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The Axophyllinae from SW Spain: a review

Los Axophyllinae del Suroeste de España: una revisión

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Key words: Axophyllinae, Rugosa, Carboniferous, Systematics, Palaeogeography, Evolution.

Resumen

Se ha abordado una revision de los corales solitarios de la subfamilia Axophyllinae y la descripción de los axophyllinos recolectados en el Carbonífero de Sierra Morena (Suroeste de España). Este grupo de corales ha sido mencionado frecuentemente en el Cabonífero desde Australia hasta América del Norte y desde China hasta Europa Occidental. Sin embargo, muchos de los supuestos registros correponden a otras familias de corales rugosos tales como Geyerophyllidae o Aulophyllidae. Tras una detallada revisión que ha incluido el estudio de algunos de los tipos, los géneros que se incluyen en esta familia son: *Axophyllum, Gangamophyllum, Pareynia, Semenophyllum, Protocarcinophyllum* y el nuevo género *Morenaphyllum*. El género *Axoclisia* se considera como dudoso miembro de esta familia.

Los Axophyllinae son frecuentes en el suroeste de España. Se han citado y descrito en el Área del Guadiato y en la Cuenca de Los Santos de Maimona en rocas del Asbiense, Brigantiense y Serpukhoviense, pero la mayoría de los hallazgos no han sido descritos aún. El registro de Axophyllinae en Sierra Morena comprende diez especies de *Axophyllum* (cuatro nuevas), dos especies de *Gangamophyllum*, una de *Pareynia* (nueva) y dos del nuevo género *Morenaphyllum*.

La distribución estratigráfica de los Axophyllinae en Sierra Morena es consistente con la distribución de las mismas especies en otras áreas (básicamente Europa Occidental y Norte de África), con tres excepciones. *A.mendipense* aparece más tarde que en las islas Británicas y Bélgica y *A. tazoultense* y *A.pseudokirsopianum* aparecen antes que en el Norte de África. Se ha establecido un árbol filogenético tentativo para los Axophyllinae. Parece claro que el género *Axophyllum* es el ancestor de los demás géneros de la subfamilia y se proponent al menos cinco líneas evolutivas desde la especie más antigua y posible ancestro de todo el grupo (*Axophyllum simplex*) hasta el registro más moderno, *A. moroccoense*. Los Axophyllinae deben ser considerados como marcadores del Palaeotethys , porque todas las citas externas a este océano son erróneas. La distribución estratigráfica de los Axophyllinos va desde el Viseense inferior hasta el Bashkiriense, estando su apogeo, tanto en abundancia como en diversidad, en el Viseense superior. Las menciones en el Bashkiriense son registros locales en algunos refugios antes de su definitiva extinción.

Abstract

A revision of the state of knowledge of the solitary axophyllids that have been grouped in the subfamily Axophyllinae (family Axophyllidae) and the description of the specimens collected in Sierra Morena (south-western Spain) is accomplished. This group of rugose corals has been reported frequently in the Carboniferous from Australia to North America and from China to Western Europe. However, some of the supposed records belong to other coral families that show some features in common, such as Geyerophyllidae and Aulophyllidae. After a detailed revision of the bibliographic references and some of the types, the genera included in this subfamily are: *Axophyllum, Gangamophyllum, Pareynia, Semenophyllum, Protocarcinophyllum* and the new genus *Morenaphyllum*. The genus *Axoclisia* remains as a doubtful member of the family.

Axophyllinae are common in south-western Spain. They have been recorded and cited from the Guadiato Area and Los Santos de Maimona Basin comprising upper Viséan (Asbian, Brigantian) and Serpukhovian rocks, but most of those records remain undescribed. The record of Axophyllinae in Sierra Morena comprises ten species belonging to *Axophyllum* (four of them are new; *A. cozari, A. julianaense, A. spinosum, A. spiralum*), two species belonging to *Gangamophyllum*, one belonging to *Pareynia* (a new one, *P. viacrucense*) and two belonging to the new genus *Morenaphyllum* (*M. antolinense, M. boyerense*).

The stratigraphic record of the Axophyllinae in Sierra Morena fits well with the distribution of the same species in other regions (mainly Western Europe and North Africa), with a few exceptions. *A.mendipense* occurs later than in Britain and Belgium and *A. tazoultense* and *A.pseudokirsopianum* occur earlier than in North Africa. A tentative phylogeny is proposed. The genus *Axophyllum* is the ancestor of all other genera of the subfamily and at least five evolutionary lineages can be traced in that genus, from the ancestor (*Axophyllum simplex*) to the youngest record, *A. moroccoense*. The Axophyllinae should be considered as biogeographic markers of the Palaeotethys, because all citations of taxa beyond that ocean are erroneous. Their stratigraphic range is from lower Viséan to Bashkirian, having an acme in the upper Viséan, both in abundance and diversity. Their occurrences in the Bashkirian are local records in some refuges before their extinction.

1. Introduction

The main subject of this paper is the revision of the state of knowledge of the solitary axophyllids that have been grouped in the subfamily Axophyllinae (family Axophyllidae) and the description of specimens collected in south-western Spain belonging to that subfamily during thirty years of research in that area. This group of rugose corals has been reported frequently in the Carboniferous from Australia to North America and from China to Western Europe. However, some of the supposed axophyllids belong actually to other rugosan families that show some features in common, such as Geyerophyllidae and Aulophyllidae. The colonial Axophyllidae (the Lonsdaleiinae) have been studied by several authors in recent times (Poty, 1975, 1981; Poty & Hecker, 2003; Hecker, 2010, 2012) and the status of most genera belonging to that family is well known. This is the main reason for the exclusion of the subfamily Lonsdaleiinae in this study. Some authors have studied the solitary representatives of the family Axophyllidae (Gorsky, 1938, 1951; Sayutina, 1973; Poty, 1981), but only Semenoff-Tian-Chansky (1974) has analysed in depth the status of the main genera (*Axophyllum-Carcinophyllum* and *Gangamophyllum*) and described the genera *Axoclisia* and *Pareynia*. However, some authors later described genera and species assigned to the Axophyllinae and the status of those genera and species needs a deep revision.

Axophyllinae are common in south-western Spain. They have been recorded and cited from the upper Viséan (Asbian, Brigantian) and Serpukhovian rocks (Rodríguez & Falces 1992, 1994, 1996; Rodríguez & Rodríguez-Curt, 2002; Gómez-Herguedas & Rodríguez, 2005, Rodríguez *et al.*, 2007; Rodríguez & Said, 2010), but only a small part of those records have been described (Rodríguez & Falces, 1992; Gómez-Herguedas & Rodríguez, 2005; Rodríguez & Said, 2010). We cover here that gap, with the description of the Axophyllinae from the Guadiato Area. The stratigraphy of the region and location of different outcrops is well known following the papers by Cózar & Rodríguez (1999a, b, 2000, 2004), Cózar *et al.* (2004, 2006, 2007) and Rodríguez *et al.* (2007), to which the reader is directed. We will not present here a detailed stratigraphic location of those outcrops, only a general map (Fig. 1) and some precise details on the stratigraphical location of each species.

The Mississippian rocks from the Guadiato Area are distributed in three different domains (Cózar & Rodríguez, 1999a): The Fresnedoso Unit (Viséan, mainly siliciclastic), The Sierra del Castillo Unit (Viséan, mainly calcareous) and the San Antonio-La Juliana Unit (Serpukhovian, partly calcareous)(Fig. 1). Only the last two units have yielded Axophyllinae. They have been recorded and/or cited in the following Viséan localities: Peñarroya olistolites (Cózar & Rodríguez, 1999b; Rodríguez & Said, 2010), in the Antolín - Sierra Boyera Block (Cózar & Rodríguez, 2000; Rodríguez & Rodríguez-Curt, 2002), in the Sierra del Castillo Block (Cózar *et al.*, 2003; Rodríguez *et al.*, 2007) and in the La Adelfilla and Cerro Cabello olistolites (unpublished data). Serpukhovian localities include: San Antonio- La Juliana section (Cózar & Rodríguez, 2004), La Cornuda section (*ibidem*, Gómez-Herguedas & Rodríguez, 2005) and Via Crucis section (unpublished).

2. Methodology

This study has been carried out in four phases: 1) Bibliographic compilation of all citations, figured material and/ or descriptions of all the genera that has been included in the subfamily Axophyllinae by any author. In that phase, more than 250 papers and monographs have been checked. 2) Construction of a data base utilising the information provided in those papers. This information has been analysed to eliminate from the study those references that include solitary corals that do not belong to the subfamily and those that are simply citations without figures and/or detailed description. 3) Analysis of the features of the genera and species belonging to the subfamily, with detailed comparison of the measurements and structures, to check the possible relationships between the different taxa and to try to identify possible synonymies. 4) Description of the material from Sierra Morena in the light of the performed revision.

For a more precise analysis of the different species and genera, some of the types were borrowed or studied *in situ*. Thus, the types of the Milne-Edwards & Haime and Semenoff-Tian-Chansky collections were studied by S. R.

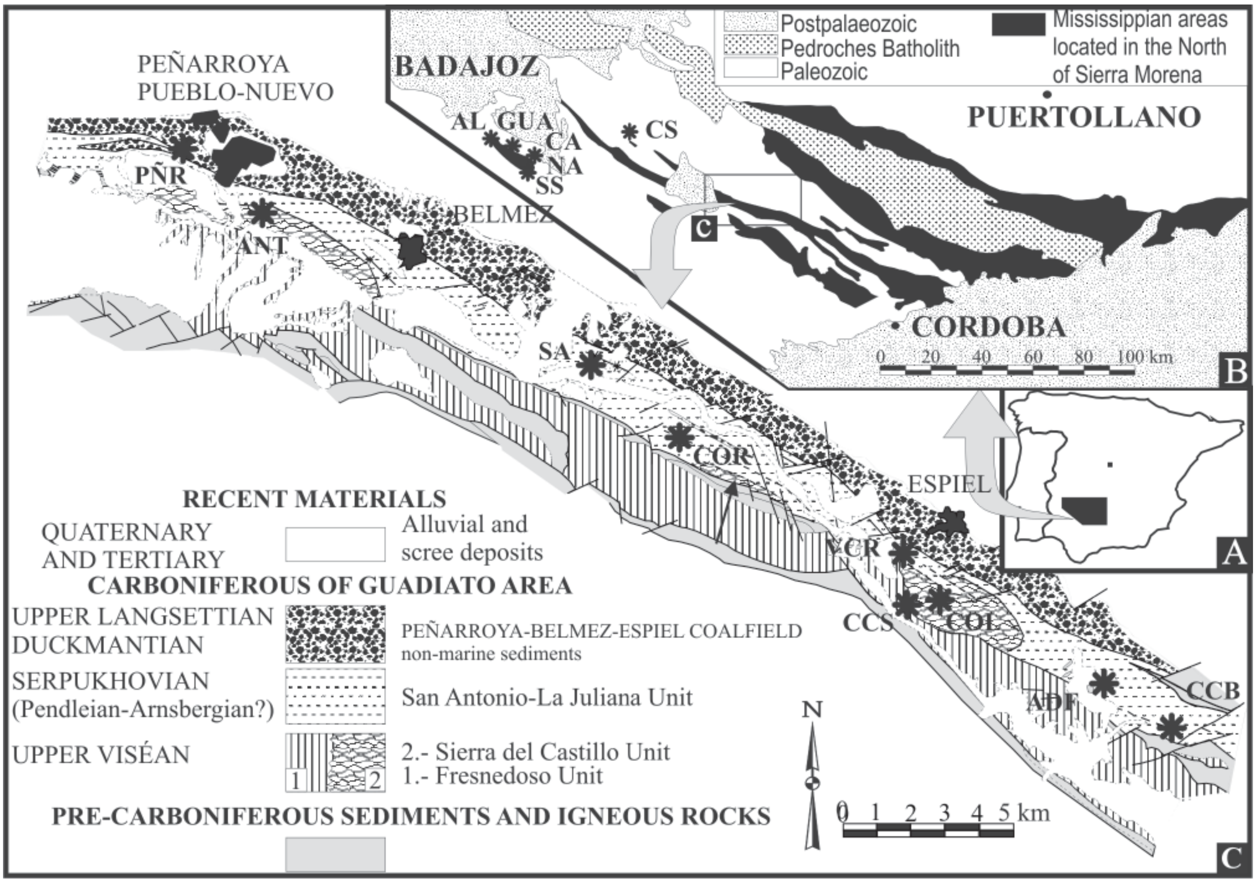

Figure 1. Carboniferous outcrops in Sierra Morena with location of the main outcrops cited in the text. A. General location. B. Carboniferous outcrops in Sierra Morena. C. Geological sketch from Guadiato Area. Abbreviations: ADF = La Adelfilla, AL = Cerro del Almendro, ANT = Antolín, CA = Cerro Almeña, CCB = Cerro Cabello, CCS = Cantera Castillo, COL = El Collado, COR = La Cornuda, CS = El Casar, GUA = Guadajira, NA= Navafría, PÑR = Peñarroya, SA = San Antonio, SS = Los Santos, VCR = Via Crucis (Modified from Cózar & Rodríguez, 1999).
— Afloramientos del Carbonífero en Sierra Morena, con la localización de los principales afloramientos citados en el texto. A. Localización general. B. Afloramientos carboníferos en Sierra Morena. C. Esquema geológico del Área del Guadiato. Abreviaturas: ADF = La Adelfilla, AL = Cerro del Almendro, ANT = Antolín, CA = Cerro Almeña, CCB = Cerro Cabello, CCS = Cantera Castillo, COL = El Collado, COR = La Cornuda, CS = El Casar, GUA = Guadajira, NA= Navafría, PÑR = Peñarroya, SA = San Antonio, SS = Los Santos, VCR = Via Crucis (Modificado de Cózar & Rodríguez, 1999).

in the MNHN from Paris, thanks to the facilities given by the authorities of the Museum, and the types of *Gangamophyllum* were checked in Saint Petersburg thanks to the facilities provided by O. Kossovaya. The types of *Axophyllum densum, A. vaughani, A. mendipense* and *A. welchi* were borrowed from NHM, London, courtesy of J. Darrell, and *A. simplex* (BGS, Keyworth, UK) checked by I.D.S..

3. Systematic Palaeontology

The morphological terminology is based on that proposed by Hill (1956, 1981), with some additions by Poty (1981) and Rodríguez (1984). The microstructural descriptions are based on the terminology proposed by Semenoff-Tian-Chansky (1974) with some refinements by Rodríguez (1984). The abbreviations used in the measurements tables are: Da = Alar diameter. Dt = Tabularium diameter. Das = Axial structure diameter. N = Number of major septa. Other abbreviations are explained in the tables and figures.

The diagnoses of the species have been modified to follow a generalised model in order to facilitate the comparison between them. Descriptions of the specimens belonging to already well-known species have been reduced to a minimum to avoid unnecessary repetition. They will only express the population variations in Sierra Morena and the main differences with the types of each species.

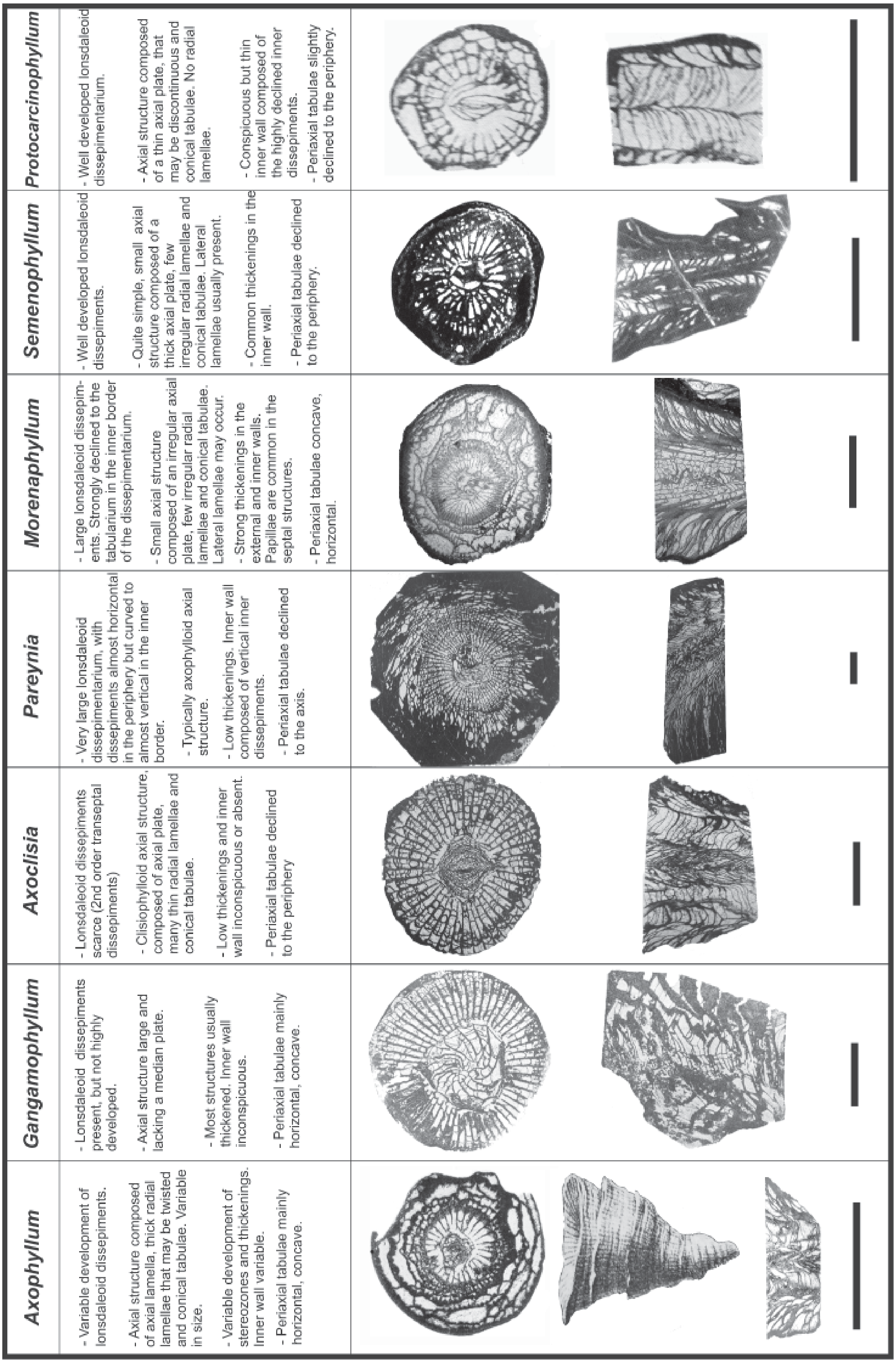

Figure 2. Genera assigned to the subfamily Axophyllinae. Scalebars = 10 mm.
— Géneros asignados a la subfamilia Axophyllinae. Escalas = 10 mm.

Class ANTHOZOA Ehrenberg, 1834
Subclass RUGOSA Milne-Edwards & Haime, 1850
Order STAURIIDA Verrill, 1865
Suborder Lonsdaleiina Spasskiy, 1974

Family Axophyllidae Milne-Edwards & Haime, 1851

Diagnosis (after Hill, 1981)**.** Solitary or colonial (fasciculate or massive). Wide axial structure composed of a medial lamella, usually continuous with the cardinal septum, radial lamellae and axial tabellae. Pericolumnar tabellae concave or subhorizontal, usually complete. Lonsdaleoid dissepimentarium with discontinuous minor septa, frequently developed as septal crests.

Subfamily Axophyllinae Milne-Edwards & Haime, 1851

Diagnosis**.** Solitary axophyllids with variable axial structure comprising median lamella joined to the cardinal septum and septal lamellae or with weak median plate to absent; axial tabellae steeply inclined, periaxial tabellae gently inclined to horizontal or concave; lonsdaleoid dissepiments commonly developed but can be scarce.

Remarks: The grouping of the solitary Axophyllidae as a subfamily was originally proposed by Hudson (1942) under the name of Carcinophyllinae. After the restoration of the genus *Axophyllum* by Semenoff-Tian-Chansky (1974), the same author indicated the priority of the name Axophyllidae over Lonsdaleiidae for the family and proposed the use of the name Axophyllinae for the solitary genera of that family.

A certain number of solitary genera have been included in the Axophyllidae (= Lonsdaleiidae) by different authors**.** After a detailed revision of all those genera, we include in the Axophyllinae the following genera: *Axophyllum*, *Gangamophyllum*, *Pareynia*, *Semenophyllum* and the new genus *Morenaphyllum* (Fig. 2). The main feature for the differentiation of those genera is the axial structure (see below).

The genus *Axoclisia,* however*,* shows intermediate features between the Axophyllinae and the subfamily Clisiophyllinae. The presence of lonsdaleoid dissepiments seem to indicate a relationship with the former, but a clisiophylloid axial structure and periaxial tabulae declined towards the dissepimentarium mark a close relationship with the Clisiophyllinae. Semenoff-Tian-Chansky (1974) and Rodríguez *et al.* (2013a,b) included this genus in the Axophyllinae. Hill (1981), Yu *et al*. (1983), Rodríguez *et al.* (2001), Said & Rodríguez (2008) and Aretz (2010), included it in the subfamily Clisiophyllinae. Here, it is provisionally retained in the subfamily Axophyllinae, but its status is at least doubtful (see details in the genus remarks).

The genus *Paragangamophyllum* Wu & Zhao, 1989 was described as being identical to *Gangamophyllum* (Gorsky, 1938), but lacking lonsdaleoid dissepiments. The type specimen of *Gangamophyllum* was described as having lonsdaleoid dissepiments, but the figures of the type do not show this feature. An examination of the type material indicates that its periphery is partly eroded but the presence of lonsdaleoid dissepiments is indubitable. However, they are scarce, as well as in other species of the genus, where they occur only in adult stages. Several species (*G. paucivesiculosum*, *G. gorskyi*, G. *latetabulatum*, etc.) would be intermediate in morphology between both genera, because lonsdaleoid dissepiments, if present, are very scarce. The differences do not seem to be a stable feature. Consequently, we regard *Gangamophyllum* and *Paragangamophyllum* as synonymous.

The genus *Protocarcinophyllum* shows most features of Axophyllinae, but the axial structure is a simple medial lamella. This feature indicates a certain proximity to the Lithostrotionidae, but it is solitary and the periaxial tabellae are not declined to the periphery, but are concave. It shows also similarities to the Petalaxidae, but it is solitary and the Petalaxidae are colonial. Consequently, we maintain this genus within the Axophyllinae.

The genus *Corphalia* was described by Poty (1975) as having evolved from *Dorlodotia*. Consequently, it was assigned to the family Lonsdaleiidae (= Axophyllidae) despite the fact that it does not have an axial structure. Hill (1981) included both genera in the Lithostrotionidae, on the basis of the relationship of the axial structure in the former is with the counter septum (not the cardinal septum, as in Lonsdaleiidae). Denayer *et al.* (2011) following that argument included both genera (*Dorlodotia* and *Corphalia*) in the Lithostrotionidae. We also follow that opinion and do not include *Corphalia* in Axophyllinae.

Yu *et al*. (1983) included in the Axophyllidae two additional genera: *Chienchiangia* and *Symplectophyllum*, but the first is a geyerophyllid (Rodríguez & Bamber 2012) and the latter is an aphrophyllid (Hill, 1981).

Genus *Axophyllum* Milne-Edwards & Haime, 1850

	1850	*Axophyllum* Milne-Edwards & Haime, p. 72
	1851	*Axophyllum* Milne-Edwards & Haime, p. 455
non	1867	*Axophyllum* Milne-Edwards & Haime 1850; White & St. John, p. 115
	1876	*Carcinophyllum* Thomson & Nicholson, p. 70
	1880	*Carcinophyllum* Thomson, p. 243
non	1882	*Axophyllum* Milne-Edwards & Haime; Barrois, p. 310

1883 *Carcinophyllum* Thomson, p. 160
1883 *Agassizia* Thomson, p. 202
non 1888 *Axophyllum* Milne-Edwards & Haime 1850; Stukenberg, p. 18
pars 1895 *Carcinophyllum* Thomson & Nicholson 1876; Stukenberg, p. 97
pars 1905 *Axophyllum* Milne-Edwards & Haime 1850; Stukenberg, p.21
1905 *Carcinophyllum* Thomson & Nicholson 1876; Vaughan, p. 147
1906 *Carcinophyllum* Thomson & Nicholson; Sibly, p. 369
1909 *Carcinophyllum* Thomson; Lee & Carruthers, p. 24
1913 *Axophyllum* Milne-Edwards & Haime 1850; Salée, p. 370
1913 *Carcinophyllum* Thomson 1880; Salée, p. 252
non 1915 *Axophyllum* Milne-Edwards & Haime 1850; Girty, p. 312
? 1915 *Carcinophyllum* Thomson 1876; Soshkina, p. 58
1923 *Carcinophyllum* Thomson 1876; Perna, p. 25.
1926 *Carcinophyllum* Thomson 1876; Parkinson, p. 250
1930 *Carcinophyllum* Thomson 1876; Ryder, p. 338
pars 1931 *Dibunophyllum* Thomson & Nicholson 1876; Chi, p. 36.
1932 *Carcinophyllum* Thomson 1880; Gorsky, p. 52
1933 *Carcinophyllum* Thomson 1880; Yu, p. 116
non 1934 *Carcinophyllum* Thomson 1880; Hill, p. 80
? 1935 *Carcinophyllum* Thomson 1880; Gorsky, p. 65
non 1937 *Axophyllum* Milne-Edwards & Haime 1860; Dobrolyubova, p. 63
1937 *Carcinophyllum* Thomson & Nicholson 1876; Yu, p. 34
pars 1938 *Carcinophyllum* Thomson & Nicholson 1876; Gorsky, p. 52
1938-1941 *Carcinophyllum* Thomson 1880; Hill, p.157
1940 *Axophyllum* Milne-Edwards & Haime 1850; Lang, Smith & Thomas, p. 27
1940 *Carcinophyllum* Thomson & Nicholson 1876; Lang, Smith & Thomas, p. 31
1942 *Carcinophyllum* Thomson & Nicholson 1876; Hudson & Fox, p. 121
non 1948 *Axophyllum* Milne-Edwards & Haime 1850; Dobrolyubova & Kabakovich, p. 32
non 1948 *Axophyllum* Milne-Edwards & Haime 1850; Dobrolyubova, p. 56
1951 *Carcinophyllum* Thomson & Nicholson 1876; Gorsky, p. 81
non 1953 *Carcinophyllum* Thomson & Nicholson 1876; Fomichev, p. 410
1956 *Carcinophyllum* Thomson & Nicholson 1876; Hill, p. F308
1960 *Carcinophyllum* Thomson & Nicholson 1876; Vassiljuk, p. 117
1962 *Carcinophyllum* Thomson & Nicholson 1876; Dobrolyubova in Orlov, p. 330
non 1963 *Carcinophyllum* Thomson 1880; De Groot, p. 94
1965 *Carcinophyllum* Thomson & Nicholson 1876; Semenoff-Tian-Chansky & Ovtracht, p. 724
1966 *Carcinophyllum* Thomson & Nicholson 1876; Bykova, p. 83
1967 *Carcinophyllum* Thomson & Nicholson 1876; Ivanovski, p. 30
1971 *Axophyllum* Milne-Edwards & Haime 1850; Perret & Semenoff-Tian-Chansky, p. 582
1973 *Carcinophyllum* Thomson & Nicholson 1876; Sayutina, p.165
1974 *Axophyllum* Milne-Edwards & Haime 1850; Semenoff-Tian-Chansky, p. 210
1975 *Carcinophyllum* Thomson & Nicholson 1876; Ivanovski, p. 64
1975 *Carcinophyllum* Thomson & Nicholson 1876; Gorsky, p. 83
1977 *Carcinophyllum* Thomson & Nicholson 1876; Jia (In Xu & Zhang), p. 222
1978 *Carcinophyllum* Thomson 1880; Fan, p. 187
non 1979 *Carcinophyllum* Thomson & Nicholson 1876; Niikawa, p. 236
1980 *Carcinophyllum* Thomson & Nicholson 1876; Fan, 29
1981 *Axophyllum* Milne-Edwards & Haime 1850; Poty, p.57
1983 *Axophyllum* Milne-Edwards & Haime 1850; Yu, Lin, Shi, Huang & Yu p. 223
1984 *Axophyllum* Milne-Edwards & Haime 1850; Rodríguez, p. 329
1985 *Axophyllum* Milne-Edwards & Haime 1851; Boll, p.36
1986 *Axophyllum* Milne-Edwards & Haime 1851; Herbig, p. 204
non 1987 *Carcinophyllum* Thomson & Nicholson 1876; Yoshida, Okimura & Kato, p. 237
non 1987 *Carcinophyllum* Thomson & Nicholson 1876; Kato, Hashimoto & Ezaki, p. 3.
1988 *Carcinophyllum* Thomson & Nicholson 1876; Huang, p. 32
1988 *Carcinophyllum* Thomson & Nicholson 1880; Lin & Wu, p. 577
1992 *Axophyllum* Milne-Edwards & Haime 1850; Rodríguez & Falces, p. 210
1994 *Axophyllum* Milne-Edwards & Haime 1850; Poty & Hannay, p. 66
1999 *Axophyllum* Milne-Edwards & Haime 1850; Liao & Rodríguez, p. 555
2002 *Axophyllum* Milne-Edwards & Haime 1850; Aretz, p. 195
2005 *Axophyllum* Milne-Edwards & Haime 1850; Cózar & Somerville, p. 51
2005 *Axophyllum* Milne-Edwards & Haime 1850; Aretz & Nudds, p. 180
2009 *Axophyllum* Milne-Edwards & Haime 1850; Rodríguez & Said, p. 14
2010 *Axophyllum* Milne-Edwards & Haime 1850; Aretz, p. 337
2010 *Axophyllum* Milne-Edwards & Haime 1850; Aretz & Herbig, p. 303
2011 *Axophyllum* Milne-Edwards & Haime 1850; Denayer, Poty & Aretz, p. 167
2012 *Axophyllum* Milne-Edwards & Haime 1850; Denayer, p. 320
2012 *Axophyllum* Milne-Edwards & Haime 1850; Rodríguez Somerville, Said & Cózar, p. 468

2012 *Axophyllum* Milne-Edwards & Haime 1850; Somerville, Rodríguez, Said & Cózar, p. 312
2013 *Axophyllum* Milne-Edwards & Haime 1850; Said, Somerville, Rodríguez & Cózar, p. 378
2013a *Axophyllum* Milne-Edwards & Haime 1850; Rodríguez, Somerville, Said & Cózar, p. 270
2013b *Axophyllum* Milne-Edwards & Haime 1850; Rodríguez, Somerville, Said & Cózar, p. 8

Diagnosis (after Semenoff-Tian-Chansky, 1974). Solitary coral, wall usually festooned. Septa of two orders, thick in the periphery where they are interrupted in adult stage by large transeptal dissepiments. Residual septal crests occur usually on the surface of the dissepiments. Fossula absent or weakly developed. Axial structure formed by thickened, irregular and anastomosed radial lamellae, crossed by a median plate, whose outline in transverse section is not clear in some instances, because of their irregularity and the junction of the radial lamellae. Long dissepiments in longitudinal section. Tabulae rising to the axis, horizontal or declined to the pericolumellar zone. Microstructure of the wall is lamellar. The festoons are composed of piled lamellae organized in fans in transverse section. Septa with fibrous mesoplasm and lamellar stereoplasm.

Diagnosis (after Hill, 1981). Solitary; axial column of irregular, curving, anastomosing septal lamellae, with a median plate and irregular conical tabellae; in marginarium peripheral parts of septa may be thickened and lonsdaleoid dissepiments may develop; pericolumnar tabulae flat or sagging.

Corrected diagnosis: Solitary corals. Septa of two orders, thick in periphery, where they may be interrupted in adult stage by transeptal dissepiments. Axial structure composed of thickened, irregular and anastomosing radial lamellae, crossed by a median plate joined to the Cardinal septum. Conical axial tabellae, concave or subhorizontal periaxial tabellae. Microstructure of the wall is lamellar; septa with fibrous mesoplasm and lamellar stereoplasm.

Remarks. The genus *Axophyllum* was proposed by Milne-Edwards & Haime (1851), who defined it based on external features of the species *A. expansum*. The poor description provoked misinterpretations by later authors and finally the abandonment of the name. Thomson & Nicholson (1876) erected the genus *Carcinophyllum* with the type species *C. kirsopianum*. For many years, most records of axophyllid corals were assigned to that genus. Hill (1940) indicated the possibility of synonymy, but being unable to check the internal structures of *Axophyllum expansum*, maintained the use of *Carcinophyllum.* Semenoff-Tian-Chansky (1974) revised the type of *Carcinophyllum kirsopianum*, housed in the Hunterian Museum in Glasgow and sectioned and studied in detail the lectotype of *Axophyllum expansum*. He compared both specimens and reached the conclusion that both belong to the same genus, but to different species (Semenoff-Tian-Chansky, 1974, p.211). However, no illustrations of *A. expansum* were provided to prove it. A further study with additional details that was projected at that time, was never published. Poty (1981) figured a transverse section of the lectotype provided by Semenoff-Tian-Chansky, and Hill (1981) illustrated the genus in the Treatise with a transverse and a longitudinal section of the lectotype.

The transverse section that was shown by Poty (1981) and Hill (1981) shows notable differences with the classical concept of the genus, based on *A. kirsopianum* and related species, but shows most of the diagnostic features of *Axophyllum*. However, that section shows an axial structure, where the median lamella is not conspicuous (Fig. 3a). Poty (1981) indicated that fact, but comparing with topotypes described by himself, indicated the identity of all other characteristics. The longitudinal section of the lectotype (Fig. 3b) and transverse sections of paralectotypes housed in the NMHN from Paris show without doubt, the presence of a median lamella.

