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First record of chambered hexactinellid sponges from the Palaeozoic

MARTIN NOSE, RADEK VODRÁŽKA, LUIS-PEDRO FERNÁNDEZ, and ISABEL MÉNDEZ-BEDIA

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A new chambered hexactinellid sponge, *Casearia devonica* sp. nov., is described from the Lower Devonian of northern Spain (Cantabrian Mountains). The fossil represents the first evidence of chambered hexactinellid sponges from the Palaeozoic and the oldest representative of the order Hexactinosida. *Casearia devonica* sp. nov. occurred within small metre-sized mud mounds that developed in deeper water below the storm wave base.

Key words: Hexactinellida, Hexactinosida, chambered sponges, mud mounds, Devonian, Northern Spain.

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Introduction

Most representatives of the polyphyletic group "Sphinctozoa", the chambered sponges, are hypercalcified animals that probably belong to the Demospongea. The "Sphinctozoa" range from the Cambrian to Recent. Senowbari-Daryan and García-Bellido (2002) provide a comprehensive overview on occurrence and distribution patterns of sphinctozoan sponges. They represent the most common sponges in late Palaeozoic and Triassic reefs and shallow-water calcareous deposits (Senowbari-Daryan and García-Bellido 2002; Senowbari-Daryan and Zankl 2010). Among hexactinellid sponges, chambered representatives are exceedingly rare; their record consists of only a few taxa from the Upper Triassic and Upper Jurassic. Five genera have been erected to date, including *Casearia* Quenstedt, 1858 (including the synonyms *Innaecoelia* Boiko, 1990 and *Monilispongia* Wu and Xiao, 1989), *Caucasocoelia* Boiko, 1990, *Dracolychnos* Wu and Xiao, 1989, *Pseudoverticillites* Boiko, 1990, and *Esfahanella* Senowbari-Daryan and Amirhassankhani 2012. The genus *Casearia* has been reported from the Upper Triassic and Upper Jurassic. Late Triassic representatives have been described from Iran, China and central Europe (Rigby et al. 1998; Senowbari-Daryan and Hamadani 1999; Senowbari-Daryan and Zankl 2010; Senowbari-Daryan and Amirhassankhani 2012), while the Late Jurassic ones come from Germany and Tadjhikistan (Schmidel 1780; Zittel 1878; Quenstedt 1858; Kolb 1910; Schrammen 1936; Müller 1974; Boiko 1990). *Caucasocoelia* and *Pseudoverticillites* have been reported from the Upper Triassic of Russia (Boiko 1990), while *Dracolychnos* comes from the Upper Triassic of China (Wu and Xiao 1989; Rigby et al. 1998). *Esfahanella* occurs in the Upper Triassic of Iran (Senowbari-Daryan and Amirhassankhani 2012).

We are not aware of any report of a chambered hexactinellid sponge older than Mesozoic. Moreover, the oldest representatives of the order Hexactinosida currently known are from the Late Devonian (e.g., Mehl and Mostler 1993; Rigby et al. 2001; Krautter 2002; Pisera 2006). The Late Ordovician hexactinellids *Wareembaia* Rigby and Webby, 1988 and *Kalimnospongia* Rigby and Webby, 1988 from Australia were initially included within the Lyssacinosida by Rigby and Webby (1988), but later placed in the family Wareembaiidae Finks and Rigby, 2004b and re-classified as Hexactinosida by Finks and Rigby (2004b). However, a number of reasons argue against hexactinosid affinity. For example, Mehl and Mostler (1993) have pointed out that the outermost

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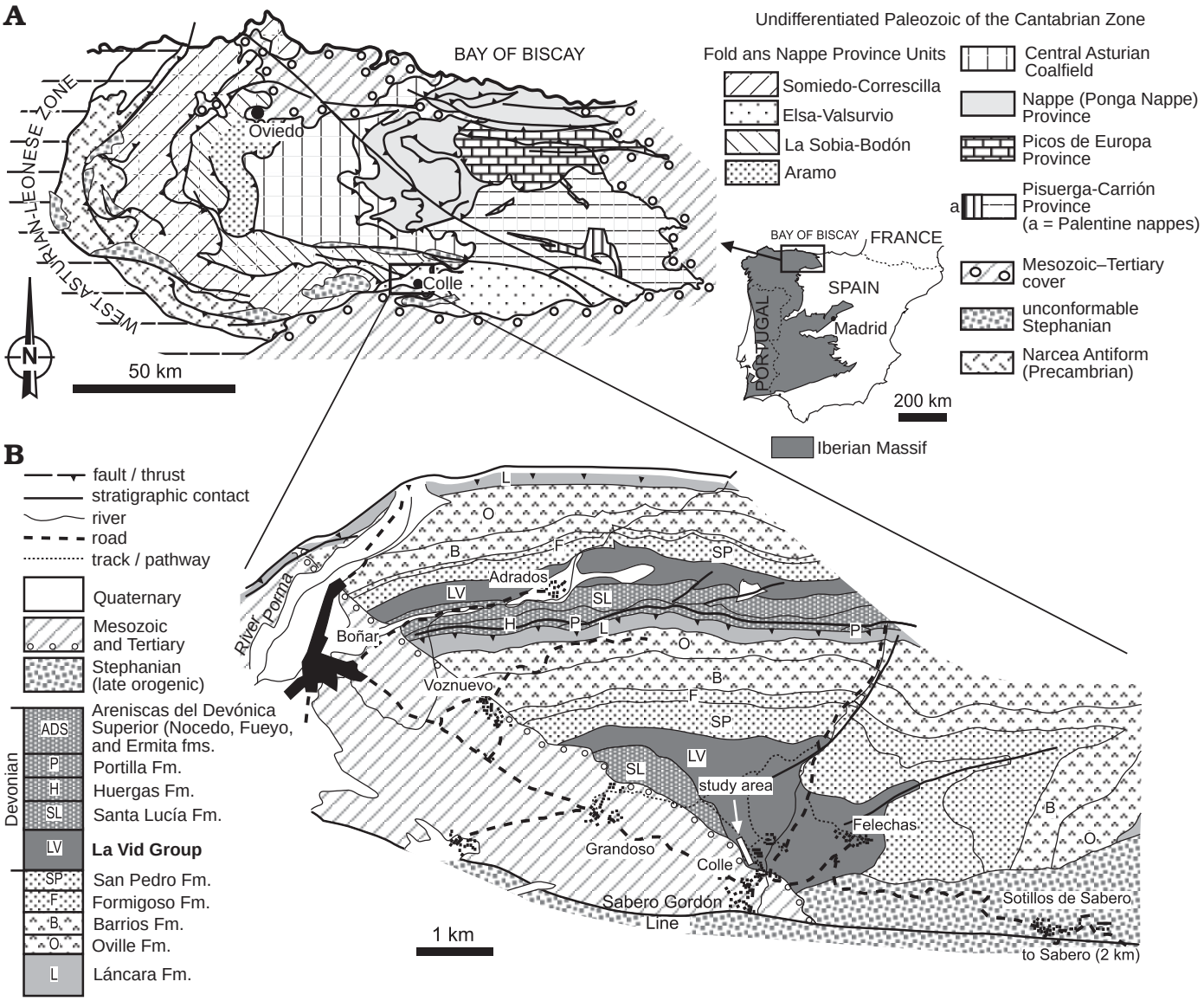


