inguanzo (Fig. 2, Table 2), situated 1 km east of Berodia. This outcrop constitutes the eastern extension of the unit exposed at the Berodia-II section.

Sierra Corisa locality

The Sierra Corisa locality belongs to the Pisuerga Carrión Unit (Fig. 1, Table 2) of the Cantabrian Zone. It is situated in the Castillería Syncline, in the northern part of the Palencia province. Samples for the present study

were collected from the Corisa Formation, a thick calcareous succession of late Myachkovian age (van Ginkel, 1965; van Ginkel and Villa, 1991).

GENERALITIES ON CALCAREOUS ALGAE

Algae are important contributors to the formation of modern bioconstructions ("reefs") and carbonate platforms and it can be inferred that they have played the same role since the Paleozoic (Wray, 1977). Taxonomic problems are present, but classification difficulties should not blur the geological importance of the microflora.

CHRONOSTRATIGRAPHIC UNITS		LITHOSTRATIGRAPHIC UNITS				MAJOR FUSULINOIDEAN ZONES
		PEN	LAS LLACERIAS	DEMUÉS	BERODIA	
GZHELIAN (part)	Pavlovoposadian				CAVANDI FM	<i>Jigulites</i> Zone
	Rusavkinian				u.m. PUENTELLÉS FM	<i>Rauserites</i> Zone
KASIMOVIAN	Dorogomilovian			PUENTELLÉS FM	l.m.	
	Khamovnikian		LAS LLACERIAS FM		Dobros Lmst.	<i>Montiparus</i> Zone
	Krevyakinian	Pen Lmst.		DEMUÉS FM		<i>Protriticites</i> Zone
MOSCOVIAN (part)	Myachkovian		PICOS DE EUROPA FM (part)	GAMONEDO FM		<i>Fusulinella</i> Zone (upper part)

Figure 3. Correlation of chronostratigraphic units, lithostratigraphic units, and fusulinoidean zones. Shaded intervals correspond to strata sampled in this study (l. m. and u. m. = lower and upper member of the Puentellés Formation).

We have also included, in this article, a number of microproblematics that play a crucial role in carbonate accumulations. We are conscious that their taxonomic position is open to question but, associated with the microflora, they equally contribute to the microfacies.

Algal proliferation is linked to various factors such as biotic turnover, nutrients, paleolatitude, turbidity, upwelling, temperature (Kroeger *et al.*, 2003). Thus, a warm low latitude photozoan association and its opposite, a cold high latitude heterozoan association, can occur in Late Paleozoic sequences (e. g., in the Carnic Alps; Samankassou, 2002).

The presently described algae are basically light dependent. The upper part of the photic zone is favorable to all categories (cyanophytes, chlorophytes, phaeophytes, rhodophytes). The euphotic/dysphotoc zone sees the progressive elimination of the first two categories. The dysphotoc zone is characterized by the latter two categories that peter out in the aphotic zone (Madi *et al.*, 1996).

As the Carboniferous succession of the Cantabrian Zone is cyclic, with concomitant variations in bathymetry/luminosity, the nearly complete gamut of algae is observed. This abundance and diversity indicate overall warm water temperature and not necessarily mixing of cold versus warm waters as suggested by Samankassou (2002) for the Auernig Group in the Carnic Alps.

The most important algal flora that contribute to Carboniferous Paleotethyan carbonates are (Mamet *et al.*, 1987; Mamet, 1992):

1. *Archaeolithophyllum*, *Kasimophyllum* and *Archaeolithoporella* (encrusting red algae) (Wahlman, 1988; Razgallah and Vachard, 1991; this paper).
2. Beresellids (*Beresella*, *Dvinella*) (green algae) (Mamet and Stemmerik, 2000).
3. *Donezella* (discussion in Della Porta *et al.*, 2002).
4. *Komia-Ungdarella* (red algae) (Mamet, 1991).
5. *Petschoria* (red alga) (Mamet *et al.*, 1987).
6. Phylloid algae (*Eugonophyllum*, *Ivanovia*, *Neoanichodidium*) (discussion in Torres, 1997, *vide* Wahlman, 2002).
7. *Tubiphytes* (for references and discussion, see Senowbari-Daryan and Flügel, 1993).
8. *Uraloporella* (green alga) (Mamet and Villa, 1995).

PREVIOUS STUDIES ON CALCAREOUS ALGAE FROM THE CANTABRIAN ZONE

As mentioned above, pioneering works on algae from the Cantabrian Zone have been those by Rác (1966a, 1966b). In these papers, Rác proposed that *Donezella* and

	MOSCOV. (part)		KASIMOVIAN			GZHEL. (part)
	Myachkovian		Kreviakian	Khamovnikian	Dorogom.	Rusavkinian
<i>Anatolipora cantabriensis</i> n. sp.	■					
<i>Anchicodium funile</i> Johnson 1948 sensu Torres & Baars 1992	■					
<i>Anthracoporella spectabilis</i> Pia 1920		■	■	■	■	
<i>Anthracoporella vicina</i> Kochansky and Herak 1960	■		■	■		
<i>Anthracoporellopsis machaevii</i> Maslov 1956	■	■				
<i>Archaeolithophyllum johnsoni</i> Rác 1966	■			■		■ ?
<i>Archaeolithophyllum delicatum</i> Johnson 1956				■		■ ?
<i>Beresella herminae</i> Rác 1966	■	■				
<i>Berestovia filaris</i> (Berchenko 1982)			■			■
<i>Claracrusta catenoides</i> (Homann 1972)				■	■	
<i>Clavaporella reinae</i> Rác 1966				■		
<i>Donezella lutugini</i> Maslov 1929		■				
<i>Ellesmerella permica</i> (Pia 1937)			■			
<i>Epimastopora symetrica</i> (Johnson 1951)						■
<i>Eugonophyllum johnsoni</i> Konishi and Wray 1961	■	■	■			
<i>Eugonophyllum mulderi</i> Rác 1966			■	■		■
<i>Fourstonella fusiformis</i> (Brady 1876)				■		
<i>Fourstonella? johnsoni</i> (Flügel 1966)					■	
<i>Gyroporella dissecta</i> (Chuvashov 1974)			■			
<i>Gyroporella? prisca</i> Kochansky-Devidé 1970		■	■			
<i>Herakella paradoxa</i> Kochansky-Devidé 1970		■				
<i>Hikorocodium kuramotoi</i> Nakamura 1994	■					
<i>Hikorocodium? sp.</i>				■		
<i>Ivanovia tenuisima</i> Khvorova 1946			■	■		
<i>Kasimophyllum demuesensis</i> n. gen., n. sp.				■		
<i>Macroporella ginkeli</i> Rác 1966				■		
<i>Palaeoberesella lahuseni</i> (von Möller 1879)		■				
<i>Pelayella multiporosa</i> n. gen., n. sp.				■		
<i>Penella pongaensis</i> n. gen., n. sp.				■	■	■
<i>Pseudokomia cansecoensis</i> Rác 1966		■				
<i>Pseudoveleitella simplex</i> (Kochansky-Devidé 1970) Mamet & Roux 1978		■	■			
" <i>Pseudogyroporella</i> " <i>annulata</i> Ishijima, Ozaki & Nakamura 1971				■		
<i>Stacheia marginuloides</i> Brady 1876	■					
<i>Tubiphytes obscurus</i> Maslov 1956					■	■
<i>Ungdarella uralica</i> Maslov 1956		■				
<i>Ungdarellita articulata</i> n. gen., n. sp.	■					
<i>Uraloporella variabilis</i> Korde 1950 emend. Mamet & Villa 1995		■				
" <i>Vermiporella</i> " <i>hispanica</i> Rác 1966						■
<i>Zaporella cantabriensis</i> Rác 1966	■			■		

Table 3. Stratigraphic distribution of the algae described in this paper. Absence of species of late Kasimovian age is due to unfavourable facies in the Dorogomilovian strata from the area investigated.

associated Paleosiphonocladales were characteristic of a restricted calm milieu and *Archaeolithophyllum*, of more agitated waters. He also postulated that algal assemblages were stratigraphically useful, a potential that has not been confirmed.

Donezella mud-mounds were described by Riding (1979), Bowman (1979), Eichmüller and Seibert (1984), and Eichmüller (1985). While Riding favored extensive reworking of the thalli, Eichmüller proposed an alternative bindstone-bafflestone effect. The associated biota in shallow platform surrounded by pelagic sediments yielded *Petschoria*-phylloids in low energy, *Komia* in intermediate energy and *Archaeolithophyllum* in high energy environments.

Rác (1966a, 1984) felt that *Donezella* had a baffling-trapping action, an opinion shared by Dingle *et al.* (1993) and Hensen *et al.* (1995). Sedimentological problems connected to *Donezella* are summarized in Della Porta *et al.* (2002) and Della Porta (2003).

Upper Carboniferous algal-bryozoan assemblages were described in the Cármenes Syncline (southern Cantabrian Mountains) by Dingle *et al.* (1993). From the same region, *Donezella* - *Anthracoporellopsis* associated with worm tubes and microbes are reported by Samankassou (2001). The red *Archaeolithophyllum* and the green *Donezella* acted as bafflestones associated with encrusting bryozoans. Cementstones were commonly produced by the *Donezella*-bryozoan associations.

Riding (1979) and Dingle *et al.* (1993) noted that algae constituted “only” 5-20% of the mud-mound, thus were unable to produce a bafflestone. However as early as 1962, Dunham documented that branching thalli could form stable boundstones. In our opinion, rocks containing 15% of branching thalli are probably *in situ* (bafflestone, bindstone) while rocks composed of >20% thalli are formed by hydrodynamically-transported fragments.

Barba Regidor (1998) described two types of carbonate mounds in the Cantabrian Zone: the *Archaeolithophyllum/Ungdarella* bindstones/bafflestones and the *Beresella* bafflestones. These floral elements can be associated with *Palaeoaplysina* (see Antoshkina, 1998), a hydrozoan (?) referred to phylloid algae plates (Davies and Nassichuk, 1973; Kiessling *et al.*, 1999), sponges (Bourque *et al.*, 1995), bryozoans (Ernst, 2000), chaetetids (Stanton *et al.*, 1994) and microbial structures (Riding, 2000; Riding and Awramic, 2000). Other biotic associations are fenestelloid-*Tubiphytes* cementstones, red-green algal-calcisponge cementstones and siliceous sponge-bryozoan-*Archaeolithoporella* cementstones.

Minwegen (2001) recognized in the Carboniferous succession of northern Spain a number of bioconstructions dominated by metazoans, algae or pelmatozoans. Metazoan-dominated buildups are: 1) Beresellidae-chaetetids mounds, 2) chaetetids biostromes, 3) *Syringopora*-chaetetids reef-mounds, 4) rugose corals, and 5) sponge-algal meadows. Algal constructions are characterized by the abundance of: 6) *Petschoria-Donzella*, 7) phylloid algae, 8) *Anthracoporella*, and 9) *Archaeolithophyllum*. Pelmatozoans mounds are: 10) undiversified dominated by pelmatozoans, or 11) diversified associated with bryozoans, brachiopods, etc. A bit surprising is the lack of recognition of algal encrusters like *Claracrusta-Berestoria* that stabilize *Donzella* mounds and the Beresellidae-chaetetids association. Also lacking is the role of *Tubiphytes*, which is an enigmatic microproblematic fossil.

Della Porta *et al.* (2002, 2003) and Della Porta (2003) describe in great detail the sedimentology of a carbonate platform/ramp in the Sierra del Cuera, with extensive microbial boundstones. Analysis of *Donzella* accumulations (Della Porta *et al.*, 2002) suggest that this organism was able to thrive over a large depth range, which led these authors to think that either *Donzella* did not belong to the green calcareous algae or, alternatively, the Sierra del Cuera depositional system was affected by particular paleo-oceanographic conditions that extended the euphotic zone below the average depth.

TAXONOMY

The material described below is held in the collections of the Département des Sciences de la Terre et de l'Environnement, Faculté des Sciences, Université Libre

de Bruxelles. Specimens are labelled U. of M., for the University of Montreal where the thin sections were made.

PHYLLUM CHLOROPHYCOPHYTA Papenfuss 1946
Genus *Anatolipora* Konishi 1956

Anatolipora cantabriensis n. sp.

Fig. 4, 7 e

Origin of name: From the Cantabrian Mountains.

Holotype: Figure 7 e. Repository number: U. of M. 823/13.

Diagnosis: Simple tapening pores with slightly irregular oblique arrangement.

Description: Thallus (cortex and medula) continuous, cylindrical. Diameter, around 400 μm . Medula, 170 μm . Cortex, 100-130 μm , perforated by numerous, regular, ploiophore pores with oblique, irregular insertion. Pores are about 15 μm thick with interpores of 20-25 μm . There are 24-27 pores per linear millimeter. The taxon belongs to the Salpingoporellinae. See idealized sections at Figure 4.

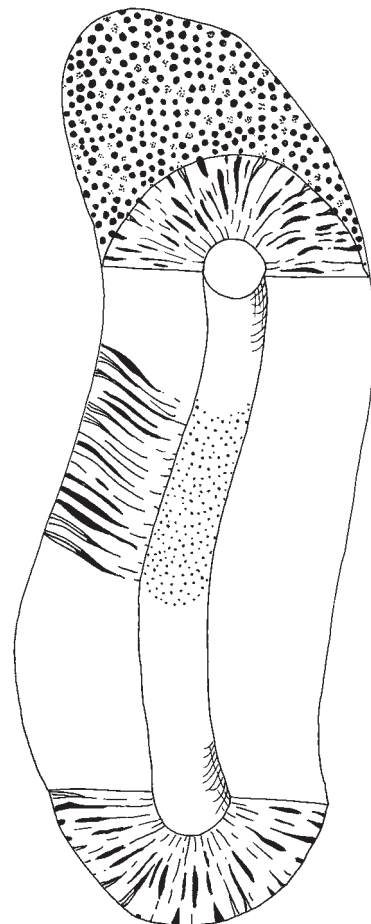


Figure 4. Idealized cross-oblique and longitudinal sections of *Anatolipora cantabriensis* n. sp. diameter of thallus around 400 μm .

Comparison: Differs from *Anatolipora carbonica*, the type of the genus, by the very regular (non-twisted) thallus, the greater number of pores per linear millimeter and the slight irregular disposition of the branches. Note that the original drawing of Konishi is somewhat idealized (Mamet, 2002).

Stratigraphic distribution and range: Known from the Late Moscovian (Miachkovian) of the Picos de Europa Formation (*Fusulinella* Zone). The highest recorded occurrence of *Anatolipora* is Namurian and *cantabriensis* extends the range into the Moscovian. The holotype is derived from the upper part of the Picos de Europa Formation (sample BM-11, Myachkovian) at Las Llacerias section, associated with algal-rich bafflestones and grainstones. The most prolific algae are *Anchicodium*, *Anthracoporella*, *Beresella*, *Donezella*, *Fourstonella*, *Hikorocodium*, *Komia*, *Pseudokomia*, *Tubiphytes* and *Ungdarella*.

Genus *Anchicodium* Johnson 1946

Anchicodium funile Johnson 1946 *sensu*
Torres and Baars 1992

Fig. 11 e

- 1946 *Anchicodium funile* Johnson, OD; 1100, pl.2, fig. 3; pl. 3, fig. 4; pl.7, fig. 1.
1974 *Anchicodium funile* Johnson; Chuvashov, 17, pl. 2, figs. 1, 2.
1992 *Anchicodium funile* Johnson; Torres and Baars, 675-677, fig. 1/1-6.

Description: Thallus grossly cylindrical, small (300-600 μm) with central stalk and irregular long and short branches (diameter 15-20 μm) forming a twig-like structure.

Stratigraphic distribution and range: From the Late Carboniferous (Virgilian) to the Early Permian (Asselian). Observed in Spain in the upper part of the Picos de Europa Formation (sample BM-12, Myachkovian) at Las Llacerias section. Considered as a central North American flora, but should be extended to the Paleotethys.

Genus *Anthracoporella* Pia 1920

Anthracoporella vicina Kochansky and Herak
1960

Fig. 9 g-j, Fig. 10 c-f

- 1960 *Anthracoporella vicina* Kochansky and Herak, OD; 69, pl.1, figs. 1-5.
1964a *Anthracoporella vicina* Kochansky and Herak; Kochansky-Devidé, pl. 3, figs. 2-3.
1966 *Anthracoporella vicina* Kochansky and Herak; Kochansky-Devidé and Ramovš, 16, pl. 6, figs. 1-4.
1970 *Anthracoporella vicina* Kochansky and Herak; Kochansky-Devidé, 212, pl. 22, fig. 4.
1971 *Anthracoporella vicina* Kochansky and Herak; Ramovš, 1387, pl.1, fig.3.

- 1978 *Anthracoporella vicina* Kochansky and Herak; Ramovš, pl. 6, fig. 1.
2000 *Anthracoporella vicina* Kochansky and Herak; Granier and Grgasovic, 15-16, figs. 2-3.
2001 *Anthracoporella* sp.; Minwegen, pl. 12, figs. 3-6.
2003 *Anthracoporella vicina* Kochansky and Herak; Khodjanyazova and Mamet, pl. 3, figs. 21, 28.

Description: Thallus important, ramose, sometimes centimetric in size. Medula occupying 4/5 of the thallus, hence a thin cortex. Pores numerous, regular, very thin (25 μm). Interpores twice the pore diameter.

Stratigraphic distribution and range: Paleotethyan flora. Reported from the "Uralian"-Kasimovian of Yugoslavia. In Spain, abundant in the upper part of the Carboniferous (upper Moscovian- lower Kasimovian). It has been recorded from the Las Llacerias section, where it occurs at the upper part of the Picos de Europa Formation and the lower-middle part of the Las Llacerias Formation (samples BM-12, BM-52, BM-72).