The diagnosis given by Semenoff-Tian-Chansky (1974) is very complete, but too detailed. If considered strictly, many of the 47 described species should be separated from the genus. The concept accepted here is basically that of the diagnosis for the family given by Hill (corals having axial structure composed of median lamella, radial lamellae and conical axial tabellae, concave or subhorizontal periaxial tabellae and common presence of transeptal (lonsdaleoid) dissepiments), plus the important subfamily feature (solitary corals). The diagnosis of Hill (1981) is very accurate, but lacks microstructural details. The microstructure in all species that have been directly studied is also quite constant, with a fibrous axial part of the septa and lamellar wall and septal thickenings.

The presence of a well-developed axial structure with a persistent median lamella distinguishes this genus from others belonging to the same subfamily (*Gangamophyllum*, *Protocarcinophyllum, Morenaphyllum* gen. nov., *Semenophyllum*; Fig. 2). Differences with *Pareynia* are more subtle; the absence of a regular external wall, irregularity of the axial structure and large size allow to distinguish the latter. The axial structure and periaxial tabellae declined to the dissepimentarium are the features that allow the distinction of *Axoclisia*.

However, the variability in the genus *Axophyllum* is extreme. There are strong variations in the size of the axial structure, the thickness and number of radial lamellae and axial tabellae, the shape of the periaxial tabellae, the number, length and thickness of major septa, the length of minor septa, the development of interseptal and transeptal dissepiments, the inclination of the dissepiments, the thickness of the wall, etc. The variation in the relationships between different measurements, such as alar diameter, tabularium diameter, axial structure diameter and number of septa is also large.

The type specimen of the type species of *Axophyllum* shows some differences with the main bulk of the genus, represented by the *Axophyllum kirsopianum*-group. *Axophyllum expansum* shows a small axial structure (<1/4 of D), whereas the species of the *Axophyllum kirsopianum*-group show large axial structures (about 1/3 of D). The inner wall is well marked (Fig. 3a) (not conspicuous in the *A. k.*-group). Lonsdaleoid dissepiments are abundant and the lonsdaleoid dissepimentarium is wide (Figs. 3a,b) (scarce and narrow respectively, in the *A. k.*-group). All those features are also present in *Morenaphyllum* gen. nov. Consequently, the latter probably evolved from *Axophyllum expansum* or a close species. In addition, the new genus shows three features that allow to distinguish it from *Axophyllum*: a thick and long cardinal septum always joined to the axial structure, which shows an irregular median plate (Fig. 2) and a peculiar microstructure (see below).

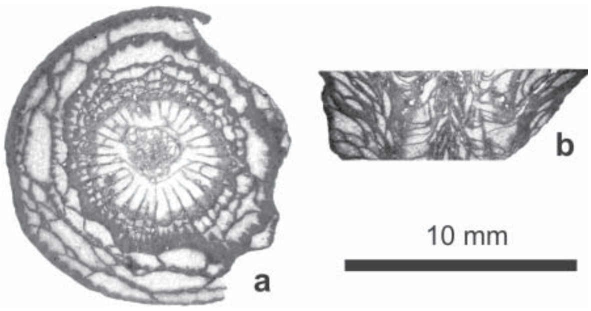

Figure 3. Lectotype of *Axophyllum expansum.* **a)** Transverse section. **b)** Longitudinal section. (located in the National Museum of Natural History of Paris). Specimen number (I. P., M.N.H.N.P. 283a/1).
— Lectotipo de *Axophyllum expansum.* **a)** Sección trnsversal. **b)** Sección longitudinal. (Depositado en el Museo Nacional de Historia Natural de París). Ejemplar número (I. P., M.N.H.N.P. 283a/1).

When beginning this study, we expected to find many coincidences in the features of some species and a high recurrence of synonymies. Thus, a completely integrated analysis comparing measurements (N, D, Dt, Das) and morphological characters (septa, axial structure, dissepimentarium, tabularium, etc.) has been carried out. The analysis is based on the examination of types, (when available), and on original diagnoses or data extracted from the figures of types. In some cases the concept of a new species is based on a single specimen, when no additional specimens were described, but in most cases, a certain variation in the features has been considered. The first part of the analysis involved the exclusion of some species that show some similarities to *Axophyllum*, but really belong to other genera or families. *Axophyllum centrotum* Chi, 1938, *Carcinophyllum onuki* Minato, 1942 and *C. welchi* Ryder, 1930 show an absence of lonsdaleoid dissepiments and show a typical aulophylloid tabularium (periaxial tabellae declining to the periphery) and must be transferred to that family. *C. coronatum* Fabre, 1955 has been transferred to the genus *Axoclisia* (Rodríguez *et al*., 2013). *C. circulare* Yu, 1933 must also be transferred to *Axoclisia*. *C. cristatum* Gerth, 1921 belongs to the genus *Verbeekiella*. *A. cylindricum* Dobrolyubova & Kabakovich, 1948, *A. infundibulum* Worthen, 1866 (In Meek & Worthen), *C. ivanitzki* Fomichev, 1953, *C. sfaiense* Termier & Termier, 1950 and *C. wagneri* De Groot, 1963 show clinotabulae and must be transferred to the Geyerophyllidae. Poty (1981) stated that *C. latevesiculosum* Salée, 1913 is synonymous with *C. lonsdaleiforme* and *C. radicatum* Milne-Edwards & Haime, 1851 is synonymous with *A. expansum*. *A. enorme* Haikawa & Ota, 1983 and *C. patella* Hill, 1934 are dendroid and seem to be closer to *Lonsdaleia*. *C. permicum* Chi, 1938 belongs to *Sakamotosawanella*. Several species have been poorly described and their illustrations are not usable for morphological analysis. These species have been also eliminated from the analysis: *A. konincki* Milne-Edwards & Haime, 1851, *A. reticulatum* Gorsky, 1938, *A. vermiculare* Thomson, 1883, and *A. volgense* Stukenberg, 1905. The only section of *A. delepini* Salée, 1913 is cut in the early stages of the development and its features are not very clear, but it will be included in the analysis.

After discarding the misidentifications and the species previously regarded as synonymous, the analysis has been carried out with the data of 37 species. Most of the checked species show clear differences in one or several of the above-mentioned features. Graphs of comparison based on different features were constructed in order to check possible synonymies, but they demonstrated to be not useful for grouping and discriminating the different species (see for instance figs. 4 and 5, based on the type of dissepiments). They are more useful though, when combined with graphs comparing measurements (Figs. 6-9). Most species may be distinguished using graphs with the relationships between different variables. The species have been divided in **two groups** to avoid graphs showing too many data. The species with a well-developed lonsdaleoid dissepimentarium have been separated from the species with scarce or absent lonsdaleoid dissepiments. **Low development (18)**: *A. barentzi* (Gorsky, 1951),

Figure 4. *Axophyllum* species with low development of lonsdaleoid dissepiments distributed by abundance of dissepiments and size of coralla. All species evaluated in the morphological analysis are included in the figure, also those that we have identified as synonyms.
— Especies de *Axophyllum* con bajo desarrollo de disepimentos lonsdaleoides, distribuidos según la abundancia de disepimentos y el tamaño del coral. Todas las especies evaluadas en el análisis se han incluido en esta figura, también aquellas que finalmente se han considerado como sinónimos. Tamaño a proximadamente a escala.

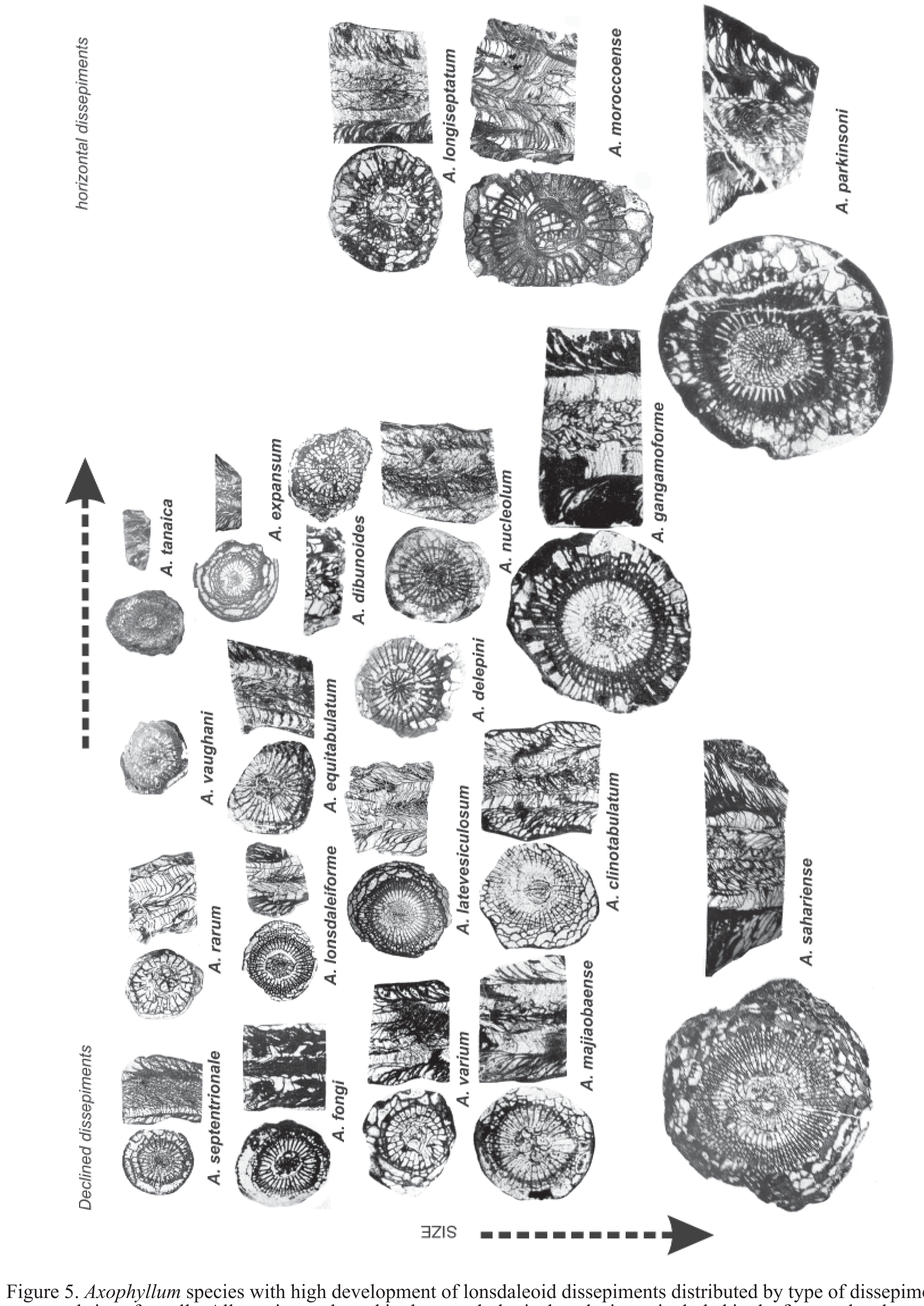

Figure 5. *Axophyllum* species with high development of lonsdaleoid dissepiments distributed by type of dissepiments and size of coralla. All species evaluated in the morphological analysis are included in the figure, also those that we have identified as synonyms.

— Especies de *Axophyllum* con alto desarrollo de disepimentos lonsdaleoides, distribuidos según la abundancia de disepimentos y el tamaño del coral. Todas las especies evaluadas en el análisis se han incluido en esta figura, también aquellas que finalmente se han considerado como sinónimos. Tamaño a proximadamente a escala.

A. begaense Semenoff-Tian-Chansky, 1974, *A. compositum* (Gorsky, 1951), *A. crassum* (Gorsky 1951), *A. curkeense* (Vaughan, 1908), *A. densum* (Ryder, 1930), *A. divisum* (Sayutina, 1973), *A. floriforme* Lin & Wu, 1988, *A. kirsopianum* (Thomson & Nicholson, 1876), *A. mendipense* (Sibly, 1906), *A. nantanaense* (Lee & Wu, 1977 In Xu & Zhang), *A. nanum* Poty, 1981, *A. pantopodum* (Perna, 1923), *A. pseudokirsopianum* Semenoff-Tian-Chansky, 1974, *A. simplex* (Garwood, 1912), *A. sphenoseptatum* Xu (In Xu & Zhang), 1977, *A. stereoseptum* Fan, 1978, *A. tazoultense* Semenoff-Tian-Chansky, 1974 and *A. zhanyiense* Wu & Zhao, 1989. **High development (19)**: *A. clinotabulatum* (Fan, 1978), *A. delepini* (Salée, 1913), *A. dibunoides* Semenoff-Tian-Chansky, 1974, *A. equitabulatum* Fan, 1978, *A. expansum* Milne-Edwards & Haime, 1851, *A. fongi* (Yu, 1933), *A. gangamoforme* Fan, 1978, *A. longiseptatum* Fan, 1978, *A. lonsdaleiforme* (Salée, 1913), *A. majiobaense* Fan, 1978, *A. moroccoense* Rodríguez *et al*., 2013, *A. nucleolum* Wu & Zhao, 1989, *A. parkinsoni* (Ryder, 1930), *A. rarum* Wu & Zhao, 1989, *A. sahariense* Semenoff-Tian-Chansky, 1974, *A. septentrionale* (Gorsky, 1938), *A. tanaica* (Vassiljuk, 1960), *A. varium* Fan, 1978 and *A. vaughani* Salée, 1913.

Some species that have been described or figured without a given name and seem to be really different species -e.g. *Axophyllum* sp. A and *Axophyllum* sp. B (= *A*. sp. of Poty, 1981) of Denayer *et al.*, 2011- were not included in the analysis.

When used in a sequence, the graphs N/D, N/Dt and N/Das, show that most species with scarce or low development of lonsdaleoid dissepiments can be clearly differentiated from each other (Figs. 6-9). It is obvious from Figure 6 that many of the 18 species show clear differences in the measurements and those differences are combined with morphological features. *A. nantanaense* shows dimensions much larger than any other species in this group. In addition, it shows a thick stereozone and relatively small axial structure. *A. sphenoseptatum* is larger than most species, and has a broad dissepimentarium combining lonsdaleoid and interseptal dissepiments and the periaxial tabulae are declined to the axial structure. *A. pseudokirsopianum* is similar to several species of this group, but it is also larger than most other species. *A. begaense* is identical to *A. kirsopianum* except in the thickening of the structures. If we do not consider the thickening of structures as an important character, both species could be regarded as synonymous. *A. floriforme* is also identical to *A. kirsopianum* in size, number of septa, scarce development of lonsdaleoid dissepiments, length of minor septa and axial structure. These species are clearly synonymous. *A. stereoseptum* shows also similar features. It is somewhat smaller, has a relatively smaller axial structure and less developed inner wall. Additionally, it occurs in China and *A. kirsopianum* in Europe; so, we maintain it as a separate species. *A. simplex* lacks dissepiments except in the very late stages, and has a lower number of septa than other species with similar diameter. Moreover, it is older than any other species and may be regarded as the ancestor of the genus. *A. divisum* shows a somewhat larger diameter for the same number of septa than other similar species. It was originally defined by Sayutina (1973) as a *Gangamophyllum*, but the median lamella is present although not conspicuous. The tabulae are conical as in *Axophyllum* but not domical as in *Gangamophyllum*. Consequently, we transfer it to the *Axophyllum* genus. *A. compositum* shows a higher number of septa and larger axial structure than other species with similar diameter. *A. crassum* has a similar diameter to *A. mendipense* (largest specimens), but has a wider dissepimentarium and smaller axial structure.

The remaining eight species show a close range of variation and must be discriminated comparing other measurements. Figure 7 confirms the different tabularium diameter of *A. divisum*. All other species in this group are very difficult to distinguish on the basis of the plots N/D and N/Dt. *A. nanum* is somewhat smaller, but the largest specimens do not differ in size and number of septa from *A. mendipense* and *A. densum*.

Similarly, when comparing the size of the axial structure, no conspicuous differences are shown in Figure 8. However, *A. zhanyiense* changes its position in the graph, because it has a relatively smaller axial structure, but a larger tabularium and alar diameter. It is clearly distinguishable in Figure 9. Consequently, *A. zhanyiense* may be regarded as a different species. Checking carefully all features of the other species, the main differences are related to the density of structures. *A. nanum* can be maintained as a separate species because it is smaller, has more lonsdaleoid dissepiments, and does not show conspicuous thickenings as some other species. *A. densum* has peripheral thickenings and a smaller axial structure in adult stages. It can be also established as a different species. *A. mendipense* and *A. curkeense* have a more dense axial structure and may be distinguished quite easily. But the differences between them are more subtle, with just slightly better developed lonsdaleoid dissepiments in the former. They are considered as synonymous. *A. pantopodum* and *A. barentzi* show similar features to the other species, but without conspicuous thickenings. Their measurements are identical and they must be regarded as synonymous. As *A. pantopodum* was described earlier, it has priority and is maintained.

The same method has been used to discriminate the 19 species with higher development of lonsdaleoid dissepiments (Figs. 10-14).

In Figure 10 some species are clearly separated from the main group because of their much larger size: *A. sahariense, A. parkinsoni, A.*

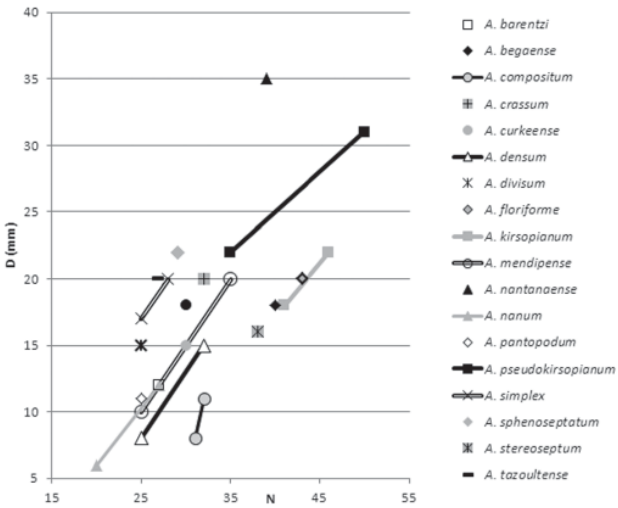

Figure 6. Graph plotting corallite diameter (D) versus number of major septa (N) for *Axophyllum* species with scarce lonsdaleoid dissepiments. Data in all graphs are taken from original diagnoses and figures.
— Gráfico de relación entre el diámetro del coralito (D) y el número de septos mayores (N) para las especies de *Axophyllum* con escasos disepimentos lonsdaleoides. Los datos en todos los gráficos se han tomado de las diagnosis y figuraciones originales.

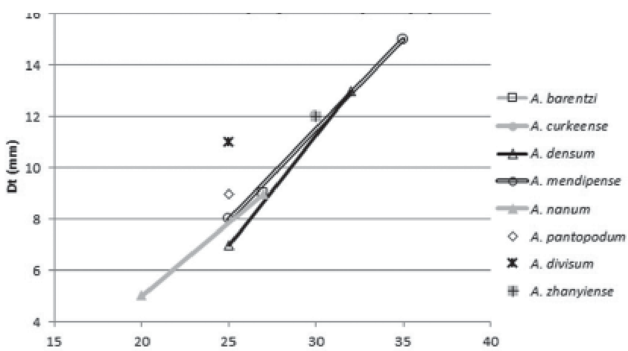

Figure 7. Graph plotting tabularium diameter (Dt) versus number of major septa (N) for *Axophyllum* species with scarce lonsdaleoid dissepiments.
— Gráfico de relación entre el diámetro del tabulario (Dt) y el número de septos mayores para las especies de *Axophyllum* con escasos disepimentos lonsdaleoides.

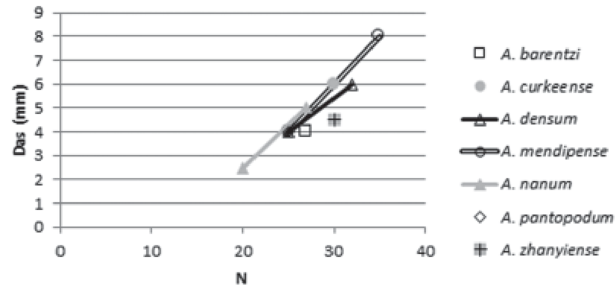

Figure 8. Graph plotting axial structure diameter (Das) versus number of major septa (N) for *Axophyllum* species with scarce lonsdaleoid dissepiments.
— Gráfico de relación entre el diámetro de la estructura axial (Das) y el número de septos mayores para las especies de *Axophyllum* con escasos disepimentos lonsdaleoides.

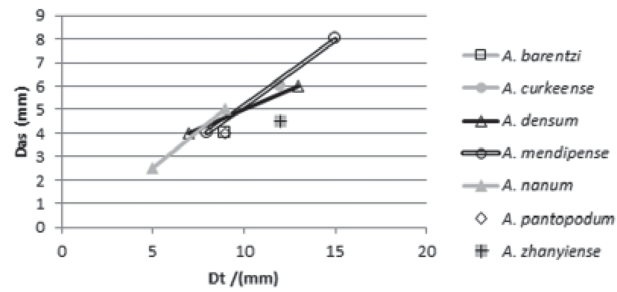

Figure 9. Graph plotting axial structure diameter (Das) versus tabularium diameter (Dt) for *Axophyllum* species with scarce lonsdaleoid dissepiments.
— Gráfico de relación entre el diámetro de la estructura axial (Das) y el diámetro del tabulario (Dt) para las especies de *Axophyllum* con escasos disepimentos lonsdaleoides.

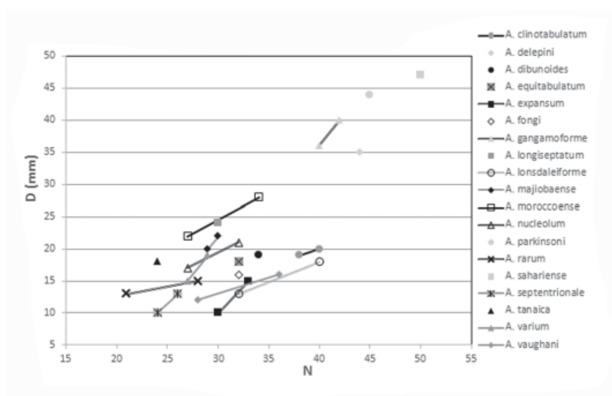

Figure 10. Graph plotting corallite diameter (D) versus number of major septa (N) for *Axophyllum* species with well-developed lonsdaleoid dissepimentarium.
— Gráfico de relación entre el diámetro del coralito (D) y el número de septos mayores (N) para las especies de *Axophyllum* con abundantes disepimentos lonsdaleoides.

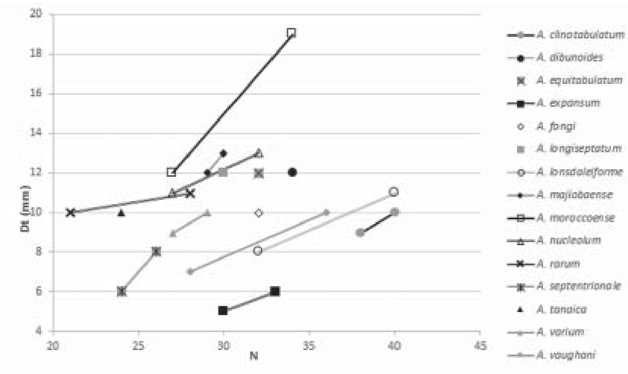

Figure 11. Graph plotting tabularium diameter (Dt) versus number of major septa (N) for *Axophyllum* species with well-developed lonsdaleoid dissepimentarium.
— Gráfico de relación entre el diámetro del tabulario (Dt) y el número de septos mayores (N) para las especies de *Axophyllum* con abundantes disepimentos lonsdaleoides.

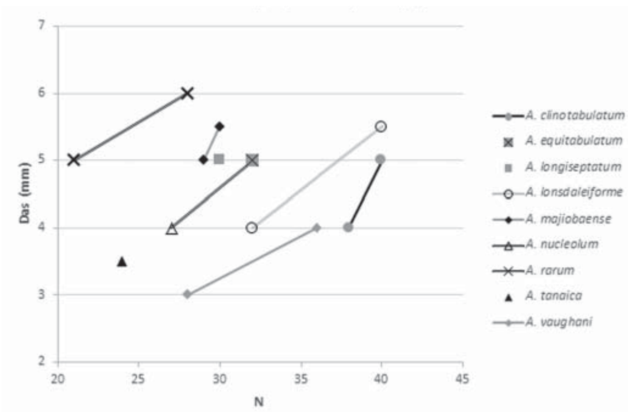

Figure 12. Graph plotting axial structure diameter (Das) versus number of major septa (N) for *Axophyllum* species with well-developed lonsdaleoid dissepimentarium.
— Gráfico de relación entre el diámetro de la estructura axial (Das) y el número de septos mayores (N) para las especies de *Axophyllum* con abundantes disepimentos lonsdaleoides.

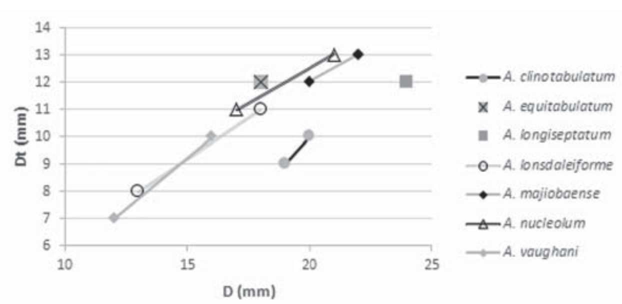

Figure 13. Graph plotting corallite diameter (D) versus tabularium diameter (Dt) for *Axophyllum* for species with well-developed lonsdaleoid dissepimentarium.
— Gráfico de relación entre el diámetro del coralito (D) y el diámetro del tabulario (Dt) para las especies de *Axophyllum* con abundantes disepimentos lonsdaleoides.

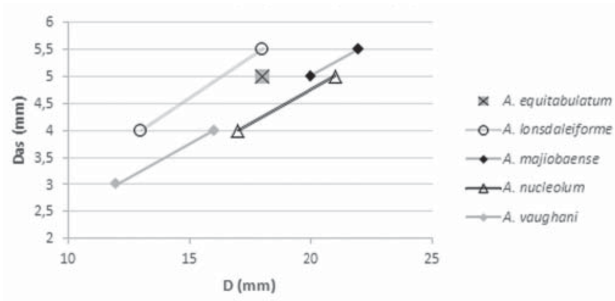

Figure 14. Graph plotting axial structure diameter (Das) versus corallite diameter (D) for *Axophyllum* species with well-developed lonsdaleoid dissepimentarium.
— Gráfico de relación entre el diámetro de la estructura axial (Das) y el diámetro del coralito (D) para las especies de *Axophyllum* con abundantes disepimentos lonsdaleoides.

gangamoforme and *A. delepini*. *A. tanaica* seems to be also separated from the other species and is confirmed in Figure 11.

When comparing the number of septa with the tabularium diameter (Fig. 11), several species show clear differences from the others. *A. moroccoense* show a larger tabularium for similar number of septa than any other species. On the other hand, *A. expansum* shows a smaller tabularium. *A. septentrionale* shows a lower number of septa and smaller tabularium than any other species. The location of *A. dibunoides* and *A. fongi* in Figure 11 clearly separate them from the others in the group (they show peculiar axial structures as well). *A. varium* is clearly separated from the group with a larger tabularium and higher number of septa.

A. rarum shows a larger axial structure, and *A. tanaica* has a quite large diameter, for one of the smallest axial structures. Both species can be easily distinguished in Figure 12. The remaining 7 species may be divided in two subgroups. The first one having fewer septa for relatively large dimensions (D, Dt, Das), that comprises *A. majiaobaense, A. longiseptatum. A. equitabulatum* and *A. nucleolum*; and a second subgroup having a higher number of septa for relatively larger dimensions, which comprises *A. lonsdaleiforme, A. clinotabulatum* and *A. vaughani*.

A. clinotabulatum and *A. longiseptatum* are clearly separated from the other species by the comparatively low value of the tabularium diameter but with a well-developed wide dissepimentarium (Fig. 13). On the other hand, the differences between *A. lonsdaleiforme* and *A. vaughani* and between *A. equitabulatum*, *A. majiaobaense* and *A. nucleolum* are even smaller.

A. vaughani is clearly separated from *A. lonsdaleiforme* because of its relatively smaller axial structure, but is related also with its longer septa (Fig. 14). However, the three Chinese species can't be clearly separated. *A. equitabulatum* shows

Table 1. Synthesis of morphological features of *Axophyllum* species. Abbreviations: Pt: Patelate; Tr.: Trochoid; Cy: Cylindrical; Cr: Ceratoid; Tn: Thin; Md: Middle/Moderate; Tk: Thick; Fs: Festooned; Sm: Smooth; Un: Undulating; St: Stereozone; Ln: Lonsdaleoid; Rg: Regular; Hr: Herringbone; El: Elongated; Gb: Globose; Ir: Irregular; No: Absence; N: near axial structure; R: Reaching axial structure; Cr: Crests on dissepiments and wall; Lg: long; Sh: Short; J: Joined to axial structure; C: Continuous; S:Straight; Spr: Spiral; Sp: Sparse; Dn: Dense; Cc: Concave; Cv: Convex; Fl: Flat; Ax: declined to the axis; H: Horizontal; P: Declined to periphery; Gr: Granulous; Fb: Fibrous; L: Lamellar.

— Síntesis de características morfológicas en las especies de *Axophyllum*. Abreviaturas: Pt: Patelate; Tr.: Trocoide; Cy: Cilíndrico; Cr: Ceratoide; Tn: Fino; Md: Medio/Moderado; Tk: Grueso; Fs: Festoneado; Sm: Liso; Un: Ondulado; St: Estereozona; Ln: Lonsdaleoide; Rg: Regular; El: Alargado; Gb: Globoso; Ir: Irregular; No: Ausencia; N:cerca de la estructura axial; R: En contacto con la estructura axial; Cr: Crestas sobre disepimentos y muralla; Lg: largo; Sh: Corto; J: Unido a la estructura axial; C: Continuo; S: Recto; Spr: Espiral; Sp: Escasos; Dn: Densos; Cc: Cóncavo; Cv: Convexo; Fl: Plano; Ax: Inclinado hacia el eje; H: Horizontal; P: Inclinado hacia la periferia; Gr: Granuloso; Fb: Fibroso; L: Lamelar.

Species	Shape	Measurements				Wall		Dissepiments				I. wall	Majors		Minors	Card.	Median plate		Radial lamellae			Axial tabellae		Periaxial tabel.			Microstr.	
		N	D	Dt	Das	Thickn.	Shape	Rows	Type	Shape	Decl.		Leng.	Thick.	Length		Thickn.	Cont.	Thickn.	Number	Outline	Thickn.	Density	Shape	Density	Decl.	Mesop.	Ster.
A. begaense	Tr	40	18	12	6	Tn-Md	Fs	1-2	Ln	El	60-90	Tk	N	Tn	Cr	J	Tk	C	Tk	15-20	Und	Tn	Sp	Cc	Sp	Ax	Gr-Fb	L
A. clinotabulatum	Cy-Cr	38-40	19-20	9-10	4-5	Tn-Md	Sm-Fs	4-6	Ln-Rg	Md	40-60	No	R	Tn	Lg	J	Tn	C	Tn	15-25	S-Un	Tn	Dn	Fl	Md	Ax	?	?
A. compositum	Cy-Cr	32	8-11	6-7	3.5-4.5	Tn-Md	Fs	1-2	Ln	El	60-90	Ir	R	Md	Sh	J	Tn	C	Tn	10-15	S-Un	Md	Dn	Cc	Sp-Md	Ax	?	?
A. cozari	Tr	34-39	24-32	16-18	7-9	Md	Fs	3-7	Ln-Rg	El	45-90	Ir	N	Md	Lg	N	Tk	C	Tk	20-30	Ir-Tw	Tn	Md	Cc	Md	Ax	Gr-Fb	L
A. crassum	Cy-Cr	32	20	13	5-6	Tk	Fs	1-3	Ln2	El	15-60	Md	R	Md	Lg	J	Md	C	Md	15-25	S	Md	Dn	Fl	Md	H	?	?
A. delepini	Tr	44	35	15	6	Th?	?	1-2	Ln	?	?	Tk	N	Tn	Sh?	J	Md	C	Md	15-20	S	?	?	?	?	?	?	?
A. densum	Tr	20-32	5-15	4-13	2-3	Tk	St	1-2	Ln	El	45-90	Tk	N	Tn-Md	Sh	J	Md	C	Tn-Md	15-20	S-Un	Tn	Sp	Cc	Sp	Ax	Gr-Fb	L
A. dibunoides	Tr	34	19	12	6	?	?	1-3	Ln	El	45-60	Ir	N/R	Tn-Md	Sh-Md	J	Tn	C	Tn	15-20	S-Un	Tn	Sp-Md	Fl-Cc	Sp	Ax	Gr-Fb	L
A. divisum	Tr	24-25	15-18	12-14	5-6	Tk	Sm	1	Ln	Gb	45-60	No	N	Tk	Sh	J	Tn	C/Ir	Tn	10-15	Ir	Tn	Md	Cc	Md	H	?	?
A. equitabulatum	Cr	32	18	11-12	4-5	Tn	Sm	1-2	Ln	El	60-90	Tn	R	Tn-Md	Cr	J	Md	C	Md	10-15	Ir	Md	Md	Cc	Sp	H	?	?
A. expansum	Tr	30-33	10-15	5-6	2.5-3	Tk	Fs	3-4	Ln	El	30-45	Tk	N	Tn-Md	Sh	N	Tn-Md	Ir	Md	10-15	Ir	Md	Md	Cc	Lw	H-Ax	Gr-Fb	L
A. fongi	Cr	32	16	10	3.5	Tk	Fs	2-3	Ln-Rg	Md	60-90	Tk	N	Md	Sh	N	Tk	C	Tk	10-15	Tw	Md	Md	Cc	Sp	H	?	?
A. gangamoforme	?	42	36-40	18-20	8-10	Tn	Sm	3-5	Ln-Rg	El	15-90	Tk	N	Tn-Md	Lg	J	Md	Ir	Md	15-20	Ir-Tw	Tn	Dn	Cc	Dn	H-P	?	?
A.julianaense	Tr	39-44	20-24	13-16.5	6-8	Tk	Fs	2-4	Ln-Rg	Md	60-90	Md	R	Md	Lg	J	Tn	Ir	Tn	15-25	Ir-Tw	Tn	Dn	Cc	Md	H-Ax	Fb	L
A. kirsopianum	Tr	41-46	18-22	14-16	6,5-7	Tn-Md	Un-Fs	1-3	Ln-Rg	Md	60-90	Tn	N	Tk	Sh	N-J	Md	Ir	Md-Tk	20-25	Ir	Tn-Md	Md	Cc	Md	H	Gr-Fb	L
A. longiseptatum	Tr-Cr	30	24	11-12	4-5	Md	Fs	3-4	Ln	El-Md	H-45	Ir	N	Tn	Cr	J	Tn	C	Tn	5-10	Ir	Tn	Dn	Cv-F	Dn	P	?	?
A. lonsdaleiforme	Tr	28-42	10-18	7-11	3.5-5.5	Md	Sm-Fs	2-5	Ln	El	60-90	Ir-Tn	N	Md	Sh	J	Md-Tk	C	Md	15-20	S-Tw	Tn	Md	Cc	Md	H	?	?
A. majiobaense	Cr	30	20-22	12-13	5-5.5	Tn-Md	Fs	3-4	Ln	El	60-90	Tk	R	Md	Sh	J	Md	Ir	Md	10-15	Ir-Tw	Tn	Dn	Cc	Md	P	?	?

