

## Note on the earliest occurrences of the calcareous algae *Paraepimastopora* and *Archaeolithophyllum* in Mississippian rocks

### *Nota sobre los primeros registros de las algas calcáreas Paraepimastopora y Archaeolithophyllum en materiales del Mississippiense*

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**Abstract:** The Mississippian records of the calcareous algal genera *Paraepimastopora* and *Archaeolithophyllum* are re-evaluated, as these genera are usually considered to first occur or are confined to Pennsylvanian and Permian rocks. Most specimens of *Paraepimastopora* in Mississippian rocks have been documented in open nomenclature. Revision of the taxonomic characters permits to assign them to three species: *Paraepimastopora* cf. *kansasensis* (JOHNSON) ROUX, *Paraepimastopora* cf. *noetschensis* KRAINER & VACHARD, and *Paraepimastopora* sp. nov. cf. *Paraepimastopora* sp. A *sensu* GROVES. These species, although possibly first occurring from the Tournaisian-Viséan boundary, are widespread in the late Viséan in many western Palaeotethyan basins. Revision of the taxonomic characters for *Archaeolithophyllum* suggests that the single species recorded in Mississippian rocks is *Archaeolithophyllum lamellosum* WRAY, a taxon rarely recorded in western Palaeotethyan basins, although now first recorded in Ireland and Scotland during the late Brigantian. Subsequently, the species is present in the Serpukhovian (late Mississippian) of France, Spain and Poland. In the Bashkirian (early Pennsylvanian) the genus diversified with several species recorded, and with a notable increase in the abundance of specimens elsewhere.

**Key words:** Taxonomy, Calcareous algae, Palaeobiogeography, Biostratigraphy, Mississippian, Pennsylvanian, Palaeotethys.

**Resumen:** Se analizan los registros del Mississippiense pertenecientes a especímenes de los géneros de algas calcáreas *Paraepimastopora* y *Archaeolithophyllum*, debido a que, habitualmente, estos géneros son considerados y descritos en rocas del Pensilvaniense y Pérmico. La mayor parte de los ejemplares de *Paraepimastopora* en rocas del Mississippiense se han citado en nomenclatura abierta. La revisión de los caracteres taxonómicos permite reagrupar los ejemplares en *Paraepimastopora* cf. *kansasensis* (JOHNSON) ROUX, *Paraepimastopora* cf. *noetschensis* KRAINER & VACHARD, y *Paraepimastopora* sp. nov. cf. *Paraepimastopora* sp. A *sensu* GROVES. Estas especies que, posiblemente aparecen desde el límite Tournaisense-Visense, pero sólo están bien representados en el Visense superior de muchas cuencas del Palaeotethys occidental. La revisión de los caracteres taxonómicos de *Archaeolithophyllum* sugiere que la única especie registrada en el Mississippiense es *Archaeolithophyllum lamellosum* WRAY, raras veces se cita en cuencas del Paleotethys occidental, considerándose sus primeros registros en el Brigantiense superior de Irlanda y Escocia. Con posterioridad se ha encontrado la especie en el Serpujoviense de Francia, España y Polonia. En el Bashkiriense (Pennsylvaniense inferior), el género se diversificó en varias especies y con un notable aumento en el número de ejemplares en numerosas cuencas.

**Palabras clave:** Taxonomía, Algas calcáreas, Paleobiogeografía, Bioestratigrafía, Mississippiense, Pensilvaniense, Palaeotethys.

## INTRODUCTION

The genera *Paraepimastopora* ROUX, 1979 and *Archaeolithophyllum* JOHNSON, 1956 are well-known in Pennsylvanian and Permian rocks, but their documentation in Mississippian rocks is very rare due,

either to their paucity in this epoch, or as a result of misidentification with other closely related genera. The paucity of specimens of both genera in Mississippian rocks usually prevents unquestionable identifications, and commonly, taxa are listed in open nomenclature. Furthermore, these rare specimens that occur in

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Mississippian rocks are usually too poorly preserved or the sections are not well-orientated for a definite determination.

The specimens illustrated here, plus those considered for the various species, were collected from many localities in geographically distinct basins in the western Palaeotethys and the North American realms, which makes it difficult to establish the precise geological or stratigraphical context. Nevertheless, detailed information about the location of the sections and horizons where the algal specimens were obtained are given in the text.

The purposes of this study are: (1) to document the earliest occurrences in the Mississippian of *Paraepimastopora* and *Archaeolithophyllum*, and (2) to achieve more precise taxonomic determinations, as far as the preservation of the specimens will permit.

### TAXONOMIC REMARKS ON THE ANCESTRAL *PARAEPIMASTOPORA*

The generally accepted stratigraphical range for most species of the genus *Paraepimastopora*, a Selenotellaceae KORDE emend. BASSOULLET *et al.*, 1977 (order Dasycladales), is Moscovian (Early Pennsylvanian) to early Permian (MAMET, 1991).

Many species have been described from this interval:

- *P. jewetti* (JOHNSON, 1946) ROUX, 1979 [Pennsylvanian].
- *P. kansasensis* (JOHNSON, 1946) ROUX, 1979 [Pennsylvanian].
- *P. kanumai* (ENDO *in* ENDO & KANUMA, 1954) ROUX, 1979 [Pennsylvanian-early Permian].
- *P. lateinterporosa* (ENDO, 1961) ROUX, 1979 [Permian].

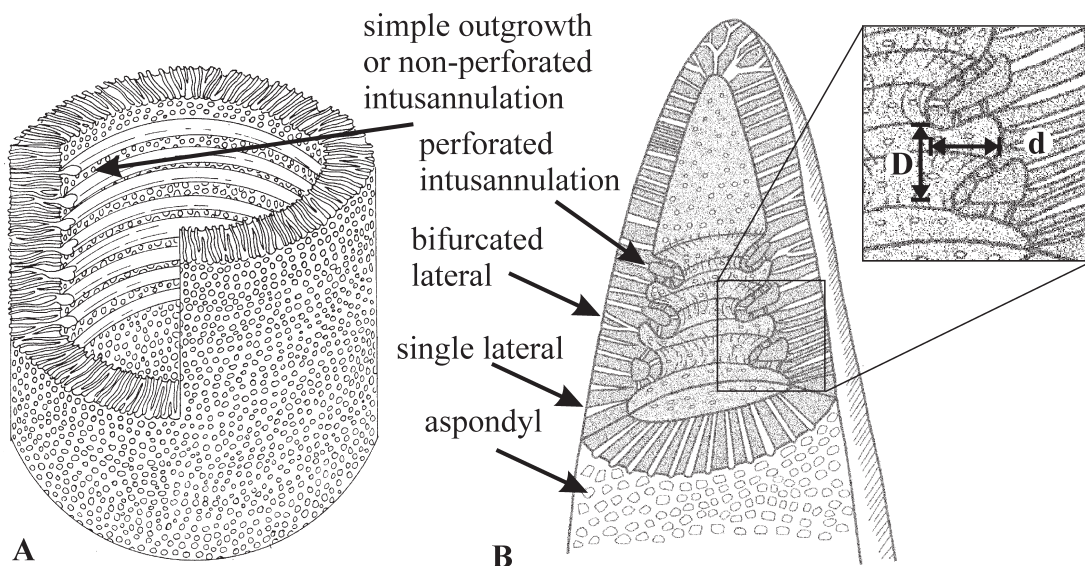


Figure 1.– A. Reconstruction of *Paraepimastopora kansasensis* (JOHNSON, 1946) ROUX, 1979 (modified from ROUX, 1989). B. Reconstruction of *Paraepimastopora noetschensis* KRAINER & VACHARD, 2002 (modified from KRAINER & VACHARD, 2002) [abbreviations: D = distance in between intusannulation, d = depth of the intusannulation]. Not to scale.

Figura 1.– A. Reconstrucción de *Paraepimastopora kansasensis* (JOHNSON, 1946) ROUX, 1979 (modificado de ROUX, 1989). B. Reconstrucción de *Paraepimastopora noetschensis* KRAINER & VACHARD, 2002 (modificado de KRAINER & VACHARD, 2002) [abreviaturas: D = distancia entre los anillos internos, d = profundidad de los anillos internos]. Sin escala.