Anthracoporella spectabilis Pia 1920

Fig. 7 a-d

For 85 illustrated references of the taxon, see Homann (1972: 189-191) and update in Granier and Grgasovic (2000: 12-15). Add to the list:

- 1984 *Anthracoporella spectabilis* Pia; Saltovskaya, pl. 31, figs. 1-3.
1985 *Anthracoporella* sp.; Mu, pl. 14, figs. 7-8.
1993 *Anthracoporella spectabilis* Pia; Perret, pl. 13, fig. 16.
1994 *Anthracoporella spectabilis* Pia; Nakamura, 15, pl. 9, figs. 7-12.
1994 *Anthracoporella spectabilis* Pia; Fontaine *et al.*, pl. 5, fig. 2.
1994 *Anthracoporella yowarensis* Nakamura, OD, 16-17, pl. 10, fig. 1; pl. 11, figs. 1-4.
1995 *Anthracoporella spectabilis* Pia; Pajic and Filipovic, pl. 51, figs. 2-5.
2001 *Anthracoporella spectabilis* Pia; Minwegen, pl. 12, figs. 1-2.
2001a *Anthracoporella spectabilis* Pia; Vachard *et al.*, 385-387, fig. 12/1-10.
2002 *Anthracoporella spectabilis* Pia; De Castro, 3-12.
2002 *Anthracoporella spectabilis* Pia; Mamet, pl. 3, figs. 1-2.
2003 *Anthracoporella spectabilis* Pia; Khodjanyazova and Mamet, pl. 3, fig. 24.

Description: Thallus cylindrical, large, plurimillimetric, bifurcated. Branches 30-50 μm , usually 40 μm , aspondyl, ramified once. Wall (100-150 μm), yellowish, of iron-rich calcite.

Discussion: De Castro (2002), Granier and Hofmann (2003), Mu *et al.* (2003) have recently questioned the dasycladale affinity of *Anthracoporella spectabilis* on the presence of calcified sheaths and perforated (?) material apparently growing in the stem. However, these characters appear to be secondary features developed after the decay of the alga, the stem being filled by bacterial (?)

micritic material. This hypothesis has been proposed again by Granier and Hofmann (2003) and by Mu *et al.* (2003). These authors compare the irregular “pores” to codiacean “filaments” (e. g. *Garwoodia*). Remnants of medular filaments are also reported which would discard a dasycladale affinity. In the Spanish material, although abundant and well preserved, the central cavity does not disclose the presence of medular tubes and their existence ought to be corroborated by further studies. The same holds true for the Carnic Alps material studied by Samankassou (2002).

Stratigraphic distribution and range: Cosmopolitan. Mid-Carboniferous to mid-Permian. Reports of the genus in the Devonian (Vachard *et al.*, 2001a) are due to confusion with other dasycladales (e.g. *Couvinianella*). The drawing (A) of an “atypical” *Anthracoporella* is indeed very atypical. Forms the *Anthracoporella* Community of Flügel (1977, p. 322 and 332). In Spain it has been recorded from the Picos de Europa Formation (upper part) and the Las Llacerias Formation at the Las Llacerias section (samples BM-12, BM-52, BM-72, BM-76).

Anthracoporellopsis machaevii Maslov 1956

Fig. 10 g-h

- 1956 *Anthracoporellopsis machaevii* Maslov, OD; 62, pl. 13, fig. 3,4.
- 1979 (non) *Anthracoporellopsis machaevii* Maslov; Muromtseva, 91, pl. 1, fig. 3, 8-10.
- 1964 (?) *Anthracoporellopsis machaevii* Maslov; Chanton, 565, pl. 17, fig. 3-4.
- 1968 (non) *Anthracoporellopsis machaevii* Maslov; Pelhate, 901, pl. 32, fig. 15.
- 1969 (non) *Anthracoporellopsis machaevii* Maslov; Pelhate, 67-68, pl. 6, figs. 74-76.
- 1974 (pars) *Donezella lunaensis* Rácz; Chuvashov, 33, pl. 20, fig. 1-2 (non 3-4).
- 1975 *Anthracoporellopsis machaevii* Maslov; Mamet and Roux, 264, pl. 13, figs. 9-11.
- 1979a *Anthracoporellopsis* aff. *machaevii* Maslov; Mamet *et al.*, 360, pl. 3, fig. 16.
- 1985 *Anthracoporellopsis machaevii* Maslov; Mamet and Pinard, pl. 1, fig. 15.
- 1987 *Anthracoporellopsis machaevii* Maslov; Shuisky, pl. 15, fig. 12.
- 1987 *Anthracoporellopsis machaevii* Maslov; Mamet *et al.*, 23, pl. 10, figs. 7-8; pl. 11, figs. 4-5.
- 1988 *Anthracoporellopsis machaevii* Maslov; Ivanova and Bogush, pl. 15, fig. 16.
- 1988 *Anthracoporellopsis machaevii* Maslov; Ivanova, pl. 2, fig. 9.
- 1988 *Anthracoporellopsis machaevii* Maslov; Deloffre, pl. 1, figs. 25-26.
- 1989 *Anthracoporellopsis machaevii* Maslov; Skompski *et al.*, pl. 2, fig. 4-7.
- 1989 *Anthracoporellopsis machaevii* Maslov; Vachard *et al.*, 706, pl. 1, fig. 6.
- 1990 *Anthracoporellopsis machaevii* Maslov; Bogush *et al.*, pl. 10, figs. 5-7.
- 1991 *Anthracoporellopsis machaevii* Maslov; Vachard and Beckary, 324, pl. 2, fig. 2.
- 1991 *Anthracoporellopsis machaevii* Maslov; Vachard and Tahiri, pl. 4, figs. 7-8.
- 1991 *Anthracoporellopsis machaevii* Maslov; Mamet, pl. 3, fig. 1.
- 1991 *Anthracoporellopsis machaevii* Maslov; Riding, pl. 3, fig. a.
- 1993 *Anthracoporellopsis machaevii* Maslov; Chuvashov *et al.*, pl. 12, fig. 5.
- 1995 (?) *Anthracoporellopsis machaevii* Maslov; Pajic and Filipovic, pl. 48, figs. 4-5.
- 1996 *Anthracoporellopsis machaevii* Maslov (*pars*); Skompski, 225-226, pl. 11, figs. 1-9; pl. 12, figs. 2-6 (non 1).
- 1996 *Anthracoporellopsis machaevii* Maslov; Vachard and Maslo, pl. 2, figs. 10-13.
- 1999 *Anthracoporellopsis machaevii* Maslov; Sebbar and Mamet, pl. 2, fig. 6.
- 2000 *Anthracoporellopsis machaevii* Maslov; Mamet and Stemmerik, pl. 3, figs. D-E.
- 2002 *Anthracoporellopsis machaevii* Maslov; Mamet, pl. 1, fig. 7.

Description: Very irregular *Anthracoporellopsis* with an external diameter of 200-400 μm . Cortex 30-60 μm . Pores simple, disposed in irregular directions (5-8 μm in diameter).

Stratigraphic distribution and range: Cosmopolitan (Mamet, 1992). Rare in Viséan, common in Middle and late Carboniferous (Moscovian, Gzhelian). Reported as late as Early Permian in the Urals. It has been recovered (uncommon) in Spain from upper Moscovian (Myachkovian) beds from the Las Llacerias section (upper part of the Picos de Europa Formation, samples BM-12, and BM-25).

Genus *Beresella* (Makhaev 1937) Maslov and Kulik 1956

Beresella herminae Rácz 1966a

Fig. 9 a-f, Fig. 10 a-b, k

- 1966a *Beresella herminae* Rácz, OD; 93, pl. 1, figs. 1-3.
- 1980 (?) *Beresella herminae* Rácz; Buchroithner *et al.*, 23, pl. 4/5, pl. 5/6.
- 1985 *Beresella herminae* Rácz; Eichmüller, pl. 9, fig. 7.
- 1986 *Beresella herminae* Rácz; Poncet, 189, pl. 2, figs. 1, 2.
- 1999 *Beresella herminae* Rácz; Sebbar and Mamet, pl. 2, fig. 2.
- 2001 *Beresella* sp.; Minwegen, pl. 4, fig. 1, 5; pl. 6, fig. 8.
- 2003 *Beresella* sp.; Della Porta, pl. 6.1.8.

Description: A heavily calcified beresellid, stouter than most representatives of the genus. Diameter 300-400 μm , reaching 500 μm . Thick (up to 100 μm) cortex. Length of clear rings, 25-50 μm . Length of dark rings (micritized pores), 70-200 μm .

Stratigraphic distribution and range: Western Paleotethyan flora (Mamet, 1992). Late Bashkirian/Moscovian where they

form bafflestones. The species is usually not as prolific as its counterparts *Beresella erecta* Maslov and Kulik 1956 and *Beresella ishimica* Kulik 1964. It has been recorded in Spain from the upper part of the Picos de Europa Formation at Las Llacerias section. Beds of late Moscovian (Myachkovian) age, samples BM-12, BM-16.

Genus *Clavaporella* Kochansky and Herak 1960

Clavaporella reinae Rácz 1966b.

Fig. 11 f

- 1966b *Clavaporella reinae* Rácz, OD; 253, pl. 1, figs. 2-7; pl. 2, fig. 6.
 1987 *Clavaporella reinae* Rácz; Mamet *et al.*, 44, pl. 14, figs. 1-11; pl. 15, figs. 1-7.
 1988 *Clavaporella reinae* Rácz; Chuvashov and Anfimov, 66-67, pl. 28, figs. 5-8.
 2003 *Clavaporella reinae* Rácz; Khodjanyazova and Mamet, pl. 3, figs. 14-15.

Description: Thallus segmented, ovoid to conical. Maximum diameter 1000-1700 μm . Upper part of the segment contains the verticillated radiating pores. Such segments reach 500-700 μm . Central part subcylindrical (300-700 μm). Pore diameter 40-60 μm , increasing towards the periphery (up to 100 μm). Vestibule present.

Stratigraphic distribution and range: Originally reported by Rácz from the Middle Moscovian ("Calcareous Zone IV"). It has been recorded in Spain from the Las Llacerias Formation, Las Llacerias section, sample BM-72, lower Kasimovian (Kreviakianian)]. Belongs to the *Orthriosiphonoides* flora (Mamet, 1992).

Genus *Donezella* Maslov 1929

Donezella lutugini Maslov 1929

Fig. 10 j

To the 24 references cited by Mamet *et al.* (1987), add the following:

- 1980 (non) *Donezella lutugini* Maslov; Buchroithner *et al.*, 25, pl. 2/5, pl. 5/7-9.
 1983 *Donezella lunaensis* Rácz; Berchenko, pl. 85, fig. 13.
 1983 (non) *Donezella lutugini* Maslov; Berchenko, pl. 86, figs. 1-4.
 1985 *Donezella lunaensis* Maslov; Eichmüller, pl. 9/9, pl. 14/1.
 1985 *Donezella lutugini* Maslov; Skipp *et al.*, pl. 7, figs. 1, 6.
 1986 *Donezella lutugini* Maslov; Groves, 484, figs. 66/11-13.
 1991 *Donezella lutugini* Maslov; Riding, pl. 2, fig. 1.
 1992 (non) *Donezella cf. lutugini* Maslov; Vachard and Berkhli, pl. 4, fig. 18.
 1993 *Donezella lutugini* Maslov; Chuvashov *et al.*, pl. 12, figs. 1-2.
 1995 *Donezella lutugini* Maslov; Pajic and Filipovic, pl. 45, fig. 4.

- 1995 *Donezella lunaensis* Rácz; Pajic and Filipovic, pl. 32, fig. 11, pl. 46, figs. 1-3.
 1996 *Donezella lutugini* Maslov; Proust *et al.*, pl. 1, fig. 1; pl. 2, figs. 1-8.
 1996 *Donezella lunaensis* Rácz; Proust *et al.*, pl. 1, fig. 4; pl. 3, fig. 1-6.
 1996 *Donezella sp.*; Proust *et al.*, pl. 3, figs. 7-9.
 1996 *Donezella lutugini* Maslov; Vachard and Maslo, pl. 2, fig. 7.
 1996 *Donezella lunaensis* Rácz; Vachard and Maslo, pl. 2, figs. 8-9.
 1996 *Donezella lutugini* Maslov; Sebbar and Mamet, pl. 2, figs. 3, 6.
 1997 *Donezella sp.*; Harris *et al.*, fig. 9/3.
 1997 *Donezella lutugini* Maslov; Harris *et al.*, fig. 9/1, 4.
 2000 *Donezella lutugini* Maslov; Mamet and Stemmerik, figs. 5/C, D, E.
 2001 *Beresella sp.*; Minwegen, pl. 7, figs. 3-4.
 2002 *Donezella sp.*; Della Porta *et al.*, fig. 3/A, C, E; pl. 26, fig. 5, 6.
 2002 *Donezella lutugini* Maslov; Mamet, pl. 1, fig. 5.
 2003 *Donezella sp.*; Della Porta, fig. 3.4 K, M; fig. 4.4 K; fig. 4.5 A, D; pl. 4.1, fig. 5; pl. 5.6, fig. 1; pl. 5.7, fig. 3; pl. 6.1, figs. 1, 5-7; pl. 6.2, figs. 6-9, 11; pl. 6.3, figs. 2-7.
 2003 *Donezella lutugini* Maslov; Khodjanyazova and Mamet, pl. 2, fig. 16.

Description: Thallus erect, a highly branching tuft. Considerable dimension variations depending on the position of the thin-section cut. External diameter ranges from 65 to 260 μm and can reach 450 μm . Perforated cortex, 12-60 μm . Pores usually micritized forming irregular "dark bands". Thin external mucilaginous coating, now transformed in cement. Spacing of the pseudo-partitions proportional to the external diameter.

Stratigraphic distribution and range: While beresellids are considered green algae forming bafflestones, the taxonomic position of their "cousin" *Donezella*, in spite of the same pore morphology, is still controversial (see Della Porta *et al.*, 2002). A common cosmopolitan taxon (Mamet, 1992) from the Bashkirian to the end of the Carboniferous. This paper records an occurrence of *Donezella lutugini* in the upper part of the Picos de Europa Formation at Las Llacerias section, sample BM-28, uppermost Moscovian, closely below the Moscovian/Kasimovian transition beds.

Genus *Dvinella* Khvorova 1949

Dvinella comata Khvorova 1949

Fig. 8 q

To the 20 references of Granier and Grgasovic (2000: 50), add:
 2000 *Dvinella comata* Mamet and Stemmerik, pl. 6, K-L.

Description: Strongly calcified beresellid alga. External diameter 200-250 μm . Thickness of cortex 50-75 μm . Pores numerous, forming a triangular "dark band". Spacing of these bands rather uniform.

Stratigraphic distribution and range: Same as *Beresella*. The two genera are usually associated in meadows and bioconstructions.

Genus *Epimastopora* Pia 1922 emend. Roux 1979

Epimastopora symetrica (Johnson 1951)

Fig. 8 p

To the 24 references of Granier and Grgasovic (2000), add:

- 1991 *Epimastopora symetrica* (Johnson); Riding, 381, pl. 3, figs. n-o.
2001 *Globuliferoporella piai* (Kordé 1951) *n. comb.*; Vachard and Krainer, pl. 3, fig. 8.

Description: An important plurimillimetric *Epimastopora* but fragile and usually encountered in small fragments. Cortex, 150-300 μm . Pores, double-gourd shaped, 75-150 μm in diameter.

Stratigraphic distribution and range: Cosmopolitan, known from the Middle Carboniferous to the Early Permian. This paper records an occurrence from the upper member of the Puentellés Formation at the Berodia-II section, sample BM-123, lower Gzhelian.

Genus *Gyroporella* (Gümbel 1872) Benecke 1876

Gyroporella dissecta Chuvashov 1974

Fig. 8 n

- 1974 *Gyroporella dissecta* Chuvashov, OD; 29, pl. 15, figs. 1-6.
1979 *Gyroporella dissecta* Chuvashov; Zadorodnjuk, pl. 2, fig. 2.
1982 *Gyroporella dissecta* Chuvashov; Mu, 226, pl. 6, figs. 7-10.
1993 *Gyroporella dissecta* Chuvashov; Chuvashov *et al.*, pl. 14, figs. 15-17.
2000 *Gyroporella dissecta* Chuvashov; Granier and Grgasovic, 72.
2001 *Gyroporella dissecta* Chuvashov; Vachard and Krainer, pl. 5, fig. 4.

Description: Elongated club-shaped thallus and similarly shaped medula (175-250 μm). Diameter rather small compared to other representatives of the genus. Pores aspondyl, vesiculiferous, 75-150 μm at the base of the cortex and twice as large at the surface.

Stratigraphic distribution and range: The species is reported from the Upper Carboniferous to the Early Permian. Our Spanish material comes from the uppermost part of the Picos de Europa Formation at the Las Llacerias section, sample BM-46, lowest Kasimovian.

Note: *Gyroporella* needs a formal taxonomic emendation. Indeed, the status of *Pseudogyroporella* (taxonomically invalid) and of *Mizzia* has to be clarified.

Gyroporella (?) *prisca* Kochansky-Devidé 1970

Fig. 8 a-g.

- 1964a *Gyroporella prisca* Kochansky-Devidé, OD; pl. 1, fig. 3 (invalid, no description).
1970 *Gyroporella prisca* Kochansky-Devidé, 14-15, pl. 1, fig. 4; pl. 4, figs. 2-6; pl. 5, figs. 1-7; pl. 6, figs. 1-2, 6; pl. 7, fig. 1 (first valid description).
1982 *Gyroporella prisca* Kochansky-Devidé; Milanovic, 21-22, pl. 8, fig. 6.

Description: Thallus very large (diameter up to 4 mm) with a prominent unsegmented medula and a comparatively thin cortex. Thick pores, heart-shaped in transverse section.

