

A new plate-like hypercalcified chaetetid demosponge (*Loiscupula bachendensi* gen. nov. sp. nov) from the Cantabrian Zone (Moscovian, Pennsylvanian, NW Spain)

Diego Corrochano and Ronald R. West

ABSTRACT

A new hypercalcified chaetetid sponge, *Loiscupula bachendensi* gen. nov. sp. nov. (Demospongiae), has been recovered from the Bachende Formation (late Kashirian/early Myachkovian) in the Cantabrian Zone, NW Spain. *Loiscupula* has a circular, concentric, platy basal skeleton, some with cylindrical features and chimneys, which sometimes branch on the upper surface. The basal skeleton is composed of polygonal (commonly hexagonal) to rounded tubules perpendicular to the surface of the skeleton producing the characteristic honeycomb pattern of chaetetids. Cathodoluminescence microscopy revealed non-luminescent calcite pseudomorphs of monoaxon and polyaxon spicules, rarely styles, which are irregularly distributed although there are occurrences that suggest that a spicular network existed. The basal skeleton is composed of neomorphic low-Mg calcite (1.7 mol% MgCO₃) and is strongly recrystallized; the tentative penicillate microstructure with relics of aragonite needles, and the high Sr content (up to 3456 ppm), suggest an original aragonite composition. *Loiscupula* is interpreted as primarily a gregarious organism with an inferred central point of attachment. This mode of growth produced small cryptic cavities between *Loiscupula* and the substrate, which were inhabited by encrusting organisms, mostly fistuliporid bryozoans. Based on the associated fossils and sedimentological features, it is suggested that *Loiscupula* inhabited an environment with a muddy bottom in the euphotic zone, where the water was well-oxygenated, of normal salinity, and the energy regime low to moderate.

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INTRODUCTION

A new chaetetid hypercalcified demosponge, *Loiscupula bachendensi* gen. nov. sp. nov., occurs in the Bachende Formation (late Kashirian/early Myachkovian, Moscovian, Pennsylvanian), in the Cantabrian Zone, León, NW Spain. Purely on the basis of its external appearance and the strong recrystallization of the skeleton, *Loiscupula* was previously described as a problematic phylloid alga (Corrochano, 2010), based on a number of similarities with the Rhodophyta and the Chlorophyta, although with certain features found in chaetetids and solenoporaceans. More recent investigation, using cathodoluminescence microscopy, revealed calcite spicule pseudomorphs, and thus they are confirmed chaetetid sponges.

Although forms identified as chaetetid sponges have been reported from rocks as old as the Cambrian (West, 2012a), valid chaetetid genera range from, questionably the Silurian (West, 2012a) to the Recent (Hartman and Goreau, 1972). Chaetetids were common reef-mound builders worldwide during the Early and Middle Pennsylvanian (West, 1988, 2012b; Wahlman, 2002). Palaeozoic chaetetids share morphological features with many groups, including extant calcified demosponges, tabulate corals, stromatoporoids, hydrozoans, trepostome bryozoans and calcareous algae, and they have had a long and complex taxonomic history (for a review see Connolly et al., 1989; West, 2011a). Documentation of spicules and soft tissue typical of demosponges in *Acanthochaetetes wellsii* by Hartman and Goreau (1972) resulted in the recognition of chaetetids as hypercalcified demosponges. The recognition of fossil chaetetids as hypercalcified demosponges is supported by documentation, in fossil forms, of astro-rhizae (Cuif et al., 1973; West and Clark, 1983), and spicule pseudomorphs (Kazmierczak, 1979; Gray, 1980; Reitner and Engeser, 1987; Wood and Reitner, 1988; Cremer, 1995; among others).

This study documents, illustrates and discusses a new genus and species of chaetetid sponge, with comments on its general morphology, preservation, diagenesis, growth habit, associated biota and palaeoecology.

COLLECTIONS AND METHODS

Twenty-eight *Loiscupula* specimens were collected in León (NW Spain), from the Bachende Formation, Lois-Ciguera sector, Cantabrian Zone (Figure 1). The collection (USAL LB) is deposited

in the Department of Geology at the University of Salamanca, Spain.

Fifteen thin sections were made and examined petrographically with both polarized and transmitted light, and measurements were made at a magnification of x 25. Two thin sections were selected and polished for study using cathodoluminescence (CL) microscopy. A cold CL unit, model CCL 8200 mkIII, with a vacuum chamber coupled to an optical microscope (Nikon Labophot 2-Pol) was employed, working under standard analytical conditions of 12 to 20 kV accelerating voltage, 200 to 400 mA beam current and vacuum of 0.2 to 0.1 torr. Three fragments of apparently well-preserved specimens were coated with gold and examined with a scanning electron microscope (SEM), model ZEISS DSM 940, following the method proposed by Reitner and Engeser (1987). One polished SEM sample was etched with a weak acid, 5% titriplex-III-solution ($C_{10}H_{14}N_2O_{18} \cdot 2H_2O$); the other two SEM samples examined were freshly fractured surfaces of the calcite skeleton. Trace element analysis (Mg, Mn, Sr, Fe) were determined from bulk samples of five specimens after dissolving the carbonate in HNO_3 and HF; samples (0.2-0.5 g) were collected using a high speed dental drill with magnification from a binocular microscope. They were analyzed using an inductively coupled plasma mass spectrometer (ICP-MS), model Perkin-Elmer ELAN 6000, with an analytical uncertainty of 2% and a standard calibration. To study the internal structure of the skeleton and its contact with the internal filling matrix, a few specimens were etched by complete immersion in 10% hydrochloric acid for 10, 30 and 60 seconds, respectively. Numerous specimens and a series of evenly spaced sections through a single specimen (USAL LB5) were used to construct an idealized three-dimensional image of *Loiscupula*.

GEOLOGICAL AND SEDIMENTOLOGICAL SETTING

The Cantabrian Zone is the external part of the Variscan Orogen in the NW Iberian Peninsula and constitutes the core of the Ibero-Armorican Arc. This area exhibits features characteristic of foreland fold-and-thrust belts, with a thin-skinned deformation and weak metamorphism (Pérez-Estaún et al., 1988). At least, during the Bashkirian-Moscovian, the Cantabrian Zone represented a wide marine foreland basin with a pronounced asymmetric profile that was in an equatorial position on the eastern coast of Pangea