Species	Shape	Measurements				Wall		Dissepiments				I. wall	Majors		Minors	Card.	Median plate		Radial lamellae			Axial tabellae		Periaxial tabel.			Microstr.	
		N	D	Dt	Das	Thickn.	Shape	Rows	Type	Shape	Decl.		Leng.	Thick.	Length		Thickn.	Cont.	Thickn.	Number	Outline	Thickn.	Density	Shape	Density	Decl.	Mesop.	Ster.
A. mendipense	Tr-Cy	25-35	10-20	8-15	4-8	Tk-Md	Fs	1	Ln-Rg	Md	60-90	Ir	N/R	Md	Sh	J	Md-Tk	C	Md-Tk	20-30	Ir-Tw	Tn-Md	Md	Cc	Md	H-Ax	Gr-Fb	L
A. morocco-ense	Tr	27-34	28	12-19	6-9	Tn	Fs	2-3	Ln	El	15-90	Tn	N	Md-Tn	Sh	J	Tn	Ir	Tn-Md	10-15	S-Ir	Tn	Md	Cc	Dn	H-P	Gr-Fb	L
A. nanum	Cr-Cy	20-27	6-12	5-9	2.5-5	Md	Fs-Sm	1	Ln	Md	60-90	Ir	N	Tn-Md	Cr	J	Md	Ir	Md-Tn	10-15	Ir	Nd	Md	Fl	Sp	P	?	?
A. pan-topodum	Cr-Tr	25	10-11	9	4	Tk	Fs-Sm	1	Ln-Rg	El	70-90	Ir	N	Md	Cr	J	Tn	C	Tn	15-20	S-Ir	Tn	Dn	Cc	Dn	H	?	?
A. parkinsoni	Pt	45	44	22	11	Tn	Sm	5-8	Ln-Rg	El-Md	0-60	Tk	N/R	Tn-Tk	Lg	J	Tn	Ir	Tn	40-50	S-Tw	Tn	Dn	Fl	Md-Dn	H	?	?
A. pseudokir-sopianum	Tr	35-50	22-31	15-20	7-13	Md	Fs	1-3	Ln-Rg	El-Md	45-90	Tk-Ir	N/R	Md	Lg	J	Md	C	Md	15-25	Ir-Tw	Tn	Md	Cc	Md	H-Ax	Gr-Fb	L
A. rarum	Tr-Cr	21-28	13-15	10-11	5-6	Md-Tk	Sm-Fs	1-3	Ln	Md-G	60-90	Tn-Ir	N	Tn-Md	Sh	J	Md	C	Tn-Md	5-15	Ir	Tn	Md	Cc	Sp	H	?	?
A. sahariense	Pt	50	47	21	12	Tn	Sm	5-8	Ln-Rg	El	30-45	No-Ir	R	Tn-Md	Lg	J	Tn	C	Tn	30-40	Tw	Tn-Md	Dn	Cc	Md	H	Fb	L
A. septentri-onale	Cr-Cy	24-26	10-13	6-8	3-4	Tk	Fs	1-2	Ln	Md	30-75	Tn	N/R	Tn-Md	Cr-Sh	J	Md	C	Tn	10-20	S-Ir	Tn	Dn	Cc	Md	H	?	?
A. simplex	Cr	28	17-20	17-20	6	Tk	Sm-St	0-1	Ln	Md	45-60	No	N	Md	Sh	J-N	Tk-Md	C	Tk-Md	10-15	Ir	Tn	Sp	Fl	Md-Dn	H	?	?
A. sphenosep-tatum	Tr	29	19-22	10	5	Tk	Sm-Fs	2-3	Rg-Ln	Md	30-60	Tk	N	Tk-Tn	Lg	J	Md	C	Tn	15-25	Ir	Tn-Md	Md	Cc	Md	H	?	?
A. spinosum	Tr	30-42	17-34	7-15	2.5-6	Tk	Fs	4-8	Ln-Rg	El-Md	60-90	Ir	R	Tn-Md	Lg	N	Tn	C	Tn	15-30	Ir-Tw	Tn	Dn	Cc	Md	Ax-H	Fb-L	L
A. spiralum	Tr	30-38	10-20	8-18	4-8	Md	Fs	1-2	Ln	El	60-90	Tk	N-R	Md	Sh	J	Tk	C	Tk	15-25	Tw	Tn	Md	Cc-Fl	Sp	Ax	Fb	L
A. stereosep-tum	Tr-Cr	38	16	11	5	Tk	St	1-3	Ln-Rg	Md-El	60-90	Ir	R	Md	Sh	J	Tk	C	Md	15-25	S-Ir	Tn	Md-Dn	Cc	Md-Dn	H-P	?	?
A. tanaica	Tr	22-24	18	10	3.5-4	Tk	St	1-3	Ln-Rg	El	60-90	Ir	R	Md	Lg	J	Md-Tn	C	Md-Tn	10-20	Ir	Tn	Dn	Fl-Cv	Md	Ax	?	?
A. tazoultense	Tr	47	20	14-15	7-8	?	?	>2	Ln-Rg	El	60-90	No	N	Tn-Md	Lg	J	Tn-Md	C	Tn	20-25	Ir	Tn	Md-Dn	F-Cc	Sp-Md	Ax	Gr-Fb	L
A. varium	Cy	27-29	15-19	9-10	4-5	Md	Ir	1-3	Ln	El-Md	45-90	Tn	R	Tn	Cr	J	Tn	C	Tn	5-15	Ir	Tn	Md	Cc	Md-Dn	H	?	?
A. vaughani	Tr	25-36	12-16	7-10	3-4	Tk	Fs	1-3	Ln	El	60-90	Ir-Tn	R	Tn-Md	Sh	J	Md	C	Tn-Md	10-20	Ir	Tn	Dn-Md	Cc	Sp-Md	H	?	?
A. zhanyiense	Tr	30	18	12	4.5	Md	Fs	2-6	Ln-Rg	El-Md	30-60	Iur	N	Tn-Md	Sh	N	Tn-Md	C	Tn	5-15	Ir	Tn	Dn-Md	Cc	Dn	P	?	?

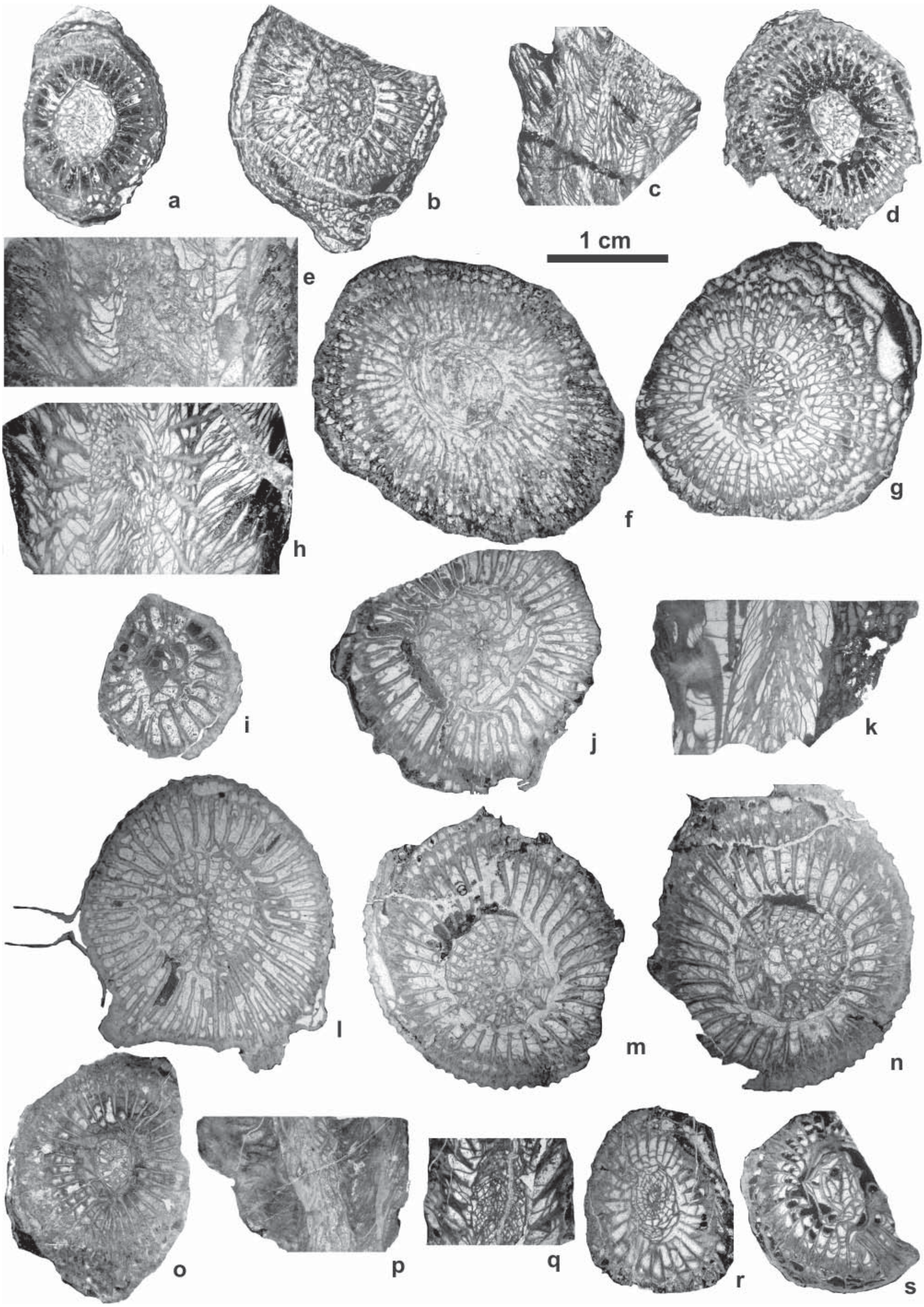
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Figure 15. *Axophyllum kirsopianum* **a)** Specimen CS/11-4, transverse section. **b)** Specimen CS/11-5, transverse section. **c)** Specimen CS/13-2, longitudinal section. **d)** Specimen CS/13-10, transverse section. *Axophyllum pseudokirsopianum* **e-f)** Specimen ANT/4-57, **e:** longitudinal section. **f:** transverse section. **g-h)** Specimen PÑR/4-14, **g:** transverse section. **h:** longitudinal section. *Axophyllum mendipense* **i-j)** Specimen ANT/1-8, **i:** transverse section, young stage, **j:** transverse section, adult stage. **k)** Specimen ANT/1-11, longitudinal section. **l:** Specimen ANT/1-22, transverse section. Note the talons and radiciform processes. **m-n)** Specimen COL/7-8, **m:** transverse section early adult stage. **n:** transverse section, advanced adult stage. *Axophyllum* densum **o-p)** Specimen NA/2-111, **o:** transverse section. **p:** longitudinal section. **q-r)** Specimen CCS/11-9, **q:** longitudinal section, **r:** transverse section. **s)** Specimen COL/7-1, transverse section. Scale bar valid for all figures.

— (izquierda). *Axophyllum kirsopianum* **a)** Ejemplar CS/11-4, sección transversal. **b)** Ejemplar CS/11-5, sección transversal. **c)** Ejemplar CS/13-2, sección longitudinal. **d)** Ejemplar CS/13-10, sección transversal. *Axophyllum pseudokirsopianum* **e-f)** Ejemplar ANT/4-57, **e: secci**ón longitudinal. **f:** sección transversal. **g-h)** Ejemplar PÑR/4-14, **g:** sección transversal. **h:** sección longitudinal. *Axophyllum mendipense* **i-j)** Ejemplar ANT/1-8, **i:** sección transversal, estadio juvenil, **j:** sección transversal, estadio adulto. **k)** Ejemplar ANT/1-11, sección longitudinal. **l:** Ejemplar ANT/1-22, sección transversal.. Observese los talones y procesos radiciformes. **m-n)** Ejemplar COL/7-8, **m:** sección transversal, estadio adulto temparano. **n:** sección transversal,. *Axophyllum* densum **o-p)** Ejemplar NA/2-111, **o:** sección transversal. **p:** sección longitudinal. **q-r)** Ejemplar CCS/11-9, **q:** sección longitudinal, **r:** sección transversal. **s)** Ejemplar COL/7-1, sección transversal. Escala válida para todas las figuras.

a slightly larger axial structure. It is joined to more regular tabulae in that species and both features taken together will be considered to accept it as a separate species. *A. nucleolum* is slightly smaller than *A. majiaobaense,* but both species share all other features, including concave periaxial tabellae predominantly declined to the periphery. These species are considered as synonymous.

In conclusion, we accept as valid species in *Axophyllum* those included in Table I (34 in total) and listed below in their respective groups:

Species with absent or poorly developed lonsdaleoid dissepimentarium (16)
A. begaense, A. compositum, A. crassum, A. densum, A. divisum, A. kirsopianum =
A. radicatum, A. mendipense = A. curkeense, A. nantanaense, A. nanum, A. pantopodum =
A. barentzi, A. pseudokirsopianum, A. simplex, A. stereoseptum, A. sphenoseptatum,
A. tazoultense, A. zhanyiense

Species with well-developed lonsdaleoid dissepimentarium (18)
A. clinotabulatum, A. delepini, A. dibunoides, A. equitabulatum, A. expansum, A. fongi,
A. gangamoforme, A. longiseptatum, A. lonsdaleiforme = A. latevesiculosum,
A. majiobaense = A. nucleolum, A. moroccoense, A. parkinsoni, A. rarum, A. sahariense,
A. septentrionale, A. tanaica, A. varium, A. vaughani.

Axophyllum kirsopianum (Thomson & Nicholson, 1876)
Figs. 15a-d; Fig. 16

1876 *Carcinophyllum kirsopianum* Thomson & Nicholson, p. 70
1940 *Carcinophyllum kirsopianum* Thomson; Hill, p. 159, pl. 8, figs. 19-24.
1974 *Axophyllum kirsopianum* Thomson & Nicholson; Semenoff-Tian-Chansky, p. 211, pl. 57, figs. 1-2.

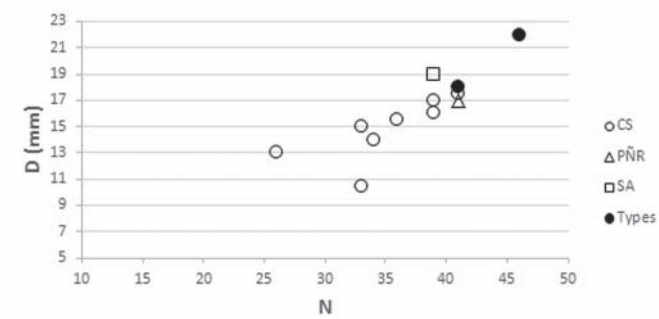

Figure 16. Graph plotting corallite diameter (D) versus number of major septa (N) for *Axophyllum kirsopianum.* CS = El Casar, PÑR = Peñarroya, SA = San Antonio.

— Gráfico de relación entre el diámetro del coralito (D) y el número de septos mayores (N) para *Axophyllum kirsopianum.* CS = El Casar, PÑR = Peñarroya, SA = San Antonio.

pars 2010 *Axophyllum* aff. *pseudo-kirsopianum* Semenoff-Tian-Chansky; Rodríguez & Said, p. 13, pl. 6, figs. 2-6.

Material. 12 specimens; 9 from El Casar (CS/11-4, CS/11-5, CS/13-2, CS/13-10, CS/14-2, CS/14-13, CS/14-27, CS/14-28, CS/16-1), 2 from Peñarroya (PÑR/1-3, PÑR/1-8 and 1 from San Antonio (SA/1-23). Brigantian, Guadiato Area.

Location, horizon and age. Located in Brigantian (upper Viséan, Mississippian) olistolites from El Casar, Peñarroya and San Antonio (Guadiato Area).

Diagnosis. *Axophyllum* 18 to 22 mm in diameter, 14-16 mm in tabularium diameter, 6-7 mm in axial structure diameter, having 41 to 46 septa of two orders. Major septa thick and withdrawn from the axial structure. Low development of lonsdaleoid dissepiments. Inner wall composed of thickened dissepiments. Axial structure large (1/3 of the diameter) and showing thick septal lamellae. Fibrous septal mesoplasm, lamellar stereoplasm.

Description. Trochoid corals with common rejuvenescences. The number of septa in adult stages varies between 33 and 41 in alar diameters from 10.5 to 19 mm. The tabularium diameter varies between 8.5 and 14.5 mm and the axial structure diameter varies from 6 to 7 mm. Undulating to festooned wall that may be doubled in thickness due to rejuvenescences. The dissepimentarium is composed of 1 or 2 rows of lonsdaleoid dissepiments plus 1 row of interseptal dissepiments that are thickened to form a conspicuous inner wall. In longitudinal section the dissepiments are regularly declined to the axis at about 45º (Fig. 15c). The major septa are long, mostly reaching the axial structure (Fig. 15a), but some are shorter (Fig. 15b, d). They are moderately thick and mostly straight, but some of them may be slightly undulating (Fig. 15d). Minor septa occur as crests on the dissepiments surface and penetrate slightly into the tabularium. The axial structure is large, reaching 1/3 or somewhat less of the alar diameter. The median plate is well developed and quite constant (Fig. 15a); the moderately thick radial lamellae are numerous. The axial tabellae are also moderately thick and conical in shape. The periaxial tabellae are concave, slightly declined to the axis (Fig. 15c). There are about 20 tabellae in one centimetre. The microstructure is typical of the genus, showing granulo-fibrous septal mesoplasm but lamellar wall and stereoplasmatic thickenings. There is little variability in the specimens assigned to this species. Only the degree of thickenings and density of elements in the axial structure show some variations.

Remarks. The specimens from Sierra Morena fit completely with the main features of this species. Large axial structure with thick anastomosed septal lamellae, reduced development of the lonsdaleoid dissepimentarium, thick septa, well-developed inner wall, etc. They are slightly smaller than the types, but some of the plots represented in Figure 15 correspond to young or early adult stages. The relationship N/D is basically the same. The Spanish specimens have been all recorded in Brigantian olistolites located in a Serpukhovian succession. Consequently, their late Viséan age is the same as the types.

Axophyllum pseudokirsopianum Semenoff-Tian-Chansky, 1974
Figs. 15e-h; Fig. 17

1974 *Axophyllum pseudokirsopianum* Semenoff-Tian-Chansky, p. 220, pl. 57, figs. 3-5; pl. 59, figs. 1-6; pl. 60, figs. 1.5; pl. 61, figs. 1-3, pl. 65, fig.1.
1981 *Axophyllum pseudokirsopianum* Semenoff-Tian-Chansky; Poty, p. 62, pl. 30, fig. 8.
1986 *Axophyllum* aff. *A. pseudokirsopianum* Semenoff-Tian-Chansky; Herbig, p. 208, Fig. 6, 1-2, fig. 7.
pars 2010 *Axophyllum* aff. *pseudo-kirsopianum* Semenoff-Tian-Chansky; Rodríguez & Said, p. 13, pl. 6, figs. 2-6.
aff. 2010 *Axophyllum* aff. *pseudo-kirsopianum* Semenoff-Tian-Chansky; Aretz, p. 337, fig. 6g-h.
2011 *Axophyllum pseudokirsopianum* Semenoff-Tian-Chansky; Denayer, Poty & Aretz, p. 168, pl. 9, fig. D.
2013b *Axophyllum* ex gr. *pseudokirsopianum* Semenoff-Tian-Chansky; Rodríguez, Somerville, Said & Cózar, p.8, fig. 5D

Material. 2 specimens; one from Antolín (ANT4/57), and other from Peñarroya (PÑR/4-14a). Brigantian, Guadiato Area.

Location, horizon and age. Recorded in Brigantian (upper Viséan, Mississippian) olistolite from Peñarroya and the Antolín Section, El Castillo Unit (Guadiato Area).

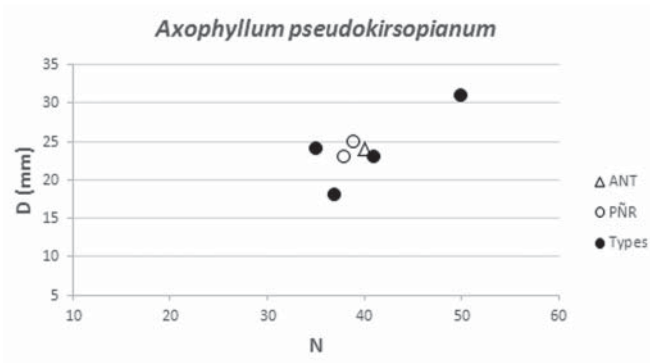

Figure 17. Graph plotting corallite diameter (D) versus number of major septa (N) for *Axophyllum pseudokirsopianum.* ANT = Antolín, PÑR = Peñarroya.
— Gráfico de relación entre el diámetro del coralito (D) y el número de septos mayores (N) para *Axophyllum pseudokirsopianum.* ANT = Antolín, PÑR = Peñarroya.

Diagnosis. Large *Axophyllum*, having 35-50 septa of two orders in 22-31 mm in diameter, 15-20 mm in tabularium diameter, and 7-13 mm in axial structure diameter. Major septa thick in the peripheral part, thinning to the axis. Minor septa long. Low development of lonsdaleoid dissepiments. Inner wall composed of thickened dissepiments. Axial structure large (1/3 of the diameter) and showing thick septal lamellae. Fibrous septal mesoplasm, lamellar stereoplasm.

Description. Trochoid corals showing common rejuvenescences and lateral expansions in young stages. There are 38 to 40 major septa in 23 to 25 mm of alar diameter. The tabularium diameter varies between 13 and 16 mm and the axial structure diameter varies between 7 and 7.5 mm. The external wall is moderately thick and festooned. The dissepimentarium is variable. In the periphery there are 1 to 3 rows of lonsdaleoid dissepiments that are variably developed in the circumference of the coral. There are 2 or 3 rows of interseptal dissepiments in the border of the tabularium that may form a slightly marked inner wall. The dissepiments are declined to the axis between 30º and 45º in the periphery, but they become almost vertical at the dissepimentarium/tabularium boundary (Fig. 15h). The major septa are long, reaching the axial structure or almost (Figs. 15f,g). They are moderately thick, thinning to the axis and frequently curved in their inner borders. The cardinal septum is always joined to the median plate of the axial structure. Minor septa are thinner than the majors and quite long (3/5 of majors), penetrating clearly into the tabularium (Fig. 15g). The axial structure is variable. The median plate is thick and constant (Fig. 15g); there are a number of radial lamellae slightly fewer than the number of septa. They may be thick and slightly twisted. The axial tabellae are thin and conical. The periaxial tabellae are concave and slightly declined to the axis. Biform tabularium, if present, is not well marked. The septal mesoplasm is granulo-fibrous and the wall and stereoplasmatic thickenings are lamellar. Differences between the specimens included in this species are related with the local development of the lonsdaleoid dissepiments and the thickness of elements in the axial structure.

Remarks. The measurements of the Spanish specimens are identical to those of the Saharan and Belgian specimens. The axial structure shows also the thick anastomosed septal lamellae and well-marked median plate. The septa are thick, but thinning to the axis and minor septa are long. The only difference is a higher development of lonsdaleoid dissepiments in one of the specimens (PÑR/4-14), but this feature is quite variable in the specimens of Semenoff-Tian-Chansky (1974). This species have been recorded in the upper Viséan from Belgium and Sierra Morena and in the upper Viséan and Serpukhovian from North Africa.

Axophyllum mendipense (Sibly, 1906).
Figs. 15i-n; Fig. 18

	1906	*Carcinophyllum mendipense* Sibly, p. 369, pl. 31, fig. 4.
	1908	*Carcinophyllum curkeense* Vaughan, p. 466.
	1909	*Carcinophyllum* sp. Douglas, p. 581, pl. 27, fig. 5.
pars	1911	Carcinophyllum θ Vaughan; Délépine, p. 400, pI. XIV, fig . 8.
	1913	*Carcinophyllum mendipense* Sibly; Salée, pI. 10, fig. 1.
	1923	*Carcinophyllum mendipense* Sibly; Demanet, p. 113.
	1930	“*Carcinophyllum*” *mendipense* Sibly; Ryder, p. 342, Fig. 2 .
	1981	*Axophyllum mendipense* (Sibly); Poty, p. 58, Fig. 28, 1-2.
	2011	*Axophyllum mendipense* (Sibly); Denayer, Poty & Aretz, p. 168, pl. 6 F.

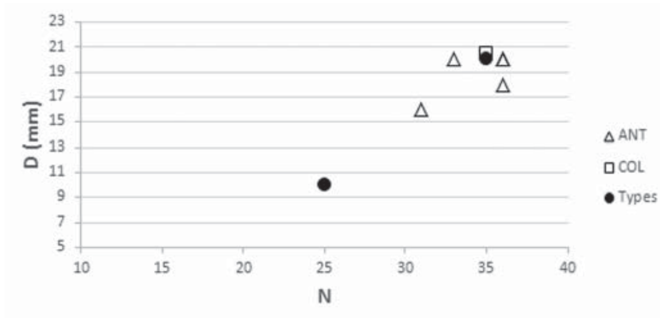

Figure 18. Graph plotting corallite diameter (D) versus number of major septa (N) for *Axophyllum mendipense.* ANT = Antolín, COL = El Collado. — Gráfico de relación entre el diámetro del coralito (D) y el número de septos mayores (N) para *Axophyllum mendipense.* ANT = Antolín, COL = El Collado.

Material. 7 specimens; 6 from Antolín, 1 from El Collado, Brigantian, Sierra del Castillo Unit, Guadiato Area.

Location, horizon and age. Recorded in Brigantian (upper Viséan, Mississippian) sections of Antolín and El Collado, El Castillo Unit (Guadiato Area).

Diagnosis. *Axophyllum*, having 25-35 septa of two orders in 10-20 mm in diameter, 8-15 mm in tabularium diameter, and 4-8 mm in axial structure diameter. Major septa thick. Minor septa short, just crests on the dissepiments and wall. Low development of lonsdaleoid dissepiments in a narrow dissepimentarium. Inner wall composed of thickened dissepiments. Axial structure 1/3 to 1/4 of the diameter. It shows a dense net composed of thick septal lamellae and conical axial tabellae. Fibrous septal mesoplasm, lamellar stereoplasm.

Description. Ceratoid to trochoid corals showing common radiciform processes and talons in their lower part (Fig. 15l). There are 31 to 36 major septa in 16 to 20 mm in alar diameter. The tabularium diameter varies from 13 to 18 mm and the axial structure diameter varies between 5 and 9 mm. The wall is thick, externally smooth to undulating. It may be reinforced with stereoplasmatic thickenings to form a septal stereozone. Dissepiments are scarce. Some lonsdaleoid and or interseptal dissepiments may occur with random distribution. When they are not covered by stereoplasm, they appear very elongated and declined between 45º and 60º to the axis. Major septa are quite thick, slightly thinning to the axis, long, reaching almost the axial structure (Fig. 15l), but rarely in contact with it, except the cardinal septum, that shows to be continuous with the median plate. Minor septa are thin, usually about 1/2 length of the majors, but mostly immersed in the septal stereozone. The axial structure is large, round?, about 1/3 of the diameter (Figs. 15m-n). It shows a moderately thick and constant median plate and numerous and thick radial lamellae. The thin axial tabellae are deeply conical and divided (Fig. 15k). The periaxial tabellae are concave and slightly declined to the axis. Septal mesoplasm is fibrous and the wall and stereoplasmatic thickenings are lamellar. The specimens recorded in Sierra Morena show little variability in most features, except in the density and declination of periaxial tabellae.

Remarks. The specimens from the Guadiato Area as well as the type specimen show general thickenings, few lonsdaleoid dissepiments, thick septa, large and dense axial structure. All measurements (D, Dt, Das, N) are the same as the type. The only difference is slightly shorter septa in adult stage. This species has been recorded from the uppermost Holkerian in Britain (Mitchell, 1989) and the upper Moliniacian from Belgium (Poty, 1981; Denayer *et al.*, 2011), basically the same stratigraphic level in the upper part of the lower Viséan. In Sierra Morena it occurs later, in the upper Asbian and lower Brigantian.

Axophyllum densum (Ryder, 1930)
Figs.15o-s; Fig. 19

Pars 1913 *Carcinophyllum vaughani* Salée, p. 256, pl. 10, fig. 4a-f, 5a-l.
1930 *"Carcinophyllum" densum*, Ryder, p. 346, fig. 4a-c.
1981 *Axophyllum densum* (Ryder); Poty, p. 61; fig. 54; Pl. 29, Fig. 8a-b.
? 1986 *Axophyllum densum* (Ryder); Herbig, p. 204, fig. 5.
1992 *Axophyllum densum* (Ryder); Rodríguez & Falces, p. 211, pl. 21, fig.3.
1994 *Axophyllum densum* (Ryder); Rodríguez & Falces, p. 196.
2005 *Axophyllum densum* (Ryder); Cózar & Somerville, fig. 12.12
2011 *Axophyllum densum* (Ryder); Denayer, Poty & Aretz, p. 167, pl. 9E.

Material. 58 Specimens; 1 from Cantera Castillo Section (CCS/11-9), 2 from El Collado Section (COL/7-1, COL/7-7), 4 from Cerro de los Santos Section (SS/1-1, 3a, 3b, 3c) 9 from Guadajira Section (GUA/1-1, 2, 5-11,), 33 from Navafría Section (NA2/1-30, 106, 111, 112), 5 from Cabezo del Almendro Section (AL/1-1, 3, 5, 7, 9), 3 from Cerro Almeña Section(CA-7-27, 37, 38) and 1 from Peñarroya Section (PÑR/3-13)

Location, horizon and age. Recorded in upper Asbian and lower Brigantian (upper Viséan, Mississippian). Cabezo del Almendro, Cerro de los Santos, Navafría, Guadajira and Cerro Almeña sections (Santos de Maimona Basin), Cantera Castillo, El Collado and Peñarroya sections (Guadiato Area).

Diagnosis. *Axophyllum*, having 20-34 septa of two orders in 5-15 mm in diameter, 4-13 mm in tabularium diameter, and 2-3 mm in axial structure diameter. Major septa almost reaching the axial structure. Thick septal stereozone in young stages that is interrupted by a few lonsdaleoid

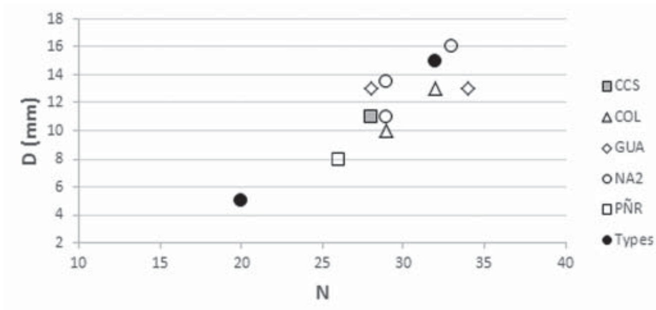

Figure 19. Graph plotting corallite diameter (D) versus number of major septa (N) for *Axophyllum densum.* CCS = Cantera Castillo, COL = El Collado, GUA = Guadajira, NA= Navafría, PÑR = Peñarroya.
— Gráfico de relación entre el diámetro del coralito (D) y el número de septos mayores (N) para *Axophyllum densum.* CCS = Cantera Castillo, COL = El Collado, GUA = Guadajira, NA= Navafría, PÑR = Peñarroya.

dissepiments in adult stage. Axial structure 1/3 to 1/5 of the diameter. Fibrous septal mesoplasm, lamellar stereoplasm.