Stratigraphic distribution and range: Occidental Paleotethyan flora. Reported from the Late Moscovian to the Kasimovian in Yugoslavia. In our material, present in shallow-water facies of the uppermost part of the Picos de Europa Formation at the Las Llacerias section, sample BM-46, lowest Kasimovian.

Genus *Pseudogyroporella* Endo 1959, invalid

“*Pseudogyroporella*” *annulata* Ishijima,

Ozaki and Nakamura 1971

Fig 8 o

- 1971 *Pseudogyroporella annulata* Ishijima, Ozaki and Nakamura, OD; p. 112-113, pl. 5, fig. 4B; pl. 6, figs. 7-11.

Description: Thallus club-shaped, small, diameter inferior to one millimeter with external annulations. Pores aspondyl, important, vesiculiferous, perpendicular to the stem and in regularly-spaced whorls.

Stratigraphic distribution and range: Originally described from the Early Permian of Japan. Recorded in Spain at the top of the Picos de Europa Formation, Las Llacerias section, sample BM-63, lower Kasimovian.

Note: As previously indicated, a taxonomic revision of *Gyroporella* and related genera is needed. The Spanish species cannot be transferred to the Triassic *Gyroporella annulata* (Schafhault 1853) Gümbel 1872 and the invalid “*Pseudogyroporella*” is tentatively used.

Genus *Herakella* Kochansky-Devidé 1970

Herakella paradoxa Kochansky-Devidé 1970

Fig. 11 a, b

- 1970 *Herakella paradoxa* Kochansky-Devidé, OD; 22-25, pl. 5, fig. 1; pl. 12, figs. 5-9; pl. 13, figs. 1-11; pl. 14, figs. 1-13; pl. 15, fig. 11-2.
1982 *Herakella paradoxa* Kochansky-Devidé; Milanovic, 23, pl. 10, fig. 5.
1988 *Herakella paradoxa* Kochansky-Devidé; Deloffre, pl. 6, fig. 13.
1990 (?) *Herakella paradoxa* Kochansky-Devidé; Bogush *et al.*, pl. 14, fig. 1.
2000 *Herakella* sp.; Forke and Samankassou, pl. 33, figs. 1-6.

- 2001 *Herakella paradoxa* Kochansky-Devidé; Vachard and Krainer, pl. 5, fig. 1.
 2003 *Herakella paradoxa* Kochansky-Devidé; Khodjanyazova and Mamet, pl. 3, figs. 25-27.

Description: Cortex cylindrical, segmented. Crescentic segments. Diameter, 1000-2000 μm . Medula continuous, cylindrical. Diameter 300-800 μm , average 500 μm . Five to ten metaspore pores in bundles perforating the cortex at an angle of 20°-40°.

Stratigraphic distribution and range: The taxon is reported in the Paleotethys from the Late Moscovian to the Kasimovian. Our Spanish material comes from the upper part of the Picos de Europa Formation at the Las Llacerias section, sample BM-28, uppermost Moscovian (upper Myachkovian).

Genus *Hikorocodium* Endo 1951

Hikorocodium kuramotoi Nakamura 1994

Fig. 11 c

- 1994 *Hikorocodium kuramotoi* Nakamura, OD; 38-39, pl. 22, figs. 6-7.

Description: Thallus nodular, around 2 mm in all specimens. Pith-like central cavity surrounded by a micritized cortex perforated by numerous anastomosed constricted tubes. Tubes thin, 20 μm at departure from central cavity and thicker towards the periphery.

Stratigraphic distribution and range: The *Hikorocodium* flora is usually connected to Permian shallow water carbonates, although Nakamura described *H. kuramotoi* from the Carboniferous of Japan (Yowora). In Spain this taxon is observed in the upper part of the Picos de Europa Formation, Las Llacerias section, sample BM-12, upper Moscovian (Myachkovian). A probable *Hikorocodium* (*Hikorocodium?* sp.) is illustrated in Fig. 11 g; the latter comes from a Khamovnikian bed of the Las Llacerias Formation, sample BM-74B.

Genus *Macroporella* Pia 1912

Macroporella ginkeli Rác 1966a

Fig. 7 g

- 1966a *Macroporella ginkeli* Rác, OD; 98-99, pl. 6, figs. 1-3.
 1981 *Macroporella ginkeli* Rác; Rauser-Chernousova and Koroljuk, 164, pl. 3, figs. 6-7.
 1988 *Macroporella ginkeli* Rác; Chuvashov and Anfimov, 64-65, pl. 27, figs. 1-2.
 1993 *Macroporella ginkeli* Rác; Chuvashov *et al.*, pl. 13, fig. 1.
 2003 *Macroporella ginkeli* Rác; Khodjanyazova and Mamet, pl. 3, fig. 20.

Description: Thallus cylindrical with a diameter ranging from 1.5 to 2 mm. Important (50-60 % of the thallus) unsegmented medula. Slightly inclined (15 °) branches without ramifications

and with a progressive diameter increase towards the outer part of the cortex.

Stratigraphic distribution and range: Originally reported from the Moscovian. Known range in the Paleotethys: Moscovian-Kasimovian. Observed in the top of the Picos de Europa Formation sample BM-63 (lower Kasimovian), Las Llacerias section.

Genus *Palaeoberesella* Mamet and Roux 1974

Palaeoberesella lahuseni (von Möller 1879)

Fig. 8 h

- 1879 *Nodosinella lahuseni* von Möller, OD; 75, pl. 5, figs. 6a-b, 7.
 1948 *Nodosinella lahuseni* von Möller; Rauser-Chernousova, figs. 4-9.
 1972 *Kamaena lahuseni* (von Möller); Mamet and Rudloff, 87, pl. 5, figs. 13-14.
 1973 *Anthracoporellopsis* sp.; Ivanova, pl. 10, fig. 2.
 1974 *Palaeoberesella lahuseni* (von Möller); Mamet and Roux, 144, 148, pl. 2, figs. 20-28; pl. 3, figs. 1-29; pl. 4, figs. 1-17.
 1975 *Nodosinella? scalaris* Malakhova, OD; 85-86, pl. 9, fig. 5-11.
 1976 *Palaeoberesella lahuseni* (von Möller); Mamet, pl. 6, fig. 2; pl. 56, fig. 3; pl. 59, fig. 3.
 1978 *Palaeoberesella lahuseni* (von Möller); Jansa *et al.*, 1434, pl. 1, figs. 15, 18.
 1979 *Paleoberesella (sic)*; Radionova, pl. 1, fig. 7.
 1979 *Paleoberesella lahuseni (sic)* (von Möller); Radionova, pl. 1, figs. 8-10.
 1981 *Palaeoberesella lahuseni* (von Möller); Mamet and Martínez, pl. 2, fig. 1.
 1981 *Palaeoberesella lahuseni* (von Möller); Vachard, 312-314, pl. 13, fig. 2.
 1983 *Palaeoberesella lahuseni* (von Möller); Cnudde and Mamet, pl. 1, fig. 5.
 1986 *Palaeoberesella lahuseni* (von Möller); Mamet *et al.*, 30, pl. 12, fig. 9.
 1987 *Palaeoberesella lahuseni* (von Möller); Shuysky, pl. 16, fig. 9.
 1988 *Palaeoberesella lahuseni* (von Möller); Flügel and Kahler, 144, pl. 20, fig. 1.
 1988 *Palaeoberesella lahuseni* (von Möller); Ivanova and Bogush, pl. 7, figs. 2-4.
 1990 *Palaeoberesella lahuseni* (von Möller); Bogush *et al.*, 96-97, pl. 8, figs. 6-11.
 1990 *Palaeoberesella scalaris* (Malakhova); Bogush *et al.*, OD; p. 97, pl. 8, fig. 12.
 1991a *Palaeoberesella lahuseni* (von Möller); Vachard, pl. 5, fig. 2.
 1992 *Palaeoberesella lahuseni* (von Möller); Mamet and Préal, pl. 1, fig. 14.
 1993 *Palaeoberesella lahuseni* (von Möller); Chuvashov *et al.*, pl. 10, fig. 6.
 1994 *Palaeoberesella lahuseni* (von Möller); Vachard and Clement, 306, pl. 2, fig. 5; pl. 3, fig. 4.
 1995 *Palaeoberesella lahuseni* (von Möller); Sanchez-Chico *et al.*, 74, pl. 1, fig. 11; pl. 2, fig. 11.

1996 *Palaeoberesella lahuseni* (von Möller); Sebban and Mamet, pl. 2, fig. 7.

1999 *Palaeoberesella lahuseni* (von Möller); Mamet *et al.*, pl. 4, figs. 3-4.

Description: Subcylindrical, long muff, straight or slightly curved. Diameter of calcified cortex, 100-200 μm . Medula composed of a succession of irregular cells (up to 25-30 μm), subcircular to subquadratic. Pores simple, thin, straight.

Stratigraphic distribution and range: Cosmopolitan (Mamet, 1992). Rare in mid-Devonian, then extremely abundant in Viséan-Serpukhovian where it forms bafflestones in lagoonal environment. Peters out in Late Carboniferous, where it is replaced by the beresellids. This paper reports its occurrence in sample P-21 (upper Myachkovian), Corisa Formation, Sierra Corisa locality, northern Palencia.

Genus *Pelayella* n. gen.

Type species: *Pelayella multiporosa* n. gen., n. sp.

Origin of name: For the name of the first Asturian king (Pelayo) who received his crown at Covadonga.

Diagnosis: A club-shaped, regular, aspondyl Salpingoporellinae. Thin pores divided in tufts.

Description: Thallus sinuous, cylindrical, unstricted. Medula continuous, cylindrical. Cortex important, perforated by a multitude of arched aspondyl pores, with slight oblique insertion. Pores enlarge slowly, then divide in a tuft of 5-6 branches.

Comparison: By its morphology, *Pelayella* is similar to *Anatolipora* and belongs to the same tribe (Salpingoporellinae). It differs from the latter by the nature of the pore dichotomy.

Stratigraphic distribution and range: Known from the Kasimovian of the Las Llacerias Formation (sample BM-72), Las Llacerias section (vicinity of Covadonga), where it is associated with a very rich flora of *Anthracoporella variabilis*, *A. vicina*, *Archaelithophyllum delicatum*, *A. johnsoni*, *Claracrusta*, *Cuneiphyucus*, *Epimastopora symetrica*, *Ivanovia tenuissima*, *Penella pongaensis*, *Tubiphytes obscura* and *Zaporella cantabriensis*.

Pelayella multiporosa n. gen., n. sp.

Fig. 11 d

Origin of name: From the multiple pores.

Holotype: Figure 11 d. Repository number U. of M. 728/2

Diagnosis: See the genus.

Description: Thallus cylindrical, club-shaped, sinuous, with a diameter of 900-1000 μm . Medula continuous, 270-300 μm . Cortex, 300-350 μm . There are 21-24 aspondyl pores per lin-

ear millimeter. Pores are very thin, 3-5 μm , with oblique insertion. They enlarge progressively up to two-thirds of their length, then form a tuft of 5-6 (3-5 μm) branches. Due to heavy micritization, the tufts are dissolved and form an epidermic cone that reaches up to 30 μm in diameter.

Stratigraphic distribution and range: See the genus.

Genus *Pseudovelebitella* Mamet and Roux 1978

Pseudovelebitella simplex (Kochansky-Devidé 1964b) Mamet and Roux 1978

Fig. 8 i-j

1964b *Velebitella simplex* Kochansky-Devidé, OD; 136-137, pl. 1, fig. 1, a-h; pl. 2, fig. 1-9.

1964a *Velebitella simplex* Kochansky-Devidé, 188, pl. 19, fig. 1.

1977 *Velebitella* sp.; Vachard in Termier *et al.*, 15, pl. 2, fig. 7.

1978 *Pseudovelebitella simplex* (Kochansky-Devidé); Mamet and Roux, 75.

1985 *Velebitella simplex* Kochansky-Devidé; Vachard, 273, pl. 2, figs. 5-7.

1988 *Pseudovelebitella simplex* (Kochansky-Devidé); Deloffre, fig. 12.

2000 *Pseudovelebitella simplex* (Kochansky-Devidé); Granier and Grgasovic, 147, figs. 24-25 (reproduction of part of Kochansky's material).

2003 *Pseudovelebitella simplex* (Kochansky-Devidé); Khodjanyazova and Mamet, pl. 3, figs. 22-23.

Description: Diplopore composed of a succession of barrel-shaped articles (diameter 500-600 μm). Medula very large and poorly developed "napkin-ring" cortex. Divergent bundles of thin pores, starting from a small vestibule and concentrated in the median part of the articles.

Stratigraphic distribution and range: Belongs to the Paleotethyan flora. Moscovian to Early Permian. Quite scarce in the Asturian material; it occurs in the upper part of the Picos de Europa Formation, samples BM-14 (upper Myachkovian), and BM-46 (lowest Kreviakian).

Genus *Vermiporella* Stolley 1893 *sensu* Pia 1927

"*Vermiporella*" *hispanica* Rácz 1966b

Fig. 11 h

1966b *Vermiporella hispanica* Rácz, OD.; 257, pl. 5, figs. 23-26.

Description: Thallus millimetric, tubular, irregular, sinuous, ramified. Cortex uniform, much less important than the medula (150-200 μm), perforated by simple cylindrical branches, perpendicular to the stem (20-40 μm). Interpore length, half that of the pores.

Note: *Vermiporella* is an Early Paleozoic Dasyporellaeae, abundant in Ordovician-Silurian, that peters out in the Devonian. Its

presence in the Carboniferous is debatable and the Cantabrian material ought to be transferred to a new genus.

Stratigraphic distribution and range: Rác reports *hispanica* from the Late Moscovian. It is also present in the Kasimovian. Our material comes from sample BM-101, upper member of the Puentellés Formation, lower Gzhelian, Berodia-I section.

Genus *Uraloporella* Kordé 1950

Uraloporella variabilis Kordé 1950 *emend.*

Mamet and Villa 1995

Fig. 10 i

For taxonomy, refer to the 23 references in Granier and Grgasovic (2000: 160-161), and add:

- 2000 *Uraloporella variabilis* Kordé; Mamet and Stemmerik, fig. 4, A-I.
 2001 *Uraloporella variabilis* Kordé; Minwegen, pl. 4, fig. 1 (*pars*), 6-7.
 2001 *Uraloporella* sp.; Minwegen, pl. 6, fig. 8 (*pars*), pl. 15, fig. 4.
 2003 *Uraloporella* sp.; Della Porta, fig. 3.5. A (*pars*).
 2003 *Uraloporella variabilis* Kordé; Khodjanyazova and Mamet, pl. 2, fig. 19.

Description: Long, unsegmented, cylindrical thallus with an external diameter ranging from 150 to 600 μm . Internal cavity unsegmented. Cortex perforated by “innumerable” micrometric pores (up to one hundred in a single axial section!) The species has been emended from the upper Moscovian (Podolian) of La Huelga beach section, Asturias, where it forms extensive boundstones.

Stratigraphic distribution and range: Reported from the Middle Carboniferous in the Paleotethyan and Arctic realms. Very abundant in the Moscovian, usually associated with beresellids. Similar distribution in Spain. Present material comes from the upper part of the Picos de Europa Formation, sample BM-19 (upper Moscovian, upper Myachkovian), Las Llacerias section.

Genus *Zaporella* Rác 1966a

Zaporella cantabriensis Rác 1966a

Fig. 7 h-k

- 1966a *Zaporella cantabriensis* Rác, OD; 102-103, pl. 1, figs. 4-7.
 1985 *Zaporella cantabriensis* Rác; Eichmüller, pl. 14, fig. 8.

Description: Thallus grossly cylindrical, unbranched. Diameter millimetric (1.5-5 mm). Cortex thick, medula reduced. Pores simple, undivided, 50 μm in diameter. Interpores of similar magnitude.

Comparison: Our material has fewer and thicker pores than the microfossils illustrated by Rác and Eichmüller. Note: Granier and Grgasovic (2000) indicate 1964 as the valid date of the genus. The correct date appears to be 1966, when the formal description “became available”.

Stratigraphic distribution and range: Quite rare. Previously reported from the Moscovian. Observed in our material from the upper part of the Picos de Europa Formation (sample BM-11, upper Moscovian, Myachkovian) and Las Llacerias Formation (sample BM-72, lower Kasimovian, top of Krevyakinian) at Las Llacerias section.

PHYLLUM CHLOROPHYCOPHYTA? Papenfuss 1946

or RHODOPHYCOPHYTA? Papenfuss 1946

Genus *Eugonophyllum* Konishi and Wray 1961

Eugonophyllum johnsoni Konishi and Wray

1961

Fig. 12 f-i

For 11 previous references to the taxon, see Flügel and Flügel-Kahler (1980: 117), and add:

- 1981 *Eugonophyllum johnsoni* Konishi and Wray; Milanovic, 19, pl. 7, figs. 8-9.
 1982 *Eugonophyllum johnsoni* Konishi and Wray; Milanovic, 19, pl. 7, figs. 8-9.
 1983 *Eugonophyllum* cf. *E. johnsoni* Konishi and Wray; Toomey, 170, pl. 21, figs. 7, 11-12.
 1987 *Eugonophyllum johnsoni* Konishi and Wray; Mamet *et al.*, 17-18, pl. 5, figs. 7-12; pl. 6, figs. 1-8; pl. 8, figs. 6-7.
 1993 *Eugonophyllum johnsoni* Konishi and Wray; Vachard *et al.*, pl. 1, fig. 1.
 1994 *Eugonophyllum johnsoni* Konishi and Wray; Nakamura, 35, pl. 18, figs. 10-12.
 1995 “*Eugonophyllum* “*johnsoni* Konishi and Wray; Pajic and Filipovic, pl. 50, figs. 8-9.
 2001 Phylloid algae (*pars*); Minwegen, pl. 1, fig. 6.
 2003 *Eugonophyllum johnsoni* Konishi and Wray; Khodjanyazova and Mamet, pl. 4, fig. 10.