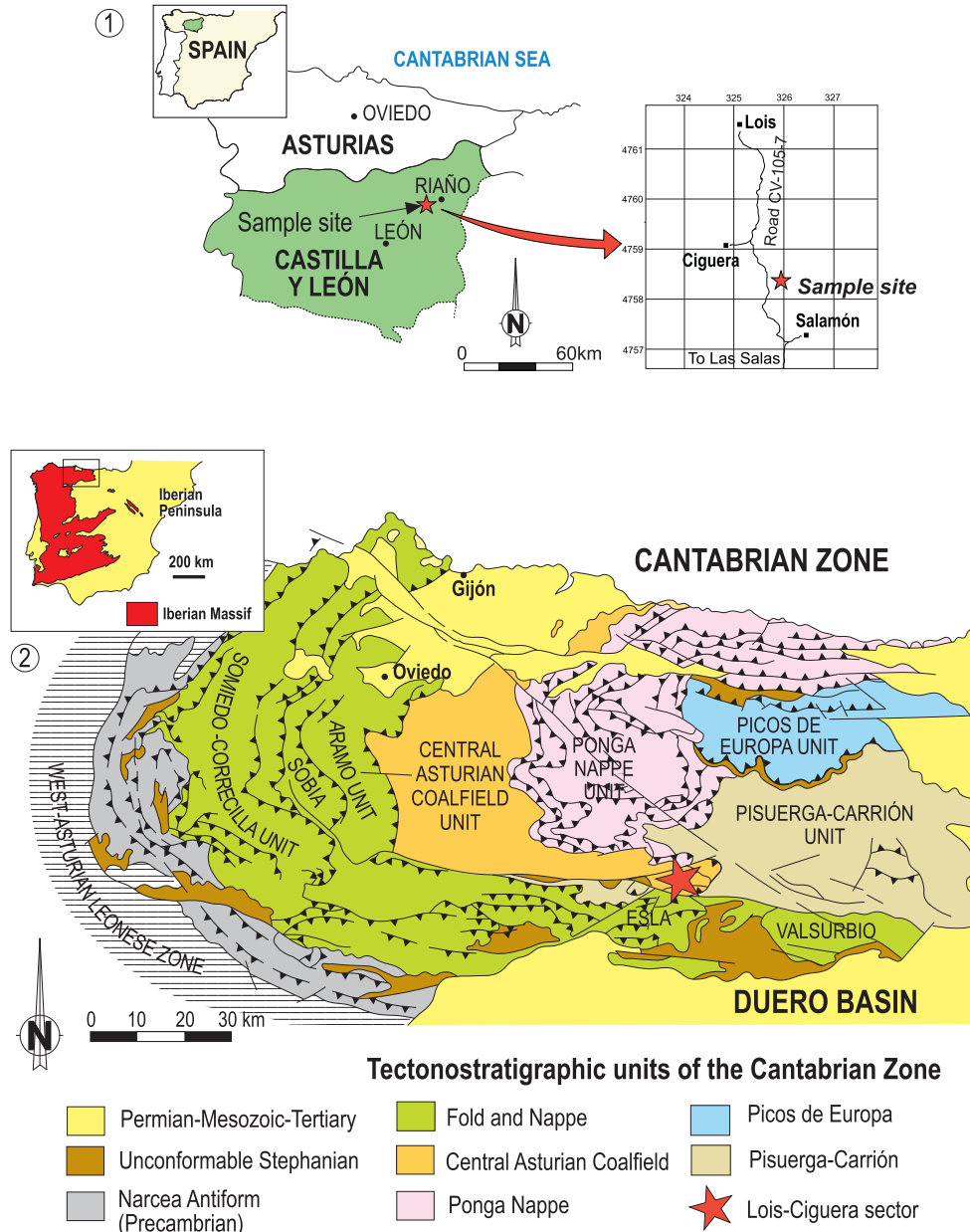


FIGURE 1. 1, Geographical setting of the collection site, a roadcut on the eastern side of the Salamón-Lois road (León, NW Spain). 2, Geological sketch map of the Cantabrian Zone showing the location of the Lois-Ciguera sector (modified from Pérez-Estaún et al., 1988).

(Colmenero et al., 2002). It was mostly filled by thick siliciclastic and paralic wedges that pass laterally into limestones. These limestones were deposited on high-rising carbonate platforms in the slowly subsiding most distal areas (Della Porta et al., 2004; Bahamonde et al., 2007; among others).

The Bachende Formation (late Kashirian/early Myachkovian) represents a delta-top carbonate platform developed on the distal shelf areas of the foreland basin. Landward (to the W), carbonate platform sediments alternate and interfingered with

deltaic sandstones and shallow marine mudrocks (Lena and Sama Groups). Distally (to the E), the carbonate platform overthrusts the siliciclastic succession of the Pisuerga-Carrión Province that is composed mostly of basinal mudrocks with local turbidites and olistoliths. The Bachende Formation is sandwiched between two major and relatively shallow-water clastic units. The Bashkirian, Lois Formation, a thick (300-700 m) interval composed of mudrocks and some sandstones underlies the Bachende Formation, and it is overlain by the

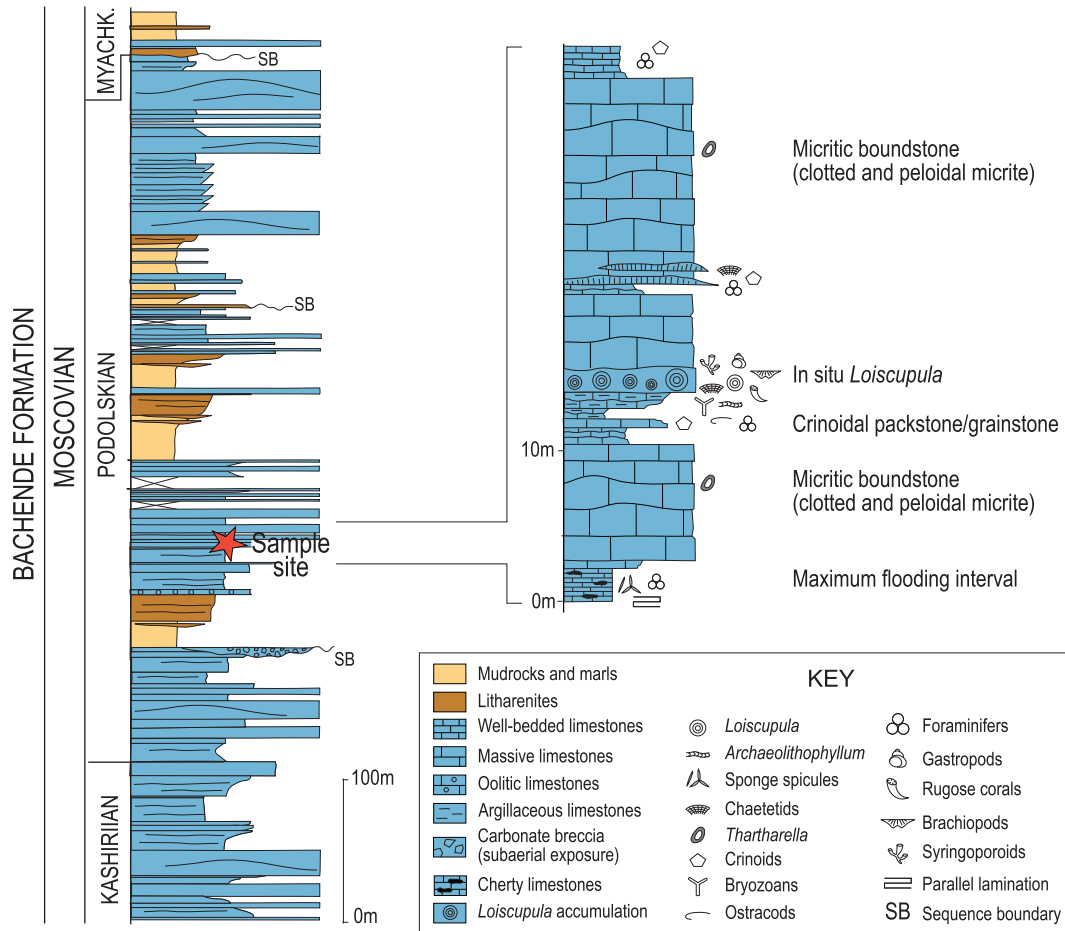


FIGURE 2. Schematic section of the Bachende Formation showing the stratigraphic position of the type locality.

Dueñas Formation, a 300 m thick succession of deltaic siliciclastics, with some interbedded limestones at the base.

Over 650 m of shallow subtidal limestones and deltaic siliciclastics compose the Bachende Formation and cycles of stacked shallowing-upward, metre-scale (10.6 m average thickness) sequences, with a moderate amplitude (~40 m), and high-frequency (15-110 ky) can be recognized (Corrochano et al., 2012). These cycles compose the basic genetic unit of the platform and can be grouped into three major depositional sequences that are bounded by extensive subaerial unconformities. In situ specimens of *Loiscupula* in the Bachende Formation appear only in the highstand system tract of the second major sequence (late Podolskian) and are located 13 m above the maximum flooding surface (Figure 2). This sequence (200 m thick) is characterized by a basal carbonate, dominated by oolitic grainstones and bioclastic wackestones/packstones, and an upper part, composed of several mixed carbonate-siliciclastic

cycles, with conspicuous micritic boundstones at the base. *Loiscupula* specimens occur in two lithologies: 1) a lower one, composed of crinoidal packstones/grainstones with abundant fenestellid bryozoans and sparse and broken fragments of *Loiscupula* (a winnowing occurrence); and 2) an upper one, of bioturbated and argillaceous wackestones (minor packstones), with fragments and complete specimens in presumed life position of *Loiscupula* (an in situ occurrence).

Organisms occurring with in situ *Loiscupula* are: phylloid algae (*Archaeolithophyllum lamellosum*), encrusting algae (*Claracrusta*), crinoids, brachiopods, bryozoans (fistuliporid and fenestellid), laminar chaetetids, ostracods, syringoporid corals, colonial rugose corals, gastropods, stacheinacean algae (problematic red algae), *Shamovella* and diverse foraminifers (paleotextulariids, *Ozawainella*, *Tetrataxis*, *Palaeonubecularia*, calcitornellids, lasiodiscids and *Tuberitina*). The matrix is a homogeneous micrite, with some microsparite.

The lithology immediately overlying the in situ *Loiscupula* is a massive micritic boundstone, characterized by a clotted and peloidal micrite resulting from microbial activity (auto-micrite sensu Wolf, 1965; Reitner and Neuweiler, 1995) and homogeneous micrite with scattered bioclasts (allomicrite). The biota associated with this lithology is mainly small crinoid ossicles, agglutinated worm tubes (*Thartharella* or *Therebella*) and calcified cyanobacterial filaments of *Girvanella*. The contact between the substrate containing in situ specimens of *Loiscupula* and the smothering lithology, is an irregular, sharp non-erosional surface, suggesting that *Loiscupula* was smothered by the microbial assemblage that produced the microbial boundstone.

SYSTEMATIC PALAEOONTOLOGY

Class Demospongiae Sollas, 1875
Order and Family Incertae sedis
Genus *Loiscupula* gen. nov.

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Type species. *Loiscupula bachendensi* gen. nov. sp. nov. *Loiscupula* is a monotypic genus, established to include *L. bachendensi*.

Etymology. The name is derived from a village close to the collection site (Lois), and the cup-shape of the individual specimens.