Description. Small trochoid corals showing mostly eroded external surfaces. There are 26 to 33 major septa in 8 to 16 mm in alar diameter. The tabularium diameter varies from 6.5 to 14 mm and the axial structure diameter varies from 2.5 to 4 mm. The external wall is moderately thick. Its external surface is mostly smooth. It may be reinforced by stereoplasmatic thickenings. The dissepimentarium is narrow, composed of one discontinuous row of lonsdaleoid dissepiments and/or one row of interseptal dissepiments. The inner border of the dissepimentarium shows stereoplasmatic thickenings to form an inner wall. The major septa are moderately thick, showing thinning to the axis (Fig. 15r). They reach or almost reach the axial structure. Minor septa are mostly immersed in the septal stereozone and penetrate slightly into the tabularium. The cardinal septum is continuous with the median plate of the axial structure (Fig. 15s). It is 1/3 to 1/4 of the alar diameter and shows an irregular median plate and few radial lamellae variable in thickness. The thin axial tabellae are deeply conical. The periaxial tabellae are flat or slightly concave and somewhat declined to the axis (Figs. 15p-q). Septal stereoplasm is fibrous and wall and stereoplasmatic thickenings are lamellar. The variability of the specimens from Sierra Morena is located in the degree of thickenings, in the density of periaxial tabellae and in the number and density of radial lamellae.

Remarks. The specimens from Sierra Morena show slightly less dense septal stereozone than the types, but their measurements fit well with those of the types. *Axophyllum densum* is one of the most abundant species of this genus in Sierra

Morena. It has been recorded in Los Santos de Maimina Basin (Rodríguez & Falces 1992) and in several localities from the Guadiato Area. It has been recorded in the upper Asbian and lower Brigantian. It is quite common in the upper Viséan from Western Palaeotethys.

Axophyllum vaughani (Salée, 1913)
Figs. 20a-e; Fig. 21

1905 "*Clisiophyllum" (Carcinophyllum*) θ Vaughan, p. 285, pI. 24, fig. 3-3b.
1911 *Carcinophyllum* θ Vaughan, p. 337, pI. 31, fig. 5.
pars 1913 *Carcinophyllum vaughani* Salée, p. 256, pI. 10, fig . 2a, b, 3.
1925 *Carcinophyllum vaughani* Salée; Smyth, pI. 3, fig. 5a, b.
1930 "*Carcinophyllum*" *vaughani* Salée; Ryder, p. 340, fig. 5 a-l.
1938 *Carcinophyllum* aff. *vaughani* Salée; Gorsky, p. 82, pl. 17, fig. 5.
1950 *Carcinophyllum vaughani* Salée; Termier & Termier, p. 93, pl. 42, fig. 23, pl. 43, figs. 15-16.
1973 *Carcinophyllum vaughani* Salée; Sayutina, p. 108, pl.17, figs. 3, 4.
1981 *Axophyllum vaughani* (Salée); Poty, p. 59, fig. 52, pl. 28, figs. 3, 4.
1989 *Axophyllum vaughani* (Salée); Wu & Zhao, p. 141.
1992 *Axophyllum* cf. *vaughani* (Salée); Rodríguez & Falces, p. 210, pl. 21, fig. 2.
1997 *Axophyllum vaughani* (Salée); Somerville, pl. 2, fig. 3.
2011 *Axophyllum vaughani* (Salée); Denayer, Poty & Aretz, p. 168, pl. 7A.

Material. 12 specimens; 1 from El Collado (COL/2-2), 2 from El Casar (CS/14-15, CS/24-7), 3 from Guadajira (GUA/1-1, GUA/1-3, GUA/1-4), 4 from Navafría (NA2/31, 32, 107, 108,) 2 from Peñarroya (PÑR/4-2, PÑR/4-11).

Location, horizon and age. Recorded in upper Asbian and lower Brigantian (upper Viséan, Mississippian). Navafría and Guadajira sections (Santos de Maimona Basin), El Collado, El Casar and Peñarroya sections (Guadiato Area).

Diagnosis. *Axophyllum*, having 25-36 septa of two orders in 12-16.5 mm in diameter, 7-10 mm in tabularium diameter, and 3-4 mm in axial structure diameter. Major septa reaching or almost reaching the axial structure. Minor septa short to absent. Dissepimentarium showing moderate development of the lonsdaleoid dissepiments. Axial structure 1/3 to 1/5 of the diameter. Fibrous septal mesoplasm, lamellar stereoplasm.

Description. Trochoid corals with irregular external surface, partly eroded, partly showing longitudinal wrinkles and common transversal furrows and rejuvenescences. There are 28 to 37 major septa in 12 to 18 mm in alar diameter. The tabularium diameter varies from 9 to 13 mm and the axial structure diameter varies from 3.5 to 7 mm. The wall is thick, festooned when the septa do not reach it. The dissepimentarium is composed of 1 or 2 rows of lonsdaleoid dissepiments that form a discontinuous lonsdaleoid ring, and 1or 2 rows of interseptal dissepiments somewhat thickened in some cases, but the inner wall is not continuous (Figs. 20a-d). Major septa long and moderately thick. Cardinal septum is longer and connected with the median plate of the axial structure. Minor septa short and thin occur as crests on the surface of the lonsdaleoid dissepiments and penetrate slightly into the tabularium (Fig. 20d). The axial structure is 1/3 to 1/4 of the alar diameter. It shows a moderately thick median plate that may be shortened and a few irregular radial lamellae (Fig. 20b). Axial tabellae are thin and deeply conical. Periaxial tabellae are declined to the axis (Fig. 20e). Septal mesoplasm is granulo-fibrous; stereoplasm thickenings and wall are lamellar. The population from Los Santos de Maimona Basin is very homogeneous, showing little variation in the density of elements in the axial structure and in the development of the lonsdaleoid dissepiments. The specimens from the Guadiato Basin show better developed inner wall, slightly longer minor septa, denser axial structure and somewhat higher number of septa for similar diameter, but also very close to the measurements of the British types.

Remarks. The measurements of the Spanish specimens fit completely with those of the types. The development of the lonsdaleoid dissepiments is highly variable in North-western Europe; the specimens described by Poty (1981) from Belgium show a much larger dissepimentarium than the type from Britain. However, the measurements are similar, and young stages are identical. The Spanish specimens show a moderate development of the lonsdaleoid dissepiments, similar to that of the type. In Sierra Morena *Axophyllum vaughani* has a similar stratigraphic range as *A. densum* (upper Asbian-lower Brigantian). This species has one of the largest geographical distributions, because it has been recorded as far as China to the East and as far as North Africa to the South. The Chinese specimens show basically identical features to the Western Palaeotethys specimens. Its stratigraphical distribution is restricted to the Asbian and Brigantian.

Axophyllum tazoultense Semenoff-Tian-Chansky, 1974
Figs. 20f-k; Fig. 22

1935 *Carcinophyllum* cf. *welchi* Ryder; Menchikoff & Hsu, p. 249, Pl. 10, fig. 8.
1974 *Axophyllum tazoultense* Semenoff-Tian-Chansky, p. 212, fig. 81, pl. 54, figs. 1-4.
1999 *Axophyllum tazoultense* Semenoff-Tian-Chansky; Liao & Rodríguez, p. 555, fig. 6.5a-c, 6-a-d

Material. 6 specimens from El Casar (CS/2-1, 3; CS/12-3; CS/13-1, 4; CS/22-5)

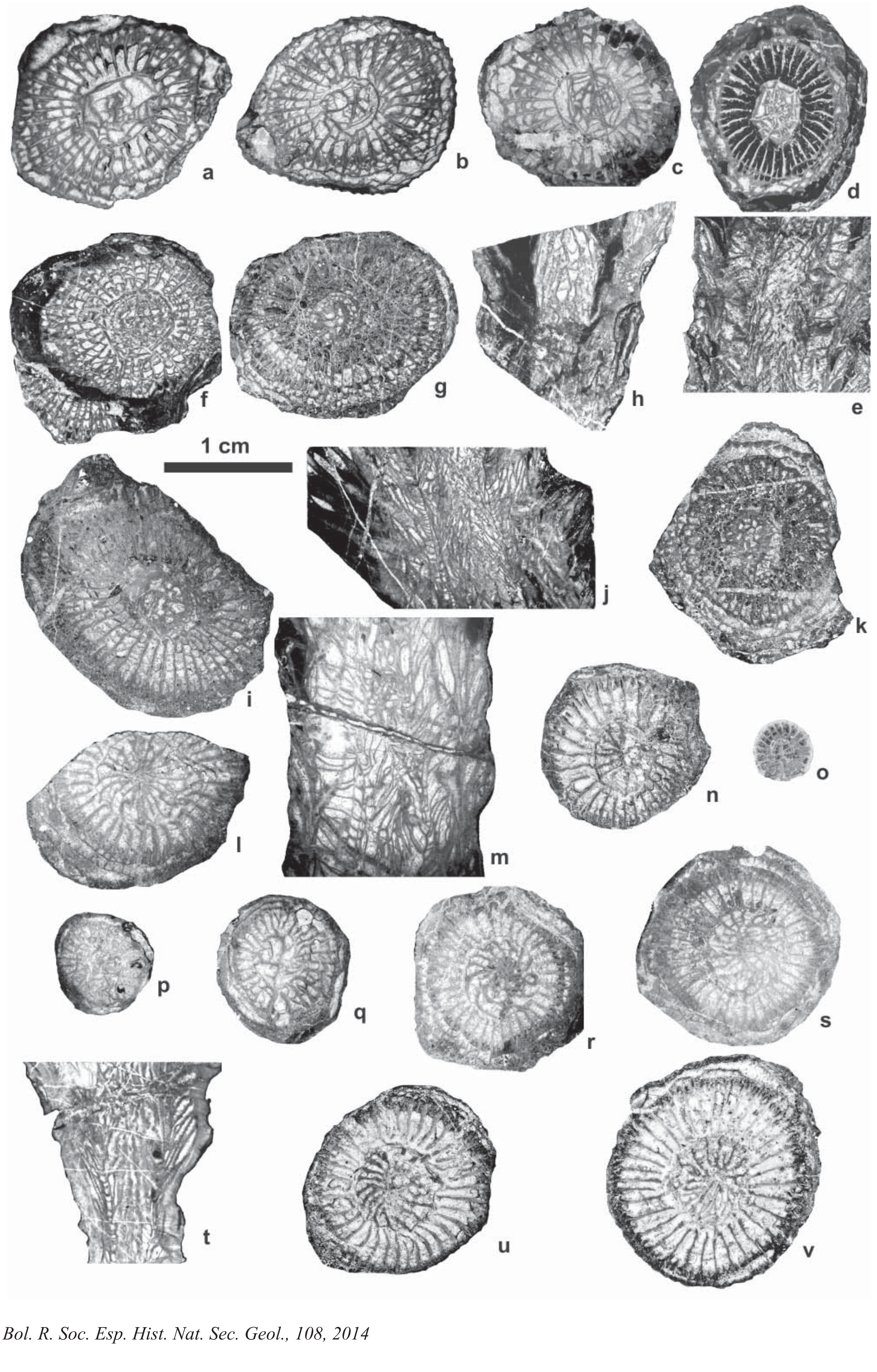
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Figure 20. *Axophyllum vaughani* **a)** Specimen GUA/1-1, transverse section. **b)** Specimen GUA/1-4, transverse section. **c)** Specimen NA/2-107, transverse section. **d-e)** Specimen CS/14-15, **d:** transverse section, **e:** longitudinal section. *Axophyllum tazoultense* **f)** Specimen CS/2-3, transverse section. **g-h)** Specimen CS/12-3, **g:** transverse section, **h:** longitudinal section. **i-j)** Specimen CS/13-1, **i:** transverse section, **j:** longitudinal section. **k)** Specimen CS/13-4, transverse section. *Axophyllum spiralum* sp. nov. **l-m)** Specimen CS/5-1 (paratype), **l:** transverse section, **m:** longitudinal section. **n-o)** Specimen CS/9-9 (paratype), **n:** transverse section, adult stage, **o:** transverse section, early young stage. **p-s)** Specimen CS/9-1 (paratype), transverse serial sections from late young stage to adult stage. **t-u)** Specimen CS/15-2 (holotype), **t:** longitudinal section, **u:** transverse section. **v)** Specimen CS/25-11 (paratype), transverse section. Scale bar valid for all figures.

— *Axophyllum vaughani* **a)** Ejemplar GUA/1-1, sección transversal. **b)** Ejemplar GUA/1-4, sección transversal. **c)** Ejemplar NA/2-107, sección transversal. **d-e)** Ejemplar CS/14-15, **d:** sección transversal, **e:** sección longitudinal. *Axophyllum tazoultense* **f)** Ejemplar CS/2-3, sección transversal. **g-h)** Ejemplar CS/12-3, **g:** sección transversal, **h:** sección longitudinal. **i-j)** Ejemplar CS/13-1, **i:** sección transversal, **j:** sección longitudinal. **k)** Ejemplar CS/13-4, sección transversal. *Axophyllum spiralum* sp. nov. **l-m)** Ejemplar CS/5-1 (paratipo), **l:** sección transversal, **m:** sección longitudinal. **n-o)** Ejemplar CS/9-9 (paratipo), **n:** sección transversal, estadio adulto, **o:** sección transversal, estadio juvenil temprano. **p-s)** Ejemplar CS/9-1 (paratipo), secciones seriadas transversales desde el estadio juvenil tardío hasta el estadio adulto. **t-u)** Ejemplar CS/15-2 (holotipo), **t:** sección longitudinal, **u:** sección transversal. **v)** Ejemplar CS/25-11 (paratipo), sección transversal. Escala válida para todas las figuras.

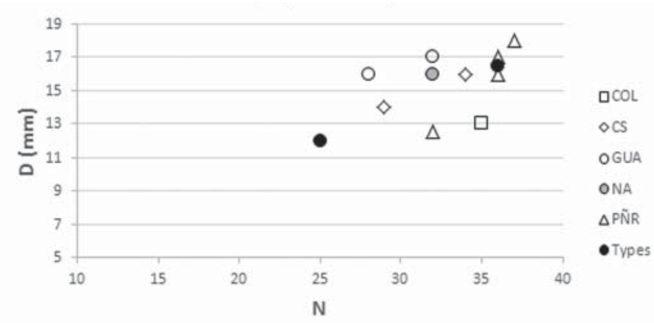

Figure 21. Graph plotting corallite diameter (D) versus number of major septa (N) for *Axophyllum vaughani*. COL = El Collado, CS = El Casar, GUA = Guadajira, NA= Navafría, PÑR = Peñarroya.

— Gráfico de relación entre el diámetro del coralito (D) y el número de septos mayores (N) para *Axophyllum vaughani.* COL = El Collado, CS = El Casar, GUA = Guadajira, NA= Navafría, PÑR = Peñarroya.

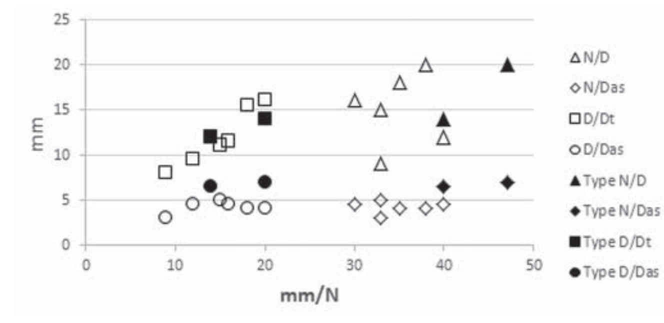

Figure 22. Graph plotting corallite diameter (D)/ tabularium diameter (Dt)/axial structure diameter (Das) versus number of major septa (N) for *Axophyllum tazoultense*.

— Gráfico de relación entre el diámetro del coralito (D)/ el diámetro del tabulario (Dt)/el diámetro de la estructura axial (Das) y el número de septos mayores (N) para *Axophyllum tazoultense*.

Location, horizon and age. Recorded in Brigantian (upper Viséan, Mississippian) from El Casar north-western extension of the Guadiato Area).

Diagnosis. *Axophyllum*, having 40-47 septa of two orders in 14-20 mm in diameter, 12-14 mm in tabularium diameter, and 7-8 mm in axial structure diameter. Major septa reaching or almost reaching the axial structure. Minor septa penetrating into the tabularium. Dissepimentarium showing interseptal dissepiments, lonsdaleoid dissepiments if present eroded in the type. Axial structure large, with irregular median plate; densely packed in the periphery, loosely packed in the axis. Axial tabellae gently declined to the periphery in the axis, but steeply declined in the periphery. Periaxial tabellae concave and declined to the axis. Fibrous septal mesoplasm, lamellar stereoplasm.

Description. Partly eroded trochoid corals showing deep calices and common rejuvenescences. There are 30 to 40 major septa in 9 to 20 mm in alar diameter. The tabularium diameter varies from 8 to 16 mm and the axial structure diameter varies from 3 to 5 mm. The external wall is thick and festooned. The dissepimentarium is variable. Usually not very wide, composed of 1 or 2 rows of lonsdaleoid dissepiments and 1 to 3 rows of interseptal dissepiments (Figs. 20g,k). The inner border may be thickened to form an inner wall (Fig. 20k), but in some specimens it is inconspicuous. The dissepiments are elongated and steeply declined to the axis (Figs. 20h,j). The major septa are long, reaching the axial structure and in many cases in contact with it (Fig. 20f). The cardinal septum is continuous with the median plate (Fig. 20f). Length of minor septa are about 1/2 that of majors. Both types of septa are quite thin and slightly undulating; minor septa thinner than majors. The axial structure is composed of a well-marked and constant, but not very thick median plate and some radial lamellae; they are few in the axial part, but numerous in the periphery (Figs. 20f,g,i). Axial tabellae are thin and also more steeply declined in the periphery, giving to the axial structure a very typical aspect, much more dense in the periphery than in the axis. The periaxial tabellae are flat to concave and slightly declined to the axis (Fig. 20j). The septal mesoplasm is fibrous; the wall and stereoplasmatic thickenings are lamellar. The variability in the specimens assigned to this species in Sierra Morena is quite high, and comprise almost any structural element, except the axial structure. The development of lonsdaleoid and interseptal dissepiments vary from one specimen to another. Also, the relationship between the number of septa and alar diameter, the thickness of structures and degree of development of stereoplasmatic thickenings is variable. These specimens have been grouped under the species *Axophyllum tazoultense* due to their very characteristic axial structure, which is identical to that of the type.

Remarks. *Axophyllum tazoultense* is a very characteristic species, due to its axial structure that shows a dense peripheral zone and a loose axial zone. The specimens from Sierra Morena shows clearly that feature. Their measurements are similar to the type, but the number of septa is somewhat lower for similar diameters and the inner wall is better marked than in the type. The differences are considered here as ecological variations or acceptable differences taking into account the geographic distance. However, this species has been also recorded in the upper Viséan from Tarim Basin, China (Liao & Rodríguez 1999), where it shows closer measurements but domical, not conical axial tabellae.

Axophyllum spiralum sp. nov.
Figs. 20l-v; Fig. 23

pars 2010 *Axophyllum* aff. *pseudo-kirsopianum* Rodríguez & Said, p. 13.

Derivatio nominis. The name of this species refers to the marked spiral disposition of radial lamellae in the axial structure.

Holotype. Specimen CS/15-2. Stored in the Department of Paleontology of the Complutense University. Rest of the specimens are regarded as paratypes.

Type locality, horizon and age. El Casar, Badajoz Province, North-west extension of the Guadiato Area, Brigantian, upper Viséan, Mississippian.

Material. 9 specimens from El Casar (CS/5-1, CS/9-1, 9, CS/15-2, CS/24-8, 13a, 13b, CS/25-2, 10, 11).

Diagnosis. *Axophyllum*, having 30-38 major septa in 10-20 mm in diameter, 8-18 mm in tabularium diameter, and 4-8 mm in axial structure diameter. Major septa reaching or almost reaching the axial structure. Minor septa short, penetrating slightly into the tabularium. Narrow dissepimentarium only developed in adult stages showing lonsdaleoid dissepiments and one row of thickened interseptal dissepiments that form a conspicuous inner wall. Axial structure large (1/2 to 1/3 of the diameter), with irregular median plate, thick, anastomosed and twisted radial lamellae and thin conical tabellae. Periaxial tabellae concave and declined to the axis. Fibrous septal mesoplasm, lamellar stereoplasm.

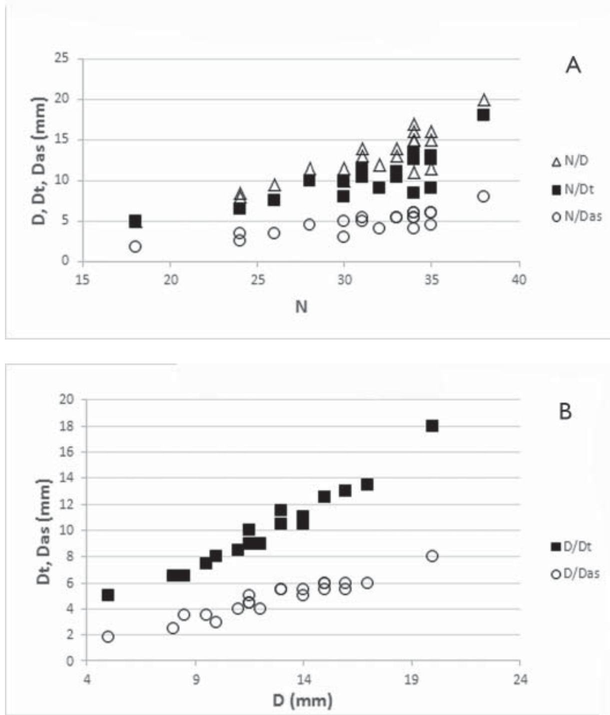

Figure 23. (A) Graph plotting corallite diameter (D)/ tabularium diameter (Dt)/axial structure diameter (Das) versus number of major septa (N) for *Axophyllum spiralum.* (B) Graph plotting corallite diameter (D) versus tabularium diameter (Dt) and axial structure diameter (Das) for *Axophyllum spiralum.*
— (A) Gráfico de relación entre el diámetro del coralito (D)/ el diámetro del tabulario (Dt)/el diámetro de la estructura axial (Das) y el número de septos mayores (N) para *Axophyllum spiralum.* (B) Gráfico de relación entre el diámetro del coralito (D), el diámetro del tabulario (Dt) y el diámetro de la estructura axial (Das) para *Axophyllum spiralum.*

Description. Ceratoid to cylindrical corals with irregular external wall showing transversal wrinkles and rejuvenescences. There are 30 to 38 major septa in 10 to 20 mm in alar diameter. The tabularium diameter varies from 8 to 18 mm and the axial structure diameter varies from 4 to 8 mm. The wall is moderately thick and may be doubled in thickness because of rejuvenescences. The marginarium is composed of a septal stereozone in young stages, which is progressively substituted by one or two incomplete rows of lonsdaleoid dissepiments. The inner row is covered by stereoplasm that forms a conspicuous inner wall.

In longitudinal section the dissepiments are very elongated and steeply declined to the axis (>60º) (Figs. 20m,t). Major septa are long; some of them reach the axial structure (Figs. 20l,n,s,u,v), some others are very close to it. They are moderately thick, thinning to the axis, but some of them may have a rhopaloid inner end. In young stages, both the cardinal and the counter septa are in continuity with the median plate of the axial structure (Fig. 20q). In adult stages, only the cardinal septum is in contact with it (Fig. 20v). Minor septa are short and thin. In young stages they are immersed in the septal stereozone, in adult stages they occur as crests on the surface of the lonsdaleoid dissepiments and in the inner wall (Figs. 20s,v). The axial structure shows a median plate that in some cases is indistinguishable from the radial lamellae. These are thick, anastomosed, twisted and numerous (Figs. 20l,r,s,u,v) (their number is somewhat fewer than the major septa). The axial tabellae are thin, conical, becoming vertical or almost in the external border of the axial structure (Fig. 20m). The periaxial tabellae show a low density (10-15 each cm). They are concave to flat and horizontal or slightly declined to the axis (Fig. 20t). Septal mesoplasm is fibrous; wall and stereoplasmatic thickenings are lamellar. The specimens from El Casar show a low variability, reflected only in the degree of twisting of the radial lamellae, the development of one or two lonsdaleoid rows and the density of elements in the axial structure.

Remarks. *Axophyllum spiralum* is close to species of the *Axophyllum kirsopianum* group, which have scarce lonsdaleoid dissepiments and a large axial structure. From *A. mendipense* it differs in having a higher number of septa for identical diameters, and a less dense axial structure having more twisted radial lamellae. From *Axophyllum kirsopianum* it differs in having a smaller size, lower number of septa for similar diameters and larger axial structure with more twisted radial lamellae. From *Axophyllum pseudokirsopianum* it differs in having a smaller size and larger axial structure. It has been recorded in a single locality, where it is the most abundant species. Its features indicate a possible evolution either from *Axophyllum kirsopianum* by the development of a larger axial structure or from *Axophyllum pseudokirsopianum* by the reduction of its size. As its only record is in the lower Brigantian, which is slightly later than the first occurrence of *A. kirsopianum* and earlier than the first occurrence of *A. pseudokirsopianum* (specimens from the Sahara are Serpukhovian, but recorded specimens from Belgium (Poty, 1981, Denayer et al., 2011) are located in the upper Warnantian = upper part of the lower Asbian), the first hypothesis is the most probable one. *A. spiralum* has close measurements and development of lonsdaleoid dissepiments to *A. compositum* from the Urals and *A. stereoseptum* from China, but it differs from those species in possessing a much larger axial structure and more twisted radial lamellae. In addition, it is somewhat larger than the Russian species and smaller than the Chinese species. The axial structure of *A. spiralum* shows high similarities with that of *Gangamophyllum spiroidea*. However, the latter lacks a median plate and has domical, not conical axial tabellae.

Axophyllum cozari sp. nov.
Figs. 24a-d; Fig. 25

Derivatio nominis. The name of this species refers to Dr. Pedro Cózar, who found the coral locality (Antolín 1) and collected the first specimens.

Holotype. Specimen ANT2/1-39. Rest of the specimens are regarded as paratypes. Stored in the Department of Paleontology of the Complutense University.

Type locality, horizon and age. Antolín Section, Córdoba Province, Sierra Boyera Block, Guadiato Area, Brigantian, (upper Viséan, Mississippian).

Material. 5 specimens from Antolín Section (ANT1/1-22b, ANT1/1-39, ANT2/1-39, ANT2/1-74, ANT4/2-1).

Diagnosis. *Axophyllum*, having 34-39 major septa in 24-32 mm in diameter, 16-18 mm in tabularium diameter, and 7-9 mm in axial structure diameter. Major septa reaching or almost reaching the axial structure. Minor septa long, penetrating clearly into the tabularium. Wide lonsdaleoid dissepimentarium and 1 to 3 rows of interseptal dissepiments; the inner one forms a conspicuous inner wall. Axial structure 1/3 to 1/4 of the alar diameter, with strongly thickened median plate, thick, anastomosed and twisted radial lamellae and conical tabellae. Periaxial tabellae concave and declined to the axis. Fibrous septal mesoplasm, lamellar stereoplasm.

Description. Trochoid to cylindrical corals showing discontinuous external wall that show numerous rejuvenescences. The external walls partly eroded in all specimens. There are 34 to 39 major septa in 24 to 28 mm in alar diameter. The tabularium diameter varies from 16 to 18 mm and the axial structure diameter varies from 7 to 9 mm. The wall is moderately thick, discontinuous and may comprise 2 or 3 rings in one single transverse section, due to rejuvenescences. The dissepimentarium is composed of 2-4 rows of large lonsdaleoid dissepiments and 1 to 3 rows of interseptal dissepiments that may be thickened in a discontinuous inner wall (Figs. 24b,c). The major septa are moderately thick, slightly thinning to the axis and long, almost reaching the axial structure, but rarely being in contact with it. The cardinal septum is somewhat thicker (Fig. 24b). In young stages it is connected with the median plate, but in adult stages it becomes separated from the axial structure. Minor septa are thin and long (2/3 length of majors), clearly penetrating into the tabularium (Figs. 24b,c), but they are only multiple crests

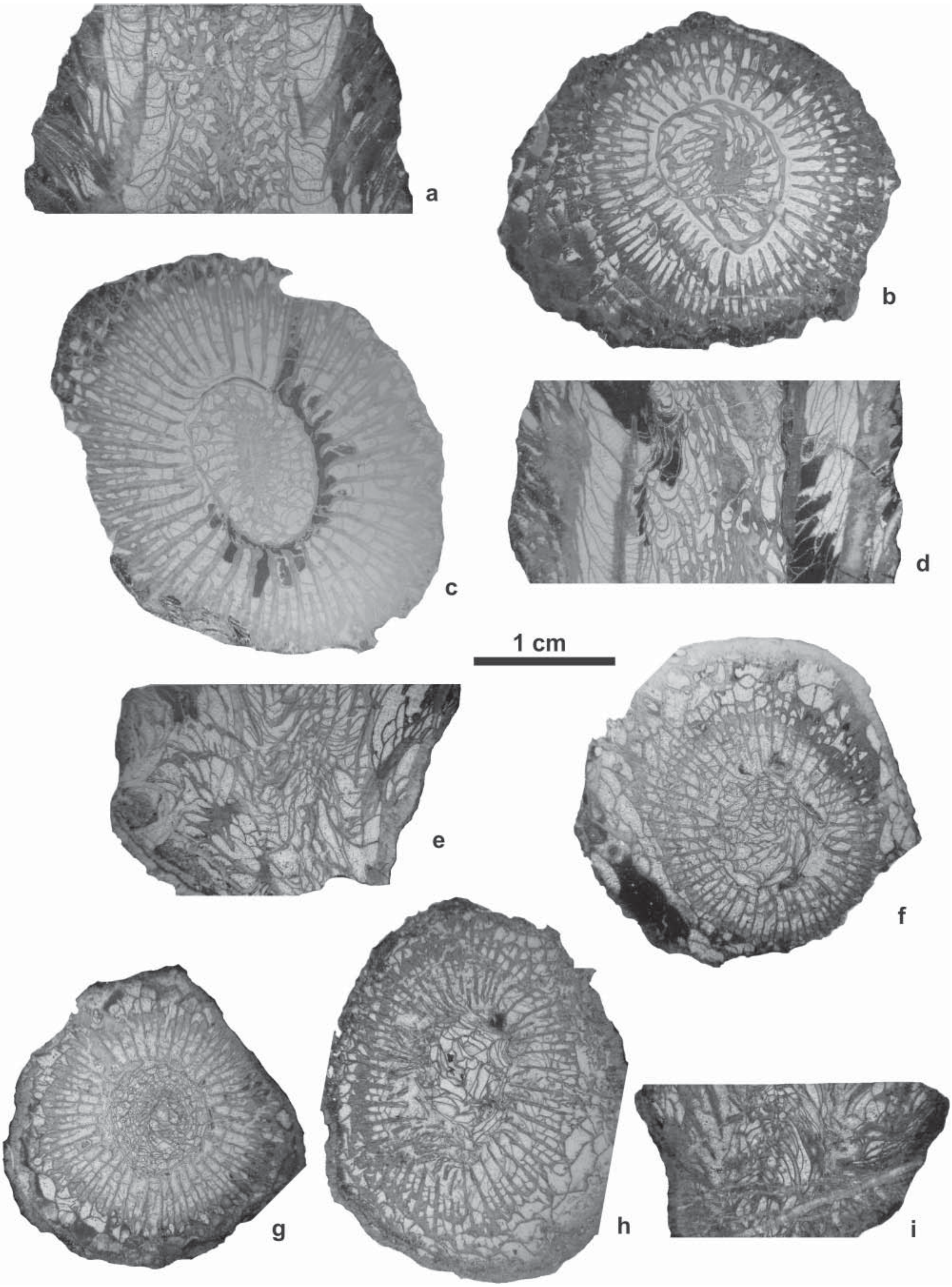
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Figure 24. *Axophyllum cozari* sp. nov. **a-b)** Specimen ANT2/1-39 (holotype), **a:** longitudinal section, **b:** transverse section. **c-d)** Specimen ANT1/1-39 (paratype), **c:** transverse section, **d:** longitudinal section. *Axophyllum julianaense* sp. nov. **e-f)** Specimen SA/2-3 (holotype), **e:** longitudinal section, **f:** transverse section. **G)** Specimen SA/0-42 (paratype), transverse section. **h-i)** Specimen SA/2-48 (paratype), **h:** transverse section, **i**: longitudinal section. Scale bar valid for all figures.

— *Axophyllum cozari* sp. nov. **a-b)** Ejemplar ANT2/1-39 (holotipo), **a:** sección longitudinal, **b:** sección transversal. **c-d)** Ejemplar ANT1/1-39 (paratipo), **c:** sección transversal, **d:** sección longitudinal. *Axophyllum julianaense* sp. nov. **e-f)** Ejemplar SA/2-3 (holotipo), **e:** sección longitudinal, **f:** sección transversal. **G)** Ejemplar SA/0-42 (paratipo), sección transversal. **h-i)** Ejemplar SA/2-48 (paratipo), **h:** sección transversal, **i**: sección longitudinal. Escala válida para todas las figuras.