Description: Plurimillimetric to pluricentimetric phylloid blade. Thickness 500-1500 μm . External cortex thin, 30-50 μm . Internal cortex 30-100 μm . Utricles 20-60 μm .

Stratigraphic distribution and range: Cosmopolitan. Total range Moscovian to Mid-Permian (same as *Ivanovia*). In NW Spain, Moscovian and earliest Kasimovian where it proliferates and forms boundstones. Recorded in the Las Llacerias section from the Picos de Europa Formation (sample BM-12, upper Myachkovian, and sample BM-46, lowest Krevyakinian). It has been also recorded from the Corisa Formation in Sierra Corisa locality, northern Palencia (sample P-21, upper Myachkovian).

Eugonophyllum mulderi Rác 1966a

Fig. 12 b-e

- 1966a *Eugonophyllum mulderi* Rác, OD; 106, pl. 12, figs. 1-4.
 1970 *Eugonophyllum mulderi* Rác; Kochansky-Devidé, 10-11, pl. 2, fig. 1.
 1978 *Eugonophyllum mulderi* Rác; Kulik, 185-186, pl. 1, figs. 4-5.
 1980 *Eugonophyllum mulderi* Rác; Flügel and Flügel-Kahler, 120, pl. 1, fig. 8.

2003 *Eugonophyllum mulderi* Rácz; Khodjanyazova and Mamet, pl. 4, fig. 11.

Description: Small, irregular, phylloid blade. Thickness 200-450 μm . Medula sometimes reduced to less than 200 μm . External cortex 30-50 μm , with utricles of the same dimensions.

Stratigraphic distribution and range: Known from the western part of the Paleotethyan Realm. Late Moscovian for Rácz. Extended to the Kasimovian by Kochansky-Devidé and to the Asselian by Khodjanyazova and Mamet. Forms phylloid algae mounds in the Cantabrian Mts. and in Yugoslavia. Present material has been collected from the lowest Kasimovian of the Las Llacerias section (sample BM-47, top of Picos de Europa Formation), the Kasimovian of Demués section (sample BM-276, Demués Formation), and the lower Gzhelian of Berodia-I section (sample BM-105, upper member of the Puente de los Hornos Formation).

Genus *Ivanovia* Khvorova 1946

Ivanovia tenuissima Khvorova 1946

Fig. 12 a, j-n

To the 8 references in Mamet *et al.* 1987, 19-20, add:

- 1991 *Ivanovia tenuissima* Khvorova; Riding, pl. 3, fig. f.
 1995 *Ivanovia tenuissima* Khvorova; Pajic and Filipovic, pl. 47, figs. 6-7.
 1995 *Ivanovia tenuissima* Khvorova; Forke, 240, pl. 20, figs. 1-4.
 1996 *Ivanovia tenuissima* Khvorova; Mamet, pl. 1, fig. 8.
 2000 *Ivanovia tenuissima* Khvorova; Mamet and Stemmerik, fig. 9A.
 2003 *Ivanovia tenuissima* Khvorova; Khodjanyazova and Mamet, pl. 4, fig. 9.

Description: Plurimillimetric to pluricentimetric phylloid blade. Thickness 500 to 1500 μm . Cortical zone reduced to 100 μm . Angular utricles perpendicular to cortex (15-30 μm).

Note: For a detailed discussion on *Ivanovia*, refer to Torres (1997).

Stratigraphic distribution and range: Originally created from the Upper Carboniferous of the Moscow Basin. Probable range, Moscovian to mid Permian (Artinskian or younger). In NW Spain, abundant in the Kasimovian and forms mounds associated with *Tubiphytes*. Present material was collected at Las Llacerias section from the uppermost part of the Picos de Europa Formation (sample BM-47) and Las Llacerias Formation (samples BM-69, BM-70, BM-72), lower Kasimovian (Krevyankinian).

PHYLLUM RHODOPHYCOPHYTA Papenfuss 1946

Genus *Fourstonella* Cummings 1955

Fourstonella fusiformis (Brady 1876)

Fig. 14 e

1876 *Stacheia fusiformis* Brady, OD; 114, pl. 8, figs. 12-16.

- 1955 *Fourstonella fusiformis* (Brady 1876); Cummings, 7, figs. 4, 5, F-G.
 1956 *Stacheia fusiformis* Brady; Braznikhova, 50, pl. 2, fig. 9; pl. 10, fig. 9.
 1964 *Fourstonella fusiformis* (Brady 1876); Loeblich and Tappan, C331, fig. 246.
 1967 *Fourstonella fusiformis* (Brady 1876); Eickhoff, 37-38, pl. 3, fig. 5; pl. 4, figs. 6-8.
 1977 *Fourstonella fusiformis* (Brady 1876); Perret and Vachard, 114, pl. 5, fig. 3.
 1977 *Fourstonella fusiformis* (Brady 1876); Mamet and Roux, 222-223, pl. 2, fig. 4.
 1978 *Fourstonella fusiformis* (Brady 1876); Jansa *et al.*, 1436, pl. 1, fig. 21.
 1986 *Fourstonella fusiformis* (Brady 1876); Skompski, pl. 15, figs. 1-5.
 1988 *Fourstonella fusiformis* (Brady 1876); Ivanova and Bogush, pl. 18, fig. 14.
 1989 *Fourstonella fusiformis* (Brady 1876); Skompski *et al.*, pl. 2, fig. 3.
 1990 *Fourstonella fusiformis* (Brady 1876); Bogush *et al.*, 126-127, pl. 26, fig. 8-9; pl. 27, figs. 1-2.
 1995 *Fourstonella fusiformis* (Brady 1876); Sanchez-Chico *et al.*, 76, pl. 3, figs. 10-11; pl. 4, figs. 9-10.
 1996 *Fourstonella fusiformis* (Brady 1876); Mamet, pl. 3, fig. 1.

Description: Thallus fusiform, with a regular addition of curvilinear rows that overlap each other. The alga is attached to a central support, usually a (now) dissolved phaeophyte or a sponge megasclere. Overall diameter 400-600 μm and length 600 μm to 1-3 mm. Thickness of interlaminae 10 μm . Height of rows, 20-25 μm .

Stratigraphic distribution and range: A widespread and long ranging species observed from the Visean to the Early Permian? Our illustrated Spanish material is from the Kasimovian.

Genus *Fourstonella*? Cummings 1955

or *Cuneiphycus*? Johnson 1960

or *Efluegelia*? (Vachard in Massa and Vachard 1979)

Ramovš and Kochansky-Devidé 1981 *nom. corr.*

Fourstonella? johnsoni (Flügel 1966)

Fig. 14 f

- 1966 *Cuneiphycus johnsoni* Flügel, OD; 17-19, pl. 2, figs. 1-5.
 1969 *Cuneiphycus* sp. cf. *C. johnsoni* Flügel; Toomey, 1318, pl. 151, figs. 3-4.
 1972 *Cuneiphycus johnsoni* Flügel; Homann, 165-169, pl. 2, fig. 12.
 1974 *Cuneiphycus johnsoni* Flügel; Chuvashov, 32, pl. 21, figs. 1-8.
 1977 *Cuneiphycus johnsoni* Flügel; Mamet and Roux, 238, pl. 9, figs. 8-11.
 1978 *Cuneiphycus johnsoni* Flügel; Mamet and Roux, 83, pl. 7, figs. 11-12.

- 1979 *Eflugelia (sic) johnsoni* (Flügel); Vachard in Massa and Vachard, 34, pl. 9, fig. 10.
- 1980 *Eflugelia (sic) johnsoni* (Flügel); Flügel, pl. 7, fig. 2; pl. 9, fig. 1.
- 1980 *Eflugelia (sic) johnsoni* (Flügel); Flügel and Flügel-Kahler, 163-164, pl. 8, figs. 9-10.
- 1981 *Eflugelia johnsoni* (Flügel); Ramovš and Kochansky-Devidé, 97, pl. 1, fig. 2.
- 1981 *Eflugelia (sic) johnsoni* (Flügel); Vachard and Montenat, 60, pl. 9, fig. 1; pl. 10, figs. 1-3, 5-6; pl. 12, fig. 10.
- 1982 *Eflugelia johnsoni* (Flügel); Milanovic, pl. 7, fig. 10; pl. 10, fig. 3.
- 1983 *Eflugelia* sp. (*sic*); Groves, 29-30, pl. 8, figs. 6-9.
- 1985 *Cuneiphycus johnsoni* Flügel; Mamet and Pinard, pl. 1, figs. 18-21; pl. 3, fig. 1.
- 1986 *Fourstonella johnsoni* (Flügel); Groves, 488, fig. 8/3-8.
- 1986 *Eflugelia (sic) johnsoni* (Flügel); Skompski, 268-269, fig. 6; pl. 10, figs. 1-2.
- 1987 *Cuneiphycus johnsoni* Flügel; Mamet *et al.*, 55-56, pl. 28, figs. 5-10.
- 1987 *Eflugelia (sic) johnsoni* (Flügel); Chuvashov, pl. 21, fig. 5.
- 1989 *Eflugelia (sic) johnsoni* (Flügel); Sebbar and Lys, pl. 1, fig. 7.
- 1990 *Eflugelia (sic) johnsoni* (Flügel); Sebbar, pl. 1, fig. 5.
- 1993 *Eflugelia (sic) johnsoni* (Flügel); Vachard *et al.*, pl. 2, figs. 6-8.
- 1993 *Eflugelia (sic) johnsoni* (Flügel); Chuvashov *et al.*, pl. 12, fig. 14.
- 1995 *Eflugelia (sic) johnsoni* (Flügel); Forke, pl. 15, fig. 8.
- 1996 *Eflugelia (sic) johnsoni* (Flügel); Vachard and Maslo, pl. 1, fig. 11.
- 2001 *Eflugelia (sic) johnsoni* (Flügel); Vachard and Krainer, pl. 3, fig. 12.
- 2001a *Eflugelia (sic) johnsoni* (Flügel); Vachard *et al.*, pl. 18, fig. 17.
- 2002 *Cuneiphycus? johnsoni* Flügel (or *Fourstonella?*); Mamet, pl. 6, fig. 9.
- 2003 *Cuneiphycus? johnsoni* Flügel (or *Fourstonella?*); Khodjanyazova and Mamet, pl. 5, fig. 4.

Description: Thallus attached on a support: shapes vary from hemispheric to "lemon-like". Length up to one millimeter. Laminae of slightly irregular subquadratic cells. Cell height 12-25 μm and width, 10-20 μm . Horizontal cells much thicker (15 μm) than vertical partitions (5 μm).

Discussion: Groves (1986) attributed the morphological variations to the shape of the substrate and questioned the existence of the genus *Eflugelia* ("Eflugelia" of the literature). The situation is further complicated by the unsolved status of *Cuneiphycus*, a genus that requires emendation. The disappearance of its type and the obscure relation with *Foliophycus* does not improve the taxonomic chaos.

Stratigraphic distribution and range: Cosmopolitan and common (Mamet, 1992). Carboniferous/Upper Permian in Eurasia. Our illustrated material is from the Kasimovian as is that of Khodjanyazova and Mamet (2003). It has been collected from

the upper part of the Las Llacerias Formation (sample BM-77B, upper Khamovnikian) at Las Llacerias section.

Genus *Archaeolithophyllum* Johnson 1956

Archaeolithophyllum johnsoni Rácz 1966a

Fig. 13 c-e

1966a *Archaeolithophyllum johnsoni* Rácz, OD; 87-88, pl. 9, figs. 1-4.

1986 *Archaeolithophyllum johnsoni* Rácz; Poncet, 190, pl. 2, figs. 7-8.

Description: Thallus branching, 500-800 μm thick, with poor development of small regular perithallic cells (10-15 μm). Polygonal hypothallic cells, 60-80 μm in length.

Stratigraphic distribution and range: Bashkirian-Moscovian of Spain and Algerian Sahara. Extends probably up to lower Gzhelian in the Picos de Europa area of Spain (samples BM-72, Las Llacerias section, and BM-257, Inguanzo).

Archaeolithophyllum delicatum Johnson 1956

(*nom. corr.*)

Fig. 13 f-i

1956 *Archaeolithophyllum delicatum* Johnson, OD; 53, pl. 14, figs. 4, 6.

1980 *Archaeolithoporella delicatum* (Johnson); Flügel and Flügel-Kahler, p. 157, pl. 8, fig. 5.

Description: Thallus slender (300-400 μm thick), arched, branching. Rather small peri- and hypothallic cells, poorly differentiated (respectively 10-15 and 15-40 μm).

Stratigraphic distribution and range: Reported from the Late Carboniferous and Late Pennsylvanian of the Carnic Alps and American Midcontinent. Observed in Spain in the Las Llacerias Formation (sample BM-72, Khamovnikian) at Las Llacerias section, in the Demués Formation (sample BM-281, Khamovnikian) at the Demués section, and in the Puente de Ibañeta Formation (sample BM-128, lower Gzhelian?) at Berodia-II section.

Remark: Vachard *et al.* (2001a) have suggested a *continuum* between *Archaeolithophyllum* and the Anchicodiaceae. Such transition is not substantiated by the study of our material.

Genus *Kasimophyllum* n. gen.

Type species: *Kasimophyllum demuesensis* n.gen., n.sp.

Origin of name: From the Kasimovian succession, from which the type is derived.

Diagnosis: Crustose Archaeolithophyllum Chuvashov, 1987, composed of irregular bundles of hypothallic cells.

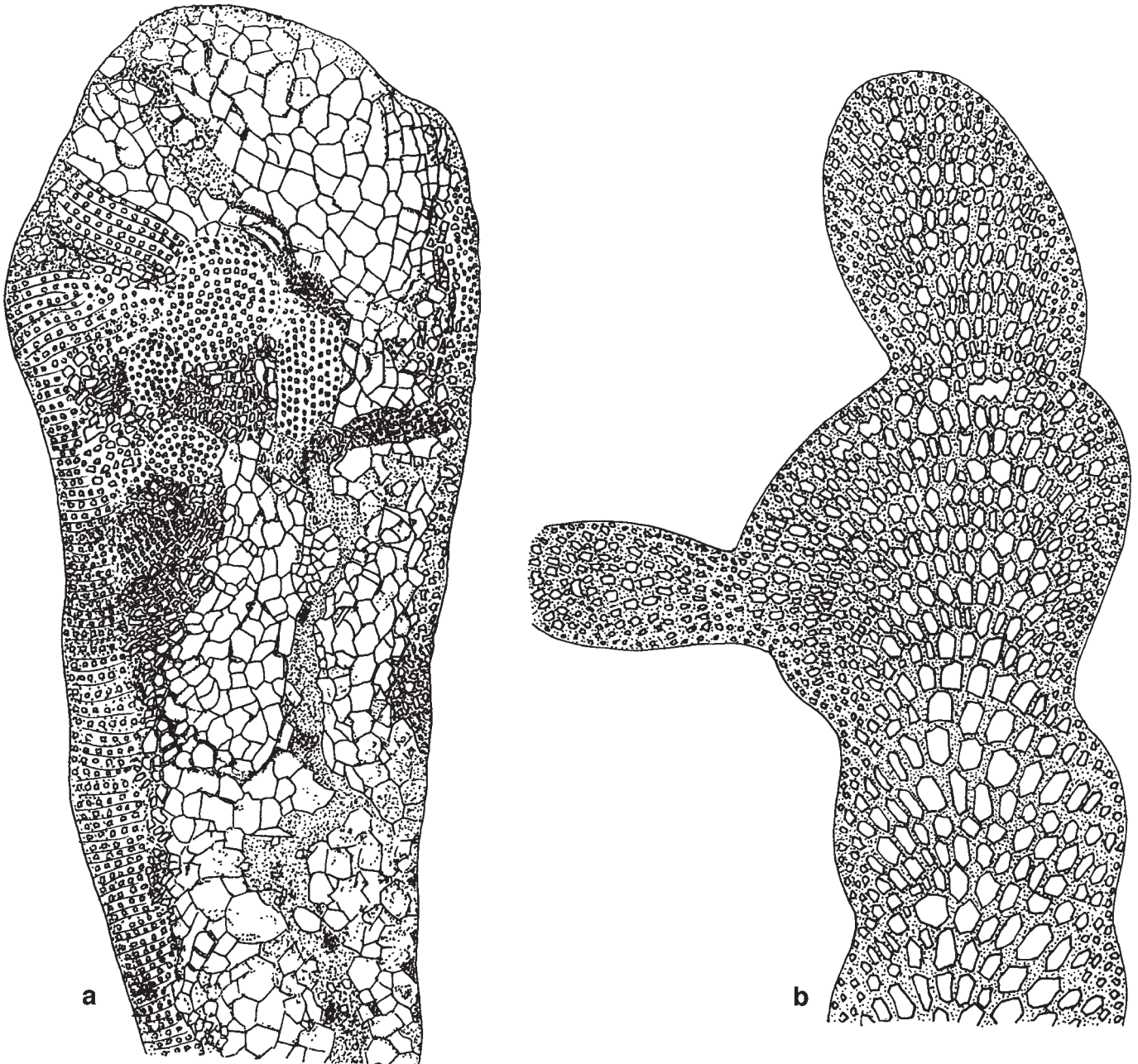


Figure 5. a, Idealized drawing of the type of *Kasimophyllum demuesensis* n. gen., n. sp. Order of magnitude of the thallus diameter: 1 mm. b, Compare with an idealized section of *Archaeolithophyllum*. Order of magnitude of the thallus diameter: 900 μ m.

Description: Crustose interwoven sheets or bundles of differentiated angular cells. Hypothallus composed of large, polygonal cells with no apparent growth patterns and of angular, irregular smaller cells. Perithallic cells as rows of very small, thin, subquadratic cells. Conceptacles not observed. See idealized section at figure 5 a and compare with *Archaeolithophyllum*, figure 5 b.