Diagnosis. Specimens with round, concentric and platy basal skeleton, with cylindrical and branching features (extended mamelons/chimneys) growing upward. Basal skeleton with polygonal to round tubules arranged perpendicular to skeleton producing a honeycomb pattern; tabulae irregularly spaced. Skeletal growth by intertubule increase and peripheral expansion. Inferred spicules, monoaxon oxea (some styles) and polyaxons, occur without a preferred orientation within the basal skeleton.

Loiscupula bachendensi sp. nov.
Figures 3-8

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Etymology. The species name derives from the Bachende Formation.

Holotype. USAL LB1 (Figures 3.2-3.6, 4.5, 4.6). Complete specimen.

Type locality. León, Spain, in a roadcut on the east side of the Salamón-Lois road, 1 km south-western of the small village of Ciguera, León (UTM coord. 325555/4758054), (Figure 1.1).

Occurrence. Currently, *Loiscupula* is only known from the late Moscovian, Pennsylvanian, Carboniferous, in the Cantabrian Zone, NW Spain.

Diagnosis. As for the genus.

Description. Plate-like forms that vary considerably in size; up to 5 cm high, 32 cm across, and from 0.7 to 2.9 mm thick in cross section, averaging 1.1 mm. Laterally, the skeleton is a flat cup-shape, with the central part several centimetres lower than the outer edges (Figure 3.2). A series of regular rings around a central point on the underside of the plate-like skeleton are produced by a regular pattern of concentric grooves and ridges (Figure 3.4). The symmetry of most specimens is exceptionally regular, although in some the central point is tilted to one side. These plate-like skeletons may have more than 15 concentric rings, each one about 1.5 cm across and 1 cm high. Conical structures (2.2 cm length and 1 cm diameter, Figure 3.5, 3.6) are concentrically distributed around the basal surface, although they are usually preserved as eroded protuberances (truncated cones) 1 cm across and 0.6 cm high, tilted approximately 30° towards the central base (Figure 3.6). These features are unevenly spaced in each ring and increase in number toward the outer rings of the fossil. In the holotype, the number of these features in each ring is (from the inner to the outer ring): 3, 5, 7, 10 and 13 (Figure 3.4).

Cylindrical features, which are similar to extended mamelons/chimneys reported in other chaetetids (West, 2011b, 2011c), occur sporadically on the upper surface of the plate-like skeleton (Figure 3.7, 3.8). They are simple or branched, and can reach a length of at least 3.4 cm. An internal cavity within these features is filled with a micrite matrix or with a sparry calcite mosaic. Their outer diameter is up to 5 mm, whereas the inner diameter is up to 3.1 mm.

The internal structure of *Loiscupula bachendensi* (Figure 4.1-4.8) is composed of narrow polygonal (some hexagonal) to slightly rounded tubules in transverse section, with shared walls between adjacent units. They are straight or gently curved in longitudinal section, and are arranged perpendicular to the surface of the skeleton resulting in a characteristic honeycomb pattern (Figure 4.1). The tubules may be partitioned horizontally at different levels by poorly developed tabulae that may occur at the same or different levels as those in adjacent tubules (Figure 4.2, 4.5-4.8). The tubule walls are approximately 10–15 µm thick, with a 70–120 µm cross-sectional area (averaging

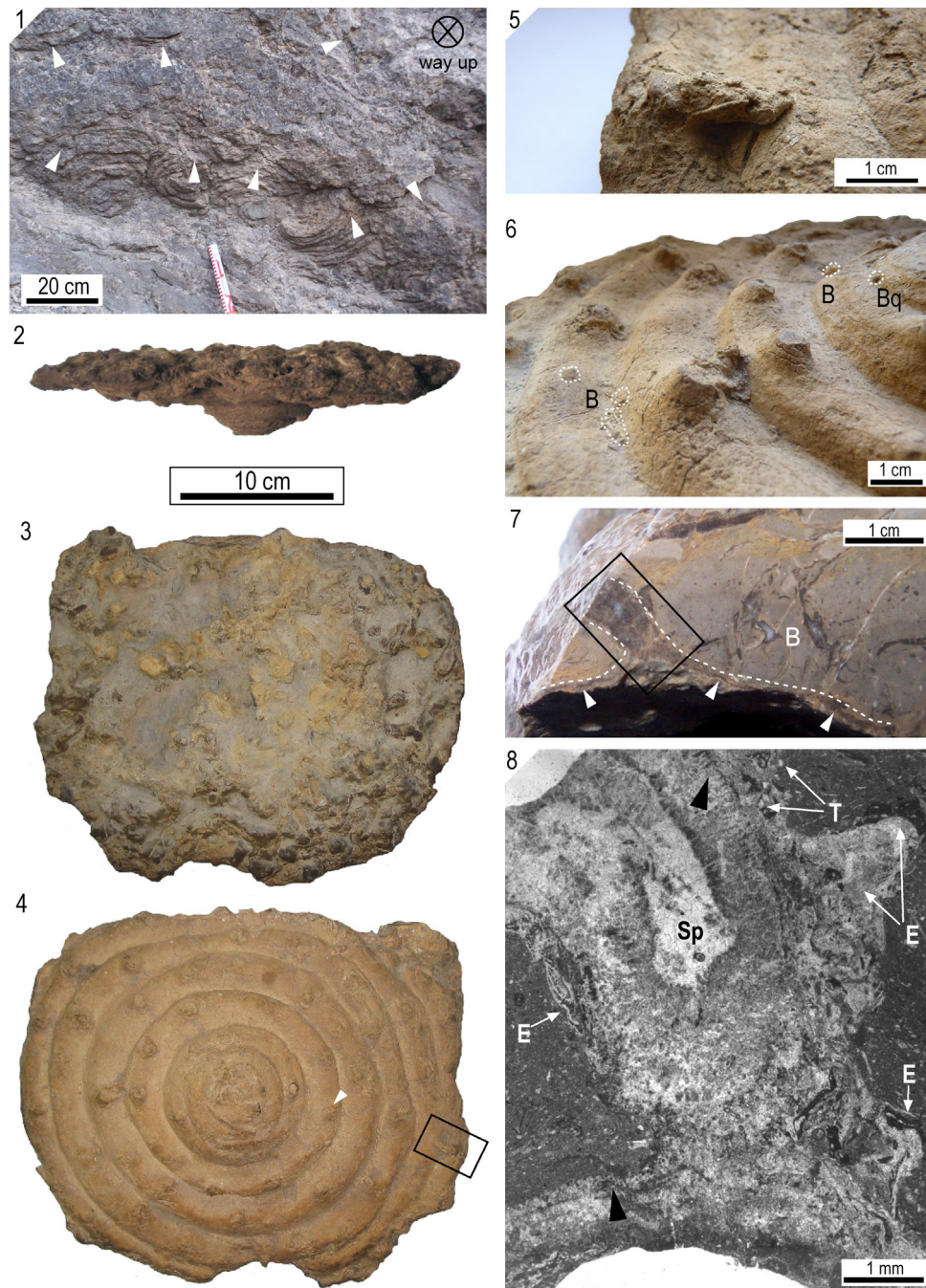


FIGURE 3. General morphologic features of *Loiscupula bachendensi* gen. nov. sp. nov. from the Bachende Formation, Cantabrian Zone, NW Spain. 1, type locality of *Loiscupula bachendensi* in the Bachende Formation, arrows point to different specimens. 2-6 Holotype USAL LB1, 2, side view showing the flat cup-shaped skeleton, with the central part of the specimen lower than the outer edges. 3, top view, showing the wackestone matrix filling the cup. 4, underside of the sponge, showing the plate-shape and the concentric rings around a central point; note the projected structures developed within each ring and usually preserved as eroded (truncated) protuberances (arrow). 5, enlargement of the rectangular area in Figure 3.4, showing in detail one of the projections on the underside of the specimen. 6, close-up of the undulating underside of the skeleton, showing the eroded protuberances and encrusting bryozoans; B= bryozoans, Bq= brachiopod. 7-8, Paratype USAL LB5, 7, cylindrical feature (rectangle) growing up from the upper surface of the skeleton of *Loiscupula* (white arrows); B= brachiopod. 8, close-up of the rectangular area in Figure 3.7; arrows point to the poorly preserved microstructure of *Loiscupula*. Note the abundant foralgal encrustations (E); T= *Tuberitina*; Sp= sparry calcite.