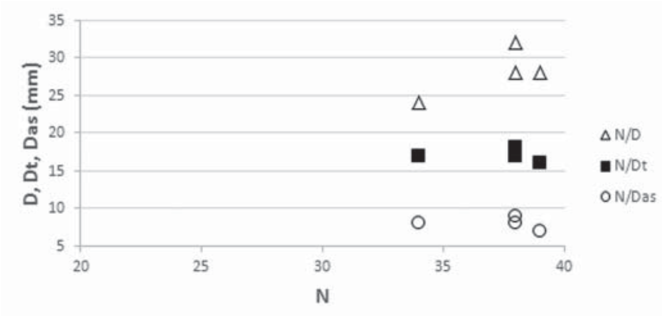


Figure 25. Graph plotting corallite diameter (D)/ tabularium diameter (Dt)/axial structure diameter (Das) versus number of major septa (N) for *Axophyllum cozari.*

— Gráfico de relación entre el diámetro del coralito (D)/ el diámetro del tabulario (Dt)/el diámetro de la estructura axial (Das) y el número de septos mayores (N) para *Axophyllum cozari.*

on the surface of the lonsdaleoid dissepiments. The axial structure is large (1/3 to 1/4 of the alar diameter) and shows a thick median plate that in adult stages is separated from the cardinal septum (Figs. 24b,c). Its outline is irregular, showing changes of direction. The radial lamellae are also thick, numerous and twisted. They are limited by a thickened axial tabella, showing a well-marked rounded boundary of the axial structure (Figs. 24b,c). Axial tabellae are conical, increasing their declination in the periphery to become vertical or almost (Fig. 24d). The periaxial tabellae are concave and declining to the axis (Figs. 24a,d). They show a clear biform organization, changing from almost horizontal to steeply declined to the axis in the tabularium/dissepimentarium boundary. The septal mesoplasm is fibrous. The thickenings and the wall are lamellar. The peripheral part of the septa show piles of microlamellae that form small spines on the surface of the lonsdaleoid dissepiments. The specimens assigned to this species show little variability, related to the number of radial lamellae in the axial structure, to the development of lonsdaleoid dissepiments and to the degree of declination of the periaxial tabellae.

Remarks. *Axophyllum cozari* shows a general appearance close to *A. pseudokirsopianum*. It differs though from the species of Semenoff-Tian-Chansky (1974) in having a higher development of lonsdaleoid dissepiments, a thicker median plate and lower number of septa for similar diameters. It is also close to *A. kirsopianum*, but differs from it also by its larger size, higher development of lonsdaleoid dissepiments and thicker median plate. From species having similar development of lonsdaleoid dissepiments, such as *A. vaughani* and *A. lonsdaleiforme*, it differs in having a larger axial structure with thicker median plate and more twisted radial lamellae, and a much larger size for similar number of septa. From *A. spiralum* that shows a similar axial structure, it differs by a higher development of lonsdaleoid dissepiments and a larger size for similar number of septa. *Axophyllum cozari* may have evolved from *Axophyllum kirsopianum* by the development of a larger lonsdaleoid dissepimentarium plus thickening of the median plate. None of the species from Middle and Eastern Palaeotethys show remarkable similarities to this species.

Axophyllum julianaense sp. nov.
Figs. 24e-i; Fig. 26

Derivatio nominis. The name of this species refers to the Juliana stream close to the San Antonio-La Juliana Section, where the specimens have been recorded.

Holotype. Specimen SA/2-3. Rest of the specimens are regarded as paratypes. Stored in the Department of Paleontology of the Complutense University.

Type locality, horizon and age. San Antonio-La Juliana Section, Córdoba Province, San Antonio-La Juliana Unit, Guadiato Area, Pendleian, Serpukhovian, Mississippian.

Material. 7 specimens from San Antonio-La Juliana Section (SA/0-42, SA/2-3, SA/2-48, SA/2-58, SA/2-210, SA/2-216, SA/4-57).

Diagnosis. *Axophyllum*, having 39-44 major septa in 20-24 mm in diameter, 13-16.5 mm in tabularium diameter, and 6-8 mm in axial structure diameter. Major septa reaching the axial structure. Minor septa long, penetrating moderately into the tabularium. Lonsdaleoid dissepimentarium and

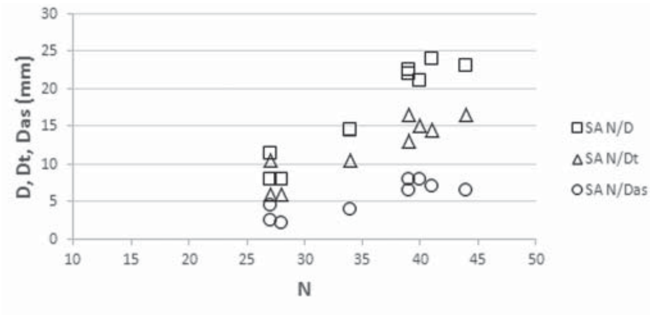


Figure 26. Graph plotting corallite diameter (D)/ tabularium diameter (Dt)/axial structure diameter (Das) versus number of major septa (N) for *Axophyllum julianaense*.
— Gráfico de relación entre el diámetro del coralito (D)/ el diámetro del tabulario (Dt)/el diámetro de la estructura axial (Das) y el número de septos mayores (N) para *Axophyllum julianaense*.

one row of thickened interseptal dissepiments that form a variable inner wall. Axial structure 1/3 to 1/4 of the alar diameter, with an irregular median plate and thin radial lamellae and conical tabellae. Periaxial tabellae biform, concave and declined to the axis. Fibrous septal mesoplasm, lamellar stereoplasm.

Description. Large solitary, trochoid corals. There are 39 to 44 major septa in 20 to 24 mm in alar diameter. The tabularium diameter varies from 13 to 16.5 mm and the axial structure diameter varies from 6 to 8 mm. The wall is very thick and mainly festooned. The dissepimentarium is composed of 1 to 3 rows of lonsdaleoid dissepiments, very variable in size and distribution and an inner row of interseptal dissepiments that show irregular thickenings producing a discontinuous inner wall (Figs. 24f,g,h). The major septa are long, many of them reaching and being in contact with the axial structure (Figs. 24f,h). They are moderately thick and some of them show rhopaloid inner ends. The minor septa are thin and long, penetrating clearly into the tabularium (1/3-1/2 length of majors). The axial structure is large (1/3 to 1/4 of the alar diameter); it is composed of a thin, irregular and inconspicuous median plate, a variable number of thin, twisted and anastomosed radial lamellae (Figs. 24f,g), and thin conical axial tabellae (Fig. 24i). Its border is not clearly marked and shows some expansions in the position of some septa, including the cardinal septum. The periaxial tabellae are concave and horizontal or slightly declined to the axis (Fig. 24e). Septal mesoplasm is fibrous; stereoplasmatic thickenings and wall are lamellar. The variability in the studied specimens affect mainly the number of radial lamellae, outline of the median plate and general density of the axial structure.

Remarks. *Axophyllum julianaense* shows a similar number of septa to *A. kirsopianum* and *A. pseudokirsopianum*, but it is larger than the former and smaller than the latter. It differs from all the other species of the *A. kirsopianum* group by a high development of lonsdaleoid dissepiments. It has similar development of lonsdaleoid dissepiments as *A. vaughani*, but it has a better marked inner wall, is larger and shows a higher number of septa. It also shows some similarities with *A. lonsdaleiforme* in the lonsdaleoid dissepimentarium and in the appearance of the axial structure, but the septa are longer, the wall is thicker and the size and number or septa are larger. It could have evolved from *A. lonsdaleiforme* by an increase in size and elongation of major septa. The species from San Antonio shows the same diameter, number of septa and development of lonsdaleoid dissepiments as *A. clinotabulatum* from China, but it differs from the Chinese species in having a thicker wall, longer major and minor septa, fewer rows of interseptal dissepiments, better developed inner wall and larger axial structure. Consequently, the similarities must be due to convergence.

Axophyllum spinosum sp. nov.
Figs. 27a-r, 28

2005 Axophyllido indeterminado sp. 1 Gómez-Herguedas & Rodríguez, p. 91, pl. 6, figs. 2,3.
2005 Axophyllido indeterminado sp. 2 Gómez-Herguedas & Rodríguez, p. 92, pl. 6, figs. 4,5.
2005 Axophyllido indeterminado sp. 3 Gómez-Herguedas & Rodríguez, p. 95, pl. 6, figs. 6,11.

Derivatio nominis. The name of this species refers to the spiny structure of the septa.

Holotype. Specimen COR/1-52. All other specimens of the same locality are regarded as paratypes. Stored in the Department of Paleontology of the Complutense University.

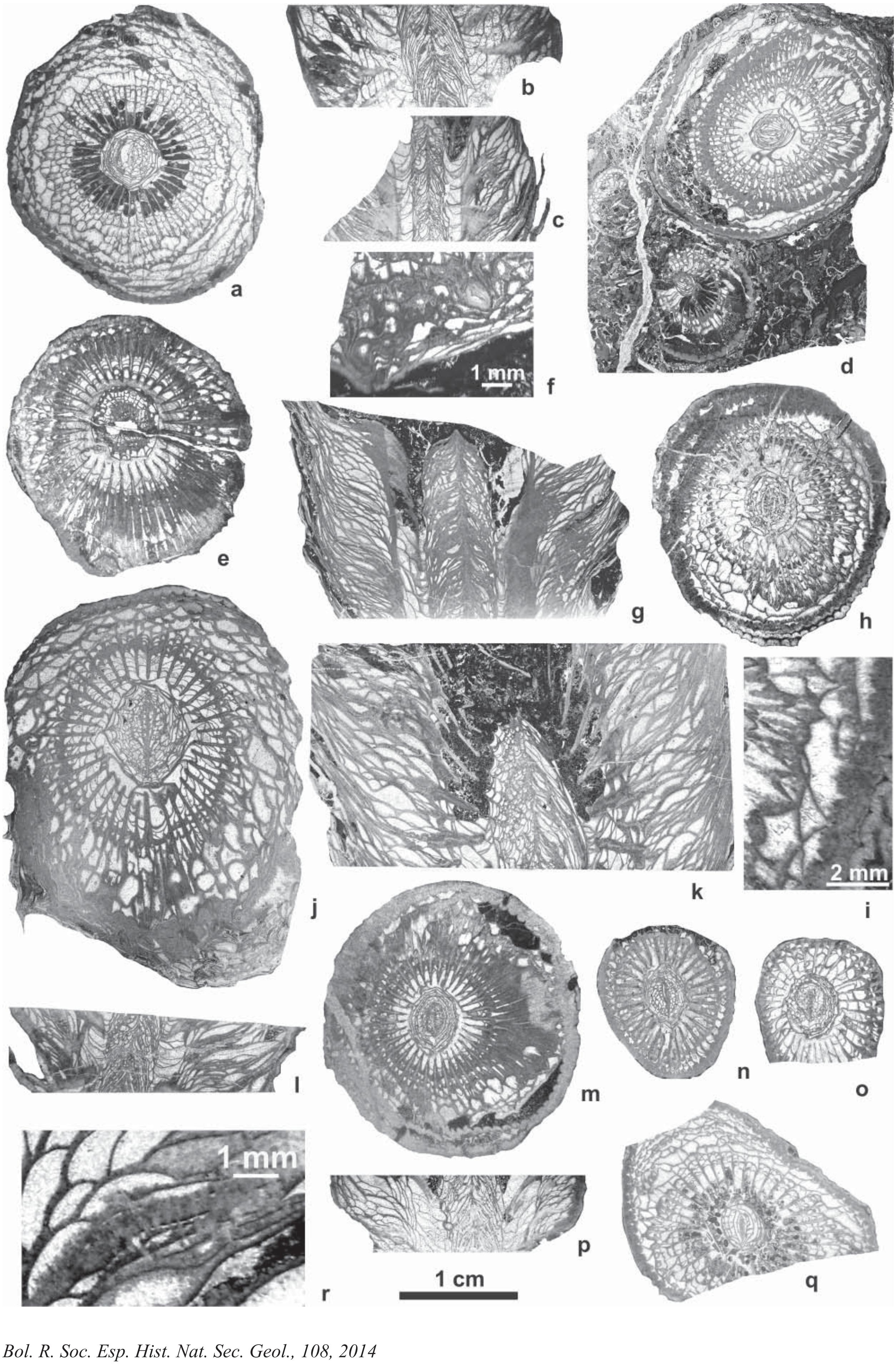
Type locality, horizon and age. La Cornuda Section, Córdoba Province, San Antonio-La Juliana Unit, Guadiato Area, Pendleian, Serpukhovian, Mississippian.

Material. 29 specimens from La Cornuda Section (COR/1-4, COR/1-15, COR/1-19 to 24, COR/1-31, COR/1-45, COR/1-52, COR/1-55, COR/1-59, COR/1-60, COR/1-66, COR/1-67, COR/1-70, COR/1-76, COR/1-79, COR/1-80, COR/1-83, COR/1-91, COR/1-92, COR/1-113, COR/1-114, COR/1-118 and COR/7-4).

Diagnosis. *Axophyllum*, having 30-42 major septa in 14-34 mm in diameter, 6-15 mm in tabularium diameter, and 2.5-7.5 mm in axial structure diameter.Major septa reaching the axial structure and some of them touching it. Minor septa thin and long, penetrating moderately into the tabularium. Lonsdaleoid dissepimentarium and 1 to 3 rows of interseptal dissepiments that may be thickened to form an inner wall. Axial structure 1/4 to 1/6 of the alar diameter. It shows a longitudinally constant median plate that varies its length in transverse section. Radial lamellae are thin and variable in number; conical tabellae are numerous, usually denser in the periphery. Periaxial tabellae concave and declined to the axis. Mesoplasm composed of bundles of microlamellae producing characteristic denticulations on the wall and lonsdaleoid dissepiments. Lamellar stereoplasm.

Description. Trochoid corals that show gregarism (Fig. 27d), some growing with walls very close one to another and showing common rejuvenescences (Figs. 27c,g,l), talons and radiciform processes (Fig. 27f). Thick, festooned wall, frequently partly eroded, which may double in thickness because of rejuvenescences (Figs. 27a,d,h). Wide dissepimentarium composed of lonsdaleoid dissepiments variable in size and shape. In the external part of the dissepimentarium some naotic dissepiments may occur. Some rows (1-3) of interseptal dissepiments occur in the inner part of the dissepimentarium (Figs. 27a,d,h,j). They may be thickened forming an inner wall (Figs. 27d,e,j), but it is not constant and some specimens lack it completely (Fig. 27a). In longitudinal section the dissepiments are mainly large, elongated and very steeply inclined to the axis, but some small semi-globose ones occur with random distribution (Figs. 27c,g,k). The major septa are thin to moderately thick and long, reaching the axial structure. Some of them touch it, but they are not in continuity with the radial lamellae. Some specimens show thick stereoplasmatic thickenings (Figs. 27d,e,m).The cardinal and counter septa are long and thick, same as the other metasepta, and they are only identifiable because of their location in the axial plane and the position of the median plate. Minor septa are thin and long, reaching 2/3 of the length of majors, but present in the dissepimentarium as crests on the lonsdaleoid dissepiments (Figs. 27a,d), although some can extend to the external wall (Figs. 27e, n, o). The axial structure is smaller than in most axophyllids, reaching between 1/4 and 1/6 of the diameter. Its shape is ellipsoidal to circular. It is composed of a median plate, radial lamellae and conical tabellae. The median plate is generally thin, occasionally thicker (Figs. 27g, j) and it is not in contact with either the cardinal and counter septa, but it is continuous in longitudinal section (Figs. 27b, c, g). Radial lamellae are also thin. They are variable in number (12 to 30). Some of them may show twisted peripheral ends (Figs. 27a,d,h,j,m,q). The axial tabellae are thin and conical. The periaxial tabellae show two different morphologies (Figs. 27b,c,g,k,l,p). The external tabellae are convex and declined to the axis (clinotabellae, Figs. 27g,p)). The most internal tabellae are concave and horizontal. The septal mesoplasm is composed of bundles of microlamellae organised in piles that form characteristic denticulations or spines on the wall and on the lonsdaleoid dissepiments (Figs. 27 I,r). Septal stereoplasm, dissepiments and tabulae are mainly lamellar. The variability is large even in different parts of a single specimen. The septa and the elements of the axial structure may be thickened; some specimens show a conspicuous but irregular inner wall. Three specimens show a slightly larger size (28 to 35 mm in diameter, compared to less than 25 in all other specimens). During growth, there is a conspicuous development of the dissepimentarium. It is quite small in young stages (1/4 of the radius or less at 10 mm in diameter, Figs. 27n,o)), but it may reach more than 1/2 of the radius in adult stages (Figs. 27m).

Remarks. Part of the collection of specimens included in this species were described by Gómez-Herguedas & Rodríguez (2005) in open nomenclature. They regarded these specimens as belonging to a new genus close to *Axophyllum*; the main differences with most species of that genus are the lamellar septal microstructure that produce “spiny” septal crests and a quite small axial structure with the cardinal and counter septa separated from the median plate. However, after a revision of the types of *Axophyllum expansum*, the microstructure is clearly identical, the size of the axial structure is also small and the cardinal and counter septa may be also separated from the median plate, as in the type species of the genus. Consequently, there are no reasons to segregate the specimens of La Cornuda from *Axophyllum*. Gómez-Herguedas & Rodríguez (2005) separated the described specimens in three species based on the large size of some specimens, and in the development of an inner wall and septal thickening in other specimens**.** A detailed analysis of the variations from young to adult stages and in different parts of single specimens indicates that such variability corresponds to intra-population variations in a highly variable species. As stated above*, A. spinosum* shows close features to *A. expansum* from which it could have evolved, but the type species has a smaller size, an even smaller and less organized axial structure, shorter minor septa and better developed and more regular inner wall. All these features allow the distinction between the two species. The new species share the microstructure type and the gregarism with the new genus *Morenaphyllum*, but the latter has a very thick and prominent cardinal septum, joined to a smaller and much more irregular axial structure.


a
b
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1 mm
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Figure 27. *Axophyllum spinosum* sp. nov. **a-b)** Specimen COR/1-52 (holotype). **a:** transverse section, **b:** longitudinal section. **c-d)** Specimen COR/1-20 (paratype). **c:** longitudinal section, **d:** transverse section. **e)** Specimen COR/1-23 (paratype), transverse section. **f, g)** Specimen COR/1-24 (paratype). **f:** Detail showing modification of structures to build talons and radiciform processes. **g:** longitudinal section. **h-i**) Specimen COR/1-91 (paratype), **h:** transverse section. **i:** detail showing the spines on the wall festoons and on the lonsdaleoid dissepiments. **j-k)** Specimen COR/1-49 (paratype). **j: t**ransverse section. **k:** longitudinal section. **l-m)** Specimen COR/1-121 (paratype). **l:** longitudinal section. **m:** transverse section. **n)** Specimen COR/1-45 (paratype). Transverse section in young stage. **o-q)** Specimen COR/1-47 (paratype). **o:** transverse section in young stage. **p:** longitudinal section. **q:** transverse section in adult stage. **r)** Specimen COR/1-83 (paratype), longitudinal section; detail showing spines in the septa as result of the microstructure. Scale bar valid for all figures except f, i and r.

— *Axophyllum spinosum* sp. nov. **a-b)** Ejemplar COR/1-52 (holotipo). **a:** sección transversal, **b:** sección longitudinal. **c-d)** Ejemplar COR/1-20 (paratipo). **c:** sección longitudinal, **d:** sección transversal. **e)** Ejemplar COR/1-23 (paratipo), sección transversal. **f, g)** Ejemplar COR/1-24 (paratipo). **f:** Detalle que muestra modificaciones en las estructuras para formar talons y procesos radiciformes. **g:** sección longitudinal. **h-i**) Ejemplar COR/1-91 (paratipo), **h:** sección transversal. **i:** detalle que muestra las espinas sobre los festones de la muralla y sobre los disepimentos lonsdaleoides. **j-k)** Ejemplar COR/1-49 (paratipo). **j:** sección transversal. **k:** sección longitudinal. **l-m)** Ejemplar COR/1-121 (paratipo). **l:** sección longitudinal. **m:** sección transversal. **n)** Ejemplar COR/1-45 (paratipo). Sección transversal en estadio juvenil. **o-q)** Ejemplar COR/1-47 (paratipo). **o:** sección transversal en estadio juvenil. **p:** sección longitudinal. **q:** sección transversal in estadio adulto. **r)** Ejemplar COR/1-83 (paratipo), sección longitudinal; detalle que muestra espinas en los septos como producto de la microestructura. Escala válida para todas las figuras excepto f, i y r.

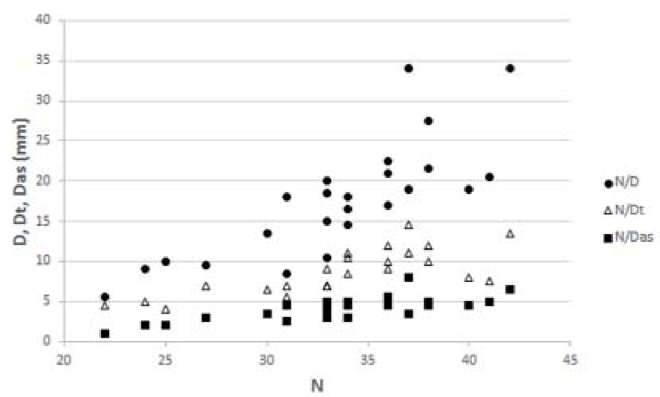

Figure 28. Graph plotting corallite diameter (D)/ tabularium diameter (Dt)/axial structure diameter (Das) versus number of major septa (N) for *Axophyllum spinosum*.

— Gráfico de relación entre el diámetro del coralito (D)/ el diámetro del tabulario (Dt)/el diámetro de la estructura axial (Das) y el número de septos mayores (N) para *Axophyllum spinosum*.

Genus *Gangamophyllum* Gorsky, 1938

1938 *Gangamophyllum* Gorsky, p. 103.
1941 *Gangamophyllum* Gorsky 1938; Volkova, p. 68.
1951 *Gangamophyllum* Gorsky 1938; Gorsky, p. 86.
1952 *Gangamophyllum* Gorsky 1938; Dobrolyubova, p. 52.
1957 *Gangamophyllum* Gorsky 1938; Kostic Podgorska, p. 71.
1958 *Gangamophyllum* Gorsky 1938; Kostic Podgorska, p. 110.
1960 *Gangamophyllum* Gorsky 1938; Vassiljuk, p. 119.
1960 *Gangamophyllum* Gorsky 1938; Zukalová, p. 335.
1962 *Gangamophyllum* Gorsky 1938; Luo & Zhao, p. 182
pars 1963 *Gangamophyllum* Gorsky 1938; Yu, Wu, Chao & Chang, p. 100.
1966 *Gangamophyllum* Gorsky 1938; Bykova, p. 85.
1967 *Gangamophyllum* Gorsky 1938; Ivanovski, p. 31.
1971 *Gangamophyllum* Gorsky 1938; Perret & Semenoff-Tian-Chansky, p. 584.
1972 *Gangamophyllum* Gorsky 1938; Degtiarev & Kropatcheva, p. 90.
1973 *Gangamophyllum* Gorsky 1938; Altmark, p. p. 42.
1973 *Gangamophyllum* Gorsky 1938; Sayutina, p. 110.
1974 *Gangamophyllum* Gorsky 1938; Semenoff-Tian-Chansky, p. 237.
1975 *Gangamophyllum* Gorsky 1938; Gorsky p. 82.
1977 *Gangamophyllum* Gorsky 1938; Jia & Hsu in Jia, p. 223.
1978 *Gangamophyllum* Gorsky 1938; Yu, Lin, Huang & Cai, p. p. 44.
1981 *Gangamophyllum* Gorsky 1938; Poty, p. 63.
1981 *Gangamophyllum* Gorsky 1938; Hill, p. F400.
1982 *Gangamophyllum* Gorsky 1938; Jiang, p. 144.
1983 *Gangamophyllum* Gorsky 1938; Yu, Lin, Shi, Huang & Yu p. 211.
1985 *Gangamophyllum* Gorsky 1938; Boll, p. 37.
1986 *Gangamophyllum* Gorsky 1938; Herbig, p. 212.
1988 *Gangamophyllum* Gorsky 1938; Lin & Wu, p. 577.
1991 *Gangamophyllum* Gorsky 1938; Fontaine, Suteethorn & Jongkanjanasoontorn, p. 54.
1992 *Gangamophyllum* Gorsky 1938; Huang & Duan, p. 160.
1998 *Gangamophyllum* Gorsky 1938; Zhao, p. 110.

Diagnosis (modified from Semenoff-Tian-Chansky, 1974). Solitary conical corals having a peripheral zone with large dissepiments sometimes lonsdaleoid. Inner wall that is reduced in adult stages. Web-like axial structure without median plate, composed of radial lamellae and axial tabellae. Large dissepiments very declined to the axis. Periaxial tabellae concave and also declined to the axis. Domical axial tabellae. Fibronormal mesoplasm, lamellar stereoplasm.

Remarks. The genus *Gangamophyllum* was erected for Axophyllinae species having an axial structure without a median plate and having domical axial tabellae. All other features are identical to those of the genus *Axophyllum*. In contrast to the latter genus, which is more common and diverse in the Western Palaeotethys, *Gangamophyllum* is more common in Central and Eastern Palaeotethys. 29 species have been assigned to this genus from which 18 have been described in Central Palaeotethys (former USSR), 9 have been recorded in East Asia and only 2 have been described in Western Europe. Of course, some of the species described in Central Palaeotethys have been also recorded in other areas, but the diversity of this genus seems to be the highest in that region.

Some of the 29 species assigned to this genus are not valid for different reasons. Some of them have been described with so poor material that they can not be verified. For instance, *G. winklerprinsi* Boll 1985 was described based on a single fragmentary and compressed specimen lacking an apex, calice and half of the adult stages. That nominal species can not be used. *Gangamophyllum divisum* Sayutina, 1973 was described also based on a single specimen lacking an apex and calice. Moreover, it was described as having a median plate, and transverse sections of the holotype (Sayutina, 1973; plate 18, fig. 2) show clearly this feature. Consequently, it has been transferred to the genus *Axophyllum*. Sayutina (1973) stated that *G. cinctum* Gorsky, 1951 is synonymous with the type species *G. boreale* Gorsky, 1938. In the same way, Sayutina (*op. cit.*) stated that *G. tenuis* Gorsky, 1951 is synonymous with *G. latum* Gorsky, 1938. *G. cinctum* and *G. tenuis* are eliminated after our analysis. *G. ultima* Gorsky, 1951 was described as a variety of *G. vesiculosum* Gorsky, 1951 and is maintained in that species. Thus, the total number of species included in the analysis is 24: *G. bodamicum* Bykova, 1966, *G. boreale* Gorsky, 1938, *G. complicatum* Zuo (*in* Jia 1977), *G. crenulatum* Bykova, 1966, *G. densitabulatum* Poty, 1981, *G. dobrolyubovae* Altmark, 1973, *G. gorskyi* Vassiljuk, 1960, *G. grandis* Vassiljuk, 1960, *G. hunanense* Jia & Hsu (*in* Jia 1977), *G. kumpani* Vassiljuk, 1960, *G. latetabulatum* Gorsky, 1951, *G. latum* Gorsky, 1938, *G.liuchengense* Kwang (*in* Jia 1977), *G. lonsdaleoidea* Lo (*in* Luo & Zhao) 1962, *G. mosquense* Dobrolyubova, 1952, *G. multiplexum* Yu, Lin, Shi, Huang & Yu, 1978, *G. oblongum* Gorsky, 1938, *G. paucivesiculosa* Gorsky, 1951, *G. pauperculum* Bykova, 1966, *G. rarilamellata* Lo (*in* Luo & Zhao) 1962, *G. retiforme* Lin & Fan, 1962 (*in* Luo & Zhao, 1962), *G. spiroidea* Lo (*in* Luo & Zhao) 1962, *G. vesiculosum* Gorsky, 1951 and *G. yamansuense* Fan & Lin (*in* Yu *et al.* 1978) (Fig. 29).

The measurements of some species (corallite diameter vs. number of septa) clearly distinguish them from the rest (Fig. 30). *G. grandis* shows a much larger diameter than any other species. On the other hand, *G. hunanense* has many more septa than any other species, including those larger than it. *G. boreale* has also a higher number of septa than most other species. In contrast, *G.liuchengense* has fewer septa than other species with similar size. The other 20 species are grouped in two clusters with similar number of septa (30-40), but with two different order of sizes (30-42 mm and 15-25 mm)(Fig. 30). Three species form an independent group with intermediate size, but higher number of septa: *G. densitabulatum*, *G.multiplexum* and *G. retiforme*. All other features are also identical in the last two species: same measurements of tabularium and axial structure, thin septa, axial structure more densely packed in the periphery having domical axial tabellae, thin, densely packed, concave periaxial tabellae and elongated dissepiments declined 45º-60º to the axis. As we did not find any substantial difference between these two species, we consider them to be synonymous, with *G. retiforme* having priority over *G. multiplexum*. *G. densitabulatum* shows some differences that make it easy to distinguish: a more irregular axial structure that is not denser in the periphery, smaller tabularium for similar diameter and number of septa, more developed lonsdaleoid dissepiments, and denser periaxial tabellae.

When comparing the tabularium diameter with the number of septa (Fig. 31), some other species show conspicuous differences: *G. yamansuense* is clearly separated because of a higher number of septa than similar-sized species. *G. crenulatum* and *G. complicatum* have similar number of septa and the difference in size is not significant. However, the tabularium is somewhat larger in *G. complicatum*, which has also less dense structures and a larger axial structure. Both can be easily distinguished. *G. bodamicum* and *G. vesiculosum* have also a close relationship Dt/N, but the corallite diameter of the latter is much larger and it possesses a wide lonsdaleoid dissepimentarium (Table II). Thus, the former is clearly distinguishable from any other species of *Gangamophyllum*. The tabularium size, number of septa and development of lonsdaleoid dissepiments are similar in *G. lonsdaleoidea* and *G. vesiculosum*. However, the former shows a larger axial structure (Table II) and a dissepimentarium with horizontal and arched dissepiments in the periphery; both differences are enough to consider these species as different.

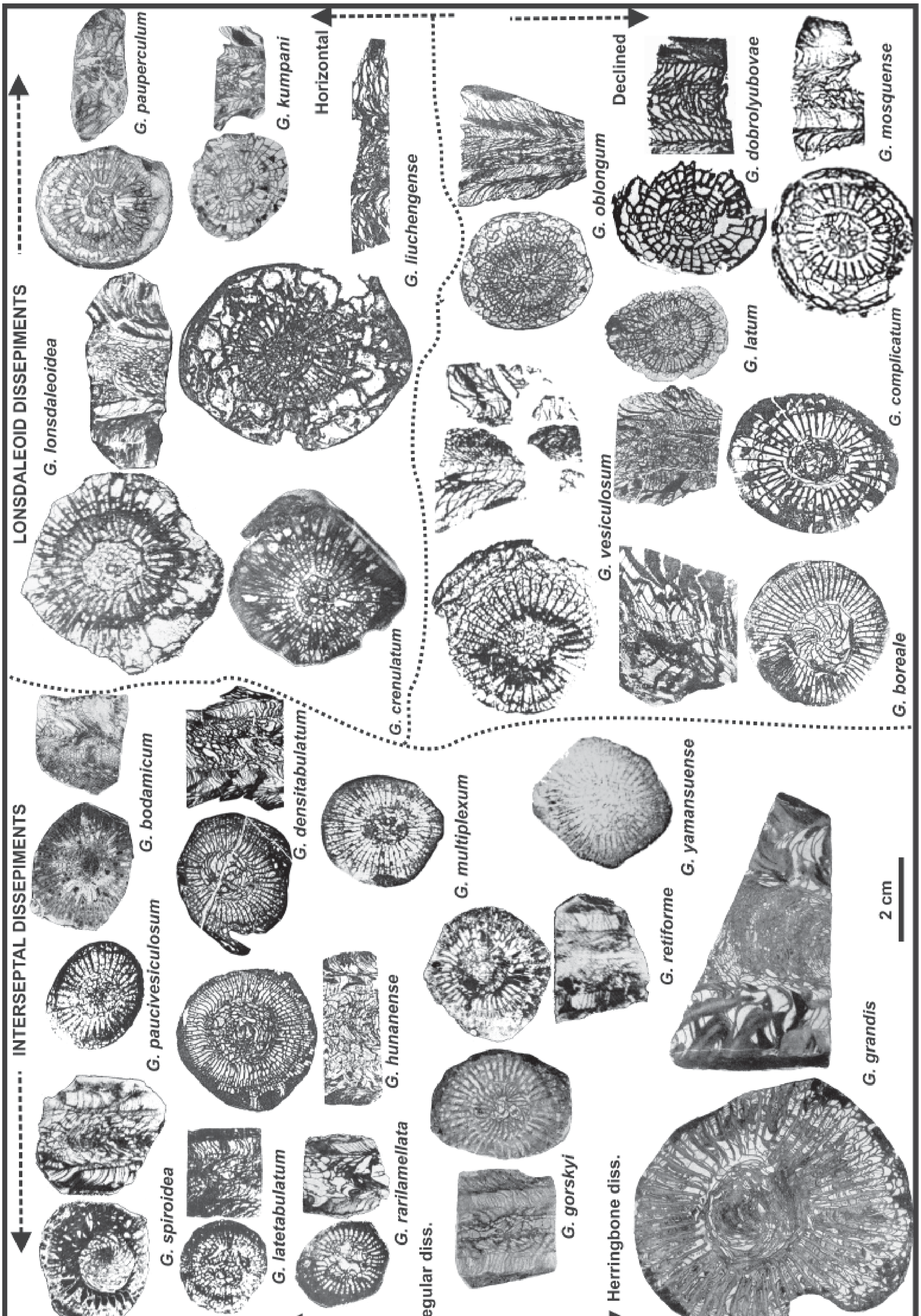

Figure 29. Species of *Gangamophyllum* included in the analysis distributed after the features of their dissepimentariums. — Especies de *Gangamophyllum* incluidas en el análisis, distribuidas según características del disepimentarium.