- *P. longituba* (ENDO, 1957) ROUX, 1979 [Permian].
- *P. regularis* (JOHNSON, 1946) ROUX, 1979 [Pennsylvanian].
- *P. urtazymensis* (CHUVASHOV & ANFIMOV, 1988) MAMET, 1991 [Moscovian].

Five of these species, *P. kansasensis*, *P. kanumai*, *P. urtazymensis*, *P. regularis* and *P. jewetti* occur in the Pennsylvanian. Some of these species (*P. regularis*, *P. jewetti* and questionably *P. kanumai*) are considered junior synonyms of *P. kansasensis* by other authors (ROUX, 1989), and *P. urtazymensis* is considered endemic to the Urals. The earliest nominal species in the fossil record is *P. noetschensis* KRAINER & VACHARD, 2002 (Figs. 1B, 2I, 2J), described from the late Serpukhovian in Nötsch (Austria), and thus, uniquely, represents the first species to be formally described from the Mississippian. In summary, therefore, it is considered that there are two species of *Paraepimastopora* which are more or less widespread during the Pennsylvanian, *P. kansasensis* and questionably *P. kanumai*, and one other species in the Mississippian, *P. noetschensis*. The latter species differs from *P. kansasensis* (Figs. 1A, 2A, 2B) by the hollow and perforate intusannulation ('annulation structure' of ROUX, 1989; more or less rounded projections or outgrowths of the medulla, which in some species form

loops; Fig. 1), smaller and more ramified branches, and perfectly random aspondyl ramifications (KRAINER & VACHARD, 2002). The overall dimensions are smaller than in *P. kansasensis* which is a much larger species (Table 1), while *P. kanumai* is an even larger species, although as ROUX (1989) recognized, the dimensions are not all that significant for the taxonomy of this genus. ROUX (1989) also synonymized other species described by JOHNSON (1946) with *P. kansasensis* (*P. jewetti* and *P. regularis*), and possibly also *P. kanumai*, with a 92% score in the computer-aided comparison of morphological descriptors. Consequently, in order to establish valid criteria for distinguishing species of *Paraepimastopora*, KRAINER & VACHARD (2002) used the type of intusannulation and the type of branches.

The tendency of *P. kansasensis* to have a euspondyl arrangement was suggested by ROUX (1989, pl. 3, figs. 1, 5), as an important characteristic. However, the differences between aspondyl and euspondyl branches have been used as a basis for suprageneric classification by some authors (BASSOULLET *et al.*, 1977; DELOFFRE, 1988). Thus, theoretically, and because of the similarities between these species, a true euspondyl arrangement does not seem to be a robust morphological criterion to use.

The hollow and size of the intusannulation requires some explanatory remarks: (1) it is a clear character,

	Wall thickness	Branch diameter	Interbranches
<i>P. kansasensis sensu</i> ROUX, 1989	700-1200 µm	65-100	15-35 µm
<i>P. kansasensis sensu</i> MAMET <i>et al.</i> , 1987	700-100 µm	65-95 µm	30 µm
<i>P. kanumai sensu</i> ENDO, 1957	1620-2052 µm	81-162 µm	41-135 µm
<i>P. noetschensis</i> KRAINER & VACHARD, 2002	~ 100-7700 µm	30 µm	45-60 µm
<i>Paraepimastopora sp. sensu</i> SÁNCHEZ-CHICO <i>et al.</i> , 1995	> 1000 µm (?)	65-95- µm	32-48 µm
<i>Paraepimastopora sp. A sensu</i> GROVES, 1983	~ 550 µm	21-51 µm	11-16 µm
<i>Paraepimastopora sp. sensu</i> MAMET <i>et al.</i> , 1987	260-395 µm	15-45 µm	25-40 µm

Table 1.– Parameters of some species of *Paraepimastopora*.

Tabla 1.– Parámetros en algunas especies de *Paraepimastopora*.

and is easy to distinguish (Fig. 1B); (2) however, in addition, the branch size or the overall dimensions can vary in conjunction with the growth of the thallus, and thus the size, and even the occurrence of the hollow, might depend on the position of the section, i.e. basal or distal; (3) the distance in between intusannulation could also change with the growth of the thallus, as representative of the distance between the outer annulation; (4) however, in many specimens, the ratio of the distance between intusannulations and depth (Fig. 1B) might be a reliable datum for distinguishing species.

Furthermore, the interbranch spaces, that can represent the density of branches, might be also considered as a valid character, because no significant changes in different parts of the same thallus can be detected.

In addition to the nominal species of *Paraepimastopora* mentioned previously, there are several species documented in open nomenclature in the lower part of the Pennsylvanian and Mississippian (GROVES, 1983; BRECKLE & GROVES, 1986; SÁNCHEZ-CHICO *et al.*, 1995; SEBBAR & MAMET, 1996, 1999; CÓZAR & SOMERVILLE, 2004, 2005a, b; VACHARD & ARETZ, 2004). In most cases, the fragmentary records or poor preservation of the specimens prevented their specific determinations, characteristics that have been acknowledged by numerous authors (e.g. ROUX, 1989).

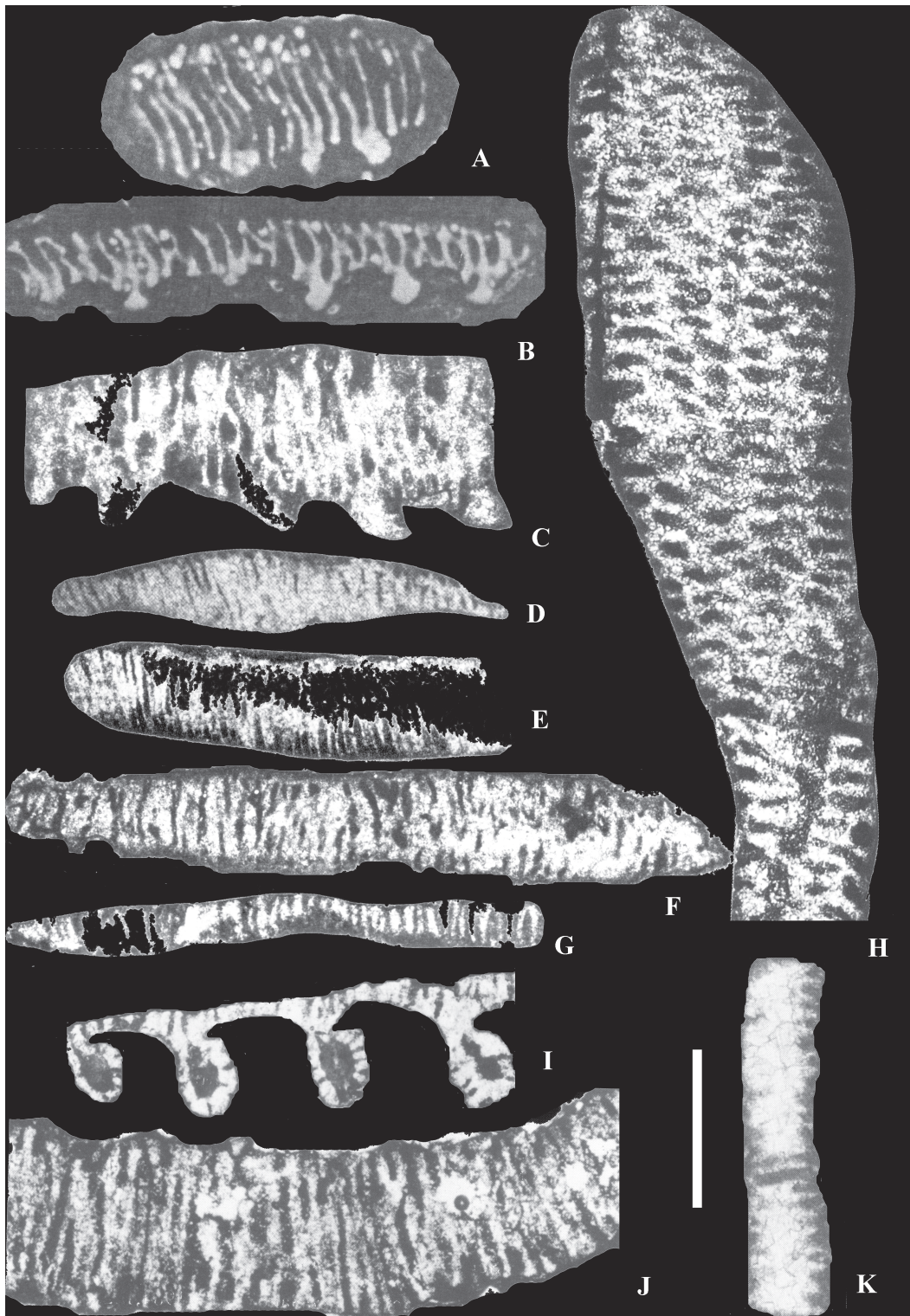
The fragmentary nature of *Paraepimastopora*, and its scarce representatives in these older rocks are the two main constraining factors in trying to determine species identifications.