Fig. 1. **A**. Geological map of the Cantabrian Zone with the provinces and units of Julivert (1971) and Pérez-Estaún et al. (1988). **B**. Simplified geological map of the Esla Nappe near Colle, showing location of study area. Based on Lobato et al. (1984). Modified after Fernández et al. (2006).

skeletal layer of *Wareembaia*, which consists of supposed dictyonal strands (Rigby and Webby 1988: pls. 41: 4; 42: 6, 43: 1, 2), does not show the typical, fused hexactines, but rather diactines interconnected by synapticulae. Even the emended diagnoses of *Wareembaia* and *Kalimnospongia* in Finks and Rigby (2004b) leave doubts about the nature of sponge spiculation, suggesting that the "dictyonal strands" rather represent "rhabdodiactines".

Zhuravleva and Pyanovskaya (1995) erected the family Tadassiidae and claimed that Tadassia from the Cambrian of Russia (South Tien Shan) is similar to representatives of Mesozoic chambered hexactinellid sponges (order Innaecoelida Boiko, 1990). Finks and Rigby (2004b) listed the Tadassiidae under class and order uncertain thus questioning their assignment to hexactinellid sponges at all. However, according to the description it seems very probable that these sponges are hexactinellids, especially when possessing stauractine spicules. But what we doubt is the chambered structure. Based on the figures it seems that variously shaped "chambers" rather represent single individuals overgrowing each other and not successive chambers within one individual.

The chambered sponges described in this paper come from the Lower Devonian (Emsian) locality of Colle in the Cantabrian Mountains. The Colle outcrops have been well known for their well-preserved and abundant invertebrate fossils since the 19th century (e.g., Verneuil 1850; Mallada 1875; Comte 1938, 1959; Truyols-Massoni 1981; Alvarez 1999; Schröder and Soto 2003). Fernández et al. (2006) conducted a facies analysis and sequence stratigraphic interpretation of the studied interval that focused on the development of reef complexes composed of coral biostromes and mud mounds. The latter yield an hexactinellid sponge fauna that

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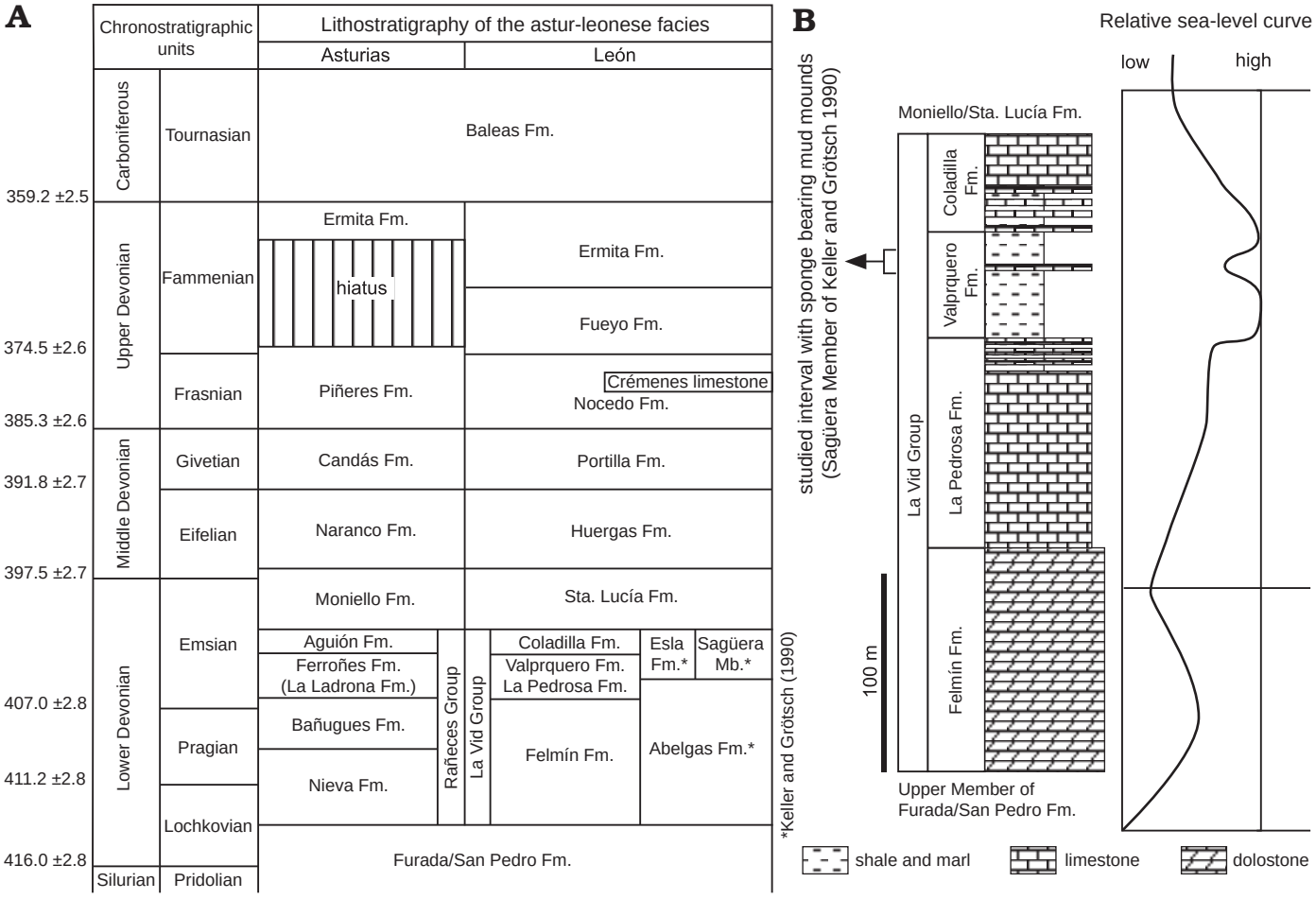


Fig. 2. **A**. Chronostratigraphic chart, showing Devonian lithostratigraphic units of Asturo-Leonese facies that have been defined in the regions of Asturias (northern part of the Cantabrian Zone) and León (southern part of the Cantabrian Zone). Absolute ages based on Gradstein et al. (2004). Stratigraphic subdivision of the La Vid Group according to Vilas Minondo (1971) and Vera de la Puente (1989), but subdivision by Keller (1988) is also shown. **B**. Simplified stratigraphy of La Vid Group in relation to sea-level development (based on Keller and Grötsch 1990) showing location of studied interval of Valporquero Formation. Modified after Fernández et al. (2006).