Comparison: Figure 5 a-b permit comparison of *Kasimophyllum* with its “cousin” *Archaeolithophyllum*. The latter has a regular coaxial hypothallus and the hexagonal

cells are disposed in somewhat regular convex rows. In *Kasimophyllum*, the sheets of radiating bundles of cells are irregular and have no consistent growth habit. Two types of hypothallic cells are present, one very coarse angular and the other smaller and irregular. The perithallic cells are well developed and disposed in regular rows.

It is probable that *Archaeolithophyllum?* sp., described in 1966 by Flügel from the Permian of the Carnic Alps and some *Archaeolithophyllum* of Minwegen, 2001, should be transferred to *Kasimophyllum*.

Stratigraphic distribution and range: The material from which the holotype is derived is a marine *Archaelithophyllum*-phyllid bafflestone with associated brachiopods, echinoderms, sponges and trilobites. There are minor amounts of bryozoans and mollusks. Foraminifers and microproblematics encountered in the level are *Biseriella*, *Bradyina*, *Bradyinelloides*, *Climacamina*, *Endothyra*, *Endothyranella*, *Globivalvulina*, *Ozawainella*, *Priscella*? *Pseudotaxis*, *Syzrania*, *Tetrataxis*. Algae and *incertae sedis* are *Anthracoporella*, *Archaelithophyllum*, *Eugonophyllum*, *Tuberitina*, *Tubiphytes*. It has been collected from the Kasimovian (probably from Khamovnikian beds) of the Demués section (sample BM-277, upper part of the Demués Formation). Minwegen (2001) illustrated "*Archaeolithophyllum*" from the Kasimovian Puentellés Formation at El Pontón section (river Cares valley, Spain). Observed in Samankassou's material from the Carnic Alps (Auernig Group, Kasimovian-Gzhelian).

Kasimophyllum demuesensis n. gen., n. sp.

Figs. 5 a, 13 a-b

2001 *Archaeolithophyllum* sp.; Minwegen, pl. 13, fig. 3; pl. 14, figs. 1, 5, 7.

Origin of name: From the Demues section.

Holotype: Figure 13 b (enlarged and with different light orientation), figure 13 a, and idealized figure 5 a. Repository number: U. of M. 827/9-11.

Diagnosis: See the genus.

Description: Thallus crustose, more than a millimeter wide and 3 millimeters long. Interwoven bundles and sheets of subhexagonal cells (50-120 μm) associated with irregular 10-40 μm cells forming the hypothallus. Perithallic cells, well developed as rows (up to 200 μm long) or grids of tiny, regular, quadratic cells (20-30 μm).

Stratigraphic distribution and range: See the genus.

Genus *Pseudokomia* Rácz 1966a

Pseudokomia cansecoensis Rácz 1966a

Fig. 14 a-d

1966a *Pseudokomia cansecoensis* Rácz, OD; 90-91, pl. 9, figs. 5-6; pl. 10, figs. 1-3.

1987 *Pseudokomia cansecoensis* Rácz; Mamet *et al.*, 51, pl. 25, fig. 5.

2003 *Komia* sp.; Della Porta, fig. 3.4. J, pl. 6.2.10.

Description: Thallus grossly cylindrical, up to one millimeter in diameter, unbranched, with strong hypo/perithallic differentiation. Perithallus composed of concentric rows of small (15-20 μm) subquadratic cells. Hypothallic cells numerous forming filaments 15-30 μm thick.

Stratigraphic distribution and range: This uncommon alga is known from the Moscovian of the Arctic Realm (*Uraloporella*

flora). The same age was originally reported by Rácz and observed in our material, which comes from the upper Moscovian of the Las Llacerias section (samples BM-18, BM-19, upper part of the Picos de Europa Formation, upper Myachkovian).

Genus *Stacheia* Brady 1876

Stacheia marginuloides Brady 1876

Fig. 14 i

For 7 taxonomic references to the taxon, see Mamet *et al.* (1987: 45), and add:

1983 *Stacheia marginuloides* Brady; Berchenko, pl. 82, fig. 5.

1986 ?*Stacheia marginuloides* Brady; Skompski, 270, pl. 14, fig. 1.

1992 *Stacheia marginuloides* (*pars*) Brady; Vachard and Berkhli, pl. 4, fig. 17 (only).

1995 *Stacheia marginuloides* Brady; Sanchez-Chico *et al.*, 75, pl. 6, fig. 1.

2002 *Stacheia marginuloides* Brady; Mamet, pl. 6, fig. 8.

Description: Thallus fusiform, with a central axis. Succession of strongly calcified arched laminae (40-60 μm in height). Lateral wall of cells quite thin (5-10 μm). Cells quadratic to subquadratic in vertical section.

Stratigraphic distribution and range: Cosmopolitan and very common from Visean to Serpukhovian. Extends into the Moscovian in the Arctic Realm and is rarely observed at that level in NW Spain. Present material was collected from the upper part of the Picos de Europa Formation at Las Llacerias section (sample BM-13, upper Moscovian, Myachkovian).

Genus *Ungdarella* Kordé 1951

Ungdarella uralica Maslov 1956 (*non* 1950)

Fig. 14 j

For taxonomy, see 20 references in Mamet *et al.* (1987: 52), and add:

1979 (*non*) *Ungdarella uralica* Maslov; Bensaid *et al.*, pl. 16, fig. 4.

1980 *Ungdarella uralica* Maslov; Buchroithner *et al.*, 26, pl. 26, fig. 1.

1981 *Ungdarella* ex.gr. *uralica* Maslov; Vachard and Montecat, 65-66, pl. 11, figs. 1, 13.

1985 *Ungdarella uralica* Maslov; Mamet and Pinard, pl. 3, fig. 1.

1986a *Ungdarella uralica* Maslov; Nguyen, pl. 10, fig. 1.

1986b *Ungdarella uralica* Maslov; Nguyen, 138, pl. 15, figs. 7-8.

1988 *Ungdarella uralica* Maslov; Flügel and Kahler, 145, pl. 20, fig. 9.

1988 *Ungdarella uralica* Maslov; Fontaine and Suteethorn, pl. 77, fig. 8.

1989 *Ungdarella* ex.gr. *uralica* Maslov; Köylüoğlu and Altiner, pl. 1, fig. 10.

1990 *Ungdarella uralica* Maslov; Flügel, pl. 3, fig. 5.

- 1990 *Ungdarella uralica* Maslov; Sebbar, pl. 1, fig. 3.
 1990 *Ungdarella uralica* Maslov; Bogush *et al.*, 124, pl. 24, figs. 1-2; pl. 25, figs. 1-5.
 1991 *Ungdarella uralica* Maslov; Riding, pl. 3, fig. R.
 1992 *Ungdarella uralica* Maslov; Vachard and Berkhli, pl. 1, fig. 21; pl. 3, figs. 13-14.
 1995 (*non*) *Ungdarella uralica* Maslov; Pajic and Filipovic, pl. 50, fig. 2.
 1996 *Ungdarella uralica* Maslov; Proust *et al.*, pl. 1, figs. 2-3; pl. 2, figs. 10-11.
 1996 *Ungdarella uralica* Maslov; Sebbar and Mamet, pl. 3, fig. 9.
 1998 *Ungdarella uralica* Maslov; Sebbar, pl. 2, fig. 6.
 2000 *Ungdarella uralica* Maslov; Mamet and Stemmerik, fig. 7, A-D.
 2001 *Ungdarella uralica* Maslov; Vachard and Krainer, pl. 5, fig. 8.
 2001 *Ungdarella* sp.; Minwegen, pl. 6, fig. 6.
 2002 *Ungdarella uralica* Maslov; Mamet, pl. 6, fig. 2.
 2003 *Ungdarella uralica* Maslov; Khodjanyazova and Mamet, pl. 5, figs. 6-7.
 2003 *Ungdarella* sp.; Della Porta, fig. 4.5.A; pl. 4.1, figs. 6, 8; pl. 4.2, figs. 1, 3, 6-8.

Description: Thallus grossly cylindrical, elongated, sometimes dichotomous. Diameter reaches one millimeter. Hypothallic single (sometimes two) row(s) of quadratic cells. They are twice the size of the surrounding cells. Multiple rows of 15-25 μ m perithallic cells. Filaments at 10°-20° angle from the hypothallus. Extensive calcification makes hazardous the estimation of cell thickness.

Note: Ungdarellae are difficult to identify (*Ungdarella* Kordé 1951, *non* Maslov 1950, *Komia*, *Pseudokomia* Rác 1966, *Chegatella* Poncet 1989, *Ungdarellina* Mamet 2002 and *Pecharella nom.nud.*) If the genera represent genuine morphological differences, they are often obscured by diagenesis. Ungdarellids are strongly calcified, hence robust carbonate stabilizers.

Stratigraphic distribution and range: A common cosmopolitan alga (Mamet, 1992) that appears in Late Viséan and is omnipresent in Bashkirian-Moscovian boundstones. It peters out in higher horizons. Observed in Spain in the upper part of the Picos de Europa Formation (sample BM-17, upper Myachkovian) at Las Llacerias section.

Genus *Ungdarellita* n. gen.

Type species: *Ungdarellita articulata* n. gen., n. sp.

Origin of name: From the relation with *Ungdarella*.

Diagnosis: A segmented articulated Ungdarellaceae with regular rectangular perithallic cells.

Description: Thallus composed of a series of annular to barrel-shaped segments growing in different directions, but with an elongated pattern of growth direction (Fig. 6). Each segment composed of a central hypothallic stem and a bundle of peripheral perithallic rectangular cells with oblique insertion. See idealized reconstruction, figure 6.

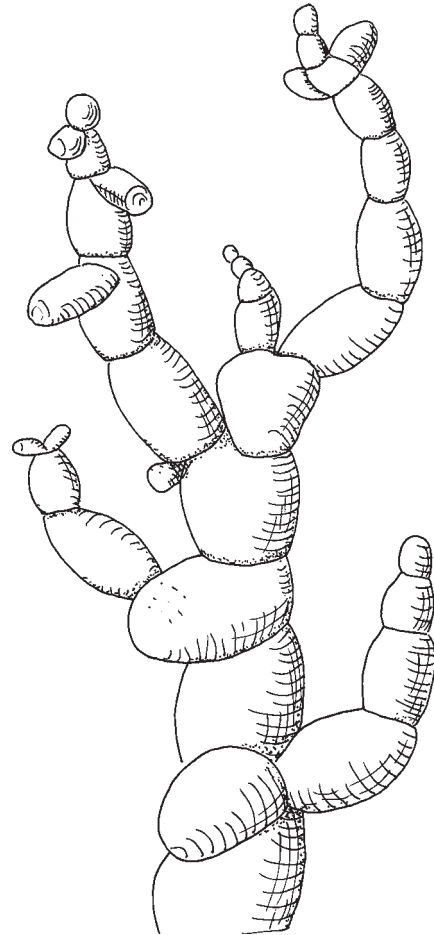


Figure 6. Idealized reconstruction of the morphology of *Ungdarellita* n. gen. Length of thallus around 2 mm.

Comparison: All previously described Ungdarellaceae (*Ungdarella*, *Chegatella*) have rather continuous rarely branched thalli. The new genus is articulated.

Stratigraphic distribution and range: Observed in a boundstone, Late Moscovian, Las Llacerias section. The type is derived from an Ungdarellid-beresellid-spongiostromid pellet bafflestone associated with sponges and chains of fenestellid bryozoans. It is associated with *Anchicodium*, *Anthracoporella*, *Beresella*, *Donezella*, *Eugonophyllum*, *Komia*, *Stacheia*, *Tubiphytes* and *Zaporella*. Foraminifers are: Apterrinellids, *Bradyina*, *Bradyinelloides*, *Climacammina*, *Endothyra*, *Eolasiodiscus*, *Ozawainella*, *Pseudobradyina*, *Syzrania* and *Tetrataxis*. Studied from the upper part of the Picos de Europa Formation, sample BM-16, upper Moscovian (Myachkovian), Las Llacerias section.

Ungdarellita articulata n. gen., n. sp.

Fig. 14 g-h

Origin of name: From its articulated stem.

Holotype: Figure 14 g. Repository number: U. of M. 815/17

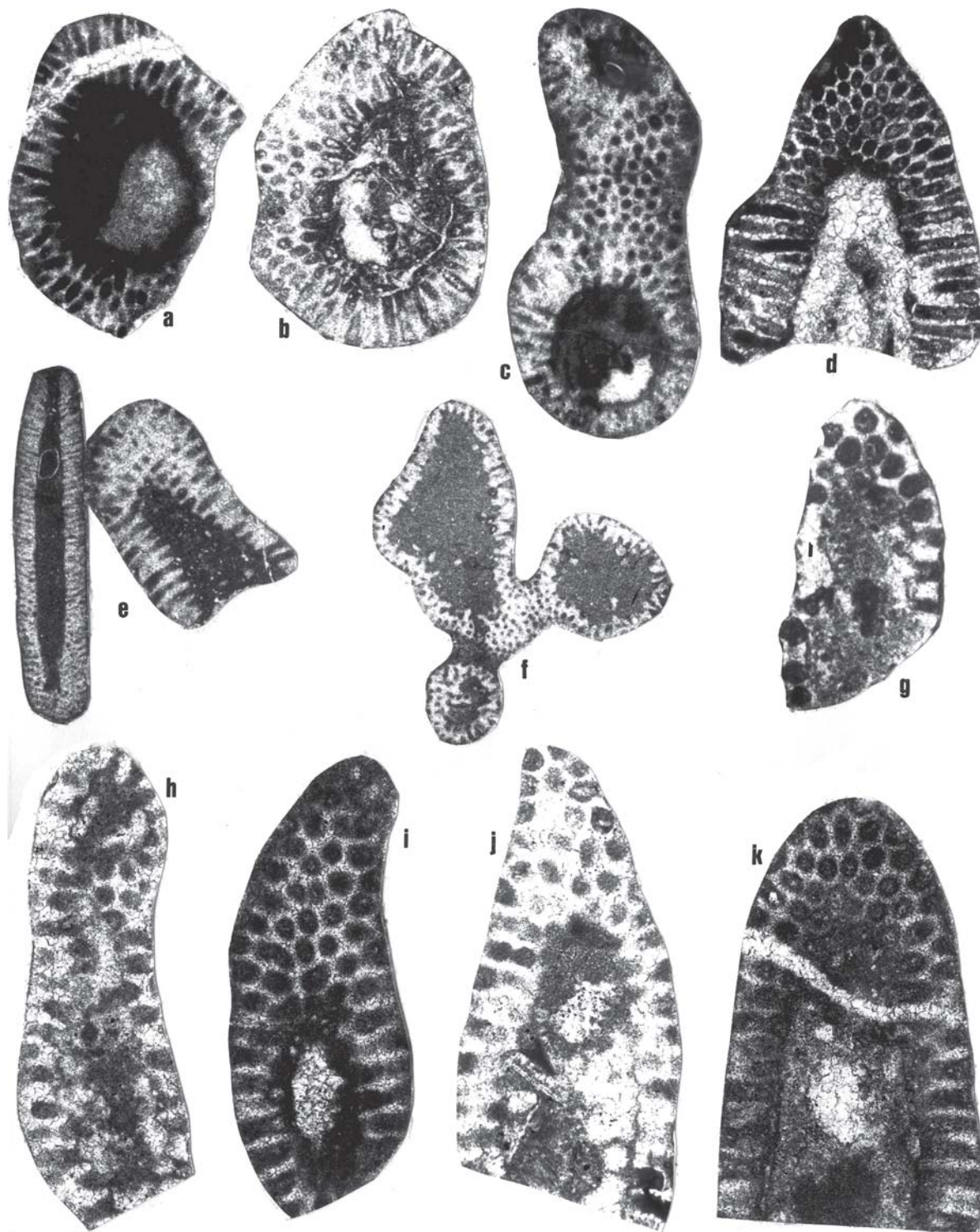


Figure 7. **a-d**, *Anthracoporella spectabilis* Pia 1920; **a**, U. of M. 728/8, BM-52, x30; **b**, U. of M. 816/0, BM-12, x30; **c**, U. of M. 728/25, BM-76, x30; **d**, U. of M. 814/24, BM-72, x41. **e**, *Anatolipora cantabriensis* n. sp., associated with *Anthracoporella spectabilis* Pia 1920; U. of M. 823/13, BM-11, x30, longitudinal section, holotype. **f**, *Anthracoporella* sp. U. of M. 815/2, BM-76, x26. **g**, *Macroporella ginkeli* Rácz 1966. U. of M. 728/16, BM-63, x30. **h-k**, *Zaporella cantabriensis* Rácz 1966; **h**, U. of M. 814/9, BM-72, x62; **i**, U. of M. 816/4, BM-11, x62; **j**, U. of M. 814/7, BM-72, x62; **k**, U. of M. 816/9, BM-11, x62. All from the Las Llacerias section.

Diagnosis: See the genus.

Description: Thallus plurimillimetric (2mm or more) composed of 20-30 (up to 45) barrel-shaped segments. At the base they have a diameter of 200-300 μm , for a length of 350 μm . They progressively diminish in size to reach 50-100 μm (or less) and a length of 100-180 μm . Each segment composed of a central stem with coarse hypothallic threads surrounded by a small number of perithallic cells disposed at 20° from the stem. There are 18-20 rows of rectangular cells in the basal segments and only half that number in the terminal segments. Rectangular cells are 20 μm wide and 40-60 μm long.

Stratigraphic distribution and range: See the genus.

INCERTAE SEDIS

Genus *Berestovia* Berchenko 1982 (*non* Berchenko 1983)

Berestovia filaris Berchenko 1982 (*non* 1983)

Fig. 14 n-o

- 1982 *Berestovia filaris* Berchenko, OD; 53-54, pl. 12, figs. 1-4.
 1983 (*non*) *Berestovia filaris* Berchenko; Berchenko, 128, pl. 84, fig. 2; pl. 86, figs. 5-6; pl. 87, fig. 1.
 1986 *Claracrusta catenoides* (Homann); Poncet, 192, pl. 3, fig. 5.
 1997 *Berestovia filaris* Berchenko; Harris *et al.*, pl. 9, fig. 12.