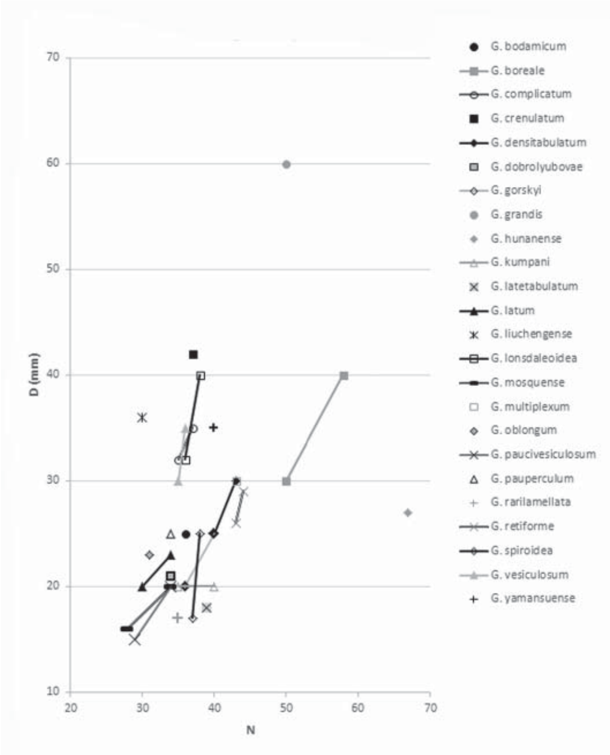

Figure 30. Graph plotting corallite diameter (D) versus number of major septa (N) for *Gangamophyllum* species.
— Gráfico de relación entre el diámetro del coralito (D) y el número de septos mayores (N) para las especies de *Gangamophyllum*.

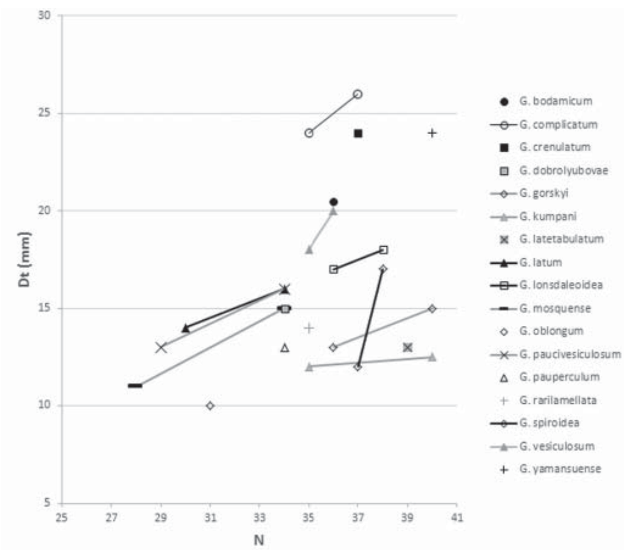

Figure 31. Graph plotting tabularium diameter (Dt) versus number of major septa (N) for *Gangamophyllum* species.
— Gráfico de relación entre el diámetro del tabulario (D) y el número de septos mayores (N) para las especies de *Gangamophyllum*.

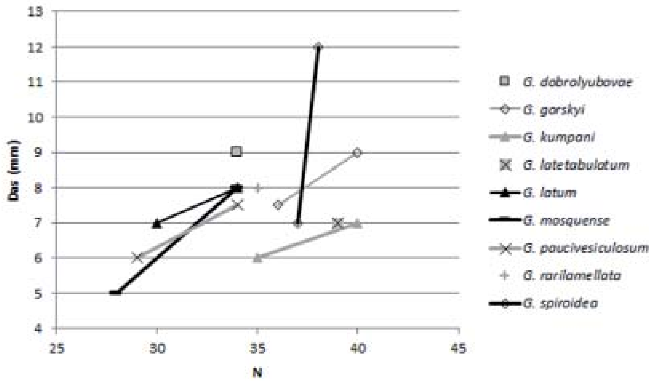

Figure 32. Graph plotting axial structure diameter (Das) versus number of major septa (N) for *Gangamophyllum* species.
— Gráfico de relación entre el diámetro de la estructura axial (Das) y el número de septos mayores (N) para las especies de *Gangamophyllum*.

G. oblongum is clearly separated from all other species by a larger alar diameter but smaller tabularium diameter for similar number of septa. It is due to a wider lonsdaleoid dissepimentarium than any other species for similar number of septa and size. In the same way, *G. pauperculum* shows a wide lonsdaleoid dissepimentarium; its alar diameter is larger than most species having 30-35 septa, but its tabularium diameter is smaller than all species having that number of septa. Moreover, it shows also horizontal dissepiments in the periphery. That feature is not present in any other species with similar dimensions.

Figures 30-32 show two compact groups of species that show similar proportions. The first one is composed of *G. dobrolyubovae, G. latum, G. mosquense* and *G. paucivesiculosum*. The last-named species is clearly different from the other three in having a narrow, mainly interseptal dissepimentarium. *G. latum* shows a quite regular inner wall, long minor septa and its periaxial tabellae are declined to the axial structure. On the other hand, *G. dobrolyubovae* and *G. mosquense* have periaxial tabellae declined to the periphery, irregular inner wall and short to absent minor septa; they must be regarded as synonymous, with the latter having priority. *G. rarilamellata* shows intermediate measurements between the two groups. It is also clearly distinguishable, because it has scarce interseptal dissepiments and extremely sparse elements in an irregular axial structure. The second group of species is composed of *G. gorskyi, G. kumpani, G. latetabulatum* and *G. spiroidea*. The latter shows a large increase of diameter with also variation of the septal number. In addition, its axial structure showing twisted radial lamellae allows an easy distinction from other species in the group. *G. gorskyi* shows somewhat larger size than *G. kumpani* and *G. latetabulatum*. In addition it has denser axial structure, with many thick radial lamellae and high density of periaxial

Table II. Synthesis of morphological features of *Gangamophyllum* species. Abbreviations: Same as in Table 1.
— Síntesis de características morfológicas en las especies de Gangamophyllum. Abreviaturas: Igual que en la Tabla 1.

Species	Shape	Measurements				Wall		Dissepiments				I. wall	Majors		Minors	Card.	Radial lamellae			Axial tabellae		Periaxial tabel.			Microstr.	
		N	D	Dt	Das	Thickn.	Shape	Rows	Type	Shape	De-clin.		Length	Thick.	Length		Thick.	Numb.	Outl.	Thick.	Dens.	Shape	Dens.	Decl.	Mes.	Ster.
G. bodamicum	Tr	36	25	20	7,5	Tn?	Fs?	1-3	Rg	El	60-90	No	R	Tk	Lg	Sh	Tn	20-25	Ir	Tn	Md	Cc	Md	Ax	?	?
G. boreale	Tr	50-58	30-40	25-27	15-18	Tn-Md	Fs	2-4	Ln-Rg	El	60-90	Ir	N	Tn	Md	J-N	Md	20-25	Spr	Tn	Sp	Cc	Sp	Ax	?	?
G. complicatum	Tr	37	32-35	24-26	10	Tk	Fs	2-5	Rg	El	H-75	Tn	N	Md	Cr	J	Ir	20-30	Ir	Tn	Md	Cc	Dn	H	?	?
G. crenulatum	Tr	37	42	20-24	6-6.5	Tk	St	4-8	Rg-Ln	?	?	No	R	Tn-Md	Lg	J	Md	25-30	S	Tn	Dn	?	Dn	?	?	?
G. densitabulatum	Cy	40-43	25-30	15-19	8-10.5	Tk	Ir-Un	3-6	Ln-Rg	El	45-90	Ir	R	Tk	Sh	J	Md	10-15	Ir-Spr	Tn-Md	Dn	Cc-Fl	Dn	H	?	?
G. gorskyi	Tr	36-40	20-25	13-15	7.5-9	Tn-Md	Sm-Fs	2-4	Rg-Ln	El	60-90	Tk	R	Md-Tk	Cr	J	Md	30-40	S-Spr	Tn	Md	F-Cc	Dn	H-Ax	Fb	L
G. grandis	Tr	50	60	40-45	20-22	Tn	Sm-Fs	6-10	Rg-Hr	Md	45-90	No	R	Tn-Tk	Lg	Sh	Tn	30-40	Ir	Tn	Dn	Ir	Md	H	?	?
G. hunanense	Tr	67	27	20	11	?	?	2-5	Rg-L2	El	H-75	Tn	R	Tn-Md	Lg	J	Md	20-30	Ir	Tn	Dn	F-Cc	Dn	P-H	?	?
G. kumpani	Tr	35-40	20	12-13	6-7	Tn	Sm-Fs	1-3	L2-Rg	El	30-90	Tn-Tk	R	Tn-Tk	Cr	J	Tn	10-20	Ir	Md	Md-Sp	Cc	Md	H-Ax	?	?
G. latetabulatum	Cy-Cr	39	18	12-13	7	Tn	Sm-Fs	2-4	Rg	Md-El	45-90	Ir	R	Tn-Md	Sh	J	Md	15-25	Ir	Md-Tk	Md	Cc	Dn	H-Ax	?	?
G. latum	Tr	30-34	20-23	14-16	7-8	Tn	Sm-Fs	4-5	Ln	El-Md	60-90	Tn	R	Tn-Md	Lg	J	Md	15-25	S-Spr	Tn	Dn	Cc	Dn	Ax-H	?	?
G. liuchengense	Tr	35	36-52	16-20	9	Tn-Md	Sm	5-8	Ln	El	H-60	Tn	R	Tn-Md	Sh	J	Md-Tn	20-25	Ir	Tn	Dn	Cv	Md	Ax	?	?
G. lonsdaleoidea	Tr	36-38	32-40	17-18	7-10	Md	Sm-Fs	2-4	Ln-L2	El-Md	H-60	Ir	R	Md	Sh	J	Tn-Md	20-30	Ir	Tn	Dn	Cc	Md	H	?	?
G. mosquense	Tr	28-34	16-20	11-15	5-8	Tk-Md	Ir-Fs	2-3	Ln	El-Md	30-75	Tn	N	Md	Cr	J	Md	10-20	Ir	Md	Md	Cc	Md	H	Fb	L
G. oblongum	Tr	31	23	10-12	5-6	Tn-Md	Sm	3-5	Ln-Rg	El	45-75	Ir	R	Md	Lg	J	Md	20-25	Ir	Md	Dn	Cc	Dn	Ax	?	?
G. paucivesiculosa	Tr	29-34	15-20	13-16	6-7.5	Md-Tk	Sm-Fs	1-2	Rg-L2	?	?	Tk	R	Tk	Sh	J	Tn-Md	15-25	S	Tn	Dn	Cc	Md	Ax	?	?
G. pauperculum	Tr-Pt	34	25	12-13	6-6.5	Tk-Md	Fs	2-4	L	El	H-60	Ir	N	Tn	Sh-Lg	J	Tn	8-15	Ir	Tn	Md	Cc	Md	H	?	?
G. rarilamellata	Tr-Cr	35	17	14	8	Tk	St	1	Rg	El	45-75	No	R	Tk	No	J	Tn	8-15	Ir	Tn	Sp	Fl	Dn	Ax	?	?
G. retiforme	Tr	44	26-29	20-22	10-12	Tk	Ir-Fs	1-3	Rg	El	45-75	No	R	Tk-Md	Sh	J	Tn	20-30	S	Md	Dn	Cc	Dn	H-Ax	?	?
G. spiroidea	Tr	38	17-25	12-17	7-12	Md	Ir-Fs	1-3	Rg	El	30-75	Tk	R	Tk-Md	Md	J	Md	15-25	Spr	Tn	Dn	Cc	Dn	H-Ax	?	?
G. vesiculosum	Tr	35-36	30-35	18-20	6-7	Md-Tn	Ir-Fs	6-8	Ln-Rg	Md	30-75	Ir	R	Md	Cr	J	Tn	20-30	Ir	Tn	Dn	Cc	Md	H	?	?
G. yamansuense	Tr	40	35	24	11	Tk	St	1-3	Rg	Gb-Md	30-75	St	R	Tk	Lg	J	Tk	15-25	Ir	Md	Md	Cc	Dn	Ax	?	?

tabellae. In spite of the fact that the dimensions and number of septa of *G. kumpani* and *G. latetabulatum* are basically identical, they are easy to distinguish because the latter shows thicker septa in the tabularium, higher development of lonsdaleoid dissepiments (large and horizontal in the periphery) and sparser periaxial tabellae.

In conclusion, 22 species belonging to the genus *Gangamophyllum* are accepted here: *G. bodamicum* Bykova, 1966, *G. boreale* Gorsky, 1938, *G. complicatum* Zuo, 1977, *G. crenulatum* Bykova, 1966, *G. densitabulatum* Poty, 1981, *G. gorskyi* Vassiljuk, 1960, *G. grandis* Vassiljuk, 1960, *G. hunanense* Jia & Hsu, 1977, *G. kumpani* Vassiljuk, 1960, *G. latetabulatum* Gorsky, 1951, *G. latum* Gorsky, *G. liuchengense* Kwang, *G. lonsdaleoidea* Lo, 1962, *G. mosquense* Dobrolyubova, 1952, (=*G. dobrolyubovae* Altmark, 1973), *G. oblongum* Gorsky, 1938, *G. paucivesiculosa* Gorsky, 1951, *G. pauperculum* Bykova, 1966, *G. rarilamellata* Lo, 1962, *G. retiforme* Lin & Fan, 1962 (=*G. multiplexum* Yu, Lin, Shi, Huang & Yu, 1978), *G. spiroidea* Lo, 1962, *G. vesiculosum* Gorsky, 1951 and *G. yamansuense* Fan & Lin, 1978.

Gangamophyllum gorskyi Vassiljuk, 1960
Figs. 33a-c, 34

1960 *Gangamophyllum gorskyi* Vassiljuk, p. 120, pl. 28, Fig. 1.

Material. 2 specimens from Adelfilla Quarry (ADF/5-8, ADF/5-11). Brigantian, Guadiato Area.

Location, horizon and age. Located in Brigantian (upper Viséan, Mississippian) olistolite from Adelfilla Quarry (Guadiato Area).

Diagnosis. *Gangamophyllum* 20 to 25 mm in diameter, 13-15 mm in tabularium diameter, 7.5-9 mm in axial structure diameter, having 36 to 40 septa of two orders. Major septa thick and in contact with the axial structure. Dissepiments mainly regular to herringbone. Conspicuous inner wall composed of thickened dissepiments. Axial structure large (1/3 of the diameter), showing thick, slightly twisted septal lamellae. Fibrous septal mesoplasm, lamellar stereoplasm.

Description. Trochoid to ceratoid corals, lacking the apex and part of the calice. They show common rejuvenescences. Moderate to very thick, festooned wall, partly eroded, which may be doubled in thickness because of rejuvenescences (Fig. 33c). Dissepimentarium partly eroded, composed of some lonsdaleoid dissepiments and some interseptal dissepiments. They and the septa are thickened to build a conspicuous inner wall (Figs. 33b,c). In longitudinal section the dissepiments are large, elongated and declined about 45º to the axis (Fig. 33a). The major septa (37-38) are long, reaching the axial structure. They are quite thick in the border of the tabularium, but they are thinner near the axis. The cardinal and counter septa are inconspicuous. Minor septa are thin, 1/3-1/2 length of majors, and they occur as crests on the lonsdaleoid dissepiments; their inner ends are immersed in the inner wall (Fig. 33b). The axial structure is about 1/3 of the alar diameter. Its shape is typically circular (Fig. 33c). It is composed of irregular, moderately thick radial lamellae that may be somewhat twisted, and domical tabellae. The periaxial tabellae are declined to the axis. The microstructure is typical for the family, granulo-fibrous septal mesoplasm and lamellar stereoplasm, dissepiments and tabulae.

Remarks. The size and number of septa of the specimens from the Adelfilla Quarry fit completely within the variability described from the types (Fig. 34). The presence of a thick inner wall and a large axial structure are also typical for this species. The only difference with the types is the presence of some lonsdaleoid dissepiments that are lacking in the Ukrainian specimens, but they are not much developed in the Spanish specimens and it is a quite variable feature in many species of *Gangamophyllum*.

Gangamophyllum mosquense Dobrolyubova, 1952
Figs. 33d-f, 35

1952 *Gangamophyllum mosquense* Dobrolyubova, p. 60, Fig. 3-6, pl. 2, Fig. 4-8, pl. 3, Fig. 2-8.
1973 *Gangamophyllum dobrolyubovae* Altmark, p. 43.
non 1977 *Gangamophyllum mosquense* Dobrolyubova; Jia & Xu in Xu & Zhang, p. 224, pl. 85, Fig. 7.
non 1982 *Carcinophyllum mosquense* (Dobrolyubova); Jiang, p. 194, pl. 94, Fig. 5.
non 1999 *Axophyllum* sp.; Liao & Rodríguez, p. 555, pl. 6, Fig. 7.

Material. 3 specimens; 1 from El Collado Section (COL/6-2), Guadiato Area; 2 from El Casar (CS/23-2, CS/25-5a), north-western extension of Guadiato Area. Lower Brigantian.

Location, horizon and age. Located in Brigantian (upper Viséan, Mississippian) from Guadiato Area and its north-western extension.

Diagnosis. *Gangamophyllum* 28 to 34 mm in diameter, 11-15 mm in tabularium diameter, 5-8 mm in axial structure diameter, having 28 to 34 septa of two orders. Major septa thick to moderately thick and long, almost reaching the axial structure. Minor septa mainly small crests on the inner wall. Wide lonsdaleoid dissepimentarium composed of large elongated dissepiments. Inner row thickened to form an inner wall. Axial structure large (about 1/3 of the diameter), showing low density of thin radial lamellae and axial tabellae. Fibrous septal mesoplasm, lamellar stereoplasm.

Description. Trochoid to ceratoid corals, lacking the apex and part of the calice; some of them also compressed. Moderate to very thick,

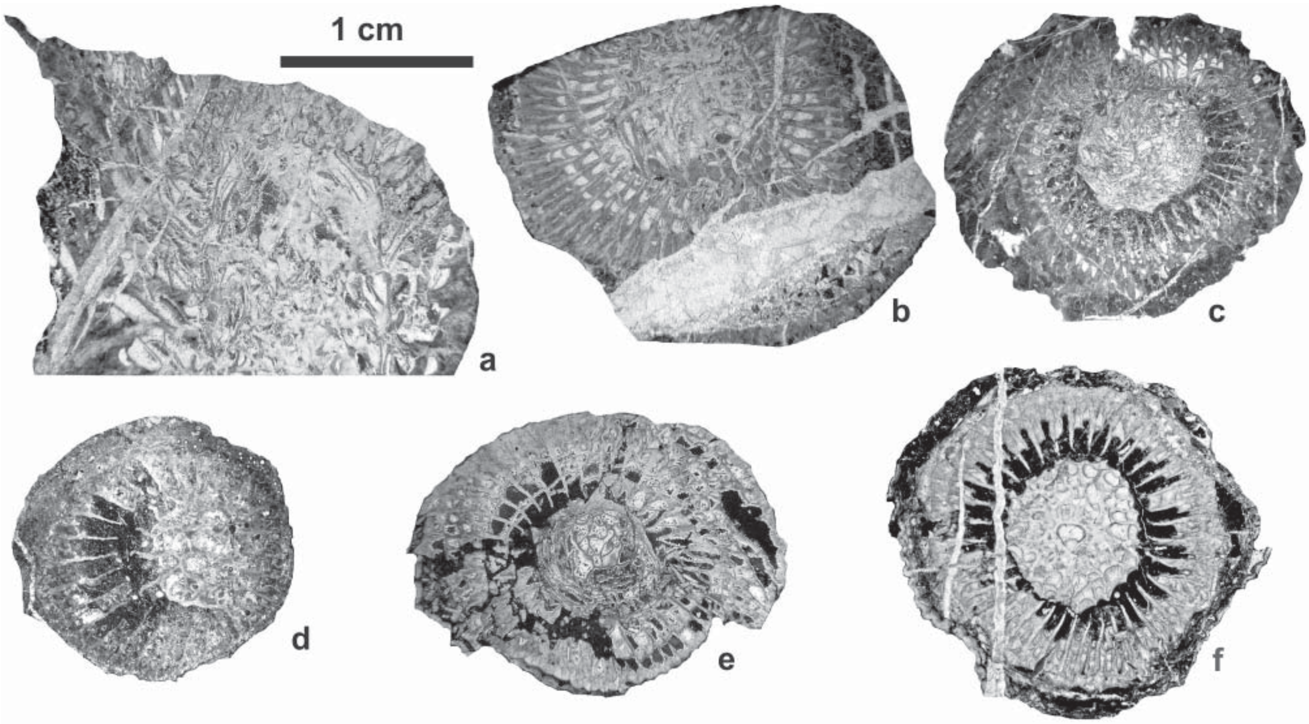

Figure 33. *Gangamophyllum gorskyi* **a-b)** Specimen ADF/5-8, **a:** longitudinal section. **b:** transverse section. **c)** Specimen ADF/5-11, transverse section. *Gangamophyllum mosquense* **d)** Specimen CS/23-2, transverse section in young stage. **e)** Specimen COL/6-2, compressed transverse section. **f)** Specimen CS/25-5, transverse section. Scale bar valid for all figures.

— *Gangamophyllum gorskyi* **a-b)** Ejemplar ADF/5-8, **a:** sección longitudinal. **b:** sección transversal. **c)** Ejemplar ADF/5-11, sección transversal. *Gangamophyllum mosquense* **d)** Ejemplar CS/23-2, sección transversal en estadio juvenil. **e)** Ejemplar COL/6-2, sección transversal comprimida. **f)** Ejemplar CS/25-5, sección transversal. Escala válida para todas las figuras.

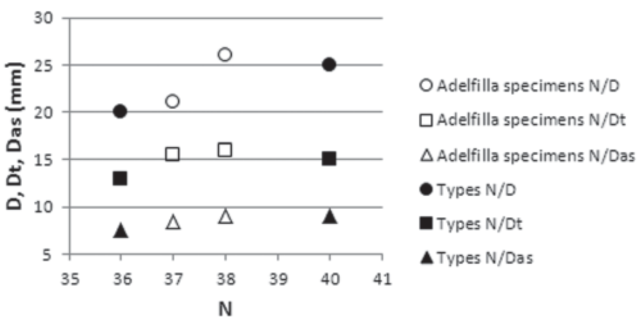

Figure 34. Graph plotting diameter (D), tabularium diameter (Dt) and axial structure diameter (Das) versus number of major septa (N) for *Gangamophyllum gorskyi*.

– Gráfico de relación entre el diámetro del coralito (D)/ el diámetro del tabulario (Dt)/el diámetro de la estructura axial (Das) y el número de septos mayores (N) para *Gangamophyllum gorskyi*.

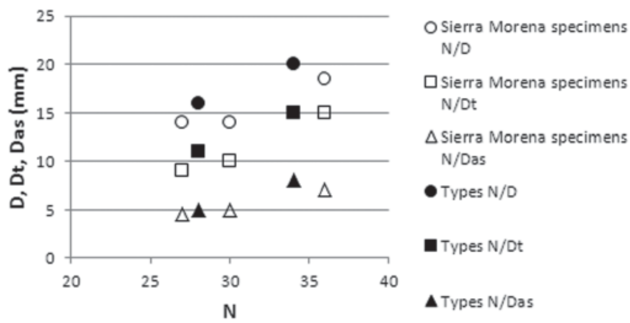

Figure 35. Graph plotting diameter (D), tabularium diameter (Dt) and axial structure diameter (Das) versus number of major septa (N) for *Gangamophyllum mosquense*.

— Gráfico de relación entre el diámetro del coralito (D)/ el diámetro del tabulario (Dt)/el diámetro de la estructura axial (Das) y el número de septos mayores (N) para *Gangamophyllum mosquense*.

festooned to undulating wall (Figs. 33e,f). It is partly eroded in all specimens. Dissepimentarium partly eroded, composed of large lonsdaleoid dissepiments that are thickened in the inner border to build a thick inner wall (Figs. 33e, f). Absence of longitudinal section impedes the analysis of their shape and declination. The major septa (27-36) are long, but rarely in contact with the axial structure. They are moderately thick, but some stereoplasmatic thickenings may occur in the periphery. They are slightly thinner near the axis. The cardinal and counter septa are inconspicuous. Minor septa are thin, 1/2 length of majors; they penetrate clearly into the tabularium (Fig. 33f). The axial structure is about 1/3 of the alar diameter. Its shape is circular to slightly ellipsoidal. It is composed of 20-25 moderately thick radial lamellae and moderately thick axial tabellae (3-5 rows). Absence of longitudinal sections impedes the description of shape and declination of axial and periaxial tabellae. The microstructure is similar to that described in *G. gorskyi.*

Remarks. The specimens from Sierra Morena show a slightly smaller diameter for the same number of septa than the types of Dobrolyubova (1952)(Fig. 35). But basically all other features are identical: thick undulated wall, large lonsdaleoid dissepiments, large axial structure and same size of tabularium. Several specimens from China have been assigned to this species by Xu & Zhang (1977) and Jiang (1982). The specimens of the former authors belong to *Gangamophyllum*, but they show thick septal stereozones and reduced development of lonsdaleoid dissepiments. The specimens described by Jiang (1982), show different measurements and smaller axial structure. Liao & Rodríguez (1999) described a similar specimen to those of Jiang (1982) and compared to it. They identified it as *Axophyllum* sp. The presence of an axial structure without median plate and domical axial tabellae indicate that it belongs to *Gangamophyllum*. It could be conspecific with the specimens of Jiang (1982), but it is also quite different from *G. dobrolyubovae*.

Genus *Pareynia* Semenoff-Tian-Chansky, 1974

1974 *Pareynia* Semenoff-Tian-Chansky, p. 240.
1977 *Pareynia* Semenoff-Tian-Chansky; Cotton, p. 24.
1981 *Pareynia* Semenoff-Tian-Chansky**;** Poty, p. 64.
1983 *Pareynia* Semenoff-Tian-Chansky; Yu, Lin, Shi, Huang & Yu p. 213.
2010 *Pareynia* Semenoff-Tian-Chansky; Aretz, p. 337.
2011 *Pareynia* Semenoff-Tian-Chansky**;** Denayer, Poty & Aretz, p. 169.

Diagnosis. Large solitary corals having axophylloid axial structure. Wide lonsdaleoid dissepimentarium composed of large transeptal dissepiments that may be thickened to form one or more irregular inner walls. Periaxial tabellae concave and horizontal in the inner part, declined to the axis in the periphery to form clinotabulae. Granulo-fibrous mesoplasm with a more fibrous tendency in the inner part of the septa and in the axial structure. Lamellar stereoplasm with some fibrous layers.

Remarks. Semenoff-Tian-Chansky (1974) erected the genus *Pareynia* for large axophyllids having a wide lonsdaleoid dissepimentarium, periaxial tabularium containing clinotabulae and apparent absence of an external wall, substituted in some cases by thickened lonsdaleoid dissepiments coming to the external part in rejuvenescences. He also indicated the existence of some offsets without further growth, showing a tendency to coloniality, not completely developed. In fact, Semenoff-Tian-Chansky (1974, p. 241) pointed out that the main differences with *Axophyllum* are the large dissepimentarium, the presence of more steeply declined periaxial tabellae including some clinotabulae, plus the possible absence of an external wall. Those features occur in isolation in different species of *Axophyllum* (e. g. *A. lonsdaleiforme*, *A. parkinsoni*, *A. sahariense*, *A. longiseptatum* and *A. moroccoense* have large lonsdaleoid dissepimentarium, and *A. clinotabulatum*, *A. cozari* sp. nov. and *A. spinosum* sp. nov. show clinotabulae). However, these features do not occur together in any *Axophyllum*. Consequently, we accept the genus *Pareynia* as valid. The oldest appearance of *Pareynia* is recorded in the lower upper Viséan from the Béchar Basin, coinciding with the acme of the subfamily. Thus, it could have evolved from a species of *Axophyllum* with high development of lonsdaleoid dissepimentarium by increasing its size and, accordingly, widening of the dissepimentarium. Two species were described by Semenoff-Tian-Chansky (1974) from North Africa: *P. splendens* (type species) and *P. gangamophylloides*.

Pareynia viacrucense sp. nov.
Figures 36a-n, 37

Derivatio nominis. The name of the species refers to the Via Crucis section, located in the Sierra del Castillo slope.

Holotype**.** Specimen VCR2/2-17; rest of specimens collected in the same section are regarded as paratypes. Stored in the Department of Paleontology of the Complutense University.

Type locality, horizon and age. Via Crucis 2 Section, located east of the road from Espiel to the Nuestra Señora de la Estrella Sanctuary, San Antonio-La Juliana Unit, Pendleian, Serpukhovian.

Material. 13 specimens (VCR2/0-4, VCR2/0-12, VCR2/0-13, VCR2/2-1, VCR2/2-4, VCR2/2-9, VCR2/2-13, VCR2/2-14, VCR2/2-16, VCR2/2-17, VCR2/4-7, VCR2/4-8, VCR2/5-1).

Diagnosis. *Pareynia* having a medium to thick wall, 34-44 major septa in 21-30 mm in diameter, 10-17 mm in tabularium diameter, and 5-7 mm in axial structure diameter. Major septa reaching the axial structure and some of them touching it. Minor septa thin, penetrating slightly into the tabularium. Large lonsdaleoid dissepimentarium and one or two rows of interseptal dissepiments usually not thickened. Axial structure about 1/5 of the alar diameter, with a thin but persistent median plate, numerous thin radial lamellae and conical tabellae. Periaxial tabellae concave and declined to the axis, with the presence of some clinotabellae. Granulo-fibrous mesoplasm and lamellar stereoplasm.

Description. Trochoid to patelloid corals showing lateral expansions of the wall in young and adult stages for supporting (Figs. 36 c,f,g,n) and rejuvenescences in adult stages (Fig. 36 b). The wall is thick to very thick in young stages (Figs. 36c,d,e), but thin to moderately thick in adult stages (Figs. 36a,f,g). It is smooth to festooned in young stages but festooned to undulating in adult stages (compare Figures 36a and c). The dissepimentarium is typically lonsdaleoid. It develops through the ontogeny. The first dissepiments appear at 8-10 mm in diameter (Fig. 36d); At 15 mm in diameter there are 1 to 3 rows of large lonsdaleoid dissepiments irregularly distributed (Figs. 36c,d,j,k). In adult stage there are 4-8 rows of lonsdaleoid dissepiments that may occupy more than 1/2 of the radius (Fig. 36a), but usually 1/3 to 1/2 (Figs. 36f,g,n). An inner wall formed by the thickening of the inner border of dissepiments may occur in young stages (Figs. 36e,j), but it disappears progressively during the ontogeny. The dissepimentarium/tabularium boundary is well marked, but no conspicuous thickenings are observed in adult stages (Figs. 36a,f,g,n). In longitudinal section the dissepiments are moderate sized to large, mainly elongated and declined to the axis. The declination increases from the periphery (15º-30º) to the interior (45º-60º) (Figs. 36b,h,I,m). The major septa occur very rarely as crests in the dissepimentarium. Otherwise, they only appear in the tabularium. They are thin to moderately thick, straight to slightly undulating and reach the border of the axial structure. Many majors touch it and some of them are in continuity with radial lamellae (Figs 36a,f,g). The cardinal septum and in some specimens the counter septum are prolongated in the median plate, but they are not thicker than other majors. The minor septa occur as short and thin laminae in the periphery of the tabularium. Like the majors, rarely they also occur as small crests on the lonsdaleoid dissepiments (Figs. 36f,n). The axial structure in young specimens may occupy more than 1/3 of the diameter (Fig. 36d), but during the ontogeny its size increases little in comparison to the dissepimentarium; in adult stages it may be less than 1/6 of the diameter (Fig, 36a). It is composed of a persistent, thin median plate, a very variable number of thin radial lamellae and thin conical tabellae. The radial lamellae increase in number during ontogeny. They are 12-15 at 10-15 mm in diameter (Figs. 36c, d), but 25-30 in adult stages (Figs. 36a,g,l). However, in some specimens the number of radial lamellae does not increase substantially during ontogeny and it is 15-20 in adult stages (Figs. 36f,n). In some cases, the radial lamellae and axial tabellae may be slightly thickened, building a more dense axial structure (Fig. 36a). The axial tabellae are conical, more steeply declined to the periphery in the border than in the axis. The periaxial tabellae are variable in shape, from convex to slightly concave and declined to the axis. Some clinotabellae occur in the periphery and some horizontal tabellae occur near the axial structure. The septal mesoplasm is granulo-fibrous and the wall, dissepiments, tabulae and septal stereoplasm are lamellar. The variability in the studied population is large in the thickness and number of the radial lamellae, in the width of the dissepimentarium (related to the size of each specimen), and in the declination of the periaxial tabellae. The aspect of the specimens varies much with the ontogeny; there are conspicuous changes during the growth of the corals that produce different appearances in different ontogenetic stages.

Remarks. The specimens from the Via Crucis Section share with *Pareynia splendens* Semenoff-Tian-Chansky, 1974 the general shape, the wide lonsdaleoid dissepimentarium and the presence of clinotabellae. All those features allow us to identify the genus *Pareynia*. However, the Spanish species show a smaller size and fewer septa, more regular and thicker wall, and smaller axial structure in the adult stage than in the type species (Fig. 37). From the other known species, *Pareynia gangamophylloides* Semenoff-Tian-Chansky, 1974, it differs in having a smaller and more regular axial structure and better developed minor septa. The previous identifications of this genus were related to the upper Viséan. The Spanish species occurs in Pendleian rocks, extending the generic range to the Serpukhovian.