Owing to these limitations, determinations of our material is equivocal, and thus, pragmatically, specimens have been identified following the previously discussed criteria. For a better visual comparison, the specimens of the earliest records have been illustrated at the same scale in figure 2 and Plate 1. The two features that can be highlighted in figure 2 and Plate 1 are the heterogeneity of the sections (variable orientation) and their preservation. Thus, some specimens are assigned to a species with some degree of uncertainty (Figs. 2D, 2F, Pl. 1, fig. 10). The ratio between different lengths has been measured in several specimens (whenever it was possible), but no diagnostic trends have been detected, being strongly influenced by the poor preservation of the specimens and their scarce number (Pl. 1, figs. 12-14), and, by a uniformity of these parameters. Consequently, the measurement of the parameters and their ratios (d/D in Fig. 1B) have been abandoned as reliable taxonomic characters.

In previously described species, the single criterion which seems to be the most valid is the density of branches, because *P. kansasensis* is clearly more densely

Figure 2.— Several specimens of *Paraepimastopora*. Scale bar for all the specimens = 1 mm. A-B. *Paraepimastopora kansasensis* (JOHNSON, 1946) ROUX, 1979; modified from ROUX (1989), upper Pennsylvanian, USA. C. *Paraepimastopora kansasensis* (JOHNSON, 1946) ROUX, 1979; modified from MAMET *et al.* (1987), Mid Moscovian, Nansen Formation, Canadian Arctic. D. (?) *Paraepimastopora* sp. nov. cf. *Paraepimastopora* sp. A *sensu* GROVES, 1983; modified from BRECKLE & GROVES (1986, as *Paraepimastopora* sp.), early Viséan, Humboldt Oolite, USA. E. *Paraepimastopora* sp. A *sensu* GROVES, 1983 (modified); Bashkirian, USA. F. (?) *Paraepimastopora kansasensis* (JOHNSON, 1946) ROUX, 1979; modified from MAMET *et al.* (1987), Mid Moscovian, Nansen Formation, Canadian Arctic. G. *Paraepimastopora* cf. *noetschensis* KRAINER & VACHARD, 2002; modified from MAMET *et al.* (1987, as *Paraepimastopora* sp.), Mid Moscovian, Canyon Fiord Formation, Canadian Arctic. H. *Paraepimastopora* cf. *kansasensis* (JOHNSON, 1946) ROUX, 1979; modified from SÁNCHEZ-CHICO *et al.* (1995, as *Paraepimastopora* sp.), Asbian (late Viséan), SW Spain. I-J. *Paraepimastopora noetschensis* KRAINER & VACHARD, 2002, modified. Nötsch, Austria. K. *Paraepimastopora* cf. *kansasensis* (JOHNSON, 1946) ROUX, 1979; modified from SEBBAR & MAMET (1996, as *Paraepimastopora* sp.), early Serpukhovian, Algeria.

Figura 2.— Algunos especímenes de *Paraepimastopora*. Barra de escala para todos los ejemplares = 1 mm. A-B. *Paraepimastopora kansasensis* (JOHNSON, 1946) ROUX, 1979; modificado de ROUX (1989), Pennsylvaniense superior, USA. C. *Paraepimastopora kansasensis* (JOHNSON, 1946) ROUX, 1979; modificado de MAMET *et al.* (1987), Moscoviense medio, Formación Nansen, Ártico canadiense. D. (?) *Paraepimastopora* sp. nov. cf. *Paraepimastopora* sp. A *sensu* GROVES, 1983; modificado de BRECKLE & GROVES (1986, como *Paraepimastopora* sp.), Viseense inferior, 'Humboldt Oolite', USA. E. *Paraepimastopora* sp. A *sensu* GROVES, 1983 (modificado); Bashkiriense, USA. F. (?) *Paraepimastopora kansasensis* (JOHNSON, 1946) ROUX, 1979; modificado de MAMET *et al.* (1987), Moscoviense medio, Formación Nansen, Ártico canadiense. G. *Paraepimastopora* cf. *noetschensis* KRAINER & VACHARD, 2002; modificado de MAMET *et al.* (1987, como *Paraepimastopora* sp.), Moscoviense medio, Formación Canyon Fiord, Ártico canadiense. H. *Paraepimastopora* cf. *kansasensis* (JOHNSON, 1946) ROUX, 1979; modificado de SÁNCHEZ-CHICO *et al.* (1995, como *Paraepimastopora* sp.), Asbiense, SO España. I-J. *Paraepimastopora noetschensis* KRAINER & VACHARD, 2002, modificado. Nötsch, Austria. K. *Paraepimastopora* cf. *kansasensis* (JOHNSON, 1946) ROUX, 1979; modificado de SEBBAR & MAMET (1996, como *Paraepimastopora* sp.), Serpukhoviense inferior, Argelia.



branched, with wider branches and thinner inter-branches than *P. noetschensis* (see Table 1). According to this criterion, specimens previously identified by other authors in open nomenclature, thus, can be classified as *Paraepimastopora* cf. *kansasensis* (Fig. 2H, 2K, Pl. 1, figs. 1-3, 5, 11), which correspond to specimens from southwestern Spain (SÁNCHEZ-CHICO *et al.*, 1995), Algeria (SEBBAR & MAMET, 1996, 1999), southeastern Ireland and northern England (CÓZAR & SOMERVILLE, 2004, 2005a, b), in rocks of Asbian, Brigantian and Brigantian to early Serpukhovian ages, respectively. Other specimens can be classified as *P. cf. noetschensis* (Fig. 2G, Pl. 1, figs. 4, 6-7, 12-14), which have been recorded from Asbian and Brigantian outcrops in southwestern Spain, Northern Ireland, northeastern Ireland and the Midland Valley in Scotland (CÓZAR & SOMERVILLE, 2005a), and from the Moscovian in the Canadian Arctic (MAMET *et al.*, 1987). In the absence of better preserved specimens which allow to observe most parts of the thalli, or rigorous statistical analysis (e.g. ROUX, 1989; MAMET & VILLA, 1995), no reliable identifications can be established.

There is a third unnamed species (Fig. 2E), exemplified by the specimens illustrated in GROVES (1983;

Bashkirian, USA). This specimen exhibits the most densely branching system of all the studied specimens, and clearly distinctive, slightly curved branches. The specimen probably belongs to a new undescribed species. The specimens included in BRENCKLE & GROVES (1986; early Viséan, USA) are also assigned to this species with some reservation (Fig. 2D), because the curved branches are not clear enough. This species is referred to as *Paraepimastopora* sp. nov. cf. *Paraepimastopora* sp. *A sensu* GROVES, 1983, because this author only recorded 4 specimens, of which only 1 was illustrated, and in our collection only 3 specimens have been recorded (Pl. 1, figs. 8-9, 10?; from the Brigantian in northern England and Brigantian to early Serpukhovian in southwestern Spain), and they are not particularly well-oriented sections. As a consequence, this material is considered to be insufficient for a proper definition of a new species. If the specimens in BRENCKLE & GROVES (1986) belong to this new species, the twelve horizons containing *Paraepimastopora* sp., recorded by these authors could provide enough material to enable a new species to be defined.