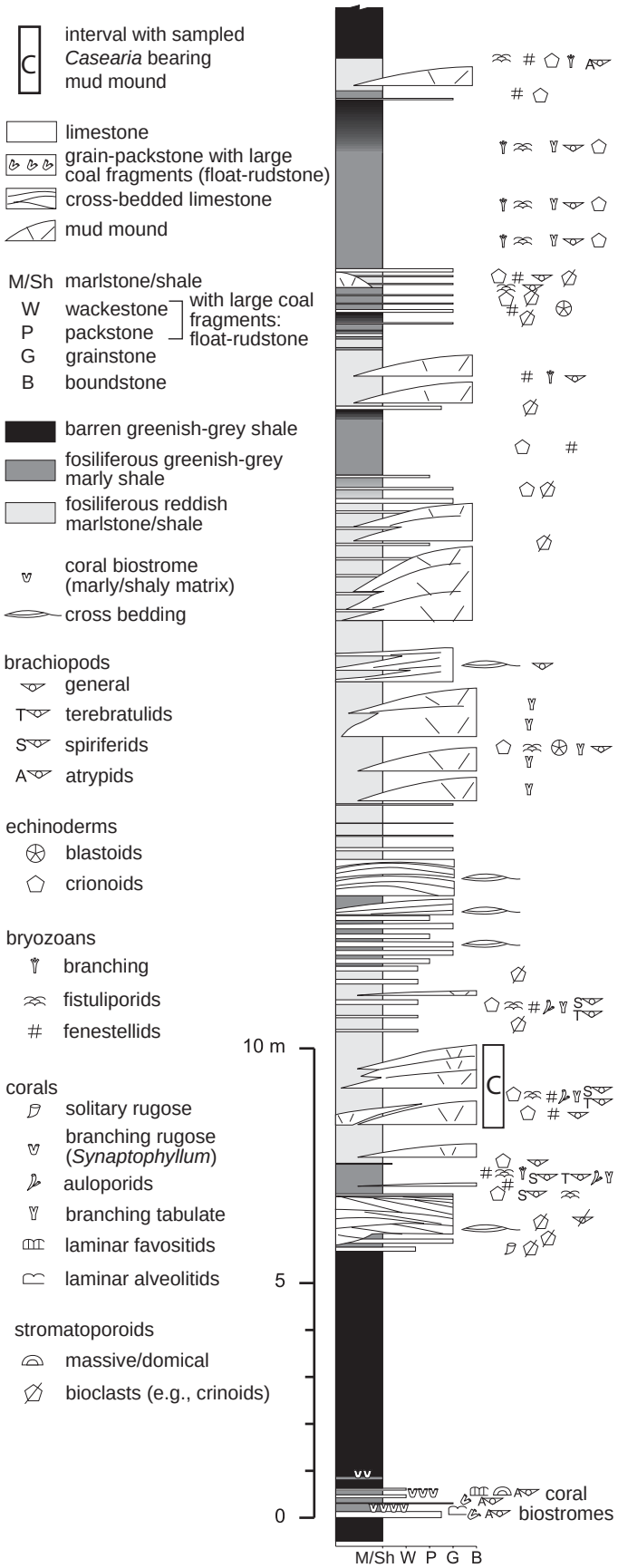
was initially reported on by Fernández et al. (2006). From these rocks we describe the first chambered hexactinellid sponge from the Palaeozoic. This fossil represents the oldest record of the order Hexactinosida.

Institutional abbreviations.—SNSB-BSPG, Bavarian State Collection of Palaeontology and Geology, Munich, Germany.

Geological setting

The fossils were collected from the Lower Devonian (Lower Emsian) succession of the upper Valporquero Formation near the village of Colle in the Cantabrian Mountains. The Valporquero Formation is part of the La Vid Group and comprises the more shaly unit in its middle and upper part. This shaly unit is rather monotonous, although its upper part contains a marly interval with limestone intercalations that constitutes the studied interval (Figs. 1, 2). These limestone beds are mostly bioclastic, although some coral biostromes and mud mounds exist as well, the latter of which contain the fossils described below (Figs. 3, 4). The coral biostromes are well understood today based on the work of Stel (1975), while the mud mounds have only been described briefly by Schmid et al. (2001). This interval corresponds to the Sagüera Member of the Esla Formation named by Keller (1988) and the Intermediate Limestone Member of Leweke (1982). According to the facies and sequence stratigraphic analysis by Fernández et al. (2006), mud mounds developed in 5th-order transgressive and early highstand systems tracts tied to 4th-order late lowstand to early transgressive systems tracts. Field relationships suggest that the mud mounds grew coevally with muddy sedimentation, with high frequency variations in carbonate vs. terrigenous mud sedimentation influencing their development. Mud mounds are encased in fossiliferous reddish shales/marls. They are dominated by microbial micrite, and fenestellid and fistuliporid bryozoans. Other metazoans such as crinoids, solitary corals, and the chambered sponges play only a minor role in mound formation and composition.

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Environment and palaeoecology

The siliceous sponge-bearing, polymicritic bryozoan mud-mounds and the surrounding fossiliferous sedimentary deposits (reddish shale/marlstone; facies C of Fernández et al. 2006) formed in a low-energy, fairly deep marine environment below the storm wave base, but apparently still under the influence of periodic storms. The latter is attested to by the occurrence of thin skeletal beds, which we interpret as distal tempestites, formed by storm-induced offshore directed bottom currents (storm surge) capable of transporting their suspension load even beyond the storm wave base (cf. Aigner 1982; Tucker and Wright 1990).

The overall faunal composition, textural features and the geometry of the Colle mounds are somewhat similar to deep water mounds constructed of microbial boundstone (Lees and Miller 1995; Monty 1995; Pratt 1995).