Genus *Morenaphyllum* gen. nov.

Derivatio nominis. The name of the genus is a double dedication: a geographical one, because it has been recorded in Sierra Morena and a personal one, because it is also in honour to Prof. Elena Moreno, distinguished palaeontologist who has worked in that area for more than 30 years.

Diagnosis. Axophyllinae with quite a small axial structure joined to a thick and long cardinal septum and having an irregular median plate, which is thick, but discontinuous, a few radial lamellae and conical tabellae. Conspicuous inner wall composed of lamellar thickenings. Wide transeptal dissepimentarium. Mesoplasm composed of bundles of microlamellae that comprise pseudofibrous structures that produce characteristic denticulations on the wall and transeptal dissepiments. Lamellar stereoplasm.

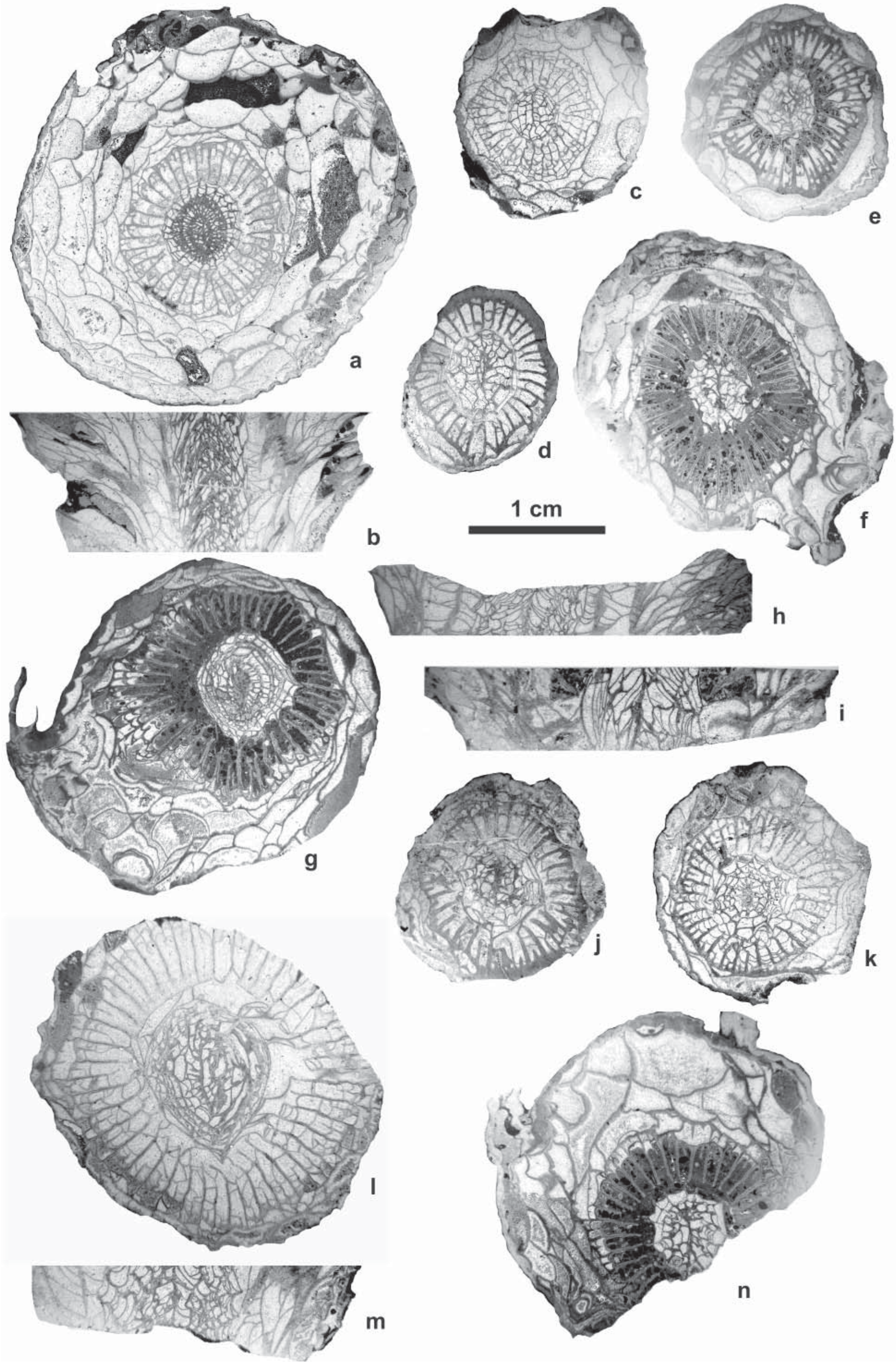
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Figure 36. *Pareynia viacrucense* sp. nov. **a-c)** Specimen VCR2/2-17 (holotype), **a:** transverse section in adult stage. **b:** longitudinal section. **c:** transverse section in young stage. **d)** Specimen VCR2/2-9 (paratype), transverse section in young stage. **e-f)** Specimen VCR2/2-14 (paratype), **e:** transverse section I early adult stage. **f:** transverse section in advanced adult stage. **g-h)** Specimen VCR2/0-13 (paratype), **g:** transverse section. **h:** longitudinal section. **i-j)** Specimen VCR2/2-16 (paratype), **i:** longitudinal section. **j:** transverse section. **k)** Specimen VCR2/4-8 (paratype), transverse section in early adult stage. **l-m)** Specimen VCR2/4-8 (paratype), **l:** transverse section. **m:** longitudinal section. **n)** Specimen VCR2/2-13 (paratype), fragmentary transverse section in adult stage. Scale bar valid for all figures.

— *Pareynia viacrucense* sp. nov. **a-c)** Ejemplar VCR2/2-17 (Holotipo), **a:** sección transversal en estadio adulto. **b:** sección longitudinal. **c:** sección transversal en estadio juvenil. **d)** Ejemplar VCR2/2-9 (paratipo), sección transversal en estadio juvenil. **e-f)** Ejemplar VCR2/2-14 (paratipo), **e:** sección transversal en estadio adulto temprano. **f:** sección transversal en estado adulto avanzado. **g-h)** Ejemplar VCR2/0-13 (paratipo), **g:** sección transversal. **h:** sección longitudinal. **i-j)** Ejemplar VCR2/2-16 (paratipo), **i:** sección longitudinal. **j:** sección transversal. **k)** Ejemplar VCR2/4-8 (paratipo), sección transversal en estado adulto temprano. **l-m)** Ejemplar VCR2/4-8 (paratipo), **l:** sección transversal. **m:** sección longitudinal. **n)** Ejemplar VCR2/2-13 (paratipo), sección fragmentaria en estadio adulto. Escala válida para todas las figuras.

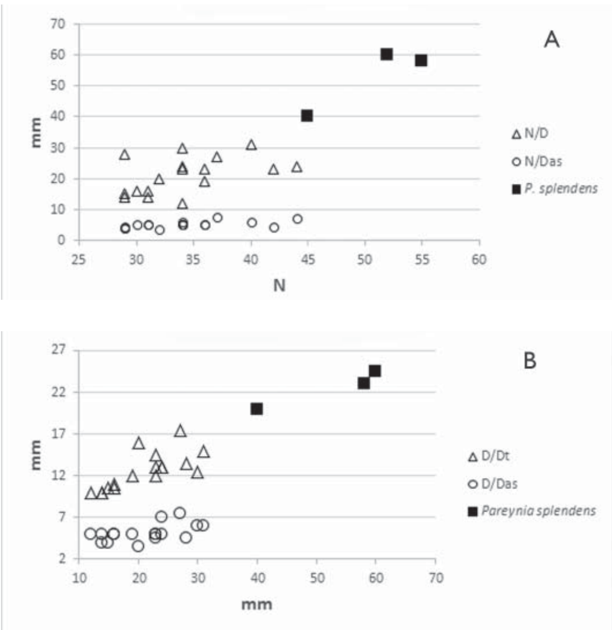

Figure 37. (A) Graph plotting corallite diameter (D)/ axial structure diameter (Das) versus number of major septa (N) for *Pareynia viacrucense.* (B) Graph plotting corallite diameter (D) versus tabularium diameter (Dt) and axial structure diameter (Das) for *Pareynia viacrucense.*

— Gráfico de relación entre el diámetro del coralito (D)/ el diámetro de la estructura axial (Das) y el número de septos mayores (N) para *Pareynia viacrucense*. (B) Gráfico de relación entre el diámetro del coralito (D)/ el diámetro del tabulario (Dt) y el diámetro de la estructura axial (Das) para *Pareynia viacrucense.*

Type species. *Morenaphyllum antolinense* Rodríguez & Somerville

Other species. *Morenaphyllum boyerense* sp. nov., *Morenaphyllum pauciseptata* (Bykova, 1966)

Locus typicus. Antolín section, Guadiato Area, SW Spain, Brigantian, upper Viséan, Mississippian.

Remarks. The new genus show indubitable features of the Axophyllinae: transeptal dissepimentarium, complex axial structure, tabularium composed of conical axial tabellae and concave periaxial tabulae slightly declined to the axis. It is close to the genus *Axophyllum*, but shows some differences to allow the distinction to be made: Small axial structure (less than 1/5 of the diameter), joined to a thick and longer cardinal septum in all stages of development. Additionally, it shows thick septal stereozones in the wall and in the border of the dissepimentarium/ tabularium, composed of lamellar stereoplasm. The microstructure is very characteristic. The inner part of the septa is granulo-fibrous and the stereoplasmatic thickenings are lamellar. The wall and the external part of the septa are composed of piles of lamellae that form pseudofibres. This type of microstructure has been previously described in some genera of the family Geyerophyllidae (Rodríguez, 1984), but it is, to date, unknown in the Axophyllinae. However, the type species of *Axophyllum, A. expansum*, as well as *A. spinosum*, show a similar microstructure that is a variation of the typical axophyllid microstructure. It is regarded here as a possible evolutive relationship between these species, but it may be also related with ecologic factors. *Morenaphyllum* and *A. spinosum* are associated with microbial mounds. Also *Axophyllum expansum* has been recorded in microbial mud mounds of Visé (Poty, pers. comm. 2015). The tendency to gregarism, which is observed in *Morenaphyllum* and in *A. expansum* has been also observed in other axophyllids recorded in mud mounds (Somerville & Rodríguez, 2010, Somerville *et al.* 2012), and it could be regarded as transitional to the development of colonialism (Rodríguez & Somerville, 2010). Two species of *Morenaphyllum* have been identified in the type locality. In addition, the specimen described by Bykova (1966) as *Carcinophyllum lonsdaleiforme pauciseptata* shows the same features and it is regarded here as an additional representative of the new genus under the name *Morenaphyllum pauciseptata* (Bykova, 1966).

Morenaphyllum antolinense gen. *et* sp. nov.
Fig. 38a-u, 39

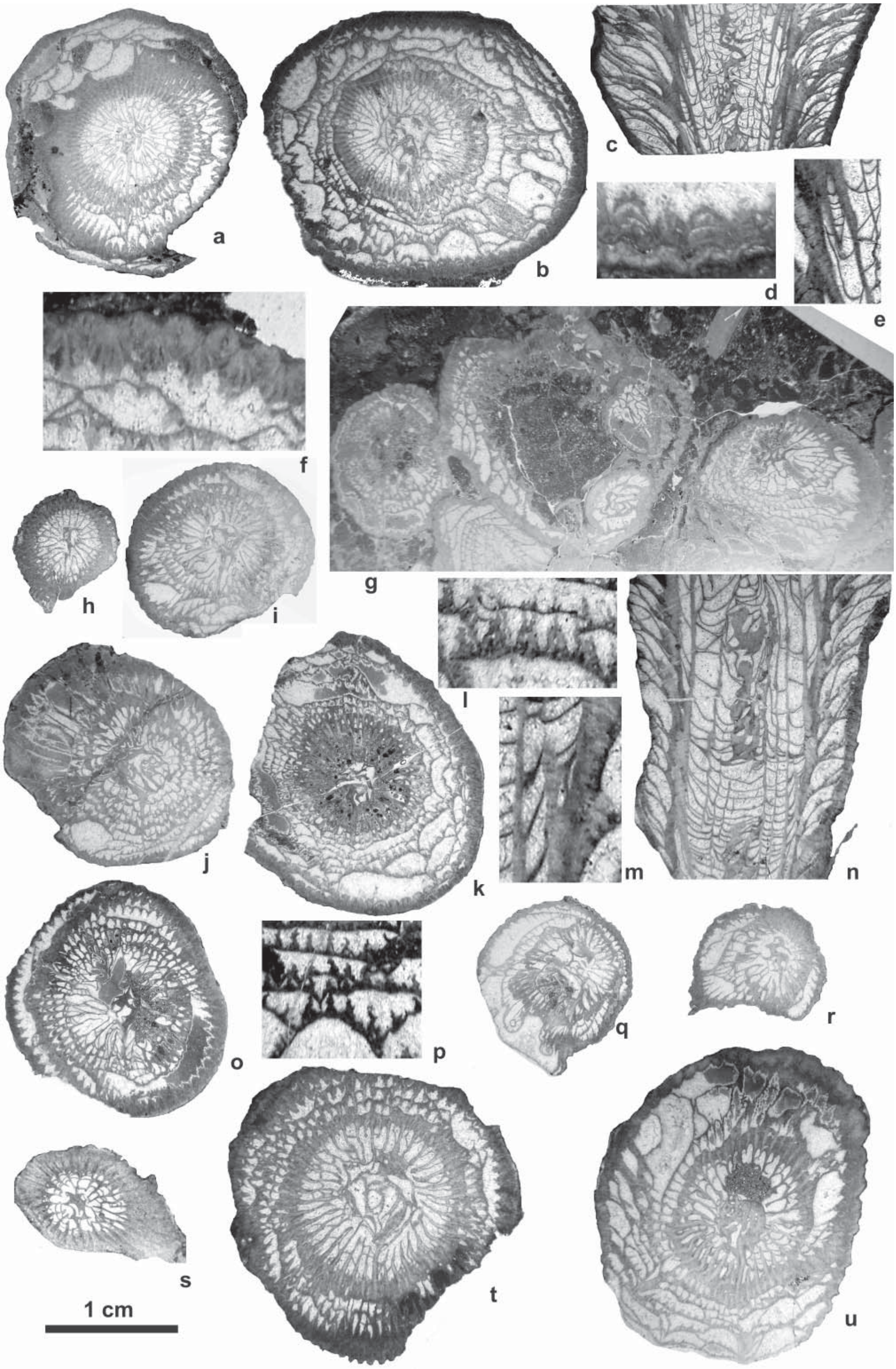
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Figure 38. *Morenaphyllum antolinense* gen. *et* sp. nov. **a-f)** Specimen ANT2/2-52 (holotype), **a:** transverse section in early adult stage. **b:** transverse section in advanced adult stage. **c:** longitudinal section. **d:** detail showing naotic septa **e:** detail showing biform tabularium in longitudinal section. **f:** detail showing septal spines in the wall, composed of piles of lamellae. **g)** Specimens ANT2/2-2a, b, c (paratypes). Transverse section showing gregarism and aborted calicular offsets. **h-i)** Specimen ANT2/2-1 (paratype), **h:** transverse section in young stage. **i:** transverse section in adult stage. **j)** Specimen ANT2/2-4 (paratype), transverse section, adult stage. **k-l)** Specimen ANT2/2-14 (paratype), **k:** transverse section in adult stage. **l:** detail showing spines on the lonsdaleoid dissepiments. **m-n)** Specimen ANT2/2-33 (paratype), **m:** detail of biform tabularium **n:** longitudinal section. **o-p)** Specimen ANT2/2-44 (paratype), **o:** transverse section. **p:** detail of the spines on the lonsdaleoid dissepiments. **q-r)** Specimen ANT2/2-40 (paratype). **q:** transverse section in early adult stage. **r:** transverse section in late young stage. **s)** Specimen ANT2/2-45 (paratype), transverse section in young stage. **t)** Specimen ANT2/2-48 (paratype), transverse section, adult stage. **u)** Specimen ANT2/2-48 (paratype), transverse section, adult stage. Scale bar valid for all figures except details.

— *Morenaphyllum antolinense* gen. *et* sp. nov. **a-f)** Ejemplar ANT2/2-52 (Holotipo), **a:** sección transversal en estadio adulto temprano. **b:** sección transversal en estadio adulto avanzado. **c:** sección longitudinal. **d:** detalle que muestra septos naóticos **e:** detalle que muestra tabulario biforme en sección longitudinal. **f:** detalle que muestra espinas septales en la muralla, compuestas de apilamientos de lamelas. **g)** Ejemplares ANT2/2-2a, b, c (paratipos). Sección transversal que muestra gregarismo y gemaciones caliculares abortadas. **h-i)** Ejemplar ANT2/2-1 (paratipo), **h:** sección transversal en estadio juvenil. **i:** sección transversal en estadio adulto. **j)** Ejemplar ANT2/2-4 (paratipo), sección transversal, estadio adulto. **k-l)** Ejemplar ANT2/2-14 (paratipo), **k:** sección transversal in estadio adulto. **l:** detalle que muestra espinas sobre los disepimentos lonsdaleoides. **m-n)** Ejemplar ANT2/2-33 (paratipo), **m:** detalle del tabulario biforme **n:** sección longitudinal. **o-p)** Ejemplar ANT2/2-44 (paratipo), **o:** sección transversal. **p:** detalle de las espinas sobre disepimentos lonsdaleoides. **q-r)** Ejemplar ANT2/2-40 (paratipo). **q:** sección transversal en estadio adulto temprano. **r:** sección transversal en estadio juvenil tardío. **s)** Ejemplar ANT2/2-45 (paratipo), sección transversal en estadio juvenil. **t)** Ejemplar ANT2/2-48 (paratipo), sección transversal, estadio adulto. **u)** Ejemplar ANT2/2-48 (paratipo), sección transversal, estadio adulto. Escala válida para todas las figuras excepto detalles.

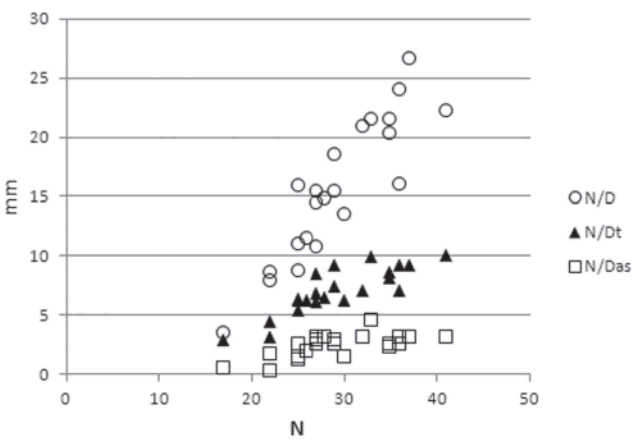

Figure 39. Graph plotting corallite diameter (D)/ tabularium diameter (Dt)/ axial structure diameter (Das) versus number of major septa (N) for *Morenaphyllum antolinense.*

— Gráfico de relación entre el diámetro del coralito (D)/ el diámetro del tabulario (Dt)/ el diámetro de la estructura axial (Das) y el número de septos mayores (N) para *Morenaphyllum antolinense.*

Derivatio nominis. The name of the species refers to the Antolín section, located near the Coal Mine of Antolín.

Holotype. Specimen ANT2/1-52; rest of specimens collected in the same bed are regarded as paratypes. Stored in the Department of Paleontology of the Complutense University.

Type locality, horizon and age. Antolín section, located near the Coal Mine of Antolín, 2 km south from Peñarroya. Sierra Boyera Block, El Castillo Unit; Brigantian (upper Viséan, Mississippian).

Material. 19 specimens (ANT 2/1-1; ANT 2/1-2; ANT 2/1-4; ANT 2/1-14; ANT 2/1-18; ANT 2/1-22; ANT 2/1-23; ANT 2/1-25; ANT 2/1-31; ANT 2/1-34; ANT 2/1-40; ANT 2/1-44;. ANT 2/1-45; ANT 2/1-46; ANT 2/1-47; ANT2/1-52; ANT 2/1-54; ANT 2/1-56 and ANT 2/1-57). 24 transverse sections and 5 longitudinal sections.

Diagnosis. *Morenaphyllum* having a thick wall and low development of stereoplasmatic thickenings. 30 to 40 major septa in 18 to 28 mm in adult stages. Axial structure 2.5-5 mm, being 1/5 to 1/7 of the diameter.

Description. Solitary, trochoid corals showing rarely calicular division, but do not develop adult corallites from them (Fig. 38g). External wall showing conspicuous longitudinal grooves. Some specimens are partly eroded. Common talons and excrescences (Rodríguez, 2004) in the lower part of the corallite Figs. 38h,q,r,s).

Thick wall, from undulating to festooned (Figs. 38a,b,d,f). Rejuvenescences that produced double and triple walls occur commonly (Fig. 38o). The dissepimentarium is wide, composed of transeptal dissepiments of first and second order (Semenoff-Tian-Chansky, 1974) in the outer part (Figs. 38a,b,k,u). Conspicuous septal crests on the wall and on the transeptal dissepiments (Figs. 38f,i,p). Up to 3 rows of interseptal, regular, locally thickened dissepiments in the inner part. Some naotic septa may occur (Fig. 38d). Thick inner wall composed of stereoplasm thickenings on the inner dissepiments and septa (Figs. 38a,b,t,u). In longitudinal section the dissepiments are elongated and declined to the axis from 30º (near the wall) to 70º (near the tabularium) (Figs. 38c,n). Two orders of septa. Major septa are straight and long, reaching the proximity of or even being in contact with the axial structure.

They are radially disposed and may be slightly undulating near the inner border (Figs. 38a,b,k,o). Minor septa penetrate into the tabularium, where they reach approximately 1/2 the length of majors (Figs. 38b,t). Both major and minor septa are thick at the dissepimentarium/tabularium boundary and build a conspicuous inner wall. They are also thick at the periphery of the coral producing a septal stereozone, mainly in young stages (Figs. 38h, s). Both, in the septal stereozone and in the crests on the surface of the transeptal dissepiments, the septa show a “spiny” aspect, because of the presence of small protuberances composed of piles of microlamellae (Figs. 38f,i). The cardinal septum is thicker and longer than other septa (Figs. 38b,I,t,u); it is joined to a median plate that is very irregular. It shows common thickenings and irregular trajectory in longitudinal section (Figs. 38b,c,n). The axial structure is completed by a few irregular radial lamellae and some axial tabellae. It is always smaller than 1/4 and usually between 1/5 and 1/7 of the alar diameter (Figs. 38b,I,k,o,t,u). The tabularium is composed of incomplete, thin tabulae. The axial tabellae are convex to slightly concave, the periaxial tabellae are concave; in the periphery they show clear biform structure, some being almost horizontal, some strongly declining from the inner wall to the axis (Figs. 38c,e,m,n). In young stages the septa are thick and form a thick peripheral stereozone interrupted by a few transeptal dissepiments (Figs. 38h,r,s). The axial structure is present from very early stages, joined to a conspicuous cardinal septum and composed of an irregular median plate and few radial lamellae. The microstructure is completely lamellar in young stages. The septa change progressively to granulo-fibrous mesoplasm. The stereoplasm is always lamellar. The festoons of the wall and the crests on the transeptal dissepiments are composed of piles of microlamellae disposed in fascicles. Those piles take on an aspect of fibres seen in conventional thin section. They produce very characteristic denticulations (Figs. 38 f,l).

Remarks. This species is different from any other axophyllid previously described. Only the species *Carcinophyllum lonsdaleiforme pauciseptata* Bykova 1966, that here is regarded as *Morenaphyllum pauciseptatum* (Bykova, 1966) shows similar structures, but the size is much larger for similar number of septa, minor septa are shorter and the inner wall is less developed.

The young stages of *Morenaphyllum* are similar to those in *Axophyllum*, but during the ontogenesis appear notable morphologic differences. The adult stages are similar to an *Axophyllum* that develop a wide lonsdaleoid dissepimentarium, but whose axial structure does not vary from the young stages. Effectively, the axial structure maintains a small size, it is always strongly joined to the cardinal septum, a few radial lamellae appear, and the axial tabellae do not develop the typical conical shape of *Axophyllum*. Consequently, the appearance of this species (and the nominal genus) can be considered as a heterochronic process (partial neoteny in this case), which are quite common in rugose corals (Poty, 1993).

Morenaphyllum boyerense gen. *et* sp. nov.
Figs. 40a-f, 41

Derivatio nominis. The name of the species refers to its occurrence in the Sierra Boyera Block, near the northern end of the Sierra Boyera Reservoir.

Holotype. Specimen ANT2/1-12; rest of specimens collected in the same bed are regarded as paratypes. Stored in the Department of Paleontology of the Complutense University.

Type locality, horizon and age. Antolín section, located near the Coal Mine of Antolín, 2 km south from Peñarroya. Sierra Boyera Block, El Castillo Unit; Brigantian (upper Viséan, Mississippian).

Material. 7 specimens (ANT2/1-8; ANT2/1-9; ANT2/1-11; ANT2/1-12; ANT2/1-13; ANT2/1-24 and ANT2/1-29). 10 transverse sections and 3 longitudinal sections.

Diagnosis. *Morenaphyllum* having 30 to 34 major septa in 18 to 20 mm in diameter, counter septum commonly joined to the axial structure, strong stereoplasmatic thickenings and irregular inner wall. Axial structure 2-3 mm being 1/6 of the diameter.

Description. Solitary, trochoid corals, showing well-marked longitudinal furrows, strong rejuvenescences and radiciform processes. Wall is thick, undulating to festooned (Figs. 40a,d,e,f). The dissepimentarium is composed of peripheral transeptal dissepiments of first and second order, showing strong septal crests on the surface of the dissepiments and 2 to 5 inner rows of interseptal, regular dissepiments that may show stereoplasmatic thickenings (Figs. 40a,d,e,f). Some parts of the peripheral dissepimentarium may be substituted by a thick septal stereozone (Fig. 40a). In longitudinal section the dissepiments are large, elongated and steeply declined to the axis in the inner part (Figs. 40b,c). The inner wall is not as conspicuous as in the type species of the genus. Major septa are straight and long, showing thinning toward the axis (Fig. 40a). In the inner zone of the tabularium they may be slightly sinuous. Cardinal and counter septa are long and may be in contact with the axial structure, and in continuity with the median plate (Figs.40a,d,f). Counter septum withdraws from the axial structure in late adult stage. Cardinal septum is thicker and stays in contact with the axial structure during all ontogenetic stages. All other metasepta reach also the axial structure, but are rarely in contact with it. Minor septa are quite long (1/2 length of majors), reaching the tabularium and penetrating slightly into it (Figs. 40a,d,e,f). Septal crests are common on the surface of the transeptal dissepiments. In some cases, the septal crests occur also in interseptal loculi.The

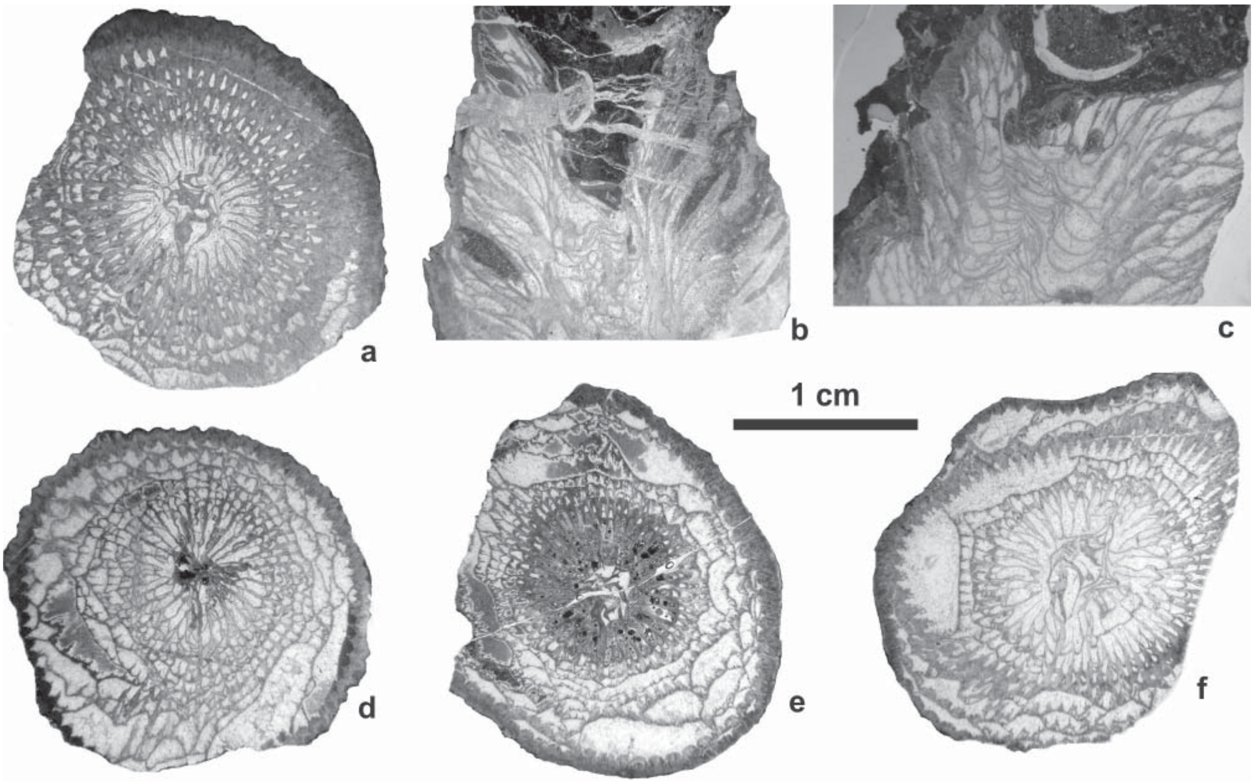

Figure 40. *Morenaphyllum boyerense* gen. *et* sp. nov. **a-b)** Specimen ANT2/2-12 (holotype), **a:** transverse section. **b:** longitudinal section. **c)** Specimen ANT2/2-8 (paratype), longitudinal section. **d)** Specimen ANT2/2-13 (paratype) transverse section. **e)** Specimen ANT2/2-14 (paratype), transverse section. **f)** Specimen ANT2/2-29 (paratype), transverse section. Scale bar valid for all figures.
— *Morenaphyllum boyerense* gen. *et* sp. nov. **a-b)** Ejemplar ANT2/2-12 (holotipo), **a:** sección transversal. **b:** sección longitudinal. **c)** Ejemplar ANT2/2-8 (paratipo), sección longitudinal. **d)** Ejemplar ANT2/2-13 (paratipo) sección transversal. **e)** Ejemplar ANT2/2-14 (paratipo), sección transversal. **f)** Ejemplar ANT2/2-29 (paratipo), sección transversal. Escala válida para todas las figuras.

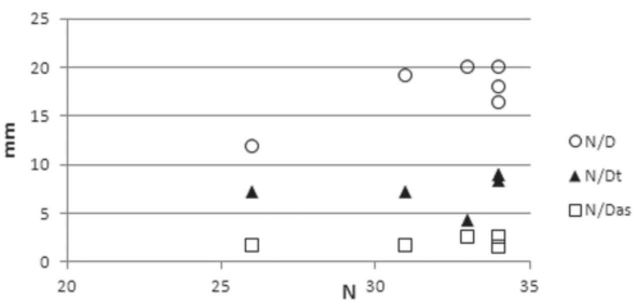

Figure 41. Graph plotting corallite diameter (D)/ tabularium diameter (Dt)/ axial structure diameter (Das) versus number of major septa (N) for *Morenaphyllum boyerense.*
— Gráfico de relación entre el diámetro del coralito (D)/ el diámetro del tabulario (Dt)/ el diámetro de la estructura axial (Das) y el número de septos mayores (N) para *Morenaphyllum boyerense.*

tabularium is composed of densely packed, thin, incomplete tabulae. The axial tabellae are conical to convex, the periaxial tabellae are concave (Figs. 40b,c). The peripheral border is biform, showing some flat tabellae and others steeply declined to the axis. The axial structure is small (about 1/6 of the alar diameter) but complex. It is composed of a median plate that shows an irregular trajectory, a few thick radial lamellae and some axial tabellae (Figs. 40a,f). The microstructure is identical to that of the type species.

Remarks. *M. boyerense* is close to the type species. The main differences are a long counter septum joined to the axial structure (except in the late adult stage), a higher development of steroplasmatic thickenings, and a less conspicuous inner wall. In addition, it shows a denser tabularium and longer septa.

4. Discussion

The distribution and variations in abundance and diversity of the Axophyllinae in Sierra Morena provide interesting biostratigraphic, evolutive and palaeobiogeographic information.