Another specimen of *Paraepimastopora* sp. illustrated in VACHARD & ARETZ (2004), shows poor preserva-

#### PLATE 1

Figs. 1-3, 5, 11.— *Paraepimastopora* cf. *kansasensis* (JOHNSON, 1946) ROUX, 1979. 1. Horizon PC-PÑR4/2a, Peñarroya 4 section (SW Spain), early Asbian (late Viséan). 2. Horizon PC-1357, Clogrenan B Borehole (SE Ireland), latest Asbian (late Viséan). 3. Horizon BGS-AH80, Allenheads N° 1 Borehole (northern England), early Brigantian (late Viséan). 5. Horizon BGS-ARE1320, Janny Wood Section (northern England), early Brigantian (late Viséan). 11. Horizon PC-1805, Fuenteobejuna section (SW Spain), latest Asbian (late Viséan).

Figs. 4, 6-7, 12-14.— *Paraepimastopora* cf. *noetschensis* KRAINER & VACHARD, 2002. 4. Horizon PC-PÑR4/2b, Peñarroya 4 section (SW Spain), early Asbian (late Viséan). 6. Horizon UCD-CKQ28, Cookstown Quarry (Northern Ireland), early Brigantian (late Viséan). 7, 13-14. Horizon PC-18/3/8, Carganamuck Quarry (northeastern Ireland), early Brigantian (late Viséan). 12. Horizon IB-743, Quarrel Hill Burn, Dailly, South Ayrshire (Scotland), late Brigantian (late Viséan).

Figs. 8-9, 10.— *Paraepimastopora* sp. nov. cf. *Paraepimastopora* sp. *A sensu* GROVES, 1983. 8. Horizon BGS-FZ6, Feizor Borehole (northern England), early Brigantian (late Viséan). 9. Horizon PC-2230, Sierra del Castillo Quarry (SW Spain), early Brigantian (late Viséan). 10. Horizon PC-VCR/0, Via Crucis section (SW Spain), Pendleian (early Serpukhovian).

Scale bar for all the specimens = 1 mm.

#### LÁMINA 1

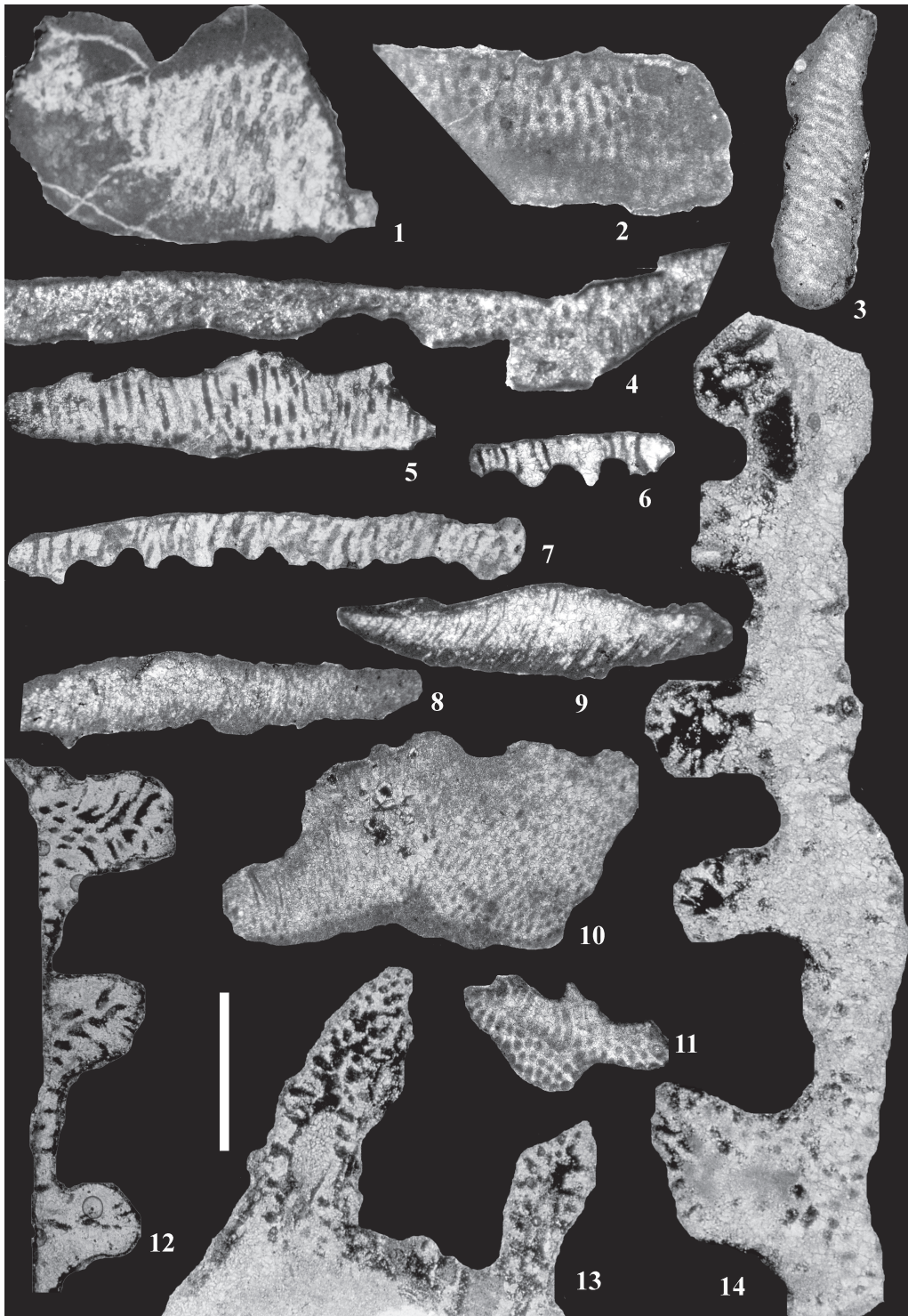
Figs. 1-3, 5, 11.— *Paraepimastopora* cf. *kansasensis* (JOHNSON, 1946) ROUX, 1979. 1. Nivel PC-PÑR4/2a, sección de Peñarroya 4 (SO España), Asbiense inferior (Viseense superior). 2. Nivel PC-1357, sondeo de Clogrenan B (SE Irlanda), Asbiense terminal (Viseense superior). 3. Nivel BGS-AH80, sondeo Allenheads N° 1 (Norte de Inglaterra), Brigantiense inferior (Viseense superior). 5. Nivel BGS-ARE1320, sección de Janny Wood (Norte de Inglaterra), Brigantiense inferior (Viseense superior). 11. Nivel PC-1805, sección de Fuenteobejuna (SW España), Asbiense terminal (Viseense superior).

Figs. 4, 6-7, 12-14.— *Paraepimastopora* cf. *noetschensis* KRAINER & VACHARD, 2002. 4. Nivel PC-PÑR4/2b, sección de Peñarroya 4 (SW España), Asbiense inferior (Viseense superior). 6. Nivel UCD-CKQ28, Cantera de Cookstown (Irlanda del Norte), Brigantiense inferior (Viseense superior). 7, 13-14. Nivel PC-18/3/8, Cantera de Carganamuck (Noreste de Irlanda), Brigantiense inferior (Viseense superior). 12. Nivel IB-743, Quarrel Hill Burn, Dailly, South Ayrshire (Escocia), Brigantiense superior (Viseense superior).

Figs. 8-9, 10.— *Paraepimastopora* sp. nov. cf. *Paraepimastopora* sp. *A sensu* GROVES, 1983. 8. Nivel BGS-FZ6, sonde de Feizor (Norte de Inglaterra), Brigantiense inferior (Viseense superior). 9. Nivel PC-2230, Cantera de Sierra del Castillo (SO España), Brigantiense inferior (Viseense superior). 10. Nivel PC-VCR/0, sección de Via Crucis (SW España), Pendleense (Serpukhovense inferior).

Barra de escala para todos los ejemplares = 1 mm.

PLATE 1 / LÁMINA 1



tion, but according to the description by the authors, it shows less densely packed branches, and it might be a different species.

### TAXONOMIC REMARKS ON THE ANCESTRAL *ARCHAEOLITHOPHYLLUM*

Several species of *Archaeolithophyllum* (Fig. 3A) have been described in the literature (MAMET, 1991):

- *A. delicatum* JOHNSON, 1956 ['mid-late' Carboniferous].
- *A. donbassicum* KOSENKO in KOSENKO *et al.*, 1972 [Mississippian-Pennsylvanian].
- *A. johnsoni* RÁCZ, 1965 [Pennsylvanian].
- *A. lamellosum* WRAY, 1964 [Pennsylvanian].
- *A. missouriense* JOHNSON, 1956 [Pennsylvanian].
- *A. vailhani* MAMET & ROUX, 1977 [Mississippian].