The assumption that these formations developed in relatively deep water is further corroborated by the scattered occurrence of the hexactinosidan sponge *Casearia* within the mounds (see systematic palaeontology below). In general, hexactinellids are indicative of deep water environments, not only in the Palaeozoic but also in the Meso- and Cenozoic (e.g., Wendt et al. 1989; Pratt 1995; Krautter 1997). In Recent environments, the order Hexactinosida proliferate in water depths between 100 and 6860 metres and range from the Arctic to Antarctic (e.g., Vodrážka and Crame 2011).

The environmental settings of the Mesozoic (Late Triassic, Jurassic) *Casearia* species are generally characteristic of deep water (e.g., Müller 1974; Rigby et al. 1998; Senowbari-Daryan and Hamadani 1999), although one species has been described from the shallow water Dachstein reef limestone (Senowbari-Daryan and Zankl 2010).

Mounds are known to have been formed predominantly by semi-lithified cyanobacterial micritic crusts and fenestellid and fistuliporid bryozoans (Fernández et al. 2006). Mud mound growth and its early lithification by bacterially precipitated peloidal crusts were essentially coeval with the sedimentation of the surrounding fossiliferous reddish shales/marlstone. The small mounds (up to 0.8 m thick) grew during relatively short periods of time, and under generally reduced background sedimentation rates. However, clay fallout rates varied with time, giving rise to periods of mud mound growth and encroachment onto the substrate, and periods of mound inactivity and clay veneering of its surface. Intermittent sedimentation rates and/or sediment winnowing during mound growth are indicated not only by the shaly partings within the mounds, but also by the ragged margins of both the mounds and the mushroom-like morphotypes of coral and multilayered bryozoan colonies (e.g., fistuliporids) in the inter-mound-facies. The mounds lack layering and zonation patterns, and it seems that they

Fig. 3. Stratigraphic section of Valporquero Formation at Colle, showing facies distribution including polymicritic mud mounds and part of section from which chambered hexactinellid sponge *Casearia* has been collected from mud mound facies. Modified after Fernández et al. (2006).

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Fig. 4. Field image of a small polymicritic mud mound containing *Casearia devonica* sp. nov., Colle, Cantabrian Mountains; Lower Emsian.

did not evolve beyond an embryonic developmental stage, and it is likely that largely uniform ecological conditions prevailed over the mud mounds' lifetime (Fernández et al. 2006). Moreover, undisturbed conditions during mud mound formation are also evidenced by the ecological requirements of hexactinosidan sponges, which are fragile, sessile suspension feeders.

It is noteworthy that numerous recent studies have reported hexactinosidan-dominated Mesozoic sponge faunas associated with sea-level highstands and accompanied by low sedimentation rates (e.g., Vodrážka et al. 2009; Schneider et al. 2011). The hexactinosidan sponges described in this paper proliferated under similar sedimentological conditions: mud mounds developed during transgression and subsequent stillstand with reduced but still existing background clay sedimentation (Fernández et al. 2006).

The dominance within the mounds of encrusting bryozoans over reef builders such as rugose and tabulate corals, as well as the common occurrence of mushroom-shaped, heavily calcified bryozoans in the contemporaneous intermound facies, might be due to (i) water depths exceeding those suitable for coral and stromatoporoid growth and/or (ii) a temperate shelf environment, which is a typical habitat for bryozoan communities (e.g., Smith 1995; Reguant and Zamarreño 1987). It has been speculated that the Colle mounds grew in somewhat cooler water based on the deeper-water setting, the fact that extant siliceous sponges grow exclusively in waters colder than 15° C and the palaeolatitudinal position of northern Spain at the southern margin of the tropical/subtropical belt (Krautter 1997; Copper 2002). However, sea surface temperature calculations for Early Devonian localities (including the Cantabrian Mountains) reveal a mean temperature of 25° C typical for modern tropical/subtropical surface waters VanGeldern et al. (2006).

The overall dominance of heterotrophs (bryozoans, crinoids, sponges), as well as the growth of mound-forming microbialites, point to slightly increased nutrient input with mesotrophic conditions (Wood 1993; Copper 2002; Webby 2002). Moreover, Mesozoic microbialites are believed to have generally developed under slightly increased input of nutrients (Leinfelder et al. 1993; Dupraz and Strasser 1999; Olivier et al. 2005).

Systematic palaeontology

At high taxonomic levels, we follow the classification system for Mesozoic and Cenozoic hexactinellid sponges introduced by Reid (2004). It is noteworthy, that non-hexactinellid origin of the studied material was tested, too, especially because some Paleozoic "lithistid" demosponges may produce skeletons that could resemble hexactinosidan frameworks. This is the case of anthaspidellids (Paleozoic demosponges of the order Orchocladina Rauff, 1895; e.g., Finks and Rigby 2004a), which possess skeletons composed of regularly arranged dendroclones and trabs cored by monaxons. However, no one of these features have been identified in studied thin sections.

Class Hexactinellida Schmidt, 1870
Subclass Hexasterophora Schulze, 1887
Order Hexactinosida Schrammen, 1903
Family Caseariidae Schrammen, 1936

Remarks.—The classification of Reid (2004) comprises four subfamilies (including Caseariinae) within the family Craticulariidae, although he illogically listed only 3 subfamilies at the beginning of the chapter without mentioning the Caseariinae. However, in accordance with Senowbari-Daryan and Zankl (2010), we use *Casearia* as the type genus for a separate family, the Caseariidae, primarily based on the unique chambered structure.

Genus *Casearia* Quenstedt, 1858

Type species: *Spongia articulata* Schmidel, 1780. Reid (2004) erroneously indicated *Scyphia articulata* Goldfuss, 1826 as the type species of the genus (Senowbari-Daryan and Zankl 2010), Franconian Alb, southern Germany; Late Jurassic.

Emended diagnosis.—Cylindrical to top-shaped or open, funnel-shaped hexactinosidans in which body consists of a superimposed series of hemispherical to annular or discoidal growths, usually with a common, paragastral cavity; dermal surface may be constricted transversely at segment junctions; skeletal surfaces may be formed by tangential networks of ankylosed stauractines, interpreted as dermalia and gastralia; stauractine network of outside, continuous to paragastral margin at top of body, and extending through wall to paragastral surface between each segment; ostia and postica of radial canals, arranged quadrately in some examples under surface networks.

Remarks.—The studied specimens correspond to the diagnosis in Kolb (1910: 186) and Reid (2004: 486) for the genus *Casearia*. Minor differences in skeletal organization, including the poorly developed exhalant canals and the absence of

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paratangential network formed by fused stauractines (e.g., Müller 1974), cannot be regarded as diagnostically significant for the discrimination of these fossils from *Casearia.* Moreover, also some other *Casearia* species do not posses tangential networks formed by ankylosed stauractines (dermalia and gastralia) on the skeletal surfaces (e.g., *Casearia pamirica* [Boiko, 1990], *C. alpina* Senowbari-Daryan and Zankl, 2010). For this reason, which was neglected by earlier authors, the genus diagnosis has been slightly emended herein (compare with Reid 2004).