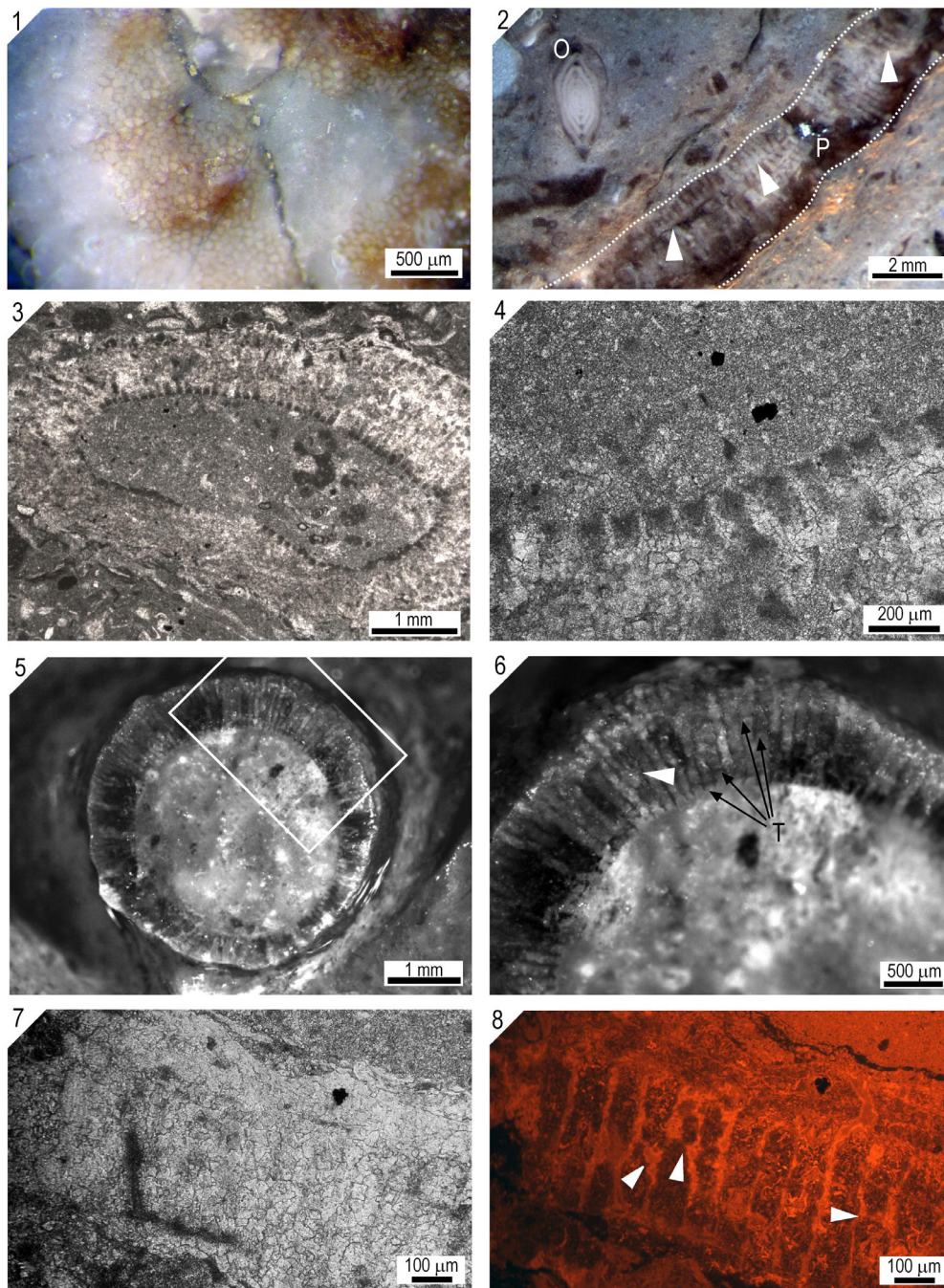


FIGURE 4. Internal structure of *Loiscupula bachendensi* gen. nov. sp. nov. 1, paratype USAL LB22, close-up showing the honey-comb pattern of the surface of *Loiscupula bachendensi*. 2, paratype USAL LB5, internal structure of the plate-like basal skeleton (enclosed by white dashed lines); white arrows point to vertical growth interruptions of the tubules; O= *Ozawainella*; P= pyrite. 3-4, paratype USAL LB29, 3, photomicrograph showing the internal structure of a cylindrical feature developed on the upper surface of the skeleton. 4, close-up of tubules at the upper edge of the skeleton. 5-6, Holotype USAL LB1, 5, transversal section of a cylindrical form; note the internal cavity, filled-up with micritic matrix, and the internal structure of *Loiscupula* composed of tubules. 6, close-up of the rectangular area in Figure 4.5 (rotated 45° counterclockwise); note the increasing of new tubules by intertubule increase (white arrow) and their horizontal partitions at different levels (T= tabulae). 7-8, paratype USAL LB5, 7, plane polarized light photo-micrograph showing the overall recrystallization of the basal skeleton. 8, cathodoluminescence image of same field of view as Figure 4.7, showing the internal structure of the skeleton with development of poorly defined tabulae (arrowed).

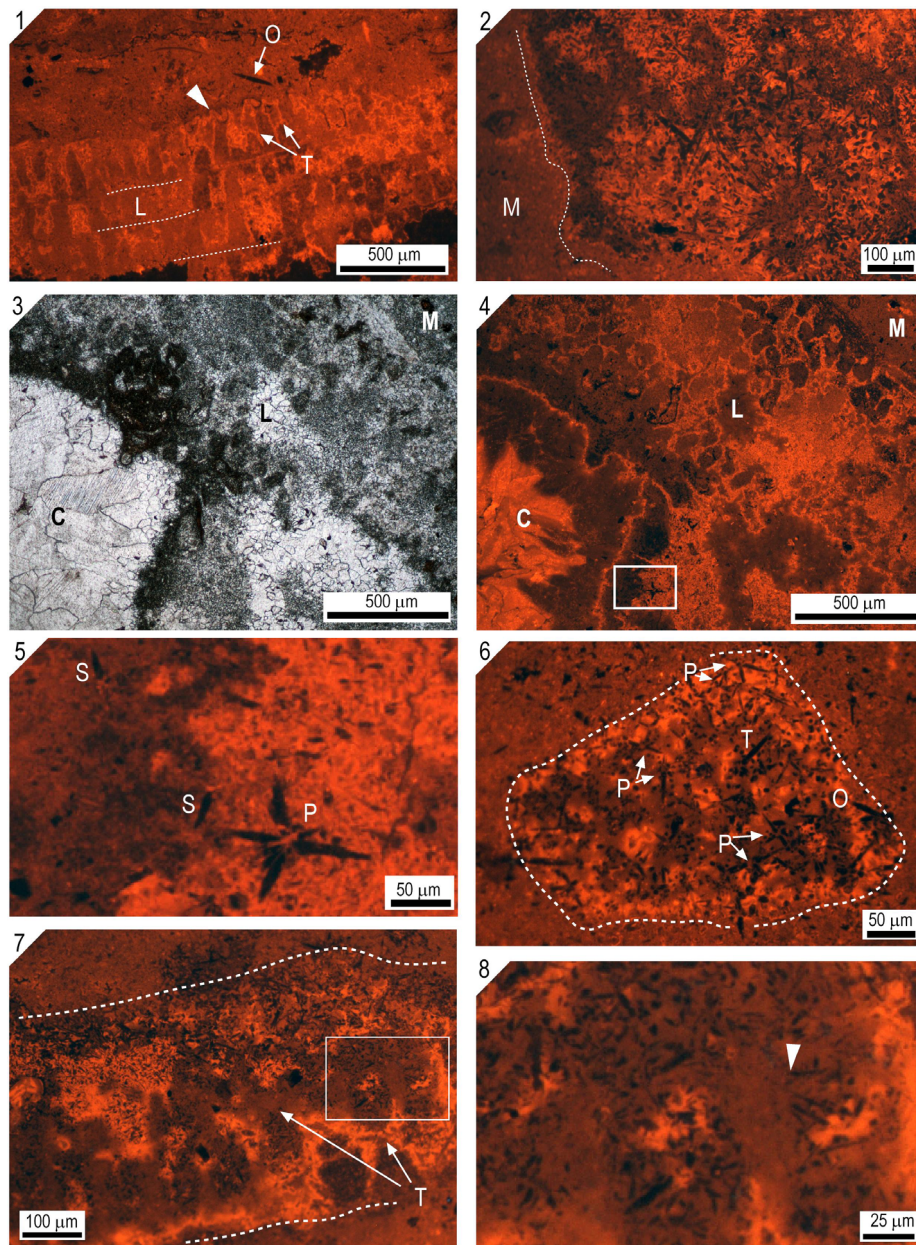


FIGURE 5. 1-8, Paratype USAL LB 5, spicule pseudomorphs of *Loiscupula bachendensi* gen. nov. sp. nov. All the images, except Figure 5.3, are cathodoluminescence photomicrographs. 1, Oxea (O) spicule pseudomorph floating in the surrounding matrix; white arrow is pointing to an (algal?) encrustation on the upper surface of the skeleton; T= tabulae; L=laminae, indicated by white dashed lines; note that tubules may be continuous or discontinuous across the growth interruptions. 2, intraskeletal non-luminescent spicule (mostly oxeas) pseudomorphs in a fragment of *Loiscupula*; white dashed line indicates the outer edge of the basal skeleton of *Loiscupula*; M= micritic matrix. 3, 4, plane polarized light and cathodoluminescence photomicrographs showing the internal structure of the plate-like basal skeleton; C= void filling cement; L= *Loiscupula*; M= micritic matrix. 5, close-up of the rectangular area in Figure 5.4, showing in detail a polyactine (P) and pseudomorphs of style spicules (S) embedded in the basal skeleton. 6, Oxea (O) and reduced polyaxon (P) spicule pseudomorphs and a probable pseudomorph of tylostyle spicule (T); dashed line indicates a fragment of *Loiscupula*. Note the dull appearance of the surrounding matrix and the bright to yellow-dull CL of the skeletal calcite. 7, Spicule pseudomorphs concentrated towards the upper edge of the basal skeleton; dashed line indicates a transversal section of *Loiscupula*; T= tabula. 8, Close-up view of the rectangular area in Figure 5.5; arrow points to spicule pseudomorphs projecting into a tubule.