Description: Encrusting, wavy, irregular, thread-like rows of contiguous cells. Rows about 40-60 μm thick, containing interconnected cells.

Note: There is confusion in the literature as the original description of the genus by Berchenko (1982) is different from the subsequent description of 1983 that is to be referred to Vachard's *Claracrusta* 1981. Both genera have similar encrusting habits.

Stratigraphic distribution and range: Widespread, cosmopolitan (Eurasia-Arctic-North America. Serpukhovian to Kasimovian. It has been recorded in Spain from the Moscovian/Kasimovian transition at the Las Llacerias section (Picos de Europa Formation, sample BM-40), and from the lower Gzhelian at the Berodia-I section (upper member of the Puentellés Formation, sample BM-103).

Genus *Claracrusta* Vachard 1981

Claracrusta catenoides (Homann 1972)

Fig. 14 k-m, Fig. 15 o

- 1972 *Girvanella catenoides* Homann, OD; 237-241, pl. 8, fig. 59 a-c.
 1980 *Girvanella catenoides* Homann; Flügel, pl. 9, figs. 2-5.
 1981 *Claracrusta catenoides* (Homann); Vachard, 392-393, pl. 3, fig. 1?; pl. 7, fig. 5?; pl. 25, fig. 1?; pl. 26, figs. 1-3.
 1981 *Claracrusta catenoides* (Homann); Vachard and Montenat, 57-58, pl. 1, fig. 1; pl. 8, figs. 8, 10-11; pl. 9, fig. 1; pl. 12, fig. 10.
 1983 *Berestovia filaris* Berchenko; Berchenko, 128, pl. 86, figs. 5-6; pl. 87, fig. 1.

- 1984 *Iberiaella carbonica* Rácz, 338, fig. 3, a-f.
 1986 (*non*) *Claracrusta catenoides* (Homann); Poncet, 192, pl. 3, fig. 5.
 1990 *Claracrusta catenoides* (Homann); Flügel, pl. 1, fig. 4.
 1990 (?) *Claracrusta catenoides* (Homann); Bogush *et al.*, 84, pl. 5, fig. 10.
 1991 *Claracrusta* sp.; Legrand-Blain and Poncet, 776, pl. 2, figs. 3-4.
 1992 "Osagia" - Filaments encrusting *Kansaphyllum*; Baars, figs. 2-4.
 1993 *Claracrusta catenoides* (Homann); Vachard *et al.*, pl. 2, fig. 5.
 1995 *Claracrusta catenoides* (Homann)(*pars*); Forke, pl. 17, fig. 5; (*non*) pl. 15, fig. 7.
 1996 *Claracrusta catenoides* (Homann); Mamet, pl. 2, figs. 8-14; pl. 3, figs. 6-7.
 1996 *Claracrusta catenoides* (Homann); Sebbar and Mamet, pl. 1, figs. 4-5.
 1996 (?) *Claracrusta catenoides* (Homann); Vachard and Maslo, 369, pl. 1, fig. 1?.
 2001 (*non*) *Claracrusta catenoides* (Homann); Vachard and Krainer, pl. 5, fig. 8.
 2001 *Iberiaella* sp.; Minwegen pl. 5, fig. 5.
 2003 *Claracrusta catenoides* (Homann); Khodjanyazova and Mamet, pl. 5, figs. 8-9.

Description: Encrusting, thread-like rows of irregular cells, around 60-80 μm in height. Base of rows is planar, while the top is wavy. Cells reported in the literature as tubular, but they are apparently circular-subquadratic (50-60 μm). Dimensions difficult to estimate due to calcification. Wall yellowish, Fe-rich calcite.

Stratigraphic distribution and range: *Claracrusta* is a very common component of the *Otonosia-Osagia* oncolitic structures. Apparently world-wide. Serpukhovian? to Early Permian. In NW Spain, very abundant in association with *Donezella* in Bashkirian-Moscovian strata. Illustrated here from the Kasimovian of Las Llacerias section (samples BM-76, BM-77B, uppermost part of the Las Llacerias Fm, upper Khamovnikian), and the Pen section (sample BM-78, Pen Limestone, Kreviakian).

Genus *Ellesmerella* Mamet, Roux and Nassichuk 1987

Ellesmerella permica (Pia 1937)

Fig. 15 p

- 1937 *Girvanella permica* Pia, OD; 816, 820, pl. 9, fig. 1.
 1963 *Girvanella permica* Pia; Johnson, pl. 78, fig. 3.
 1963 *Girvanella permica* Pia; H. Flügel, 91-92, pl. 22, fig. 5
 1966 *Girvanella permica* Pia; E. Flügel, 45-51, pl. 8, figs. 4-5.
 1972 *Girvanella permica* Pia; Homann, 243-324, pl. 8, fig. 61; pl. 9, fig. 65
 1981 *Girvanella permica* Pia; Vachard, 323, pl. 7, fig. 4.
 1983 *Girvanella permica* Pia; Jenny-Deshusses, 160, pl. 16, fig. 1; pl. 24, fig. 2.
 1987 *Ellesmerella permica* (Pia); Mamet, Roux and Nassichuk, 15-16, pl. 3, figs. 9-11.

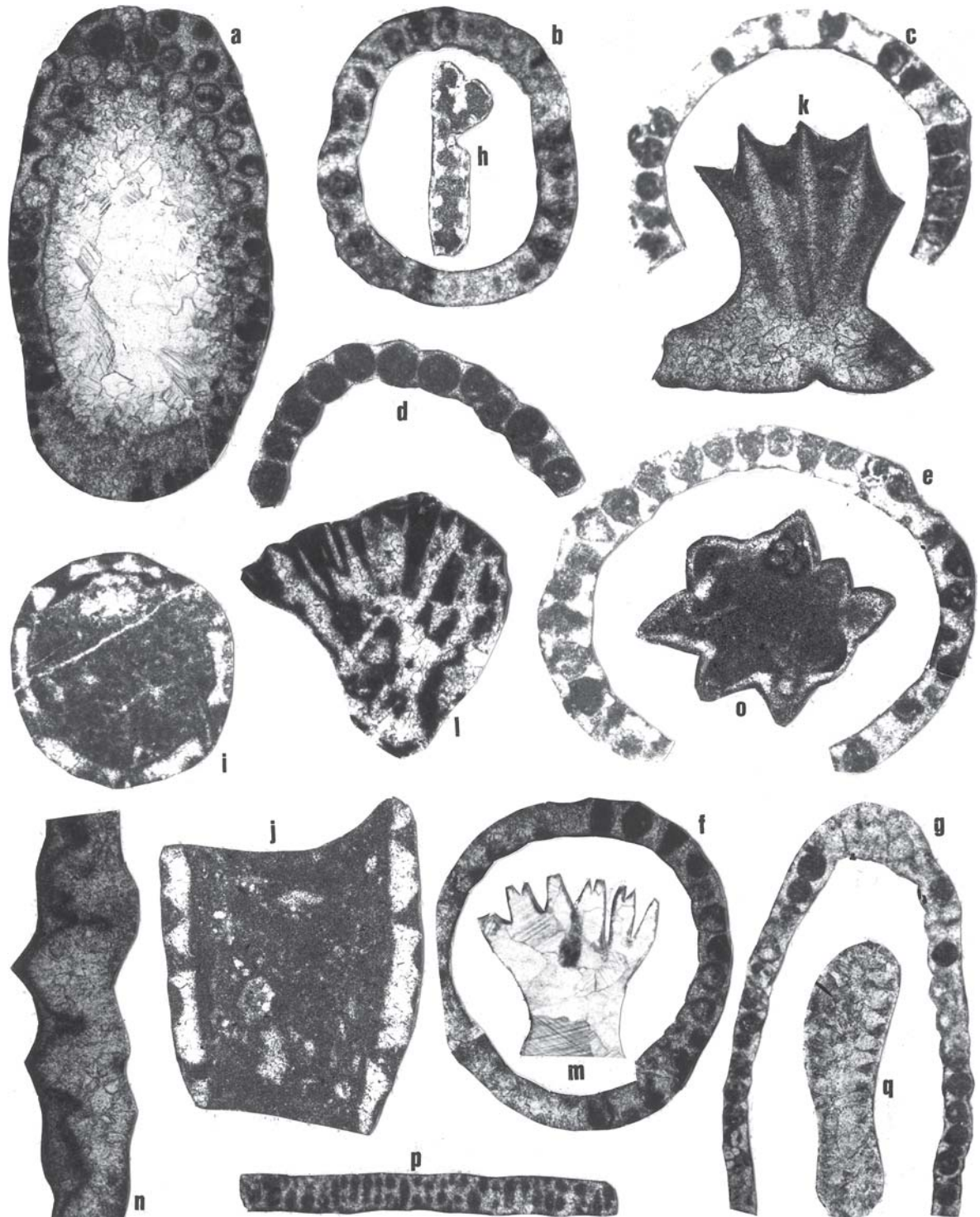


Figure 8. a-g, *Gyroporella? prisca* Kochansky-Devidé 1970; a, U. of M. 815/19-20, BM-46, x26. b, U. of M. 810/16, as a. c, U. of M. 810/17, as a. d, U. of M. 810/8, BM-39, x41; e, U. of M. 810/13-14, as a; f, U. of M. 815/21, as a; g, U. of M. 810/7, BM-38, x26. h, *Palaeoberesella lahuseni* (von Möller 1879); U. of M. 813/17, P21-39, x62. i-j, *Pseudovelebitella simplex* (Kochansky-Devidé 1970); i, U. of M. 833/37, BM-46, x41; j, U. of M. 816/13, BM-14, x62. k, m, *Clavaporella reinae* Rác 1966; k, U. of M. 833/12, BM-28, x62; m, U. of M. 728/17, BM-72, x30. l, Dissolved Albertaporelleae; U. of M. 814/19, BM-74, x41. n, *Gyroporella dissecta* (Chuvashov 1974); U. of M. 833/4, BM-46, x62. o, «*Pseudogyroporella*» *annulata* Ishizima, Ozaki and Nakamura 1971; U. of M. 728/15, BM-63, x62. p, *Epimastopora symetrica* (Johnson 1951); U. of M. 818/17, BM-123, x30. q, *Dvinella comata* Khovorova 1949; U. of M. 727/13, Las Llacerias section, BM-18, x61. All from the Las Llacerias section, except P-21 (Sierra Corisa), and BM-123 (Berodia-II section).

- 1995 *Girvanella permica* Pia; Partoazar, pl. 1, fig. 1; pl. 6, fig. 13; pl. 8, fig. 11.
 2000 *Ellesmerella* sp.; Mamet and Stemmerik, pl. 3, B.
 2001 *Ellesmerella permica* (Pia); Vachard and Krainer, 190, pl. 3, figs. 1-4.
 2003 *Ellesmerella permica* (Pia); Khodjanyazova and Mamet, pl. 5, fig. 13.

Description: Oncolitic encrustation, composed of subhorizontal files of continuous, unsegmented irregular tubes. Height of tubes variable, 10 to 40 μm . Micritized wall, 10-20 μm .

Stratigraphic distribution and range: Widespread in Eurasia-Arctic. Up to now, observed only in the Permian (see Vachard and Krainer, 2001). The Spanish material extends this range slightly lower in the Kasimovian; it has been recorded from the uppermost part of the Picos de Europa Formation at Las Llaceras section (sample BM-52, lower Kasimovian, Krevianinian).

Genus *Tubiphytes* Maslov 1956

Tubiphytes obscurus Maslov 1956

Fig. 15 a, l-m

To the 29 references reported by Homann (1972) and 26 references in Senowbari-Daryan and Flügel (1993), update the list by adding:

- 1989 *Tubiphytes obscurus* Maslov; Köyliüoglu and Altiner, pl. 1, fig. 12.
 1989 *Tubiphytes obscurus* Maslov; Razgallah *et al.*, pl. 1, fig. D.
 1991 *Tubiphytes obscurus* Maslov (*pars*); Vachard and Ferrière, pl. 1, fig. 1, (non) 4.
 1993 *Tubiphytes obscurus* Maslov (*pars*); Vachard and Clift, pl. 3, fig. 1-3, 6, (non) 4.
 1993 *Shamovella obscura* (Maslov); Riding, p. 72.
 1993 *Tubiphytes obscurus* Maslov; Chuvashov *et al.*, pl. 14, figs. 2-5.
 1993 (*non*) *Tubiphytes obscurus* Maslov; Vachard *et al.*, pl. 3, figs. 1-2.
 1993 *Tubiphytes obscurus* Maslov; Vachard, pl. 8, fig. 17.
 1995 *Tubiphytes obscurus* Maslov; Forke, pl. 15, fig. 9.
 1995 *Tubiphytes obscurus* Maslov; Pajic and Filipovic, pl. 50, fig. 10.
 1996 *Tubiphytes obscurus* Maslov; Sano and Kanmera, pl. 59, figs. 1-2; pl. 61, fig. 1-2?
 1997 *Tubiphytes obscurus* Maslov; Vachard and Fourcade, pl. 12, fig. 1.
 1999 *Tubiphytes obscurus* Maslov; Weidlich and Fagerstrom, fig. 5, E-G, fig. 6, F, fig. 8, B-D.
 2000 *Tubiphytes obscurus* Maslov; Mamet and Stemmerik, fig. 9, H-J.
 2001 *Tubiphytes obscurus* Maslov; Vachard and Krainer, pl. 1, fig. 2.
 2001b *Tubiphytes obscurus* Maslov; Vachard *et al.*, pl. 3, figs. 2-3.
 2001 *Tubiphytes* sp.; Minwegen, pl. 10, fig. 6; pl. 16, figs. 6-7.
 2002 *Tubiphytes* sp.; Vennin *et al.*, 2002, Fig. 5, E-H, Fig. 6, C.

- 2002 *Tubiphytes* sp.; Wahlman and Konovalova, fig. 7 A-B, fig. 8 A, fig. 9 B-E, fig. 11 A-D, fig. 12 A-D, fig. 13 A, C, E, fig. 14 E, fig. 15 C, fig. 16 A.
 2003 *Tubiphytes obscurus* Maslov; Khodjanyazova and Mamet, pl. 5, fig. 10.

Description: Crustose, erect, cellular micritic organism, encrusting various supports (the most common being sponge spicules). When the support is segmented, growth bands are present. Microfabric composed by a reticular network of very small cells, usually obscured by micritization (hence the dark aspect, origin of the *obscurus* taxon).

Note: Little has been added by the numerous (137!) contributions to the original straight-forward description of Maslov (1956): "This is an encrusting (epiphyte) organism, that forms dark calcite bands around other organisms" (translated). While the genus is also reported from the Mesozoic, there are significant ultrastructure differences and the Maslov taxon is probably restricted to the Paleozoic.

Taxonomic note: It seems appropriate to attempt to bring here some light to the origin of *Tubiphytes* (= *Shamovella*). This *microproblematicum* has been the subject of numerous hypothesis that are summarized in Senowbari-Daryan and Flügel, 1993. The controversial taxon is indeed abundant in Late Paleozoic time and omnipresent in Carboniferous-Permian bioconstructions. Its ultrastructure is observed (*Tubiphytes obscurus*!) by intense micritization.

Tubiphytes encrusts various organisms such as foraminifers, sponges, bryozoans, phaeophytes, and has been erroneously attributed to various phyla.

An exceptionally well-preserved sample from the Permian Cache Creek is here illustrated in figure 14 a. Although derived from a very distant locality, it shed some light on our Spanish material. Associated with "normal" *Tubiphytes* encrustations, some of the thalli have well-preserved cellular files that strikingly resemble those of *Ungdarella-Komia*. Ungdarellaceae however develop strong sparitic encrustations, while *Tubiphytes* is highly micritized.

If our hypothesis is correct, *Tubiphytes* is related to encrusting red algae. This fits the known wide bathymetric distribution of this baffler-guild. *Tubiphytes* is abundant in the upper euphotic zone associated with bacteria, in the lower euphotic zone attached to dasycladales or to phylloids, and in the dysphotic zone with *Archaeolithophyllum*. It reaches the dysphotic/aphotic boundary, as could be anticipated from a rhodophyte.

Stratigraphic distribution and range: An important cosmopolitan microproblematic often associated in mounds with *Archaeolithoporella* and epimastoporids (Razgallah and Vachard, 1991). Abundant from the Moscovian to the Late Permian. Our Asturian illustrated material comes from the upper part of the Las Llaceras Formation at Las Llaceras section (sample BM-76B, Kasimovian, upper Khamovnikian) and the upper member of the Puentellés Formation at Berodia-II section (sample BM-122, probably lower Gzhelian).