Casearia was first described from the Upper Jurassic of Germany (Quenstedt 1858; Zittel 1878; Kolb 1910; Müller 1974, 1990). Later, Boiko 1990; Wu 1990; Rigby et al. 1998; Senowbari-Daryan and Hamadani 1999; Senowbari-Daryan and Zankl 2010; and Senowbari-Daryan and Amirhassankhani 2012 reported *Casearia* species (including the synonyms *Innaecoelia* and *Monilispongia*) also from the Jurassic of Tadjhikistan and Upper Triassic of the Pamir Range, Sichuan/China, Iran, and the Northern Calcareous Alps. Other valid genera such as *Dracolychnos*, *Caucasocoelia*, *Pseudoverticillites*, and *Esfahanella* differ from the Early Devonian fossils from northern Spain in several respects, as follows.

Pseudoverticillites exhibits low, empty chambers, which are of regular size and shape, contrasting the higher chambers of irregular shape with skeletal filling of dictyonal hexactine network in the fossils from Spain. The chambers of *Caucasocoelia* are also regular in size and shape, and thus differ from the chambers of the sponge described here. Moreover, *Caucasocoelia* is characterized by a considerably larger axial spongocoel, and wider hexactinosidan meshes. In addition, the character of the skeletal chamber filling differs from that seen in *Casearia*. Both genera have been described by Boiko (1990) from the Upper Triassic (Norian–Rhaetian) of Russia (northern Caucasus). *Dracolychnos* from the Upper Triassic (Carnian) of China/Sichuan exhibits a different funnel-shaped morphology (Wu and Xiao 1989) and also differs from *Casearia* with regard to the character of the spiculation of the dermal and gastral surfaces. *Esfahanella* from the Upper Triassic of Iran (Senowbari-Daryan and Amirhassankhani 2012) is distinguished from *Casearia* mainly by its very wide spongocoel.

Stratigraphic and geographic range.—Early Devonian (Cantabrian Mountains, NW Spain); Late Triassic (Pamir, Iran, China, central Europe); Jurassic (Germany, Tadjhikistan).

Casearia devonica sp. nov.

Figs. 5–8.

Etymology: After the report of *Casearia* in the Devonian.

Type material: Holotype: BSPG 2012 I 46; from the holotype specimen three thin sections were prepared (Fig. 5A–C). Paratypes: BSPG 2012 I 47, BSPG 2012 I 48, BSPG 2012 I 49; two thin sections of each.

Type locality: Hillside immediately north of Colle, between Bonar and Sabero (road CL-626), NW Spain.

Type horizon: Upper Valporquero Formation, La Vid Group, Lower Emsian (= Sagüera Member, Esla Formation sensu Keller 1988).

Diagnosis.—Cylindrical to conical, frequently branched multi-chambered sponge with axial spongocoel. Outer morphology reflecting internal segmentation. Stacked annular chambers variable in size and shape; some chambers fully encasing previous chamber. Cortex on dermal surface formed by single layer of hexactines with spherically-enlarged multiradiate nodes producing triangular meshes. Fused hexactines on gastral surface, within spongocoel, producing polygonal to rounded meshes, possibly representing exhalant canal openings. Chamber fillings characterized by dictyonal hexactine network with rectangular meshes.

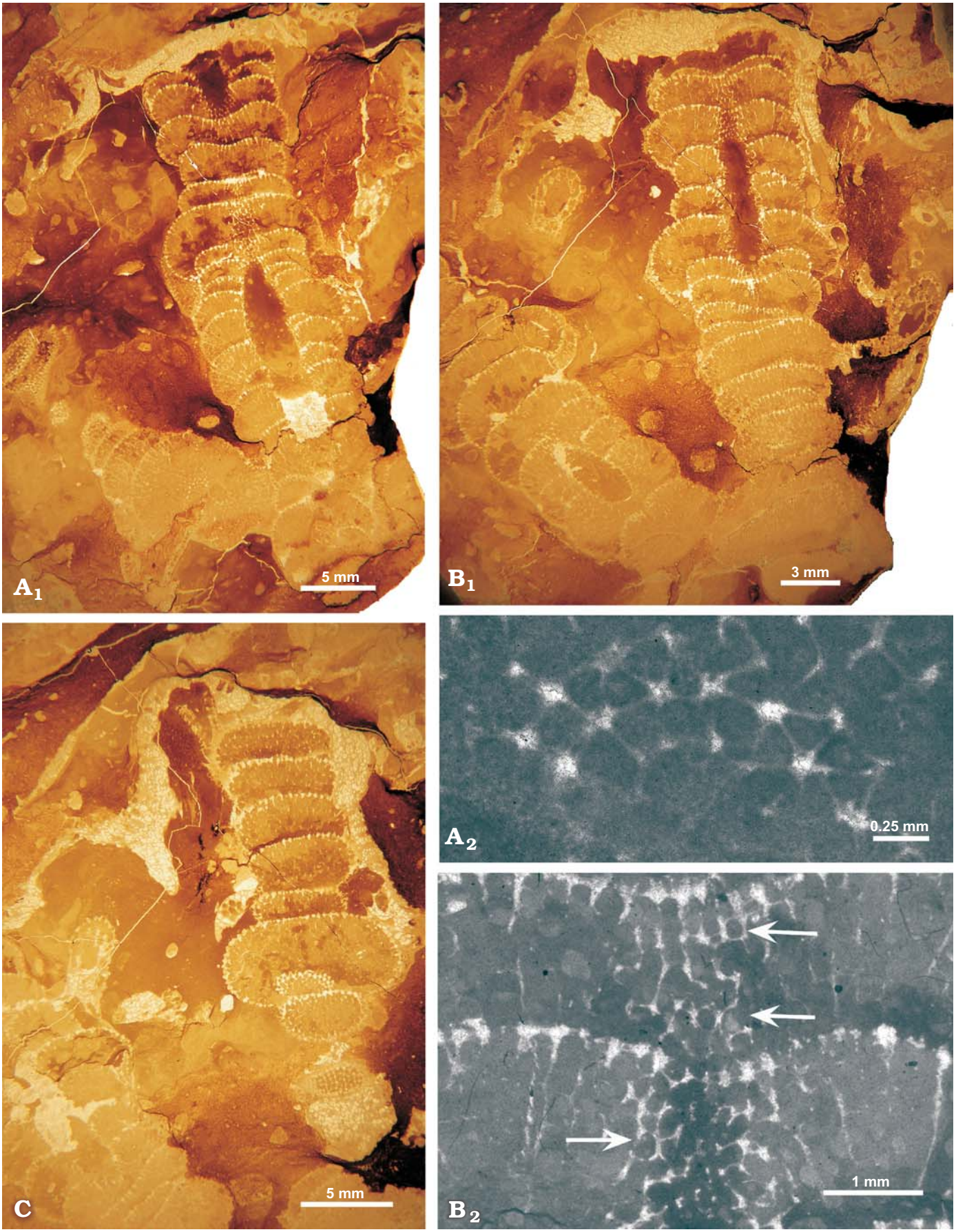
Description.—Scattered sponge bodies occur within polymictic mud mound limestone rocks. The sponges are usually preserved complete, although in some cases not in life position. The gross morphology of the sponges is characterized by successive addition of annular chambers. Chambers are highly variable in size and shape (Fig. 5A–C). There is a characteristic alternation of smaller, tabular annular chambers with larger, discoidal to crescent-shaped chambers (e.g., Fig. $5A_1$); in some specimens the size of the chambers gradually increases from the base to the top (Fig. 7). In a few instances, younger chambers may entirely enclose older chambers (Fig. 6B). Three of the four specimens are branched. Branches originate from basal chambers as well as from chambers higher up, in the middle part of the main branch. The total height of the sponge bodies reaches 3.5 cm. The height of the chambers ranges from 0.5 to 5 mm and their diameter varies between 6 and 12 mm. Up to 18 subsequent chambers may be developed.