80-90 μm) and a length of up to (at least) 1.9 mm (Figure 4.3, 4.4). New tubules may arise by intertubule increase (Figure 4.6) or peripheral expansion. Growth interruptions are sporadically present in some specimens and define poorly developed laminae (Figure 5.1). Tubules may be continuous or discontinuous across these interruptions (Figure 5.1).

Cathodoluminescence microscopy reveals non-luminescent calcite structures that are interpreted as spicule pseudomorphs (Figures 5 and 6.1-6.5). These spicule pseudomorphs are only found in the *Loiscupula* horizon and have not been observed in the overlying and underlying rock units. They appear floating in the matrix, embedded in the skeleton of *Loiscupula* or projecting into the tubules (Figure 5.7, 5.8). These spicule pseudomorphs do not occur in associated calcareous components, such as void-filling cements or phylloid algae (e.g., *Archaeolithophyllum*). Spicule pseudomorphs are not visible with transmitted polarized light, and under CL microscopy, they contrast sharply with the bright to yellow-dull CL calcite of the skeleton of *Loiscupula*, with the cement filling the tubules spaces (non-luminescent or orange-dull CL) and with the surrounding matrix (orange-dull CL). These pseudomorphs are found in large numbers toward the upper edge of the skeletons, and they have been observed in both the plate-like skeleton and the cylindrical and branching forms (extended mamelons and/or chimneys) that project upward from the upper surface. Although frequently the distribution of these pseudomorphs is irregular (Figure 5.2), there are occurrences that suggest that a spicular network existed. Monoaxon oxea spicule pseudomorphs predominate, but styles and polyaxon spicule pseudomorphs are also present (Figures 5.5, 5.6, 6.4, 6.5).

Although the preservation of the spicule pseudomorphs is relatively good, no convincing axial canals have been observed (Figure 6.3); most of the pseudomorphs exhibit dissolution features, such as irregular edges, deep corrosion or reduction of axial rays (Figure 6.5). In addition, some of them are discontinuous. Pseudomorphs of monoaxon spicules are 190 to 24 μm long, and 22 to 4 μm wide (25 spicules measured). Polyaxon spicules have several equal rays radiating from a central point, and are 190 to 64 μm long, and 11 to 9 μm wide (4 spicules measured). The dimensions of the spicule pseudomorphs were taken from an enlarged CL image, and thus are only approximate and probably underestimated. These dimensions

are conservative because it is unlikely that the spicule pseudomorphs were sectioned in a plane that allowed viewing their full and real size.

The basal skeleton is a mosaic of sparry calcite, and the degree of preservation is usually best near the upper margin of the skeleton. The original microstructure was almost completely destroyed during diagenesis, although SEM microscopy revealed patches of the relic fascicular penicillate-type microstructure, which is composed of closely packed needles that fan out from points of calcification in a longitudinal view. These needles are usually encased in coarse calcite crystals as a result of diagenetic overprinting (Figure 6.6), and range in diameter from less than one micrometer to two micrometers.

Discussion and remarks

Hypercalcified chaetetid demosponges are a group with a diverse and complex taxonomic history with different Paleozoic and post-Paleozoic histories (Fischer, 1970; Gray, 1980; West, 2011a) that has been further complicated by Riding (2004) who assigned *Solenopora* to the chaetetids (for a detailed history of chaetetid taxonomy see Connolly et al., 1989; and West, 2011a).

As summarized by West (2011a), the valid taxonomic placement of chaetetid sponges should be based in (in order of decreasing usefulness): 1) spicule composition and morphology; 2) the original mineralogy and microstructure of the secondary skeleton; and 3) skeletal and morphological features, such as shape, size and arrangement of the tubules, thickness of the tubule walls, thickness of the tabulae, and absence of septa and mural pores. The first and second features are traditionally used at all levels in the classification of sponges. Unfortunately, in most fossil chaetetid skeletons, spicules (or their pseudomorphs) are usually absent (West and Clark, 1983; West, 2011b), and thus, they have not been usually used as diagnostic criteria in most chaetetid taxonomic classifications. This absence may be due to several biological and diagenetical factors, such as the non-incorporation of the spicules into the skeleton or dissolution during diagenesis. The third set of morphological diagnostic criteria is usually available in fossil chaetetids and has been employed in most chaetetid taxonomic classifications. However, it has been demonstrated that some criteria, such as the diameter of the tubes (properly cross-sectional areas of the tubes) and thickness of the tube walls, are not valid to differentiate Carboniferous