Two of these species are typically recorded in the Mississippian, *A. donbassicum* and *A. vailhani*, but the structure and composition of the wall of both species are distinct from the typical Pennsylvanian *Archaeolithophyllum*. These differences led BRECKLE in BRECKLE *et al.* (1982) to define a new genus, *Principia* (Fig. 3B), which was subsequently emended by CÓZAR & VACHARD (2003), who also considered it to be composed of *P. donbassicum* (KOSENKO in KOSENKO *et al.*, 1972) BRECKLE in BRECKLE *et al.*, 1982, *P. cf. donbassicum* (KOSENKO in KOSENKO *et al.*, 1972) BRECKLE in BRECKLE *et al.*, 1982, and *P. vailhani* (MAMET & ROUX, 1977) CÓZAR & VACHARD, 2003. Differences used by BRECKLE in BRECKLE *et al.* (1982) and CÓZAR & VACHARD (2003) to distinguish this genus from *Archaeolithophyllum* are based on the morphology and arrangement of the medulla cells, shorter thallus laminae, rare bifurcations of the thallus, and different wall composition (Fig. 3B). Another related genus is *Neoprincipia* CÓZAR & VACHARD, 2003 (Fig. 3C), which is similar to *Principia*, but has a different wall composition and thallus differentiation into cortex and medulla, as in *Archaeolithophyllum*. Species included in *Neoprincipia* are:

- *N. guadiatica* CÓZAR & VACHARD, 2003.
- *N. tethysiana* CÓZAR & VACHARD, 2003.
- *N. fluegeli* (KRAINER & VACHARD, 2002) CÓZAR & VACHARD, 2003.
- *N. petschoriaeformis* VACHARD & ARETZ, 2004.
- *N. claviformis* VACHARD & ARETZ, 2004.

Taxonomic characters used to distinguish the four species of true *Archaeolithophyllum* are well established (Table 2). *A. missouriense* is the largest species with subquadratic cells and marked medulla and cortex zones; *A. delicatum* is similar, but is a much smaller species; *A. johnsoni* is a relatively large species, but with elongated cells and a poorly defined contact between the medulla and the cortex; and *A. lamellosum* is a small species, similar to *A. delicatum*, but it developed a supe-

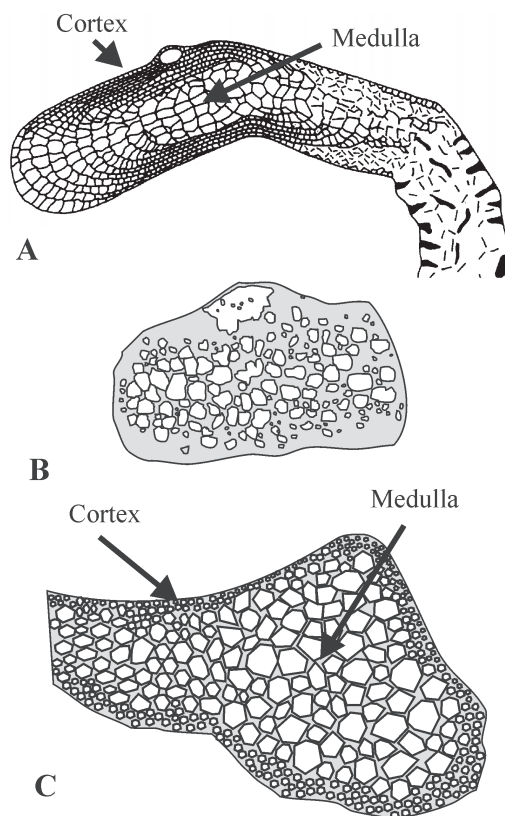


Figure 3.— Reconstruction of: A. *Archaeolithophyllum* (modified from VACHARD *et al.*, 2001). (N.B. specimen on the right hand side shows the effects of progressive loss of cellular detail during recrystallisation). B. *Principia* (modified from CÓZAR & VACHARD, 2003). C. *Neoprincipia* (modified from CÓZAR & VACHARD, 2003). Not to scale.

Figure 3.— Reconstrucción de: A. *Archaeolithophyllum* (modificado de VACHARD *et al.*, 2001) (El espécimen en el lado derecho muestra los efectos de la pérdida progresiva del detalle de las células durante la recristalización). B. *Principia* (modificado de CÓZAR & VACHARD, 2003). C. *Neoprincipia* (modificado de CÓZAR & VACHARD, 2003). Sin escala.



	Length medulla cells	Wide medulla cells	Length cortical cells	Width cortical cells	Diameter of the thallus
<i>A. delicatum</i>	14-36 $\mu\text{m}$	14-22 $\mu\text{m}$	13-15 $\mu\text{m}$	8-10 $\mu\text{m}$	~ 200 $\mu\text{m}$
<i>A. lamellosum</i>	20-58 $\mu\text{m}$	18-40 $\mu\text{m}$	12-18 $\mu\text{m}$	10-15 $\mu\text{m}$	30-400 $\mu\text{m}$
<i>A. missouriensis</i>	37-108 $\mu\text{m}$	29-90 $\mu\text{m}$	7-16 $\mu\text{m}$	7-14 $\mu\text{m}$	500-1800 $\mu\text{m}$
<i>A. johnsoni</i>	55-80 $\mu\text{m}$	35-47 $\mu\text{m}$	Transitional from the medulla cells		315-780 $\mu\text{m}$

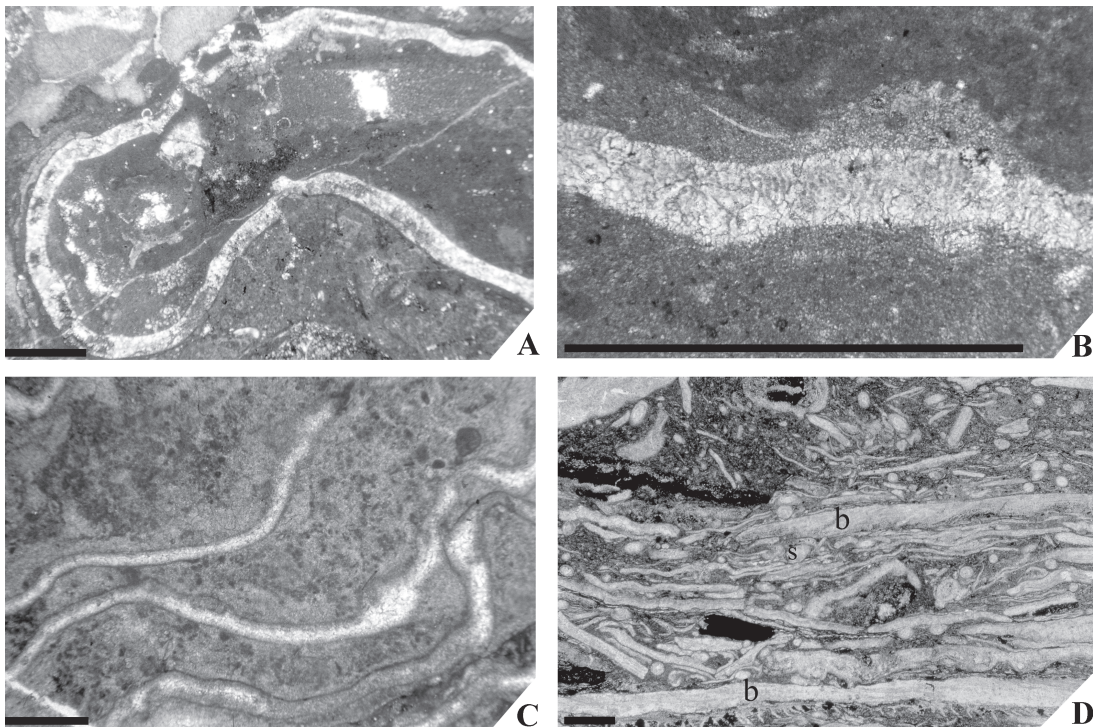
Table 2.– Parameters of the four species of *Archaeolithophyllum*.Tabla 2.– Parámetros de las cuatro especies de *Archaeolithophyllum*.