The axial spongocoel is developed throughout the entire length of the sponge and measures approximately 1 mm in diameter at the base and up to 2.5 mm at the top. The gastral and dermal surfaces show strong diagenetic alteration in some of the thin-sections, with the outermost hexactine layer(s) sometimes lacking (e.g., Figs. 7, 8A). However, the dermal surface still exhibits annulations reflecting the internal chambered construction.

The cortex on the dermal surface, which is also represented by the wall between the individual chambers, is formed by a single layer of hexactines (e.g., Fig. 8A, B) with spherically-enlarged multiradiate nodes producing triangular meshes (Figs. $5A_2$, 6B). The distance between the centers

Fig. 5. Holotype of chambered hexactinellid sponge *Casearia devonica* sp. nov. from the Lower Emsian at Colle, Cantabrian Mountains, NW Spain; in → three serial thin sections (**A**–**C**). Main branch sectioned almost parallel to axial spongocoel, exhibiting stacked annular chambers. Serial sections of branch in lower left, which although not parallel to the axial spongocoel, shows changing growth direction. Overgrowth by cementing bryozoans (e.g., fistuliporids). **A**. BSPG 2012 I 46a; A_2, detail of A_1, showing tangential section of wall between chambers (i.e., dermal cortex) formed by spherically-enlarged multiradiate nodes producing triangular meshes. **B**. BSPG 2012 I 46b; B_2, detail of B_1, focusing on two subsequent chambers and gastral surface within spongocoel; fused hexactines produce polygonal to rounded meshes (examples arrowed). **C**. BSPG 2012 I 46c.

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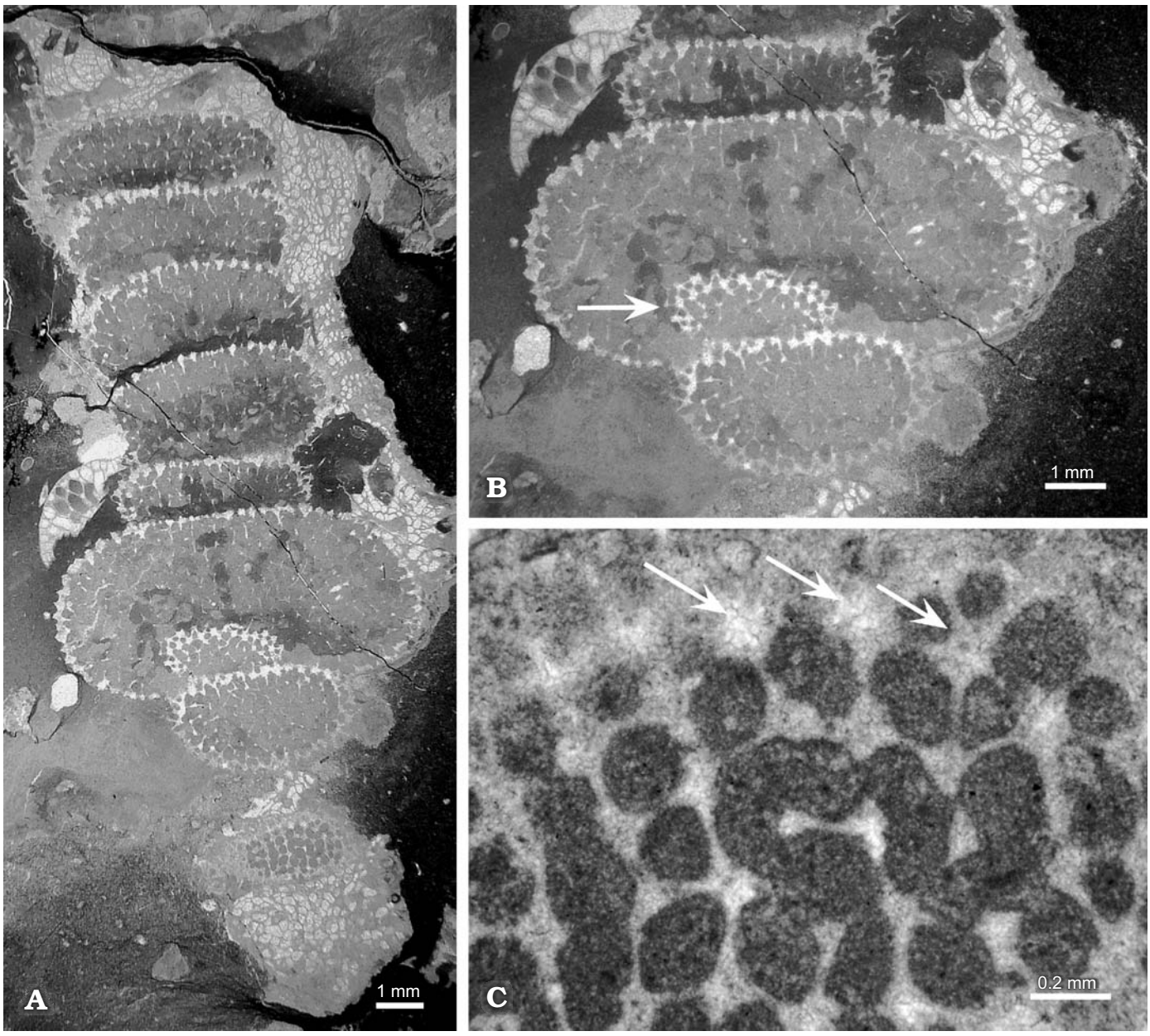