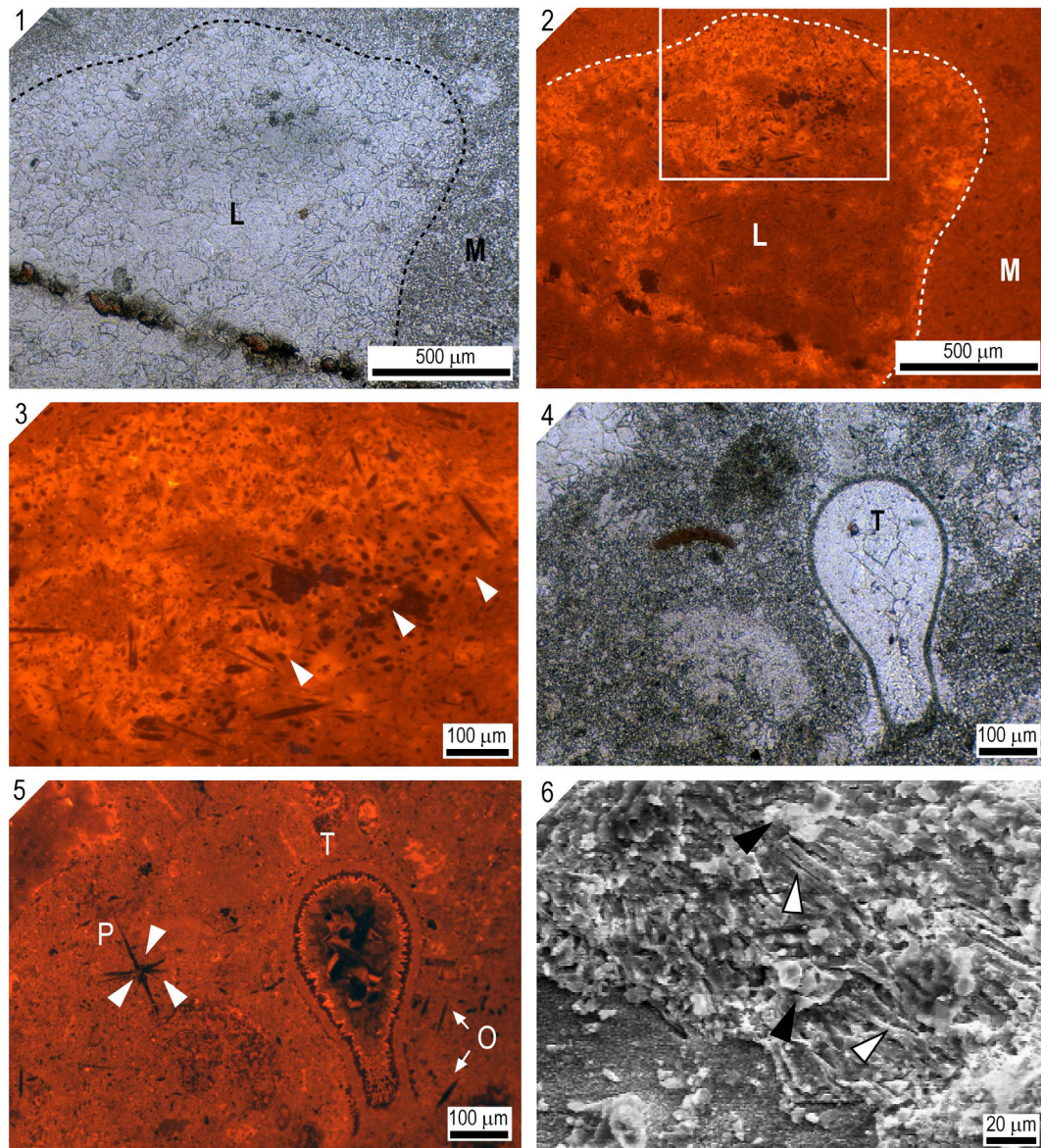


FIGURE 6. 1-6, Paratype USAL LB 5, spicule pseudomorphs and microstructure of *Loiscupula bachendensi* gen. nov. sp. nov. All the images are cathodoluminescence photomicrographs, except Figure 6.6, which is a scanning electron micrograph. 1, strongly recrystallized fragment of *Loiscupula* (L) floating in a microspartic matrix (M). 2, cathodoluminescence image of same field of view as Figure 6.1, showing abundant spicule pseudomorphs embedded in the basal skeleton; note that they are absent in the surrounding matrix; L= *Loiscupula*; M= matrix. 3, close-up of the rectangular area in Figure 6.2, showing in detail several pseudomorphs of oxea pseudomorphs; arrows point to spicule cross sections. 4, 5, plane polarized light and cathodoluminescence photomicrographs showing a *Tubertina* specimen (T) with well developed cathodoluminescence zonation; (P) polyaxon spicule pseudomorph floating in the surrounding microspartic matrix with some rays shortened and others missing (arrows); O= pseudomorphs of oxea spicules with irregular edges. 6, Relic fascicular penicillate microstructure of *Loiscupula*, composed of fibers, inferred to be aragonite needles (white arrows) within coarse calcite crystals (black arrows).

species of the genus *Chaetetes* (West 1994, 2011a).

Currently, there are 22 chaetetid genera and subgenera from which spicule pseudomorphs, and the original microstructure and mineralogy of the

basal skeleton, have been reported (West 2011a, table 3). Calcite, silica or pyritic monoaxoan spicule pseudomorphs (mainly tylostyles or styles) in Carboniferous chaetetids have been reported in *Chaetetes* (*Boswellia*) by Gray (1980), from the

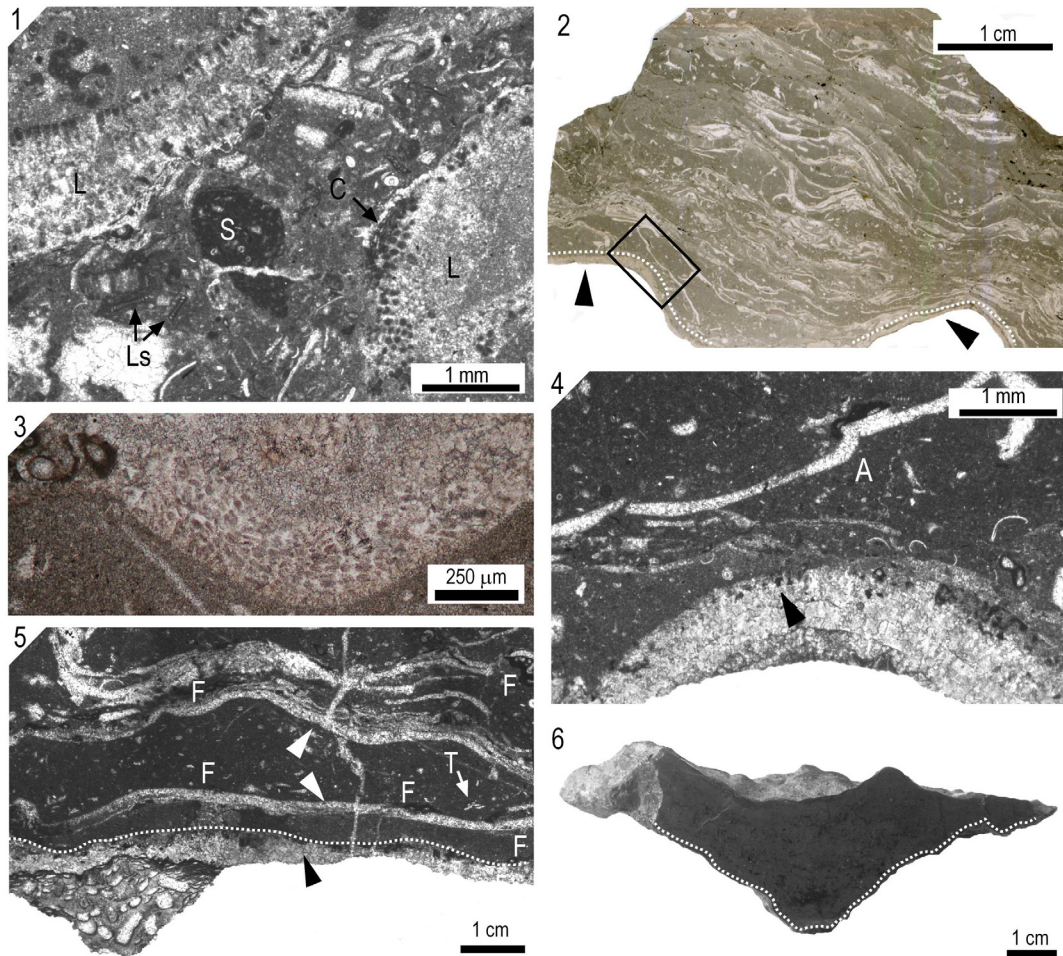


FIGURE 7. 1, Paratype USAL LB 5, *Loiscupula* (L) fragments floating in a muddy matrix; Ls= lasiodiscs; C=cyanobacteria filaments (*Girvanella*?); S= *Shamovella*. 2-4, USAL LB34, 2, polished slab showing the matrix that filled the cup-like skeleton of *Loisphyllum* (arrowed), with a complex intergrowth of *Archaeolithophyllum lamellosum*; note the undulating morphology of the *Loiscupula* skeleton (white dashed lines), representing the circular and concentric rings (grooves and ridges) in transverse section. 3, *Archaeolithophyllum* thallus showing relics of coaxial perithallum and hypotallum organization. 4, close-up view of the rectangular area in Figure 6.2; note the neomorphic calcite forming the basal skeleton and the poor preservation of the tubules (arrow); A= blade fragments of *Archaeolithophyllum*. 5, paratype USAL LB38-1, polished slab of a *Loiscupula bachendensi* specimen (black arrow and dashed line) with a fistuliporid bryozoan encrusting (lower left of the image) the underside of the specimen; note the development of the complex intergrowth of *Archaeolithophyllum lamellosum* (white arrows) in the wackestone matrix and the encrustations of small foraminifers (F), usually developed on the upper surface of the phylloid blades and *Loiscupula*. T= small specimen of *Tetrataxis*. 6, paratype USAL LB24, transversal section of a small specimen of *Loiscupula bachendensi*, showing the internal wackestone matrix filling the cup-shaped skeleton (dashed lines).

British Dinantian. *Loiscupula bachendensi* differs from these chaetetids in containing oxea, style and polyaxon spicules forming a complex and irregular network, and justifies the new genus and species as described herein. Furthermore, the extremely regular and concentric basal skeleton, the occurrence of ventral projections (actually preserved as eroded protuberances), and the inferred central point of attachment, are features not reported in

other chaetetid hypercalcified sponges. Until the composition of the original microstructure of *Loiscupula* and the type and arrangement of spicules are better known, the taxonomic placement of these fossils within the Class Demospongiae is uncertain.

Alternatively, although the spicular objects are best candidates for spicule pseudomorphs and *Loiscupula* shows numerous similarities with other

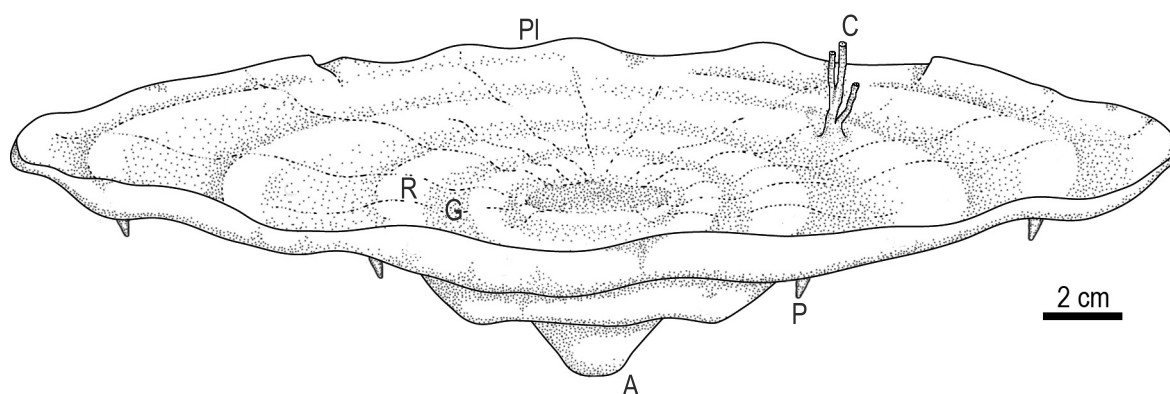


FIGURE 8. Idealized reconstruction of *Loiscupula bachendensi* gen. nov. sp. nov. Note the low conical growth form; A= presumed attachment point; P= projections on lower surface; G= grooves; R= ridges; PI= plate-like skeleton; C)= cylindrical/branching features (extended mamelons/chimneys) on upper surface.

chaetetid demosponges, there is not conclusive evidence to verify the original silica composition of the spicules. Thus, these pseudomorphs could represent in reality diagenetic alteration of originally calcareous spicules. In that case, the systematic placement of *Loiscupula* within the Demospongiae would be invalid.