Figure 4.– *Archaeolithophyllum lamellosum* WRAY, 1964. Scale bar for all the specimens = 1 mm. A. The specimen is part of an oncoide; horizon PC-670, San Antonio section (SW Spain), Pendleian (early Serpukhovian). B. Close up view of specimen in Fig. A, note the ghost of the typical reticulate medulla cells. C. Horizon UCD-ARTS-18.2 m, top of mud-mound, Ardagh Quarry (northeastern Ireland), late Brigantian (late Viséan). D. Note that there are also some fragments of brachiopods (b) and *Saccaminopsis* (s). Horizon IB-2, Hawthorn Limestone, Scotland, late Brigantian (late Viséan).

Figura 4.– *Archaeolithophyllum lamellosum* WRAY, 1964. Barra de escala para todos los ejemplares = 1 mm. A. El ejemplar es parte de un oncoide; nivel PC-670, sección de San Antonio (SO España), Pendleense (Serpukoviense inferior). B. Detalle del ejemplar en Fig. A donde se observan fantasmas del reticulado típico de las células medulares. C. nivel UCD-ARTS-18.2 m, techo de un montículo microbiano, cantera de Ardagh (noreste de Irlanda), Brigantiense superior (Viseense superior). D. Los ejemplares están intercalados con fragmentos de braquiópodos (b) y *Saccaminopsis* (s). Nivel IB-2, Hawthorn Limestone, Escocia, Brigantiense superior (Viseense superior).

rimposed, multilayered encrusting growth, not present in other species of the genus (WRAY, 1964). It is also notable, that preservation of the specimens of *A. lamellosum* is always poor (Fig. 4A-B), and cells are difficult to distinguish because of the effects of recrystallization (WRAY, 1964; SKOMPSKI, 1996; VACHARD & ARETZ, 2004). Some of the palaeoecological features of *Archaeolithophyllum* summarized by WRAY (1964) are: (1) encrusting, locally attached, or free forms, (2) flexible crusts capable of providing a self-supporting skeletal framework and a sediment-binding function, and (3) the genus most probably inhabited the inner sublittoral platform, being able to tolerate appreciable wave agitation.

In the study of SOMERVILLE *et al.* (1996, figs. 9E, 9F), specimens were identified as *Archaeolithophyllum*, but no specific determination was stated. These specimens were later transferred to *Archaeolithophyllum* ex gr. *lamellosum* by CÓZAR & SOMERVILLE (2005a). In fact, although cells are not preserved (Fig. 4C), the specimens can be classified as *A. lamellosum* supported by two morphological and another two palaeoecological similarities:

- (1) Dimensions of the thalli are the same (Table 2).
- (2) They are interpreted to be flexible crusts, similar to those recorded in the early Serpukhovian in southwestern Spain, and in which, internal cell structures are exceptionally preserved (Fig. 4B).

(3) Palaeoecologically, they occur in the upper part of a mud-mound complex, resulting in bindstone fabrics due to the fact that *Archaeolithophyllum* lines cavity walls. In addition, they are associated with the profusion of encrusting fauna and cyanophytes, as well as colonial rugose corals acting as baffles (SOMERVILLE *et al.*, 1996). This typical binding-habit is commonly observed in other specimens of Serpukhovian age (SKOMPSKI, 1996; CÓZAR *et al.*, 2003; CÓZAR & RODRÍGUEZ, 2004; VACHARD & ARETZ, 2004; CÓZAR, 2005).

(4) The palaeoecological setting in which *Archaeolithophyllum* was recorded at the top of the Ardagh mud-mound ('reef') complex (Kingscourt, NE Ireland), was compared with the evolved diversification stage of WALKER & ALBERSTADT (1975), being adapted to turbulent water crests of banks (SOMERVILLE *et al.*, 1996).

The species has not been recovered in others basins in Ireland, but it has been also recorded at equivalent levels in the late Brigantian in the Midland Valley of Scotland (thin-section IB-2, Hawthorn Limestone, Fig. 4D).

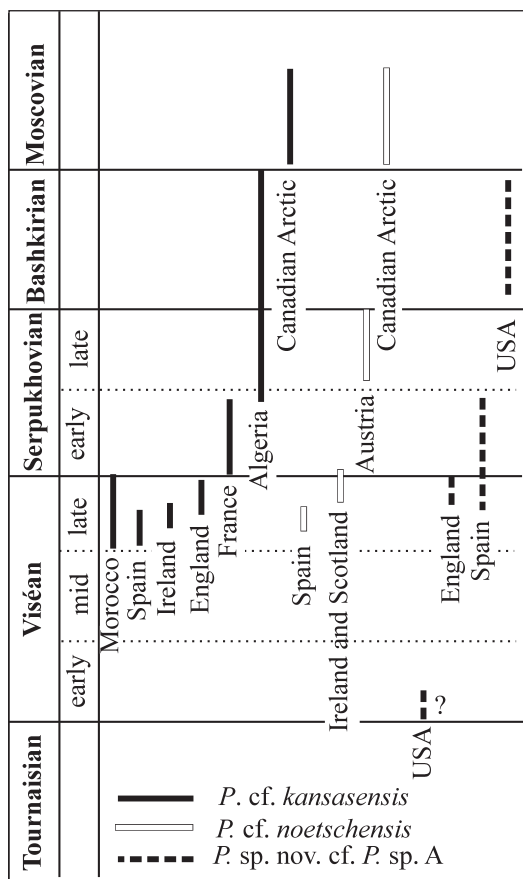


Figure 5.— The earliest occurrences of *Paraepimastopora* cf. *kansasensis* (JOHNSON, 1946) ROUX, 1979, *Paraepimastopora* cf. *noetschensis* KRAINER & VACHARD, 2002, and *Paraepimastopora* sp. nov. cf. *Paraepimastopora* sp. A sensu GROVES, 1983.

Figura 5.— Registros más antiguos de *Paraepimastopora* cf. *kansasensis* (JOHNSON, 1946) ROUX, 1979, *Paraepimastopora* cf. *noetschensis* KRAINER & VACHARD, 2002, y *Paraepimastopora* sp. nov. cf. *Paraepimastopora* sp. A sensu GROVES, 1983.

### PALAEOGEOGRAPHIC AND BIOSTRATIGRAPHIC IMPLICATIONS

In the three ancestral Mississippian species of *Paraepimastopora*, their stratigraphic ranges and geographic distributions considered in this study are modified (Fig. 5).

The widely accepted stratigraphic range for the first species *Paraepimastopora kansasensis* (JOHNSON,

1946) ROUX, 1979, is mostly restricted to the Pennsylvanian, being the previous earliest record of the species in the Moscovian of the Nansen Formation in the Canadian Arctic (MAMET *et al.*, 1987), but exceptionally it has been documented in the Permian (MAMET & ROUX, 1982). However, other specimens which have been attributed here to the same species, as *P. cf. kansasensis*, come from the early Asbian (?) to Brigantian (late Viséan) in Morocco, Asbian (late Viséan) of the Guadiato Area (Pl. 1, figs. 1, 11) and Los Santos de Maimona Basin (SW Spain), late Asbian (late Viséan) from Co. Carlow (SE Ireland) (Pl. 1, fig. 2), Brigantian (late Viséan) in northern England (Pl. 1, figs. 3, 5), early Serpukhovian in La Serre (France), and upper early Serpukhovian to Bashkirian in Béchar Basin (Algeria) [see 'Taxonomic remarks on the ancestral *Paraepimastopora*' Section].

The second species *Paraepimastopora noetschensis* KRAINER & VACHARD, 2002 is recorded in the late Serpukhovian of Austria, but oblique sections attributable to this same species, as *P. cf. noetschensis*, have been recorded in the Moscovian of the Nansen Formation of Arctic Canada, in the Brigantian (late Viséan) of Ireland and Scotland (Pl. 1, figs. 6-7, 12-14), and in the early Asbian (late Viséan) of SW Spain (Pl. 1, fig. 4).