4.1. *Biostratigraphy*

The Carboniferous marine outcrops in Siera Morena are restricted to the upper Viséan and Serpukhovian. The first studies on the Carboniferous from Sierra Morena indicated the possible presence of Tournaisian and lower Viséan rocks (Ortuño, 1971, Gabaldón *et al.*, 1983), but detailed studies on conodonts and foraminifers (Cózar, 1998; Cózar & Rodríguez, 1999a,b; Bermúdez-Rochas *et al.*, 2004) demonstrated that the marine sedimentation in that region began with the upper Viséan transgression. Consequently, the first axophyllids in Sierra Morena occur in Asbian rocks. They are common in most studied outcrops and locally abundant (Antolín, La Cornuda, Via Crucis, El Casar sections). Most species occur in several localities, but some of them have been recorded in only a single locality (*Axophyllum tazoultense* and all the new species). The stratigraphic range of the species identified in Los Santos de Maimona Basin and Guadiato Area (Fig. 42) fits well in most cases with the previously known range in other regions, with three exceptions. *A. mendipense* occurs at the top of the lower Viséan and at the base of the upper Viséan in North-western Europe (Ryder, 1930; Mitchell, 1989), but it occurs in lower Brigantian rocks in Sierra Morena. It could be explained in two ways. It could have originated by a slow migration southwards, or it could be a homeomorphic form. On the other hand, *A. tazoultense* occurs in Sierra Morena somewhat earlier than in the Saharan basins (Semenoff-Tian-Chansky, 1974). The difference is small and it can be explained easily by a slow migration. *A. pseudokirsopianum* occurs in North Africa in Serpukhovian rocks (Semenoff-Tian-Chansky, 1974), but in Brigantian rocks in Sierra Morena. It also occurs in Upper Viséan rocks in Belgium (Poty, 1981). Consequently, it seems to have a long range; it appears in the upper Asbian in North-western Europe and migrated to the south, reaching the Saharan Basins during the Serpukhovian. It accords well with slow migrations southwards of both *A.mendipense* and *A. tazoultense.*

The oldest axophyllid occurrences in Sierra Morena are located in the Asbian from Los Santos de Maimona Basin, where *A. densum* and *A. vaughani* occur. Both species are also recorded in the Asbian from Guadiato Area, where they reach the lower Brigantian. Only one additional species occurs also in the Asbian from Sierra Morena, *A. kirsopianum*. The Lower Brigantian represents the acme in the axophyllid distribution from Sierra Morena. The maximum abundance and diversity is located in the Lower Brigantian from the Guadiato Area, where 11 species belonging to three genera occur (Fig. 42). The two richest and most diverse outcrops are Brigantian in age. El Casar (more than 40 specimens, 5 species belonging to 2 genera) and Antolín (more than 50 specimens, 5 species belonging to 2 genera). The upper Brigantian sediments in the Guadiato Area are mainly terrigenous and did not yield axophyllids, but the Serpukhovian was again a favourable time for them. In spite of the reduction of outcrops compared to the Viséan, they occur in several outcrops, being abundant in at least two of them. The assemblages show peculiar forms, with special features that seem to be developed locally. Thus, only one species has been recorded in each outcrop and all three are new (Fig. 42).

4.2. *Evolution*

The record of Axophyllinae in the Palaeotethys is abundant and diverse. The Axophyllinae show quite variable features and many of them show variations not only between individuals, but also in their growth. It implies that in many cases the differentiation of species is not easy to discriminate. Some populations show intermediate features between two or three species (Rodríguez & Said, 2009; Denayer, 2012). But some species appear at different stratigraphical levels and are substituted by other species after periods of co-existence. It means that there are evolutionary lines from some species to others, not that all species should be synonymyzed. The abundance of specimens and the precise knowledge of the stratigraphic position of most species in the Western Palaeotethys allow the proposal of some evolutive lines that are shown in Figure 43. The precision of stratigraphic location is not as high in some species in the Eastern Palaeotethys. Consequently, some tentative lines are proposed for those species (Fig. 44).

The oldest species is *A. simplex* that shows a low development of the dissepimentarium and a quite simple axial structure. It seems to be the ancestor of all Axophyllinae. Three main evolutive lines are proposed here: 1) A main line of species having large axial structures and low development of lonsdaleoid dissepiments in which the increase in size through time is conspicuous (*Axophyllum kirsopianum* species group). 2) A line of species that maintain small size, moderate axial structures and moderate development of lonsdaleoid dissepiments (*A. pantopodum* species group). 3) A line of species developing large lonsdaleoid dissepiments and also notable an increase in size (*A. lonsdaleiforme* species group).

The development of an evolutionary pattern in which many intermediate forms occur through time is well expressed in the so-called *Axophyllum kirsopianum* species group. It comprises *A. mendipense*, *A. begaense*, *A. kirsopianum*, *A. spiralum* and *A. pseudokirsopianum*. All of them show low development of lonsdaleoid dissepiments and large axial structures with quite thick elements. The oldest species is *Axophyllum mendipense* from which *A. begaense* seems to be an ecologic variant with strongly thickened structures. During the Upper Viséan an increase in size and spiralation of axial structure originated *A. kirsopianum* (intermediate) and *A. pseudokirsopianum* (the largest one). The development of an even larger

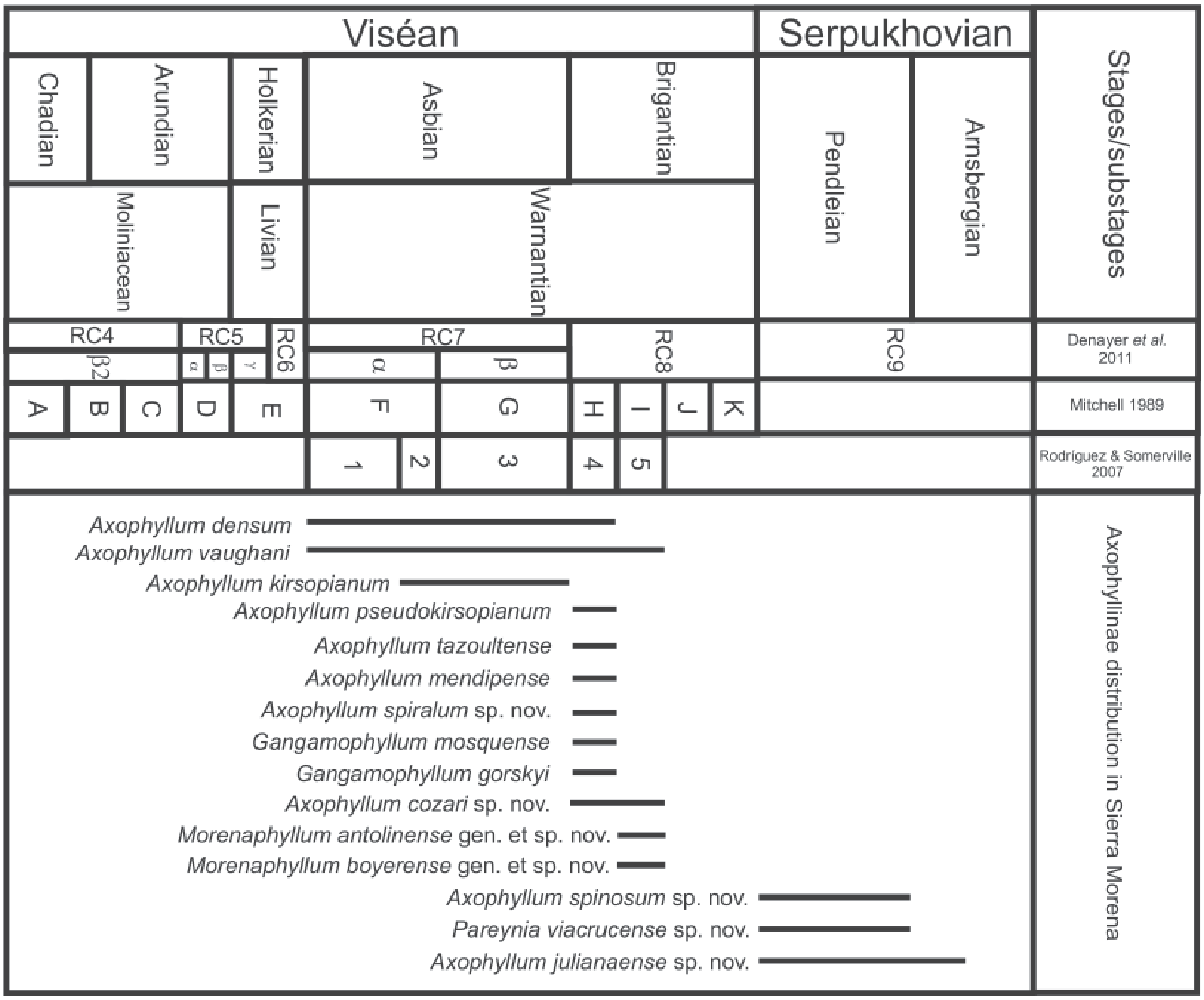

Figure 42. Stratigraphic distribution of Axophyllinae in Sierra Morena.
— Distribución estratigráfica de los Axophyllinae en Sierra Morena.

and more spiral axial structure without an increase in size produced the local species *A. spiralum*. Only the largest form (*A. pseudokirsopianum*) reaches the Serpukhovian. An additional species could be added in that evolutionary lineage; *A. cozari* shows also a large spiralled axial structure. It could have derived from *A. kirsopianum* by the development of a wide lonsdaleoid dissepimentarium.

The oldest species having a well-developed lonsdaleoid dissepimentarium is *Axophyllum vaughani*. The increase of the lonsdaleoid dissepimentarium is related to an increase in size and resulted in *A. lonsdaleiforme*, *A. dibunoides* and *A. julianaense*. The lower Bashkirian species *A. moroccoense* could be derived from this line by an increase in size in *A. julianaense* or from the *A. kirsopianum* species group by the development of a large lonsdaleoid dissepimentarium via *A. pseudokirsopianum* (Fig. 43).

Two very large species probably originated from this evolutionary lineage by extreme development of lonsdaleoid dissepiments, *A. parkinsoni* that shows horizontal dissepiments in the periphery that curve to vertical arrangement near the tabularium and *A. sahariense* that show regularly declined dissepiments (not included in Figure 43 because of their large size). A third large species has been described in the Eastern Palaeotethys, *A. gangamoforme*, with identical dissepimentarium, but different axial structure to *A. parkinsoni*, that could be its ancestor (Fig. 44).

The type species, *A. expansum,* could have descended from *A vaughani* by the reduction in size of the axial structure and the development of an inner wall and “spiny” septa. A larger increase in those features could have led to the origin of the Serpukhovian species *A. spinosum* (Fig. 43). In addition, the extreme development of such microstructure plus the reduction of the axial structure and the development of a longer and thicker cardinal septum could have led to the origin of the genus *Morenaphyllum* (Fig. 45).

The third evolutionary line led to the origin of small species such as *A. nanum*, *A. densum*

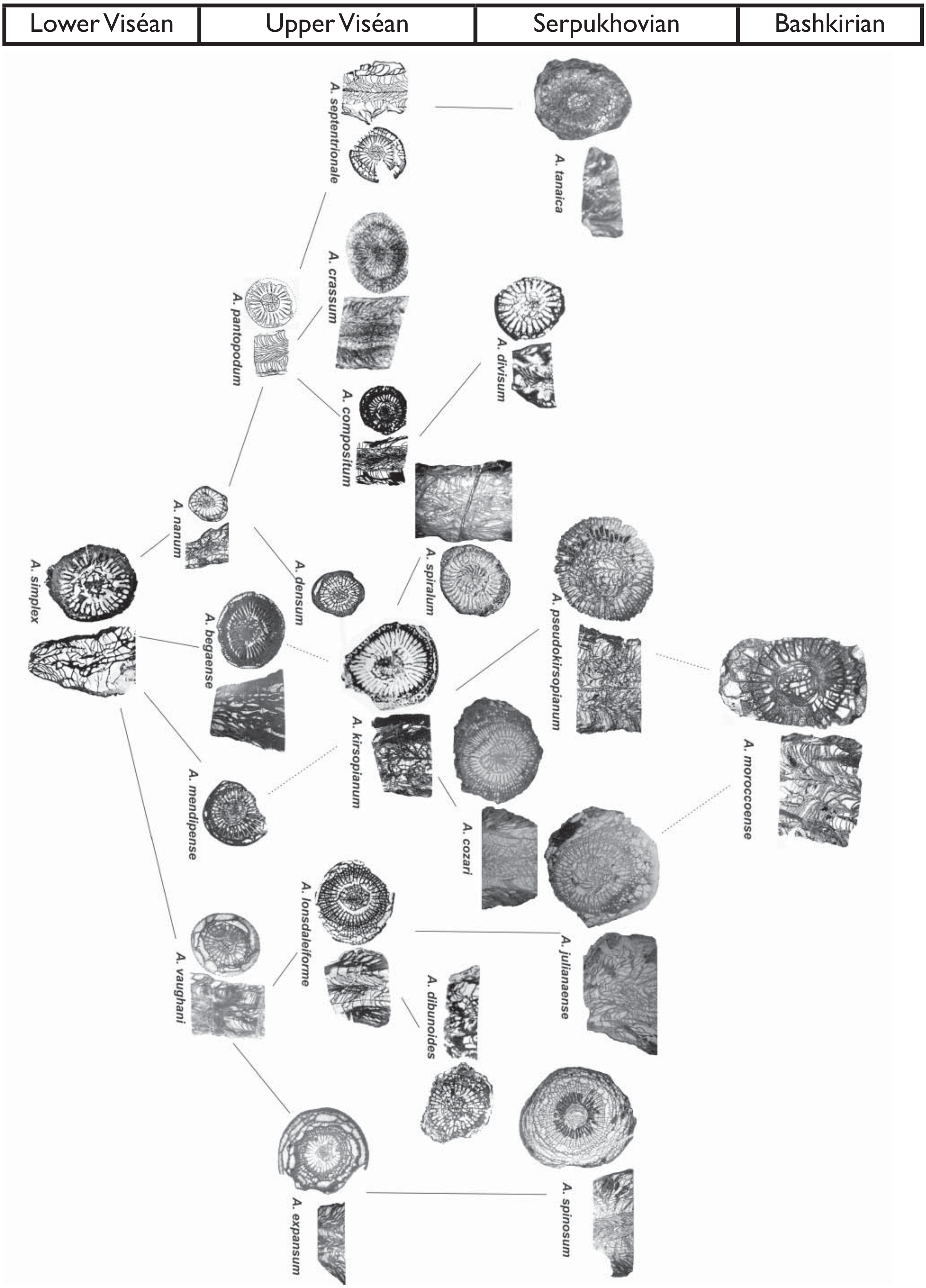

Figure 43. Proposal of evolutionary lineages of the *Axophyllum* species in Central and Western Palaeotethys.
— Propuesta de líneas evolutivas de *Axophyllum* en el Palaeotethys occidental y central.

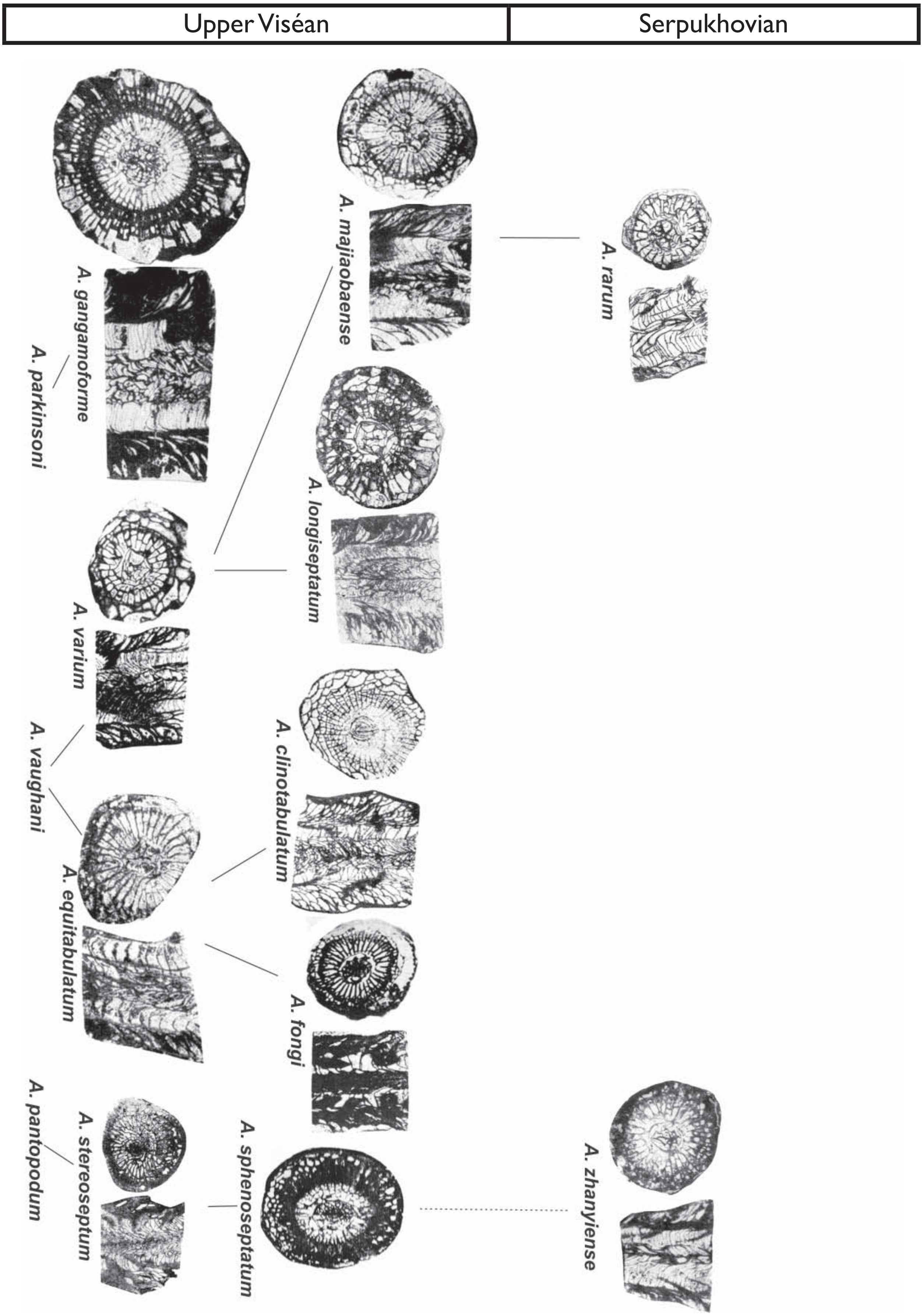

Figure 44. Proposal of evolutionary lineages of the *Axophyllum* species in Eastern Palaeotethys.
— Propuesta de líneas evolutivas de *Axophyllum* en le Palaeotethys oriental.

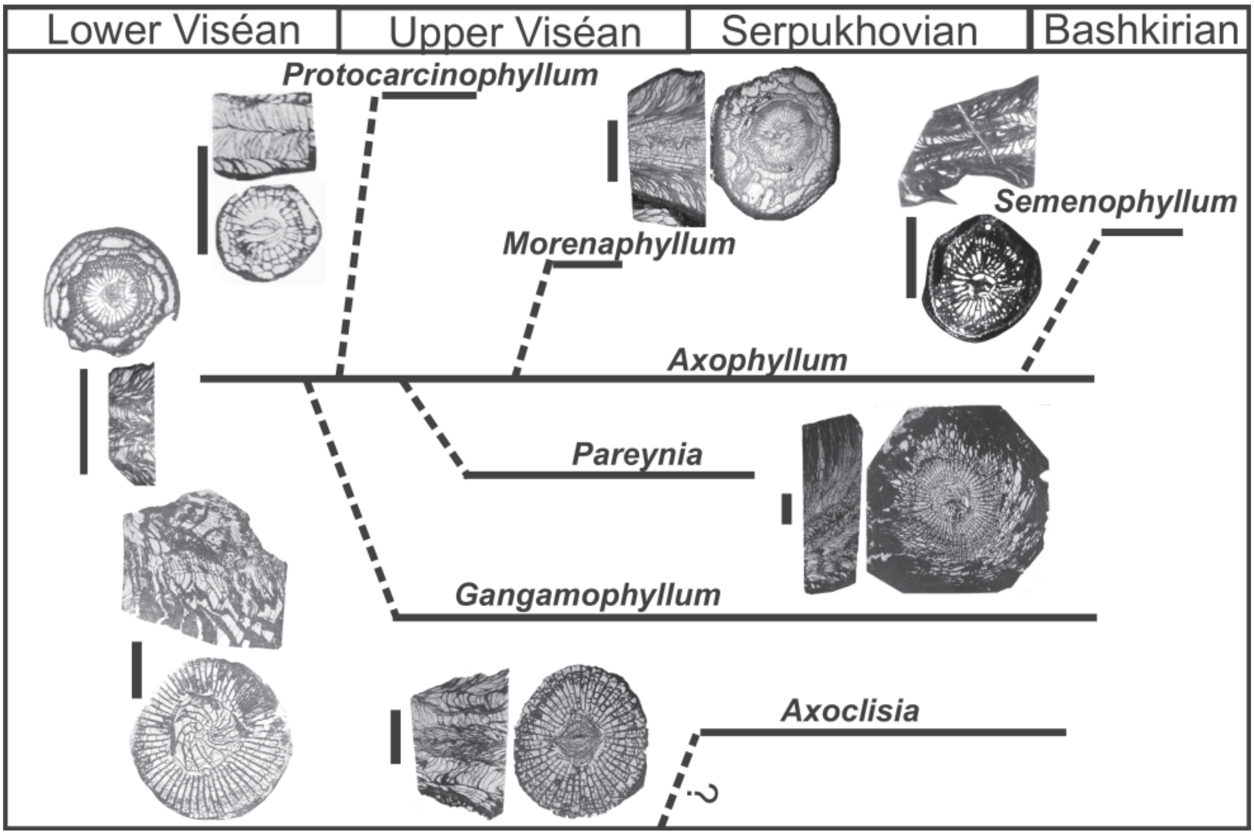

Figure 45. Evolutionary relationships between the Axophyllinae genera. The represented species are the types of each genus.
— Relaciones evolutivas entre los géneros de los Axophyllinae. Las especies representadas son las especies tipo de cada género.

and *A. pantopodum*. The last-named species was probably the ancestor of most species from North-Central Palaeotethys. All of them show moderate lonsdaleoid dissepimentarium and a small increase in size during the Brigantian-Serpukhovian interval. *A. septentrionale, A. compositum, A. divisum, A. crassum* and *A. tanaica* are typical representatives of that line.

Some species recorded in the Eastern Palaeotethys probably migrated from Western Palaeotethys. *A. vaughani* has been mentioned also in that area (Wu & Zhao 1989) and it could be the ancestor of the Chinese species having a high development of lonsdaleoid dissepiments. Some of them show a lonsdaleoid dissepimentarium with horizontal peripheral dissepiments and could represent a sub-lineage (*A. varium*, *A. longiseptatum* and *A. majiaobaense*) (Fig. 44). The Serpukhovian species *A. rarum* has been tentatively included in that evolutionary lineage. The coral described by Niikawa (1979) as *Carcinophyllum lonsdaleiforme* must be included in this group and probably represents a separate species. Other species show regularly inclined dissepiments and could represent another evolutionary subline (*A. clinotabulatum*, *A. equitabulatum*, *A. fongi*) (Fig. 44). The species having low development of lonsdaleoid dissepiments and moderate size (*A. stereoseptum*, *A. sphenoseptatum* and *A. zhanyiense*) could have descended from North-Central Palaeotethys species that are close morphologically, such as *A. pantopodum* (Fig. 44).

There is no doubt that *Axophyllum* represents the main genetic pool from which all other axophyllinae descend. Most of the Axophyllinae genera are locally developed from a geographical and stratigraphical point of view (Fig. 45). Thus, *Protocarcinophyllum* and *Semenophyllum* would be derivations that reduced the development of the axial structure at two different times (uppermost lower Viséan and lower Bashkirian respectively). The first one could have descended from *A. vaughani*, the latter from an unknown species. *Morenaphyllum* would have descended from the type species by extreme development of the cardinal septum and reduction of the axial structure. *Pareynia* could have descended from the large species that developed very large lonsdaleoid dissepimentarium (*A. sahariense*?).

The genus *Gangamophyllum* was mainly developed in the North-Central Palaeotethys. Consequently, it probably descended from an *Axophyllum* species from that area. It developed by the reduction of the median plate and the homogenization of the axial structure. However, the different species of that genus show similarities with different species of *Axophyllum* and connections between species of that genus are difficult to appreciate. Consequently, we consider *Gangamophyllum* as a polyphyletic genus, some of whose species descended from *Axophyllum* species.

Finally, the genus *Axoclisia* derived from the genus *Clisiophyllum* by the development of lonsdaleoid dissepiments, being a case of homeomorphism.

Axophyllum, *Gangamophyllum* and *Axoclisia* reach the Bashkirian, but only in the Tindouf Basin (Rodríguez *et al.*, 2013a).

4.3. *Palaeobiogeography*

The first Axophyllinae (*A. simplex* Garwood, 1912; Mitchell, 1989) appears at the beginning of the early Viséan (Chadian) in Britain, Belgium (Poty *et al.*, 2006 and Poland (Poty *et al.*, 2007) (Fig. 46). No other representative of the subfamily occurs during most of the early Viséan, but at the end of the early Viséan and in the middle Viséan (Holkerian), the species *A. mendipense* is also recorded, but only in the North-western border of the Palaeotethys (British Isles, Belgium; Mitchell, 1989; Denayer *et al.*, 2011). Thus, the Axophyllinae must be considered as an endemic group from that region during the early Viséan. But early in the late Viséan (Early Asbian), several new species occur and the geographic distribution expands to the Iberian Plate, North Africa and Eastern European platforms (Rodríguez & Falces, 1992; Semenoff-Tian-Chansky, 1974, 1985; Vassiljuk, 1960; Sayutina, 1973). It represents the first radiation of the Axophyllinae.

During the rest of the Asbian, the Axophyllinae expand to the East Palaeotethys reaching its maximum distribution and diversity at the end of the Asbian and the beginning of Brigantian, coinciding with the greatest Viséan transgression. The expansion of the representatives of the subfamily towards the East was difficult before that transgression, because of the main equatorial currents, directed to the West, would make it difficult for the transport of the planulae in the contrary direction. But the coastal currents that favour the expansion of larvae against the main oceanic currents (Teske *et al.* 2007; Langhorne & Read, 2000) were more active in larger platforms created by the transgression and supported a quicker expansion to the East. The appearance of *Protocarcinophyllum*, *Gangamophyllum*, *Morenaphyllum* and *Pareynia*, together with the maximum diversity of the genus *Axophyllum* evidence the acme of the subfamily. The genus *Gangamophyllum* expanded quickly in the North-central Palaeotethys and became dominant in that region, whereas *Axophyllum* continued being the dominant genus in West, South and East Palaeotethys (Fig. 46).

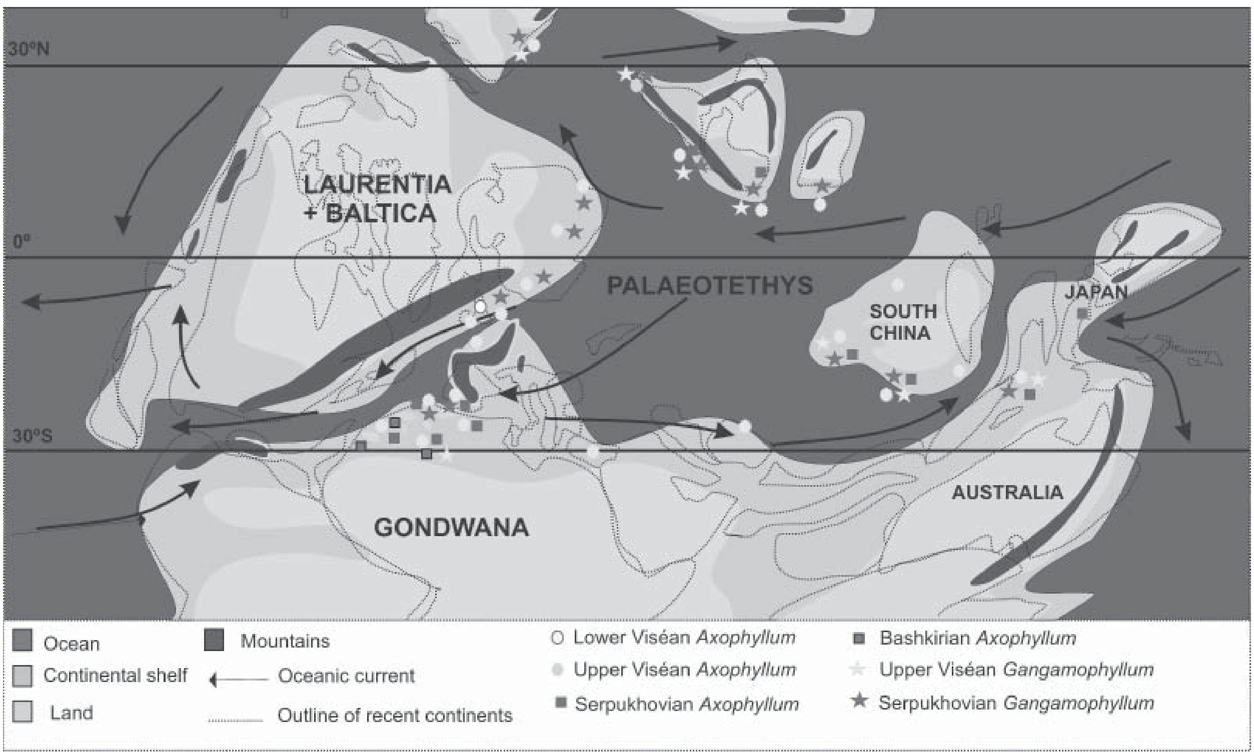

Figure 46. Palaeogeographic distribution of Axophyllinae (map based on Scotese, 202).
— Distribución palaeogeográfica de los Axophyllinae (mapa basado en Scotese, 2002).

The reduction of epicontinental platforms during the Serpukhovian because of the icehouse period and the intensive tectonic activity, providing terrigenous imputs into the remaining platforms, notably between Laurentia (Laurussia) and Gondwana (Somerville *et al.*, 2013; Cózar *et al.,* 2014) provoked the extinction of most Axophyllinae species, coinciding with the extinction of many other invertebrates (Stanley 2007; McGhee *et al.,* 2012). Consequently, the Axophyllinae disappear from the North-west Palaeotethys and distribution of the subfamily during the Serpukhovian is restricted to South-western, North-central and the Eastern Palaeotethys (Fig. 46).

The transition to the Bashkirian implies the disappearance of Axophyllinae from most Palaeotethys areas. Only some species remain in stable refuges, such as Saharan platforms (Somerville *et al*. 2013).

As a whole, the Axophyllinae are restricted to the Palaeotethys. All the references to the genera included in the subfamily beyond the Palaeotethys are misidentifications. The eastern limit of their distribution is located in Japan, at the eastern end of the Palaeotethys (Niikawa, 1979). It is a peculiar situation, because other typical Palaeotethysian families, such as Aulophyllidae or Lithostrotionidae, were able to migrate to other areas (North America, Australia), during the late Viséan transgression (Rodríguez & Kopaska-Merkel, 2014; Fedorowski *et al*., 2012). Consequently, it must be due to some intrinsic features of the Axophyllinae (persistence of the planulae, capacity to survive in environments with terrigenous imputs, etc.) that limit their capacity of migration.

5. Conclusions

The revision of the subfamily Axophyllinae allow the assignation to it of the genera *Axophyllum, Gangamophyllum, Pareynia, Semenophyllum, Protocarcinophyllum* and the new genus *Morenaphyllum*. The genus *Axoclisia* show close features to Axophyllinae, but it seems to be more closely related to the Aulophyllidae. Only 34 previously described species are included in the genus *Axophyllum* (more than 50 have been recorded in the literature). Four new species recorded in Sierra Morena are described: *A. spinosum*, *A. cozari*, *A. spiralum* and *A julianaense*. From more than 30 species assigned previously to the genus *Gangamophyllum*, only 22 are accepted here. A new species belonging to the genus *Pareynia* is described: *P. viacrucense*. A new genus, *Morenaphyllum*, is also described and two species are assigned to it, *M. antolinense* and *A. boyerense*.

The record of Axophyllinae in Sierra Morena includes 10 species belonging to *Axophyllum*, two species belonging to *Gangamophyllum*, one species belonging to *Pareynia* and two species belonging to *Morenaphyllum*.

The stratigraphical distribution of the Axophyllinae in Sierra Morena ranges from Upper Viséan to Serpukhovian. It is consistent with the distribution of the same species in other areas, except in three cases: *A.mendipense* appears later than in NW Europe and *A. tazoultense* and *A. pseudokirsopianum* appear earlier than in North Africa. It indicates a possible slow migration from north to south.

The genus *Axophyllum* seems to be the ancestor of all other Axophyllinae. Five evolutive lineages in the genus *Axophyllum* are proposed: 1) A lineage including species having large axial structures and scarce lonsdaleoid dissepiments (*A. kirsopianum* species group). 2) A lineage of small species having moderate development of lonsdaleoid dissepiments (*A. pantopodum* species group). 3) A lineage of species with large size and wide lonsdaleoid dissepimentarium (*A. lonsdaleiforme* species group). 4) A lineage of species showing small axial structures, conspicuous inner wall and "spiny" septa (*A. expansum* species group). 5) A lineage developed in Eastern Palaeotethys, showing wide lonsdaleoid dissepimentarium. That lineage splits in two sub-lineages, one showing horizontal dissepiments in the periphery (*A. majiobaense* species group), another showing regularly inclined dissepiments (*A. clinotabulatum* species group).

Pareynia may descend from the lineage 3, *Morenaphyllum* may descend from the lineage 4. *Protocarcinophyllum* and *Semenophyllum* seem to be local variants showing extreme reduction of the axial structure in two different regions and times. *Gangamophyllum* seems to be a polyphyletic genus descending from different species of *Axophyllum* and developing especially in the north-central Palaeotethys.

The Axophyllinae are typical palaeo-geographic indicators of the Palaeotethys. All references to species located in North America and Australia are erroneous identifications.

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