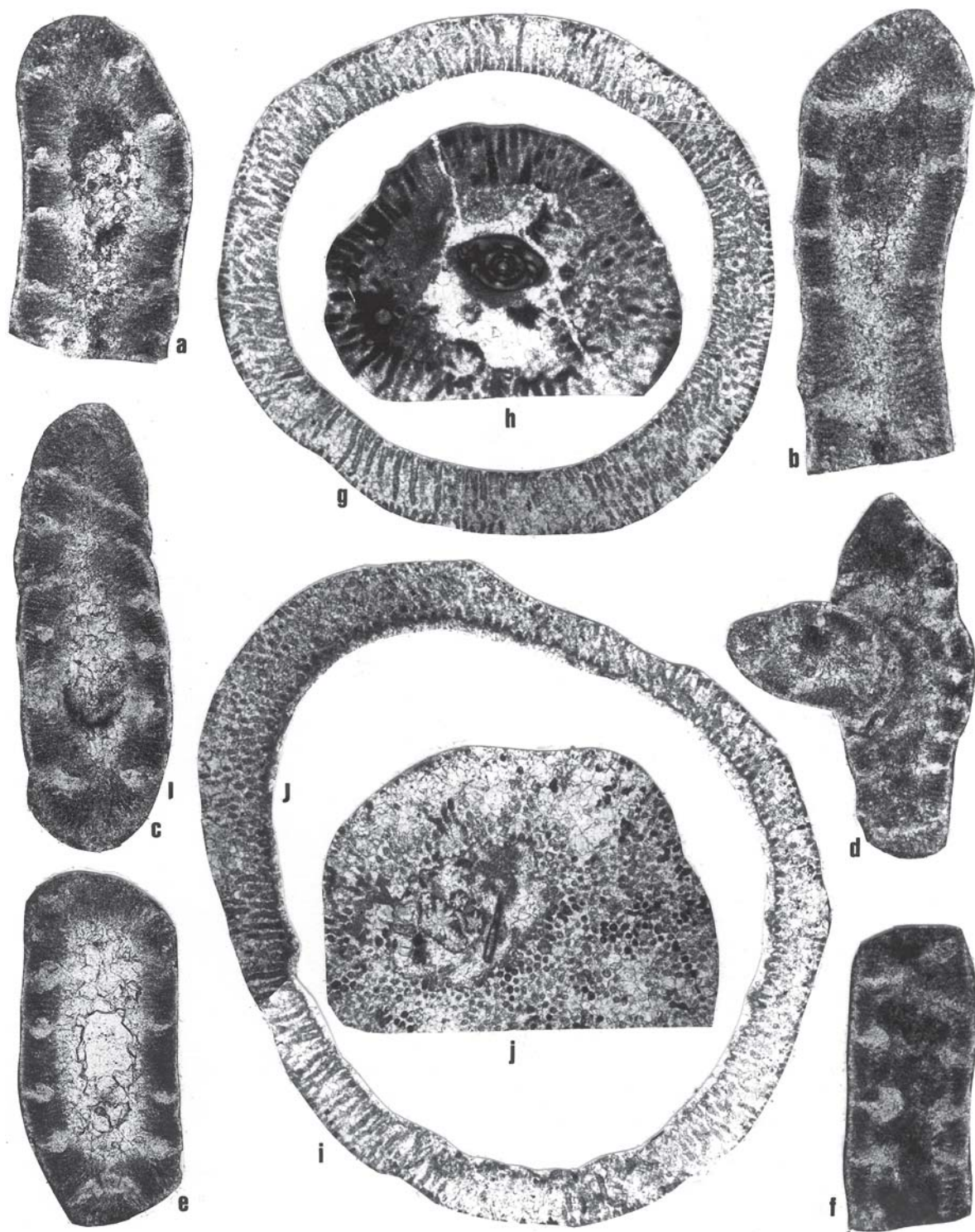


Figure 9. a-f, *Beresella herminae* Rácz 1966; a, U. of M. 809/12, BM-16, x78, with normal «dark bands» and «egg-shaped white bands»; b, U. of M. 809/9, as a, but x97; c, U. of M. 809/10, as a, with abnormally curved «egg-shaped white bands»; d, U. of M. 809/13, as a, with thallus dichotomy; e, U. of M. 809/1, as a, with «egg-shaped white bands»; f, U. of M. 809/7, BM-12, x97, with remnants of parietal conceptacles inside the medulla. g-j, *Anthracoporella vicina* Kochansky and Herak 1960; g, U. of M. 816/16-18, BM-72, x26; h, U. of M. 728/7, BM-52, x26; an axial section of *Protriticites* sp. is present. i, U. of M. 814/12-15, as g; j, U. of M. 814/3, as g. All from the Las Llacerias section.

Genus *Penella* n. gen.

Type species: *Penella pongaensis* n.gen., n.sp.

Origin of name: From the hamlet of Pen.

Diagnosis: Cluster of sphaeroidal microproblematic.

Description: Sphere or coalescent cluster of spheres of various size. Wall micritic, imperforated.

Discussion: The wall of most *Penella* is usually dissolved and replaced by neomorphic cement. However, a few exceptionally well preserved walls show that it was originally densely micritic. In most cases, the original structure is destroyed and replaced by acicular cement or blocky sparite (compare figure 15 i, j, k and same figure a-h).

Although sponge spicules are often observed in association with *Penella*, they are not responsible of swarms of spheroidal microfossils. Moreover, *Penella* has a characteristic wall-structure unknown among calcareous sponges.

Comparison: *Penella* is somewhat similar to *Calcisphaera*, but calcispheres do not form interconnected clusters of spheres. *Penella* is also somewhat similar to the *incertae sedis Tuberitina* (and the Tuberitinidae), but does not have attachment disks. Moreover, tuberitinids form chains, while *Penella* form clusters that are random. A number of similar microproblematics that form swarms are known in the Devonian and Carboniferous. For instance *Bisphaera* Birina 1948, *Baculella* Conil and Dreesen 1985 and *Saccaminopsis* Sollas 1921 (“*Saccamina*-bands”, Brady, 1871). For a discussion on *Baculella*-*Saccaminopsis* see Poncet (1989) and Skompski (1993). The “*Bisphaera* beds” are common at the Devonian-Carboniferous transition of Russia. Similarly the Kasimovian beds of Asturias are riddled with enigmatic little spheres. They are associated with sponges (*in situ* sclerites) and algae (*Anthracoporella*, *Anthracoporellopsis*).

The type material of *Penella* at Pen is rich in foraminifers such as: Apterrinellidae, *Hemigordius*, *Pseudopalaespiroplectamina*, *Syzrania*, *Syzranella*, *Tetrataxis*. The microflora and *incertae sedis* are composed of *Clara-crusta*, *Cuneiphyucus*, *Ivanovia*, *Tubiphytes* and *Zaporella*.

Penella has recently been observed in the Carnic Alps, Austria. We used the material collected by E. Samankasou (see 2002). It is abundant in fine-grained matrix bafflestone associated with *Anthracoporella* and sponge spicules. The genus is abundant in the Kasimovian-Gzhelian Auernig Group and in the Gzhelian lower *Pseudoschwagerina* Limestone, Rattendorf Group.

Stratigraphic distribution and range: Up to now, recognized from the lower Kasimovian of the Pen section (Pen limestone,

samples BM-78, BM-79, BM-85), the upper Kasimovian of the Berodia-I section (Puentellés Formation, sample BM-98), and either the upper Kasimovian or the lower Gzhelian of the Inganzo locality (sample BM-251, Puentellés Formation).

Penella pongaensis n. gen., n. sp.

Fig. 15 b-k

2001 Spiculitic wackestone with monoaxons sponge spicules. Minwegen, pl. 13, figs. 7-8.

Origin of name: From the Ponga river valley, where the locality of Pen is situated.

Holotype: Figure 15 j (here designated). The rest of figure 15 (b-i, k) are paratypes.

Diagnosis: See the genus.

Description: Micritic sphere of group of 2, 3, up to 8 spheres that communicate with each other by means of an interruption in the wall. Average dimensions of the spheres 90-150 μm , some reaching up to 310 μm . Wall micritic, 12-20 μm . When dissolved, it is enlarged and reaches 30 μm . No known functional aperture. No attachment disk.

Stratigraphic distribution and age: See the genus.

REMARKS AND CONCLUSIONS

This report is uncomplete as it is based on a rather limited number of sections. For instance, we have not observed in our material common algal builders that have been previously illustrated in the region (e. g. *Renalcis* illustrated by Della Porta, 2003, fig. 4.4.1, or *Petschoria*, reported by Minwegen, 2001, pl. 7, fig. 1.2). However, in spite of its limitation, it is a badly needed taxonomic update. Since the early work of Rácz, much progress has been made in suprageneric classification. But if there is much advance to be achieved, the study of Paleozoic algae remains a fascinating aspect of paleobotany.

The majority of the microflora is composed of dasycladales, observed in the form of reworked broken thalli or in growth position. Not only are they abundant and diverse, but they form intertwined bafflestones and frames-tones within the upper part of the euphotic zone. Denezellids and beresellids thrive in boundstones coated by *Clara-crusta* and *Berestoria* but also in associated lagoons. Phylloids are fragile but can form frameworks that indicate early marine cementation and lithification (early bacterial infestation). Red algae are more resistant than their green counterparts, hence withstand higher energy in the rarefied light of deeper waters.

The flora is typically Western Paleotethyan and is similar to that of the Carnic Alps or Central Urals. The number

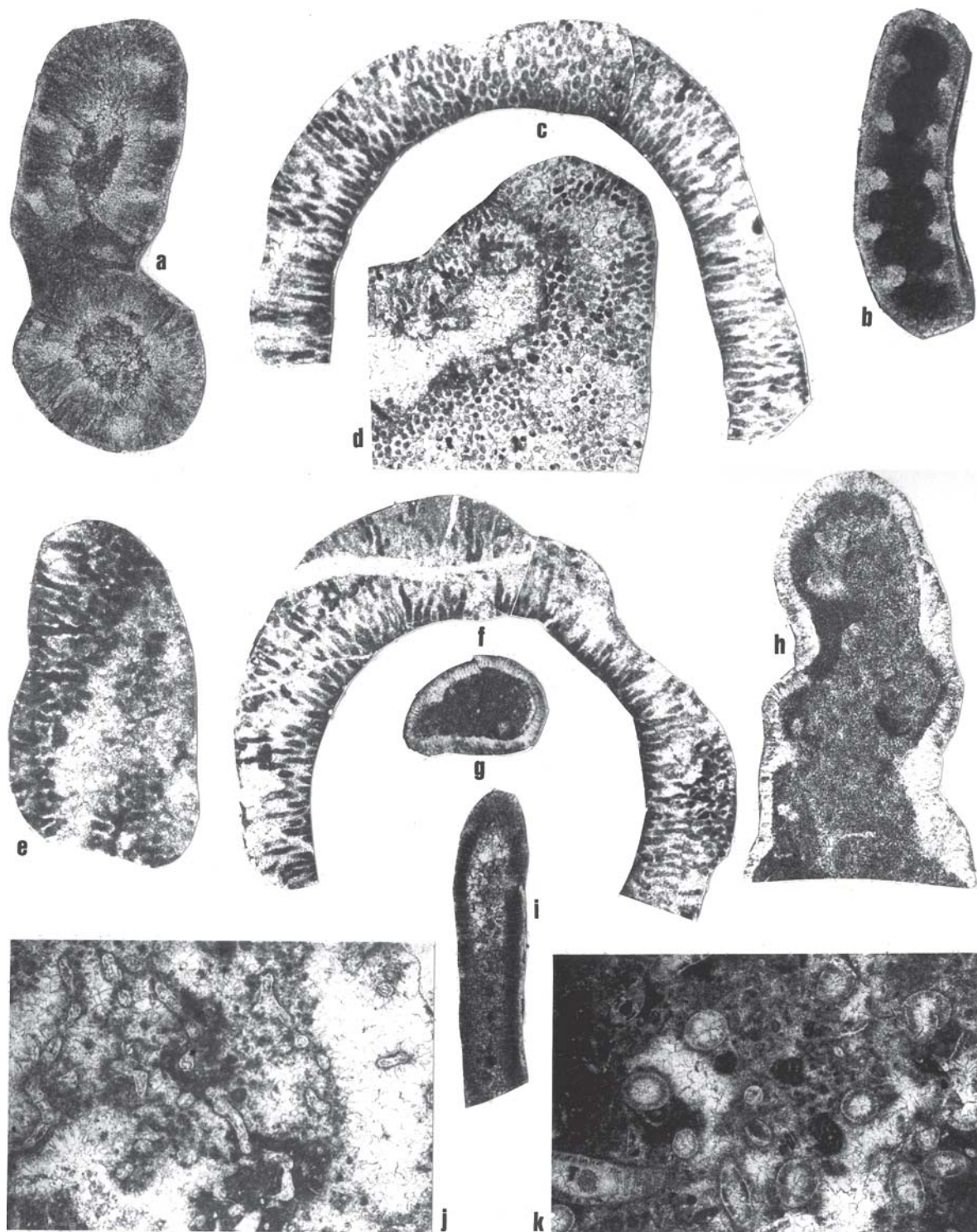


Figure 10. **a-b**, *Beresella herminae* Rácz 1966; **a**, U. of M. 815/16, BM-16, x62; **b**, U. of M. 809/6, BM-12, x97, with conceptacles simulating pseudoseptation; this *Beresella* could be confused with a *Palaeoberesellea*. **c-f**, *Anthracoporella vicina* Kochansky and Herak 1960; **c**, U. of M. 816/1-2, as b, but x26; **d**, U. of M. 814/4, BM-72, x26, epidermic section; **e**, U. of M. 814/0bis, as d, showing pore dichotomies; **f**, U. of M. 816/5-6, as b, but x26. **g-h**, *Anthracoporellopsis machaevii* Maslov 1956; **g**, U. of M. 816/10, as f, but x30, transverse section; **h**, U. of M. 807/17, BM-25, x62, longitudinal section with poorly developed pseudo-septation and extensively developed pore dichotomy. **i**, *Uraloporella variabilis* Korde 1950. U. of M. 820/22, BM-19, x62, longitudinal section. **j**, Bafflestone of *Donezella lutugini* Maslov 1929. U. of M. 833/15, BM-28, x26. **k**, Bafflestone of *Beresella herminae* Rácz 1966. U. of M. 810/3, BM-31, x26. All from the Las Llacerias section.

of endemic species is remarkably low. The close paleobiogeographic affinity of the Cantabrian Zone with the Carnic Alps confirms that observed for the brachiopods (Martinez Chacón and Winker-Prins, 1985) and the fusulinoids (Villa *et al.*, 2002).

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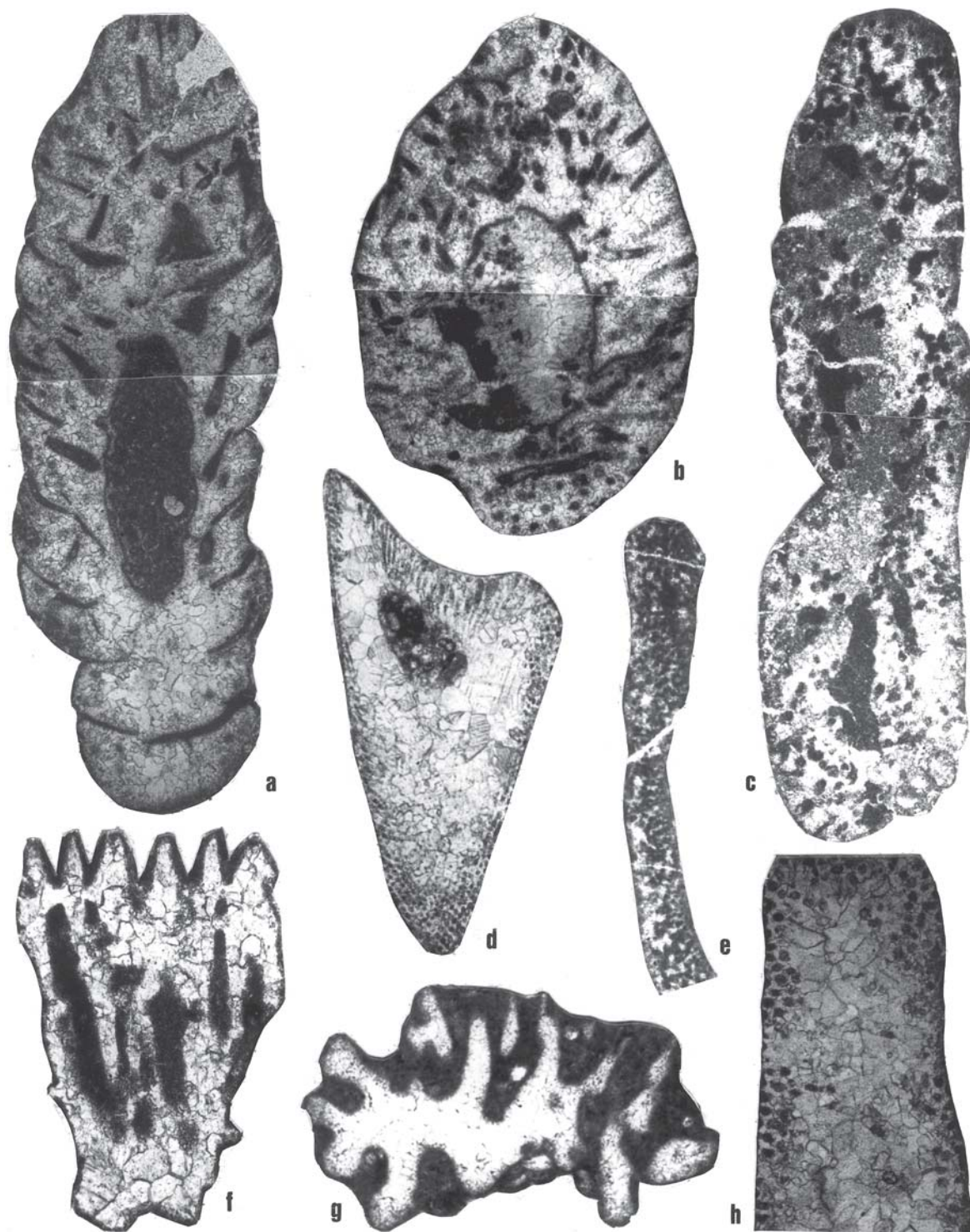


Figure 11. **a-b**, *Herakella paradoxa* Kochansky-Devidé 1970; **a**, U. of M. 833/13-14, BM-28, x26, longitudinal section; **b**, U. of M. 809/21-24, as **a**, oblique section. **c**, *Hikorocodium kuramotoi* Nakamura 1994. U. of M. 816/7-8, BM-12, x26, longitudinal section. **d**, *Pelayella multiporosa* n. gen., n. sp. U. of M. 728/22, BM-72, x30, oblique longitudinal section, holotype. **e**, *Anchicodium funile* Johnson 1948 *sensu* Torres and Baars 1992. U. of M. 833/8, as **c**. **f**, *Clavaporella reinae* Rác 1966. U. of M. 814/5, BM-72, x41. **g**, *Hikorocodium?* sp. U. of M. 728/24, BM-74B, x62. **h**, «*Vermiporella*» *hispanica* Rác 1966. U. of M. 818/3, BM-101, x26. All from the Las Llacerias section, except BM-101 (Berodia-I section).