The third species *Paraepimastopora* sp. A. *sensu* GROVES, 1983, recorded in the Bashkirian of the Bloyd Formation (USA), but specimens attributed to the same species, as *Paraepimastopora* sp. nov. cf. *Paraepimastopora* sp. A. *sensu* GROVES, 1983, has been also recorded in the Pendleian (early Serpukhovian) of SW Spain, and in the Brigantian (late Viséan) of northern England (Pl. 1, fig. 8) and Spain (Pl. 1, figs. 9-10?). Specimens documented in BRECKLE & GROVES (1986), were ascribed to the Tournaisian/Viséan Boundary in the Humboldt Oolite in the USA.

By way of contrast, the occurrence of the genus *Archaeolithophyllum* in Mississippian rocks is confined to a limited number of studies, SKOMPSKI (1996), SOMERVILLE *et al.* (1996), CÓZAR *et al.* (2003), CÓZAR & RODRÍGUEZ (2004), VACHARD & ARETZ (2004) and CÓZAR (2005).

SKOMPSKI (1996) described *A. lamellosum* from the late Serpukhovian of Poland (Fig. 6). CÓZAR *et al.* (2003), CÓZAR & RODRÍGUEZ (2004), CÓZAR *et al.* (2004) and CÓZAR (2005) documented *A. lamellosum*

from the early Serpukhovian of Spain. This taxon was also recorded by VACHARD & ARETZ (2004) from the early Serpukhovian of France. As a result, VACHARD & ARETZ (2004) considered that *A. lamellosum* first appeared in the early Serpukhovian (late Mississippian), *A. johnsoni* (e.g. in northern Spain and Ukraine; RACZ, 1965; VACHARD & MASLO, 1996), and *A. missouriense* first appeared in the early Bashkirian (e.g. in northern Spain, VACHARD & BECKARY, 1991), while *A. delicatum* first appeared in the Pennsylvanian (USA; JOHNSON, 1956).

However, the range of the last named species, *A. lamellosum*, has to be modified (Fig. 6), because it is now recorded from the late Brigantian (late Viséan) in NE Ireland and Scotland (SOMERVILLE *et al.*, 1996; CÓZAR & SOMERVILLE, 2005a).

In consequence, the stratigraphic and palaeogeographic distribution of the ancestral *A. lamellosum* can be summarized as follow (Fig. 6):

(1) the earliest occurrence is in the late Brigantian of northern Ireland and the Midland Valley of Scotland, in the extreme northwest of the western Palaeotethys region.

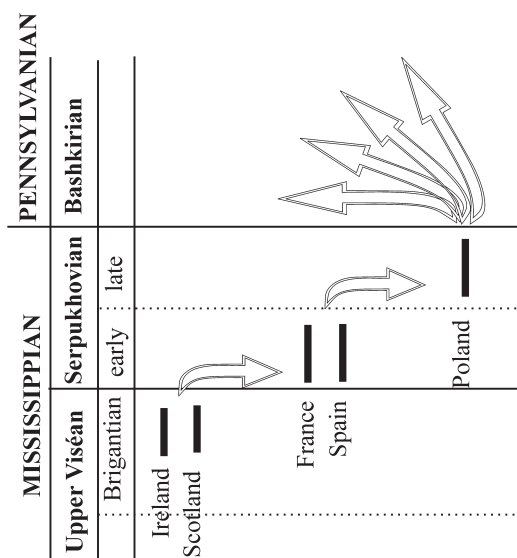


Figure 6.— The earliest occurrences of *Archaeolithophyllum lamellosum* WRAY, 1964, and possible geographic migration routes through the late Mississippian.

Figura 6.— Registros más antiguos de *Archaeolithophyllum lamellosum* WRAY, 1964, y posibles rutas de migración geográfica a través del Mississippiano superior.

(2) the species migrated south from northern Britain and Ireland to Sierra Morena in southwest Spain and to the Montagne Noire in southern France during the early Serpukhovian, both of which would have occupied southwesterly positions in the Palaeotethys region.

(3) the species migrated to Poland during the late Serpukhovian (latest Mississippian), still in the western Palaeotethys, but in a more central position.

(4) Finally, during the Bashkirian (Early Pennsylvanian), a great profusion of the genus was achieved, with many new species arising and occurring in more diverse basins in Europe and North America.

These occurrences of *Archaeolithophyllum lamellosum* suggest, that in the areas between the basins, new records could be recorded in future work. For instance, in the region between Ireland-Scotland and the Montagne Noire, *A. lamellosum* most probably inhabited the shallow-water platforms in England-Wales or northern France during the latest Brigantian or earliest Serpukhovian. Similarly, between the Montagne Noire and the Lublin Basin in Poland, *A. lamellosum* could be expected to occur in other intermediate basins, such as in Austria (e.g. Nötsch), and in intermediate ages (transition between the early to late Serpukhovian).

## CONCLUSIONS

The earliest records of the genera *Paraepimastopora* and *Archaeolithophyllum* are analysed from a taxonomical point of view. Revision of the species in open nomenclature of the genus *Paraepimastopora* permits to recognize three species: (i) *Paraepimastopora* cf. *kansasensis* (JOHNSON, 1946) ROUX, 1979, (ii) *Paraepimastopora* cf. *noetschensis* KRAINER & VACHARD, 2002, and (iii) *Paraepimastopora* sp. nov. cf. *Paraepimastopora* sp. A *sensu* GROVES, 1983. *Paraepimastopora* cf. *kansasensis* is the most common, being widely represented in the late Viséan to early Serpukhovian interval in northwestern and southwestern Palaeotethyan basins (France, Morocco, Algeria, Spain, Ireland, England). However, *Paraepimastopora* cf. *noetschensis* outside its Serpukhovian type locality, has an earlier occurrence in the latest Viséan of Ireland, but it seems to be also present in the Canadian Arctic in the Moscovian. An unnamed species from the Bashkirian of the USA

(*Paraepimastopora* nov. cf. *Paraepimastopora* sp. A *sensu* GROVES, 1983) also occurs in the latest Viséan of England and Spain, but it might occur in the USA from the Tournaisian/Viséan boundary.

On the other hand, the earliest occurrences of *Archaeolithophyllum lamellosum* WRAY, 1964 are situated in the late Brigantian of Ireland and Scotland. The same species is also present in the Serpukhovian of France, Spain and Poland. However, in the Bashkirian, the genus diversified, with several species arising in western Palaeotethyan basins in the Carnic Alps, Cantabrian Mountains and Yugoslavia.

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## REFERENCES

- BASSOULLET, J.P., BERNIER, P., DELOFFRE, R., GENOT, P., JAFFREZO, M., POIGNANT, A.F. & SEGONZAC, G. 1977. Classification criteria of fossil dasycladales. In: *Fossil algae*. E. FLÜGEL, Ed., pp. 154-166. Springer. Berlin-Heidelberg-New York.
- BRENCKLE, P. & GROVES, J.R. 1986. Calcareous foraminifers from the Humboldt Oolite of Iowa: Key to Early Osagean (Mississippian) correlations between eastern and western North America. *Palaios*, 1: 561-581.
- BRENCKLE, P.L., MARSHALL, F.C., WALLER, S.F. & WILHELM, M.M.H. 1982. Calcareous microfossils from the Mississippian Keokuk Limestone and adjacent formations, Upper Mississippi River Valley: their meaning for North American and intercontinental correlation. *Geologica et Paleontologica*, 15: 47-88.