Fig. 6. Chambered hexactinellid sponge *Casearia devonica* sp. nov., BSPG 2012 I 46c (holotype) from the Lower Emsian at Colle, Cantabrian Mountains, NW Spain. **A**. Detail of Fig. 5C; branch with irregularly-chambered structure, sectioned roughly parallel to growth direction and tangentially to dermal cortex. Upper chambers exhibiting seemingly irregular hexactinellid framework, which shows regular rectangular meshes in radial cross-sections (compare with Figs. 7 and 8A). **B**. Detail of A, showing tangentially-sectioned dermal cortex of small chamber (indicated by arrow), completely enclosed by considerably larger subsequent chamber. Triangular meshes of dermal cortex resulting from interconnecting, spherically-enlarged multiradiate nodes. **C**. Detail of lowermost chamber in A; tangential section showing enlarged nodes forming dermal cortex and producing triangular meshes (arrowed), and regular rectangular meshes directly below dermal cortex.

of these multiradiate nodes varies between 0.18 and 0.38 mm. In the section tangential to the wall surface the nodes are circular and 0.12–0.22 mm in diameter, but irregularly elongated in the section perpendicular to the wall surface (Fig. 8B).

Within the individual chambers a dictyonal hexactine network with rectangular meshes is developed. Rectangular meshes are particularly recognizable in radial cross-sections (Figs. 7, 8A), but is difficult to recognize in tangential cross-sections (e.g., Fig. 6A), except for the framework directly below the cortex on the dermal surface (Fig. 6C). Rectangular meshes within the radial cross-sections are formed by beams extending parallel to the long axis of the sponge that are 0.19–0.44 mm long and by transverse beams 0.15–0.34 mm long. Numerous spherically-enlarged nodes of hexactines reveal perforations resembling the pseudolychniscid structures typically developed in *Casearia* as it is described by Müller (1974) and Pisera (1997) (Fig. 8A).

On the gastral surface, within the spongocoel, the fused hexactines occur in the form of polygonal to rounded mesh-

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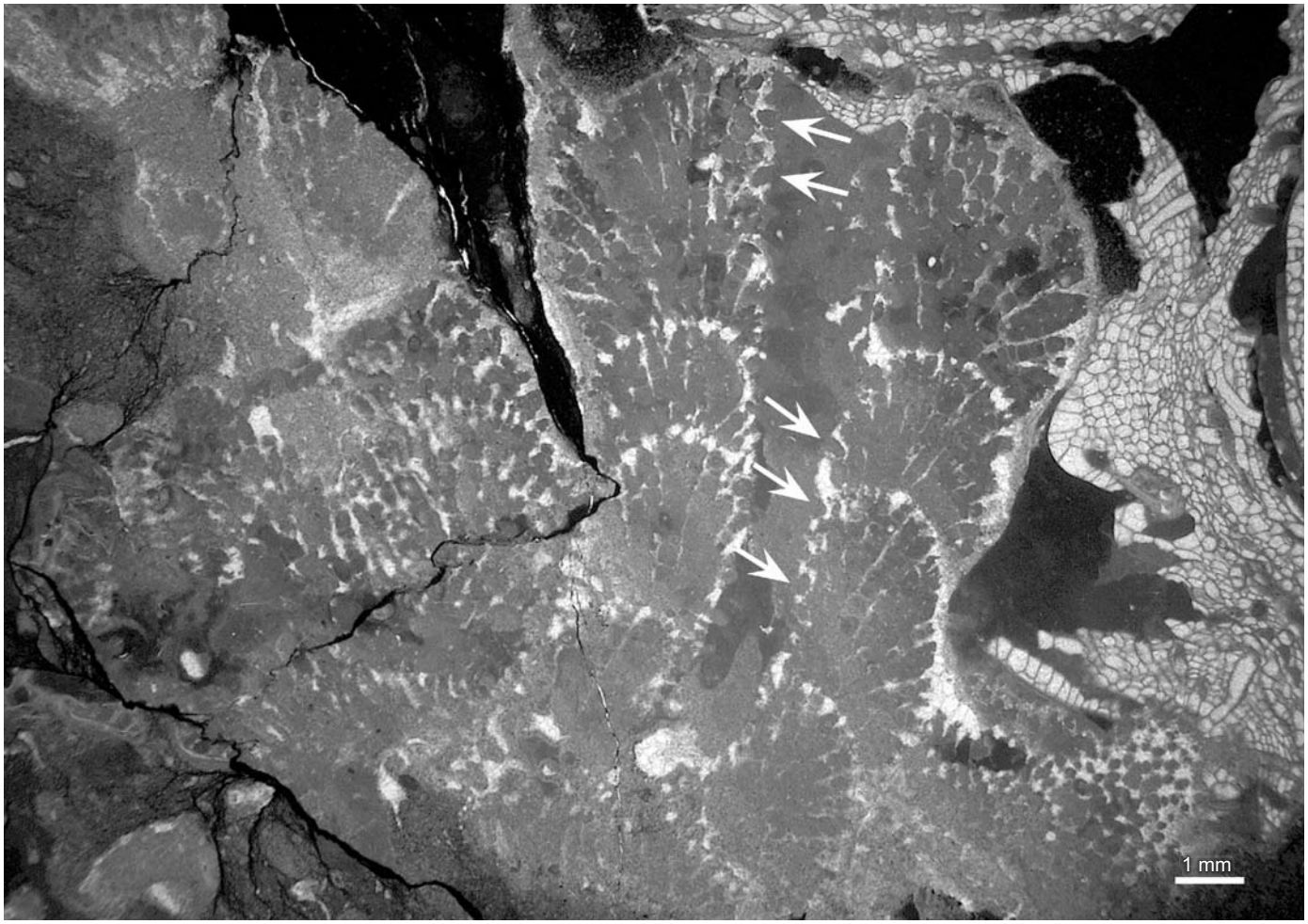


Fig. 7. Three-armed branched individual of chambered hexactinellid sponge *Casearia devonica* sp. nov., BSPG 2012 I 47a (paratype) from the Lower Emsian at Colle, Cantabrian Mountains, NW Spain. Central branch exhibiting almost longitudinal section with chambers gradually increasing in size from base to top, and axial spongocoel. Irregular gastral surface within spongocoel, showing possible openings of exhalant canals (arrows). Sponge encrusted by fistuliporid bryozoans, at least some of which colonized surface of sponge post mortem, see, e.g., bryozoan fully overgrowing the osculum.

es (Fig. $5B_2$), possibly representing exhalant canal openings. These openings, each 0.20–0.48 mm in diameter, are slightly larger than the rectangular meshes within the chambers and are randomly arranged. The size and position of the putative canal openings in radial section (e.g., Fig. 7) suggest the existence of radially arranged canals that extended outwards, but lacked skeletal expressions within the chambers.