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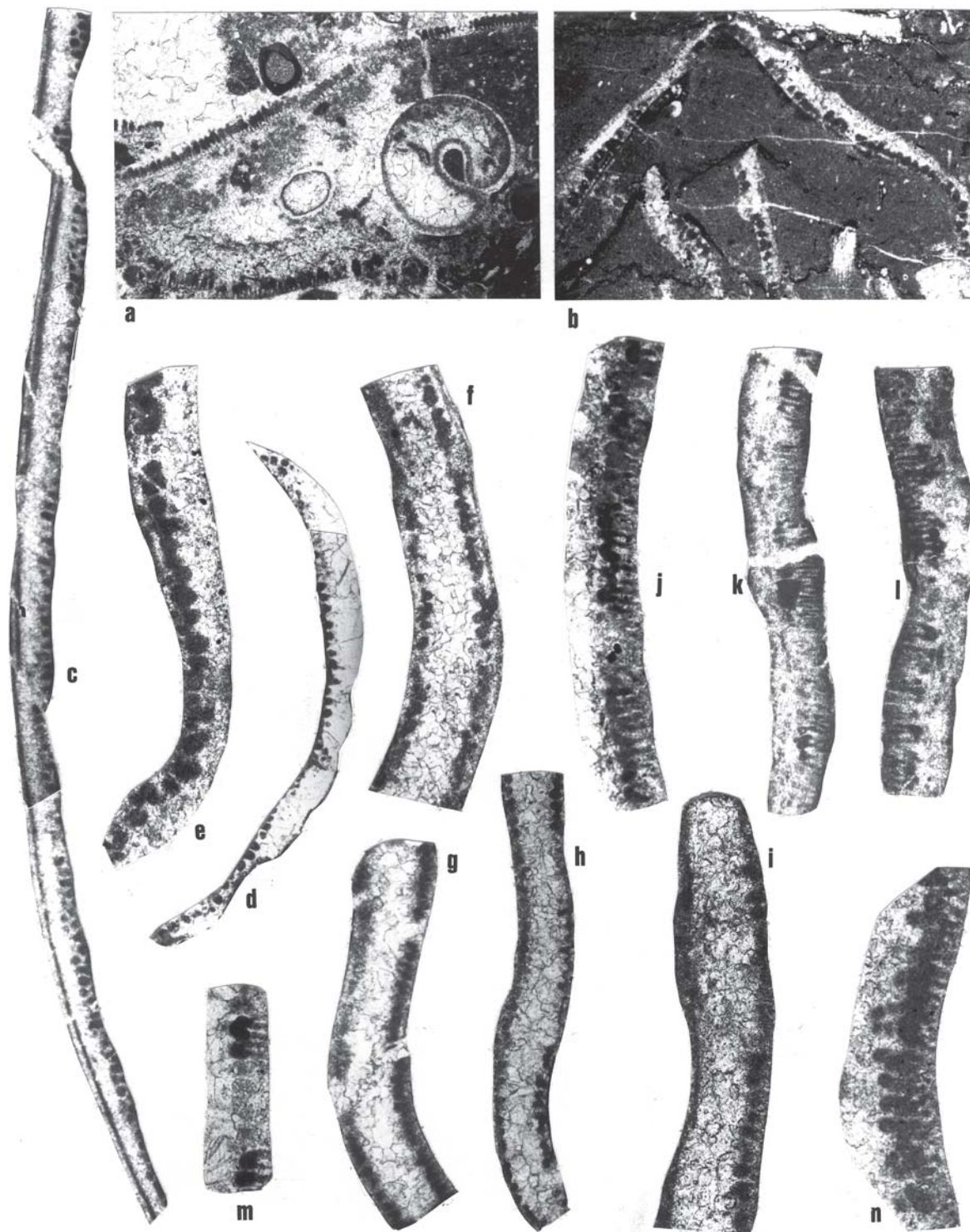


Figure 12. a, j-n, *Ivanovia tenuisima* Khvorova 1946; a, U. of M. 813/24, BM-72, x26. *Ivanovia* bafflestone with phylloid blades criss-crossing the sediment. Associated are bacterial pellets, a gastropod, *Tubiphytes*, *Syzrania*, and *in situ* sponge sclerites; j, U. of M. 728/21, BM-69, x62; k, U. of M. 813/23, BM-70, x30; l, U. of M. 813/22, as k; m, U. of M. 728/18, as a, but x62; n, U. of M. 728/3, BM-47, x62. b-e, *Eugonophyllum mulderi* Rácz 1966; b, U. of M. 827/14, BM-276, x26. *Eugonophyllum mulderi* bafflestone; scattered sessile foraminifers (one attached to the blade, obstructing the utricular packages), sponge sclerites, altered echinid spine; c, U. of M. 833/21-22, BM-47, x26; d, U. of M. 816/6-7, BM-105, x26; e, U. of M. 827/3, as b, but x62. f-i, *Eugonophyllum johnsoni* Konishi and Wray 1961; f, U. of M. 813/15, P-21, x30; g, U. of M. 833/18, BM-46, x30; h, U. of M. 813/12, as f; i, U. of M. 809/4, BM-12, x62. All from the Las Llacerias section, except BM-276 (Demués section), BM-105 (Berodia-I section), and P-21 (Sierra Corisa).

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Figure 13. **a-b**, *Kasimophyllum demuesensis* n. gen., n. sp.; **a**, U. of M. 827/9-11, BM-277, Demués section, x62, longitudinal section, enlargement of part of the holotype, with different nicol orientation; **b**, Same as a, x 26, holotype. **c-e**, *Archaeolithophyllum johnsoni* Rác 1966; **c**, U. of M. 825/3, BM-257, Inganzo, x26, longitudinal section; **d**, U. of M. 725/19-20, BM-72, Las Llacierias section, x26, longitudinal section with a fragment of *Hikorocodium*?; **e**, U. of M. 815/23, BM-11, Las Llacierias section, x26. **f-i**, *Archaeolithophyllum delicatum* Johnson 1956; **f**, U. of M. 814/6, as d, but x30, longitudinal section; **g**, U. of M. 825/14, as c, but x30, showing branches; **h**, U. of M. 818/20-21, BM-128, Berodia-II section, x26, longitudinal section; **i**, U. of M. 827/18, BM-281, Demués section, x26, with the perithallic cells.

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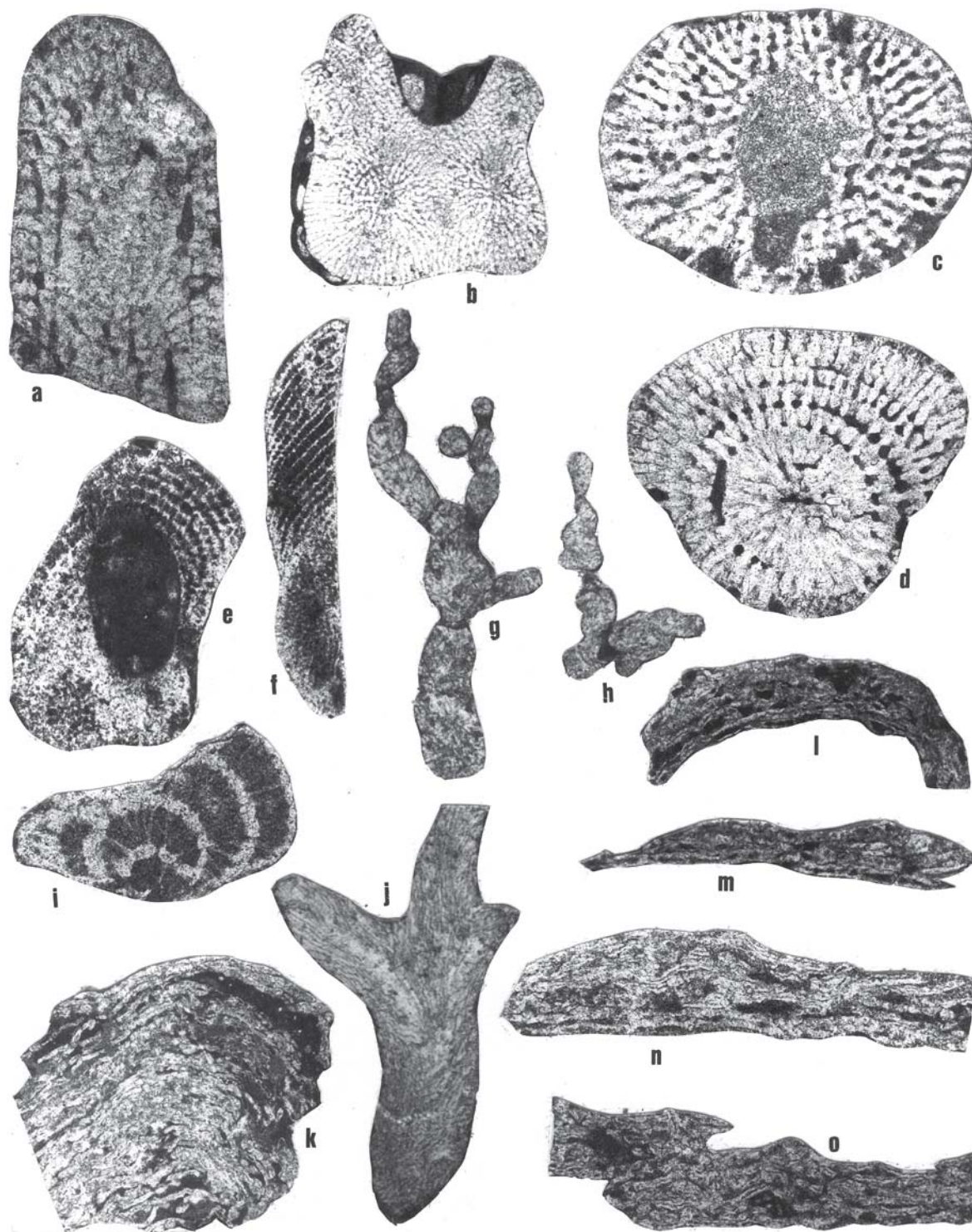


Figure 14. a-d, *Pseudokomia cansecoensis* Rácz 1966; a, U. of M. 820/17, BM-18, x62; b, U. of M. 822/18, BM-19, x26, encrusted by *Tubiphytes obscurus* Maslov 1956; c, U. of M. 822/10, as b, but x62, transverse section; d, U. of M. 822/9, as c, oblique transverse section. e, *Fourstonella fusiformis* (Brady 1876), U. of M. 814/10, BM-72, x62, oblique longitudinal section. f, «*Fourstonella*»(?) *johnsoni* (Flügel 1966) (= *Efluegelia*), U. of M. 728/29, BM-77B, x62, longitudinal section. g-h, *Ungdarellita articulata* n. gen., n. sp.; g, U. of M. 815/17, BM-16, x41, longitudinal section along growth axis, holotype; h, U. of M. 809/15, as g, but x30, oblique section, paratype; i, *Stacheia marginuloides* Brady 1876. U. of M. 809/8, BM-13, x97, longitudinal section; j, *Ungdarella uralica* Maslov 1956, U. of M. 819/10, BM-17, x30, longitudinal section. k-m, *Claracrusta catenoides* (Homann 1972); k, U. of M. 815/10, BM-78, x26; l, U. of M. 728/28, BM-77B, x62; m, U. of M. 728/26, BM-76, x62. n-o, *Berestovia filaris* (Berchenko 1982); n, U. of M. 810/10, BM-40, x62; o, U. of M. 818/4, BM-103, x62. All from the Las Llaceras section, except BM-78 (Pen section), and BM-103 (Berodia-I section).

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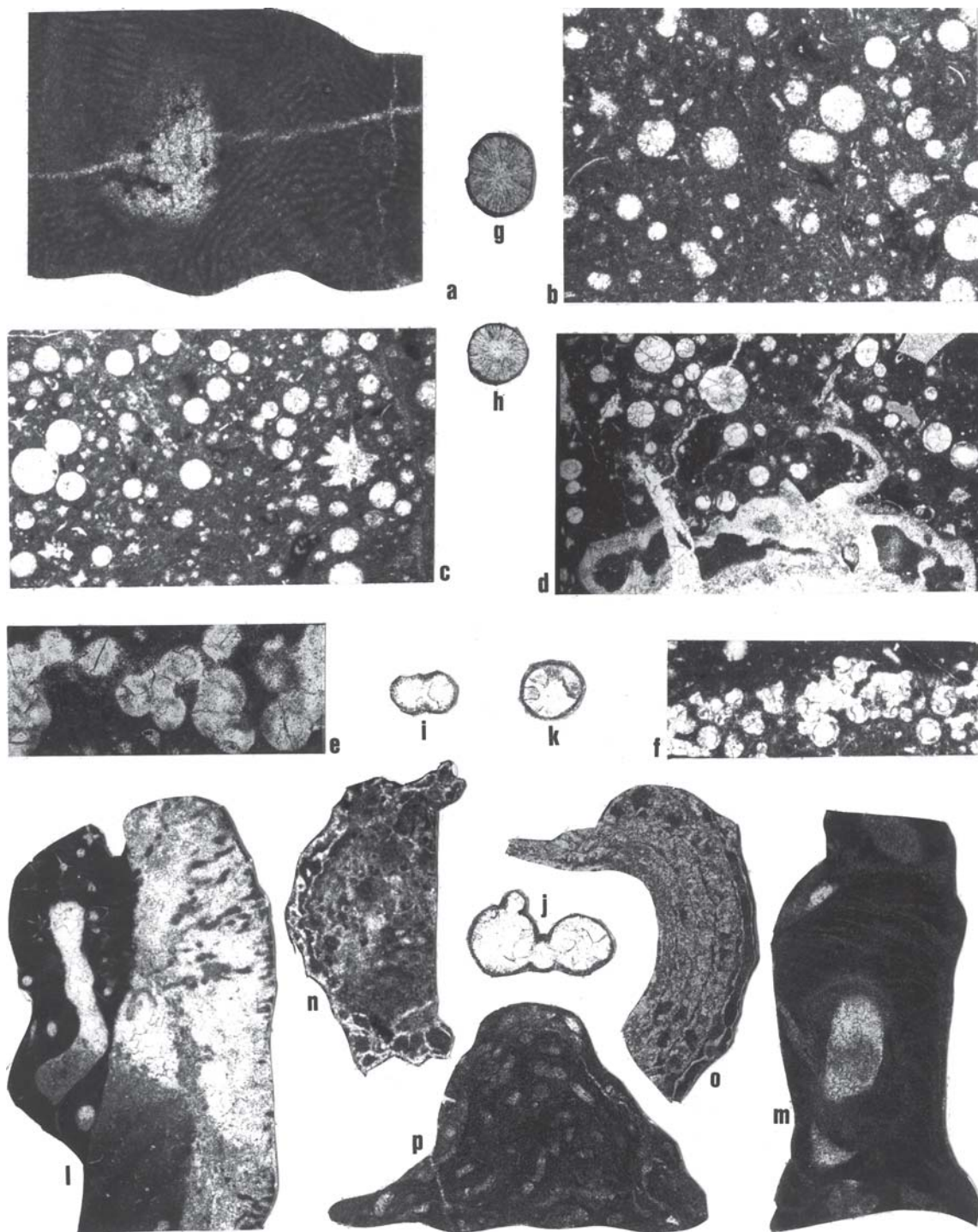


Figure 15. **b-k**, *Penella pongaensis* n. gen., n. sp.; **b**, U. of M. 825/2, BM-251, Inguanzo, x41; swarms of cement filled *Penella*, sponge spicules and ostracods; **c**, U. of M. 825/3, same as a; budding *Penella*, microscleres, macroscleres and sessile foraminifer; **d**, U. of M. 816/20, BM-85, Pen section, x62; cement filled *Penella* with remnants of wall, *Anthracoporellopsis*, sponge microscleres and echinoderm plates; **e**, U. of M. 816/18, BM-79, Pen section, x62; **f**, U. of M. 816/22, as d, but x30; **g**, U. of M. 818/1, BM-98, Berodia-I section, x97; filled by neomorphic cement; **h**, U. of M. 818/2, BM-78, Pen section, x97; **i**, U. of M. 816/21a, as d; **j**, U. of M. 816/21b, as d, Holotype; **k**, U. of M. 816/21c, as d. **a, l-m**, *Tubiphytes obscurus* Maslov 1956 [= *Shamovella obscura* (Maslov 1956)]; **a**, U. of M. 948/15, BM-FER 147, entrance of Marble Canyon, British Columbia, Cache Creek Formation, Roadian, associated with *Codonofusiella-Kahlerina*, x121; collected with C. Ross and F. Kobayashi; **l**, U. of M. 814/23, BM-76B, Las Llacerias section, x26. Encrusting *Anthracoporella*; note in the tissue the presence of sponge sclerites and of an ostracod; they do not suggest that *Tubiphytes* is either a sponge or an arthropod; **m**, U. of M. 818/16, BM-122, Berodia-II section, x30. Note the growth surfaces. **n**, *Claracrusta?* sp., U. of M. 810/0, BM-28, Las Llacerias section, x26. **o**, *Claracrusta catenoides* (Homann 1972), U. of M. 815/8, BM-78, Pen section, x62. **p**, *Ellesmerella permica* (Pia 1937), U. of M. 728/4, BM-52, Las Llacerias section, x62.

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