- CHUVASHOV, B.I. & ANFIMOV, A.L. 1988. New Late Carboniferous-Early Permian calcareous algae of the Urals and Pre-Urals. In: *Calcareous algae and Stromatolites*. V.I. DUBATOLOV, Ed., pp. 54-69. Nauka, Akademiya Nauk SSSR, Sibirsk Otdeleniye Instituta Geologii i Geofiziki. Novosibirsk.
- CÓZAR, P. 2005. Early Serpukhovian (late Mississippian) microflora from the Guadiato Area (southwestern Spain). *Geological Journal*, **40**(4): 405-424.
- CÓZAR, P. & RODRÍGUEZ, S. 2004. Pendleian (early Serpukhovian) marine carbonates from SW Spain: sedimentology, biostratigraphy and depositional model. *Geological Journal*, **39**(1): 25-47.
- CÓZAR, P., RODRÍGUEZ, S. & MAS, R. 2004. Análisis sedimentológico y bioestratigráfico de afloramientos del Serpujoviense inferior (Mississippiense) en las proximidades de Adamuz (Córdoba, SO de España). *Coloquios de Paleontología*, **54**: 115-130.
- CÓZAR, P., RODRÍGUEZ, S. & SOMERVILLE, I.D. 2003. Large multi-biotic cyanoliths from relatively deep-water facies in the early Serpukhovian of SW Spain: composition, palaeoecology and depositional setting. *Facies*, **49**: 31-48.
- CÓZAR, P. & SOMERVILLE, I.D. 2004. New algal and foraminiferal assemblages and evidence for the recognition of the Asbian-Brigantian boundary in northern England. *Proceedings of the Yorkshire Geological Society*, **55**(1): 43-65.
- 2005a. Significance of calcareous algae for the recognition of the Asbian and Brigantian Stages (Mississippian) in Ireland and Great Britain. *Revista Española de Micropaleontología*, **37**(1): 71-94.
- 2005b. Late Viséan calcareous algal assemblages in South-eastern Ireland. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **2005**(2): 95-117.
- CÓZAR, P. & VACHARD, D. 2003. *Neoprincipia* nov. gen., a new Mississippian red alga, and remarks on the Archaeolithophyllumaceae (Rhodophyta). *Geobios*, **36**(5): 505-517.
- DELOFFRE, R. 1988. Nouvelle taxonomie des algues dasycladales. *Bulletin du Centre de Recherche Exploration-Production Elf-Aquitaine*, **12**(1): 165-217.
- ENDO, R. 1957. Stratigraphical and paleontological studies of the Later Paleozoic calcareous algae in Japan, XI – Fossil algae from the Taishaku district, Hiroshima-Ken and Kitami-no-kuni, Hokkaido. *The Science Reports, Saitama University, series B*, **2**(3): 279-305.
- 1961. Stratigraphical and paleontological studies of the Later Paleozoic calcareous algae in Japan, XVII – Fossil algae from the Akiyoshi limestone Group. *The Science Reports, Saitama University, series B*, commemorative volume to Prof. R. Endo: 119-142.
- ENDO, R. & KANUMA, M. 1954. Stratigraphical and paleontological studies of the Later Paleozoic calcareous algae in Japan, VII – Geology of the Mino Mountain land and southern part of Hida Plateau, with descriptions of the algal remains found in those districts. *The Science Reports, Saitama University, series B*, **1**(3): 177-208.
- GROVES, J.R. 1983. Calcareous foraminifers and algae from the type Morrowan (Lower Pennsylvanian) region of northeastern Oklahoma and northwestern Arkansas. *Oklahoma Geological Survey, Bulletin*, **133**: 1-65.
- JOHNSON, J.H. 1946. Lime-secreting algae from the Pennsylvanian and Permian of Kansas. *Bulletin of the Geological Society of America*, **57**: 1087-1120.
- 1956. *Archaeolithophyllum*, a new genus of Paleozoic coralline algae. *Journal of Paleontology*, **30**(1): 53-55.
- KOSENKO, Z.A., PETROSIAN, N.M. & CHUMENKO, S.I. 1972. New fossil algae from the Ukraine and western Siberia. In: *New species of fossil plants and invertebrates of USSR*. I. E. ZANINA, Ed., pp. 293-326. Akademiya Nauk SSSR. Izdatelstvo Nauka.
- KRAINER, K. & VACHARD, D. 2002. Late Serpukhovian (Namurian A) microfacies and carbonate microfossils from the Carboniferous of Nötsch (Austria). *Facies*, **46**: 1-26.
- MAMET, B.L. 1991. Carboniferous calcareous algae. In: *Calcareous algae and stromatolites*. R. RIDING, Ed., pp. 370-451. Springer. Berlin-Heidelberg-New York.
- MAMET, B.L. & ROUX, A. 1977. Algues rouges dévoniennes et carbonifères de la Téthys occidentale, 4e partie. *Revue de Micropaléontologie*, **19**(4): 215-266.
- 1982. Sur la présence de *Microcodium* (Algae ?, *Incertae sedis* ?) dans le Paléozoïque de l'Arctique canadien. *Canadian Journal of Earth Sciences*, **19**(2): 357-363.
- MAMET, B.L., ROUX, A. & NASSICHUK, W.W. 1987. Algues carbonifères et permiennes de l'Arctique canadien. *Geological Survey of Canada, Bulletin*, **342**: 1-143.
- MAMET, B.L. & VILLA, E. 1995. A revision of the Dasycladale alga *Uraloporella* (Chlorophycophyta, Upper Paleozoic, Asturias, Spain). *Revista Española de Paleontología*, n° Homenaje al Dr. Guillermo Colm: 48-54.
- RACZ, L. 1965. Carboniferous calcareous algae and their associations in the San Emiliano and Lois-Ciguera formations (Prov. León, NW Spain). *Leidse Geologische Mededelingen*, **31**: 1-112.
- ROUX, A. 1979. Revision du genre *Epimastopora* "PIA, 1922" (Dasycladaceae). *Bulletin du Centre de Recherche Exploration-Production Elf-Aquitaine*, **3**(2): 803-810.
- 1989. Study of a *Paraepimastopora kansasensis* (dasyclad alga) topotypical material from the Upper Pennsylvanian of Kansas, U.S.A. *Revue de Paléobiologie*, **8**(2): 323-333.
- SÁNCHEZ-CHICO, F., MAMET, B.L., MORENO-EIRIS, E. & RODRÍGUEZ, S. 1995. Algas calcáreas del Viséense de Los Santos de Maimona. *Revista Española de Micropaleontología*, **27**(2): 67-96.
- SEBBAR, A. & MAMET, B.L. 1996. Algues benthiques calcaires du Carbonifère inférieur et moyen bassin de Béchar, Algérie. *Revue de Micropaléontologie*, **39**(2): 153-167.
- 1999. Algues benthiques calcaires et *Incertae sedis* du Carbonifère, bassin de 'Béchar-Mézarif', Algérie. Rôle sédimentologique. *Revue de Micropaléontologie*, **42**(1): 71-82.
- SKOMPSKI, S. 1996. Stratigraphic position and facies significance of the limestone bands in the subsurface Carboniferous succession of the Lublin Upland. *Acta Geologica Polonica*, **46**(3-4): 171-268.
- SOMERVILLE, I.D., STROGEN, P., JONES, G.L.L. & SOMERVILLE, H.E.A. 1996. Late Viséan buildups at Kingscourt, Ireland: possible pres-

- cursors for Upper Carboniferous bioherms. In: *Recent Advances in Lower Carboniferous Geology*. P. STROGEN, I. D. SOMERVILLE & G. L.L. JONES, Eds. Geological Society of London, Special Publication, **107**: 127-144.
- VACHARD, D. & ARETZ, M. 2004. A carbonate algal microflora (cyanobacteria, algae and pseudo-algae) from the Earliest Serpukhovian (Mississippian, Early Carboniferous) of La Serre (Montagne Noire, France). *Geobios*, **37**(5): 643-666.
- VACHARD, D. & BECKARY, S. 1991. Algues et foraminifères bachkiriens des coal balls de la Mine Rosario (Truebano, León, Espagne). Precisions biostratigraphiques et micropaleontologiques sur le Bashkirien d'Ukraine (Carbonifère Moyen). *Revue de Paléobiologie*, **10**: 315-357.
- VACHARD, D., HAUSER, M., MARTINI, R., ZANINETTI, L., MATTER, A. & PETERS, T. 2001. New algae and problematica of algal affinity from the Permian of the Aseelah Unit of the Batain Plain (East Oman). *Geobios*, **34**(4): 375-404.
- VACHARD, D. & MASLO, A. 1996. Precisions biostratigraphiques et micropaleontologiques sur le Bashkirien d'Ukraine (Carbonifère Moyen). *Revue de Paléobiologie*, **15**: 357-383.
- WALKER, K.R. & ALBERSTADT, L.P. 1975. Ecological succession as an aspect of structure in fossil communities. *Paleobiology*, **1**: 238-257.
- WRAY, J.L. 1964. *Archaeolithophyllum*, an abundant calcareous alga in limestones of the Lansing Group (Pennsylvanian), southeastern Kansas. *Kansas Geological Survey, Bulletin*, **170**: 1-13.

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