Remarks and comparisons.—Mehl (1992) synonymized *Casearia depressa* Kolb, 1910 (Upper Jurrasic), *Casearia eurygaster* Zittel, 1878 (Upper Jurrasic), *Innaecoelia pamirica* Boiko, 1990 (Upper Triassic) and *Innaecoelia kurtekia* Boiko, 1990 (Upper Triassic) with *Casearia articulata* (Schmidel, 1780) (Upper Jurrassic–Upper Triassic). Following Pisera (1997) and Senowbari-Daryan and Zankl (2010), we do not accept the synonymy list of Mehl (1992) and treat all above-mentioned taxa as a separate species of *Casearia*. Other valid species of the genus *Casearia* include the Late Triassic *C. oblata* (Wu, 1990), *C. decursiva* (Wu, 1990), *C. alpina* Senowbari-Daryan and Zankl, 2010, *C. iranica* Senowbari-Daryan and Amirhassankhani, 2012, *C. vezvanensis* Senowbari-Daryan and Amirhassankhani, 2012, and *C. delijanensis* Senowbari-Daryan and Amirhassankhani, 2012.

The Early Devonian taxon *C. devonica* sp. nov. described in this paper differs from the all other species asigned to *Casearia* in the following features: (i) stacked annular chambers that are highly variable in size and shape, and (ii) a cortex on the dermal surface that is formed by a single layer of hexactines with spherically-enlarged multiradiate nodes occurring in the form of triangular meshes.

Moreover, in comparison with the type species *C. articulata* there is also an absence of a paratangential network formed by fused stauractines on the dermal and gastral skeletal surfaces (e.g., Müller 1974). The gastral surface of *C. devonica* sp. nov., which is formed by a dense network of polygonal to rounded meshes that might represent the openings of shallow exhalant canals, is also unique in comparison to the other species of *Casearia*. The presence of this relatively "primitive" type of canalization in *C. devonica* sp. nov. is a remarkable feature since the geologically younger repre-

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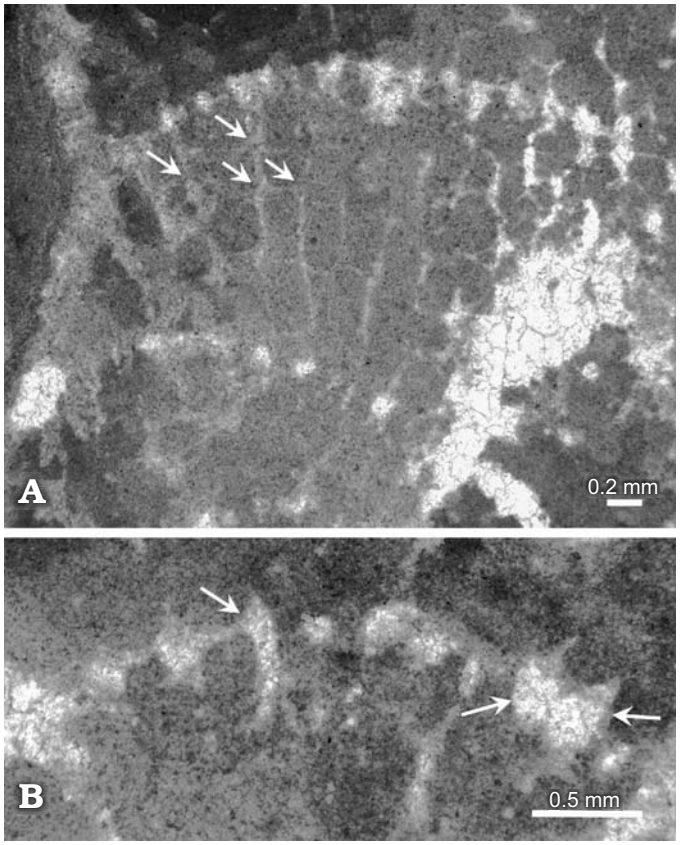


Fig. 8. Chambered hexactinellid sponge *Casearia devonica* sp. nov. **A**. BSPG 2012 I 46b (holotype); regular rectangular meshes of hexactinosidan skeleton in radial cross section. Note paragaster in lower right of image and dissolved centres of several thickened spicule nodes (arrowed) which seem to be identical with those forming pseudolychniscid structures similar to that described, e.g., by Müller (1974). **B**. BSPG 2012 I 47a (paratype); dermal cortex between two chambers, constructed of single thickened hexactine layer with spherically-enlarged nodes. Nodes often irregularly elongated perpendicular to surface of wall (arrow).

sentatives of the genus are characterized by a sophisticated canalization system that includes a skeletal expression of the canals within the wall.

Stratigraphic and geographic range.—Upper Valporquero Formation, La Vid Group, Lower Emsian; Hillside north of Colle, between Bonar and Sabero, NW Spain.

Conclusions

Deeper-water mud mounds from the Lower Devonian of the Cantabrian Mountains (Northern Spain) yield a new hexactinosidan species, *Casearia devonica* sp. nov., which represents the first Paleozoic representative of the chambered hexactinellid sponges and the oldest hexactinosidan sponge. In spite of minor differences in overall skeletal organization, we believe that, the fossils from Spain can still be assigned to the genus *Casearia* with confidence. In contrast to other species in that genus, *Casearia devonica* sp. nov. shows stacked annular chambers that are highly variable in size and shape, and a cortex on the dermal surface that is composed of a single layer of hexactines with spherically-enlarged multiradiate nodes. Moreover, *C. devonica* sp. nov. was probably characterized by shallow, "primitive" inhalant canals based on the dense network of polygonal to rounded meshes on the gastral surface. Mounds (and sponges) grew below the storm wave base under reduced, but still noticeable background sedimentation rates. The faunal association, the ecological requirements of hexactinellids and the palaeolatitudinal circumstances together are suggestive of a temperate shelf environment.

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