MINERALOGY, PRESERVATION AND DIAGENESIS OF *LOISCUPULA*

Fossil and extant coralline sponges secrete metastable carbonate like high-Mg calcite (e.g., *Merlia*, *Acanthochaetetes*, *Stromatoaxinella*) or aragonite (e.g., *Chaetetes* (*Boswellia*), *Astrosclera*, *Ceratoporella*), and thus, both are possible as the mineralogy of *Loiscupula*. Several studies have demonstrated that the alteration of high-Mg calcite to low-Mg calcite usually retains, to a high degree, the details of the original skeletal structure because the change does not involve a modification of the original crystal habit (e.g., James and Choquette, 1983; Tucker and Wright, 1990). On the other hand, early diagenetic process (usually under vadose/meteoric phreatic conditions) that converts aragonite to calcite often results in a secondary fabric formed by a mosaic of coarse-grained neomorphic spar. This mosaic commonly retains only the basic structure of the original elements, usually as organic inclusions (e.g., James, 1974). In some instances, the replacement is incomplete, and tiny crystallites of aragonite remain as relics entombed in the new calcite (Sandberg et al., 1973; Sandberg and Hudson, 1983).

The skeleton of *Loiscupula bachendensi* is now composed of a sparry calcite mosaic, and the skeletal fabric is poorly preserved, but with relics of

fascicular needles encased in coarse calcite crystals. Based on these observations, it is inferred that the original mineralogy of *Loiscupula* was probably aragonite that has undergone diagenetic alteration. In addition, the preservation of the outlines of the original structure and relics of remnant aragonite needles, suggests that the transformation process was the result of a rapid and in situ replacement of the aragonite, and not removal by solution followed by precipitation of void-filling cement.

Although CL microscopy has not been usually used as a tool to study polymorphic transformations in fossil forms (Boggs and Krinsley, 2006) it has been demonstrated that diagenesis can influence the CL signal. Richter and Zinkernagel (1981) suggested that aragonitic skeletons lose their luminescence zonation during replacement by calcite, whereas Mg-calcite skeletons may maintain part of it because their replacement preserves the original crystal fabric.

Minor element data (Mg, Mn, Fe and Sr) from bulk samples of five specimens (Table 1) indicate that the basal skeleton of *Loiscupula* is currently composed of neomorphosed low-Mg calcite (1.7 mol % MgCO_3). In all the samples, Fe values are relatively high (with an average of 5468 ppm), whereas Mn diagenetic enrichment appears to be insignificant (mean of 103 ppm). On the other hand, Sr content is high, but variable, ranging from 1492 to 3456 ppm (average 2422 ppm). When present at an anomalously high concentration in a calcitic fossil, Sr is often taken to be the chemical remnant of a primary aragonite composition (Sandberg and Hudson, 1983). Recent skeletal aragonite in coralline demosponges typically contains 8000-10000 ppm Sr (Laghi et al., 1984; Mastandrea and

TABLE 1. Minor element content (ppm) of *Loiscupula* skeletons from the Bachende Formation.

Type (ppm)	Mg	Mn	Fe	Sr
USAL LB2	3821	60	4246	2863
USAL LB4	3804	168	8477	1943
USAL LB5-5	4535	103	5717	2365
USAL LB5-13	5033	119	4636	1482
USAL LB22	4423	66	4266	3456
Average	4323	103	5468	2422

Russo, 1995; Reitner et al., 2001). Nevertheless, the diagenetic stabilization of aragonite commonly results in a Sr depletion because its incorporation in the calcite lattice is not favoured. Given that, the Sr values of *Loiscupula* are reasonably similar to the Sr values reported for other Pennsylvanian aragonitic fossils as follows: 1800-3500 ppm Sr for encrusting demosponges in Texas (Molineux, 1994), 4000 ppm Sr for cephalopods and 4800-5200 ppm Sr in molluscs from the Kendrick Shale of eastern Kentucky (Uwe, 1981). However, the Sr values for the skeleton of *Loiscupula* are much lower than the Pennsylvanian data reported by Dickson et al. (1996) for exceptionally preserved demosponges in New Mexico (7600 ppm Sr), or by Kirkland et al. (1993) for very well preserved *Eugonophyllum* specimens from the Sacramento Mountains (9090 ppm Sr), which retain abundant relics of aragonite needles, with Sr concentrations close to the concentrations of unaltered aragonite.

The tubules of *Loiscupula* are filled with fine-grained equant cements that are non-luminescent or orange-dull CL. Based on their form, size and occurrence (e.g., Figure 4.4, 4.7, 4.8) they are interpreted to have been originally calcite that had a low Sr content. Because it was not possible to separate the calcitic skeleton from early diagenetic cement that fills the tubules, the ICP-MS results indicate an alteration of the original chemistry of the basal skeleton. Therefore, the Sr in the specimens of *Loiscupula* probably shows a reduction due to diagenetic contamination.

It is suggested that the elevated content of Fe was derived from the tubule-filling cements, which reflect subsequent diagenetic changes from reducing fluids enriched in Fe. This interpretation is consistent with the observed cathodoluminescence signal, because the absence of luminescence is usually related to high concentrations of Fe²⁺ that appears to be the most important quencher of luminescence in natural carbonates (e.g., Machel et al., 1991; Boggs and Krinsley, 2006). The source of Fe is probably related to the burial transformation of

detrital clays accompanied by release of metal ions to the pore fluid. Such clays/mudstones occur in the middle part of the Bachende Formation (Figure 2) and the overlying Dueñas Formation.

The non-luminescent spicule-like structures reported herein, which are missed using conventional microscopy, are reasonable candidates for sponge spicule pseudomorphs. An alternative, however, would be that some of them, especially the polyactine forms, may represent in reality authigenic crystals formed during early diagenesis. Although their size and morphology do not rule out this possibility, the presence of these structures only within the fragments of *Loiscupula* and not in other recrystallized bioclasts (e.g., the red alga *Archaeolithophyllum*) or diagenetic cements, suggests that the authigenic crystal interpretation is improbable.

It is widely accepted that the primary mineralogy of chaetetids spicules was opaline silica (see review in Gray, 1980; Cremer, 1995; West, 2011b) that was easily and rapidly dissolved, with the resulting molds, in some cases filled by other secondary minerals (e.g., calcite, silica, pyrite). Such rapid dissolution has been observed in recent hypercalcified sponges and can occur during life (Hartman and Goreau, 1970, 1972; Reitner, 1987). After the dissolution of opaline silica, while the spicules existed as molds in *Loiscupula*, many molds were deformed. The molds were subsequently filled and cemented by non-luminescent calcite that contrasts sharply with the bright and yellow-dull luminescent calcite of the secondary skeleton (Figures 5 and 6.1-6.5). The edges of some pseudomorphs are irregular and corroded, features that were filled with dull luminescent calcite, indicating diagenetic processes that post-dated their cementation.

The diversity of spicule morphology in *Loiscupula* specimens invites discussion. Some of the spicules are discontinuous, a feature suggesting severe corrosion (as suggested by Gray, 1980). The irregular edges and shapes of some spicule

pseudomorphs are the result of diagenetic processes. Consequently, most of the oxea calcite pseudomorphs could have originally been styles (tylostyle?) or reduced derivations of polyaxon spicules.

The timing of the calcite cementation of the tubules must have occurred prior to dissolution of the siliceous spicules to allow the formation of molds that produced the spicule pseudomorphs, as noted by Wood and Reitner (1988) in specimens of *Stromatoaxinella*. However, the cement in some tubules masks the walls of the tubules and some spicule pseudomorphs, suggesting that diagenetic alteration has occurred. The timing of the cementation of the spicule pseudomorphs relative to the neomorphism of aragonite to low-Mg calcite is uncertain and requires further geochemical studies, but based on CL observations, it can be assumed that it was not contemporaneous. This assumption is in agreement with the diagenetic pathways reported by Gray (1980) in some specimens of *Chaetetes* (*Boswellia*) from the Carboniferous.

PALAEOECOLOGY

The ecology of extant hypercalcified sponges is fundamentally different from that of fossil forms. Extant forms are commonly found in cryptic habitats such as submarine caves of the reef core, and at depth on fore-reef slopes and walls in both the Caribbean and Indo-Pacific regions (Hartman and Goreau, 1975) in depths ranging from 10 to 185 m (Fallon et al., 2005). In contrast, Palaeozoic chaetetids are common open-shelf organisms, often associated with sunlight and relatively shallow-water carbonates. Therefore, the transfer of ecologic data from extant hypercalcified sponges to fossil chaetetids is tenuous and tentative, and the palaeoecology of *Loiscupula* must be inferred from the associated biota and sedimentologic evidence.

Fossil Assemblage

The relatively highly diverse fossil assemblage associated with *Loiscupula* in the micritic matrix, includes diverse foraminifers, brachiopods, crinoids, ostracods, calcareous algae, syringopod corals, colonial rugose corals, gastropods, stacheinacean algae, cyanobacteria and bryozoans (Figure 7.1). Such an assemblage is indicative of open marine conditions, with normal salinity and well oxygenated water.

Archaeolithophyllum lamellosum generally encrusts the upper surface of *Loiscupula* forming undulatory masses of superimposed crusts or thalli up to 2 cm thick, oriented subparallel to the bedding surface (Figure 7.2-7.4). It is usually associated with *Shamovella* and *Palaeonubecularia*, forming complex intergrowths in the micritic matrix. The conspicuous presence of *A. lamellosum* suggests a depositional environment within the euphotic zone. Wray (1964) described wave-resistant features formed by *A. lamellosum*, and its abundance could be indicative of environments of high to moderate energy.

Large benthic foraminifers, such as paleotextulariids, inhabited shallow and warm environments with moderate to strong hydrodynamic conditions (Gallagher, 1998; Della Porta et al., 2005; Merino-Tomé et al. 2009). *Ozawainella* (Figure 4.2) is consistent with open marine and outer platform facies below wave base, and in the Cantabrian Zone is usually associated with open-marine crinoidal accumulations (Della Porta et al., 2005). In the Carboniferous and Permian of the USA, *Tetrataxis* is a common foraminifer of shallow phylloid algal facies (Toomey and Winland, 1973), which was able to live in highly varied environments with a preference for open-marine environments (Della Porta et al., 2005). However, its distribution shows a wider range of depths than most Fusulinida (Gallagher, 1998). Della Porta et al. (2005) reported that tetrataxids in the Sierra del Cuera platform (NW Spain) occur in platform and slope facies and even at aphotic depths of 200 m below the platform break. Additionally, Cózar and Rodríguez (2003) suggested that the occurrence and abundance of tetrataxids was similar in all facies, but its relative abundance is higher in intertidal and mud mound facies because many other taxa do not inhabit these facies. The lasiodiscids mainly occur in quiet-water, low-energy open marine, subtidal facies and mud mound environments (Cózar and Rodríguez, 2003; Della Porta et al., 2005).

Chaetetids at the type locality are laminar, up to a few centimetres thick and may also encrust the upper surface of *Loiscupula*. Laminar chaetetids are believed to be better adapted to high-energy environments, although Kershaw and West (1991) suggested that this growth form remains problematic, and an interpretation of its environmental habitat depends on the type and features of the associated lithology. Chaetetids are commonly interpreted to have inhabited very shallow-water subtidal environments, close to intertidal depths where the water is somewhat agitated (Connolly et

al., 1989; Wahlman, 2002). However, these organisms were probably able to thrive over a range of depths, and chaetetid accumulations have been reported at paleowater depths of approximately 100 m in Sonora, Mexico (Almazán-Vázquez et al., 2007).

Brachiopods and fistuliporid bryozoans (rarely fenestrate/ramose bryozoans) occur on the lower surface of *Loiscupula* skeletons (Figure 7.5), and represent cryptic biota associated with small cavities formed between *Loiscupula* and the substrate. Bryozoan colonies are conical or occur as irregular patches up to 2.2 cm across and less than 1.5 mm thick. In the holotype (USAL LB1), these bryozoans cover an average area of only 0.9% of the lower surface of *Loiscupula*. The cryptic biota is similar to that reported by Hartman and Goreau (1970) found on extant hypercalcified sponges, and to cryptic faunas documented by Suchy and West (1988) on laminar chaetetids from the Pennsylvanian Pawnee Formation (Iowa), and to that reported beneath Silurian stromatoporoids in the Silurian of Gotland, Sweden, by Kershaw (1980). Suchy and West (1988) suggested that although a wide depth range could be plausible for their specimens, the cryptic community probably represents intertidal occurrences similar to those observed on extant specimens of *Acanthochaetetes*, from well oxygenated marine water of normal salinity.

Growth Mode

The lithology filling and surrounding the in situ skeletons of *Loiscupula*, is a wackestone (minor packstone), basically formed by a homogeneous micrite with some recrystallization to microsparite. This occurrence was resulted from the successive vertical accumulation of specimens of *Loiscupula* and the deposition of muddy sediment. Some algae, such as *Archaeolithophyllum*, and diverse, encrusting foraminifers, trapped and bound the sediments stabilizing it. These meter thick accumulations lack a positive relief and are interpreted as chaetetid banks.

The facies of the Bachende Formation that contains the in situ specimens of *Loiscupula* is interpreted as an environment of moderate to low energy, below wave base or a protected area in the shallow water of the platform. This interpretation is supported by the scarcity of grain-supported deposits with current structures. Fragments of *Loiscupula* in the surrounding matrix and the lithology filling the skeletons are probably the result of turbulent episodes. The orientation of *Loiscupula* relative to the substrate suggests that it grew very

close to the seabed, elevated very little above it. The growth form of *Loiscupula* is essentially two-dimensional (Figures 3.2, 7.6, 8) and therefore it could have come in direct contact with other benthic organisms, competing for space (e.g., calcareous algae). However, the well-developed regular circular geometry in plan view, would suggest that they lived in a relatively uncrowded environment where they were free to grow outward in a very regular fashion. As *Loiscupula* grew laterally, it also grew vertically, and the growth bands observed in some specimens are interpreted to be phases of such growth. The concentric rings in all the specimens studied, probably indicate successive lateral growth stages of the organism (peripheral expansion) and suggest a regular outgrowth from an initial and central point of settlement/attachment. Although there is no evidence of attachment to the substrate, the base of the skeleton that tapers downward could have served as a peduncle, such as observed in some species of *Acanthochaetetes* (e.g., Millet and Kiessling, 2009). The ecological function of the ventral projections (now mostly preserved as eroded protuberances) observed on the basal surface of *Loiscupula* remains uncertain. However, they may have served a support function, or anchoring mechanism, for the growth of the low conical form in the muddy substrate. Substrates on which chaetetids grew were hard, firm, or composed of loose and coarse grains (West and Kershaw, 1991). The absence of pressure-solution features or sutured contacts between grains indicates rapid symsedimentary cementation of the muddy sediment, resulting in a lithified firm substrate for *Loiscupula*. Early lithification of the substrate is also supported by the upper non-erosive hummocky irregular topography of the *Loiscupula* occurrence. As pointed by Almazán-Vázquez et al. (2007), such substrates would be favoured by relative strong hydrodynamic conditions that permitted rapid cementation of the granular sediments.

Cylindrical branched forms growing up from the plate-shaped basal skeleton resemble some vertical features observed in fossil chaetetids that are referred to as chimneys (West, 2011b, 2011c). These vertical developed mamelons may be related to exhalant movement of water, although it is also possible that these structures are the result of an associated symbiotic organism (West, 2011c).

CONCLUSIONS

1. A new chaetetid genus (Demospongiae) is described as *Loiscupula bachendensi* n. gen.

- n. sp., from the Moscovian Bachende Formation (Cantabrian Zone, NW Spain).
- Loiscupula* has a circular, concentric and platy (low cup-like) basal skeleton, with cylindrical and branching features (extended mamelons and/or chimneys) growing upward. The basal skeleton is composed of polygonal (often hexagonal) to slightly rounded tubules arranged perpendicular to the surface of the skeleton, resulting in the characteristic honeycomb pattern of chaetetids. Tabulae are irregularly distributed and tubules increased by intertubule increase and/or peripheral expansion.
 - Cathodoluminescence microscopy revealed non-luminescent calcite pseudomorphs of oxeas (rarely styles) monoaxon and polyaxon spicules.
 - Despite the fact that the basal skeleton is recrystallized and now composed of a low-Mg calcite (1.7 mol % MgCO₃), recognition of what appears to be a penicillate microstructure with relics of aragonite needles, and the high Sr content of the skeleton, supports the interpretation that the original skeleton of *Loiscupula* was aragonite.
 - Loiscupula* lived on or attached to a firm carbonate-mud substrate, and provided small cryptic cavities between its skeleton and the sea floor for encrusting organisms, such as fistuliporid bryozoans. The associated fossil assemblage and sedimentological features support an open marine environment within the euphotic zone for *Loiscupula* where the normally saline waters were well-oxygenated and where energy conditions were low to moderate.

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