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Sobralispongia densespiculata, a new coralline sponge from the Upper Jurassic of Portugal

Sobralispongia densespiculata, une nouvelle « coralline sponge » dans le Jurassique supérieur du Portugal

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Abstract

From the Kimmeridgian (Upper Jurassic) of Portugal, the coralline sponge *Sobralispongia densespiculata* nov. gen. and nov. sp. is described. Main characteristics are a crustose habit, a primary spicule skeleton of very densely packed styles and subtylostyles arranged in a plumose architecture, microscleres of possibly aster-type, and a microgranular to fibrous secondary calcareous skeleton. The primary mineralogy of the calcareous skeleton was probably high-Mg calcitic. An assignment to the demosponge Order Axinellida is proposed.

Résumé

Une nouvelle éponge du groupe des « coralline sponges », *Sobralispongia densespiculata* nov. gen. nov. sp., est décrite dans le Kimméridgien (Jurassique supérieur) du Portugal. Elle est caracterisée principalement par un mode de vie encroutant, un squelette spiculaire constitué de styles et subtylostyles arrangés selon une architecture plumeuse, des microsclères de type aster et d'un squelette calcaire microgranulaire à fibreux. La minéralogie du squelette calcaire était probablement calcitique. Il est proposé une attribution à l'ordre Axinellida dans les Démosponges.

Keywords: Sponges; Coralline sponges; Demospongiae; New taxon; Late Jurassic; Portugal

Mots clés : Éponges ; « Coralline sponges » ; Demospongiae ; Nouveau taxon ; Jurassique supérieur ; Portugal

1. Introduction

With the studies on Recent coralline sponges by Hartman (1969); Hartman and Goreau (1970, 1972), increased attention was focussed on the fossil stromatoporoids and chaetetids. In a series of papers dealing mainly with architecture, microstructure, and taxonomy, the comparison with the Recent coralline sponges confirmed the poriferan affinities of these two groups. Some of the fossil taxa which bear a calcareous skeleton and spicule pseudomorphs have been placed within the new class Sclerospongia Hartman, 1972 (e.g. Cuif, 1973; Dieci et al., 1977; Kazmierczak, 1979).

While the poriferan nature of Palaeozoic and Mesozoic stromatoporoids and chaetetids is now widely accepted, there still exist uncertainties as to the systematic value of the preserved skeletal features of coralline sponges. Increasing knowledge of Recent and fossil coralline sponges has proved

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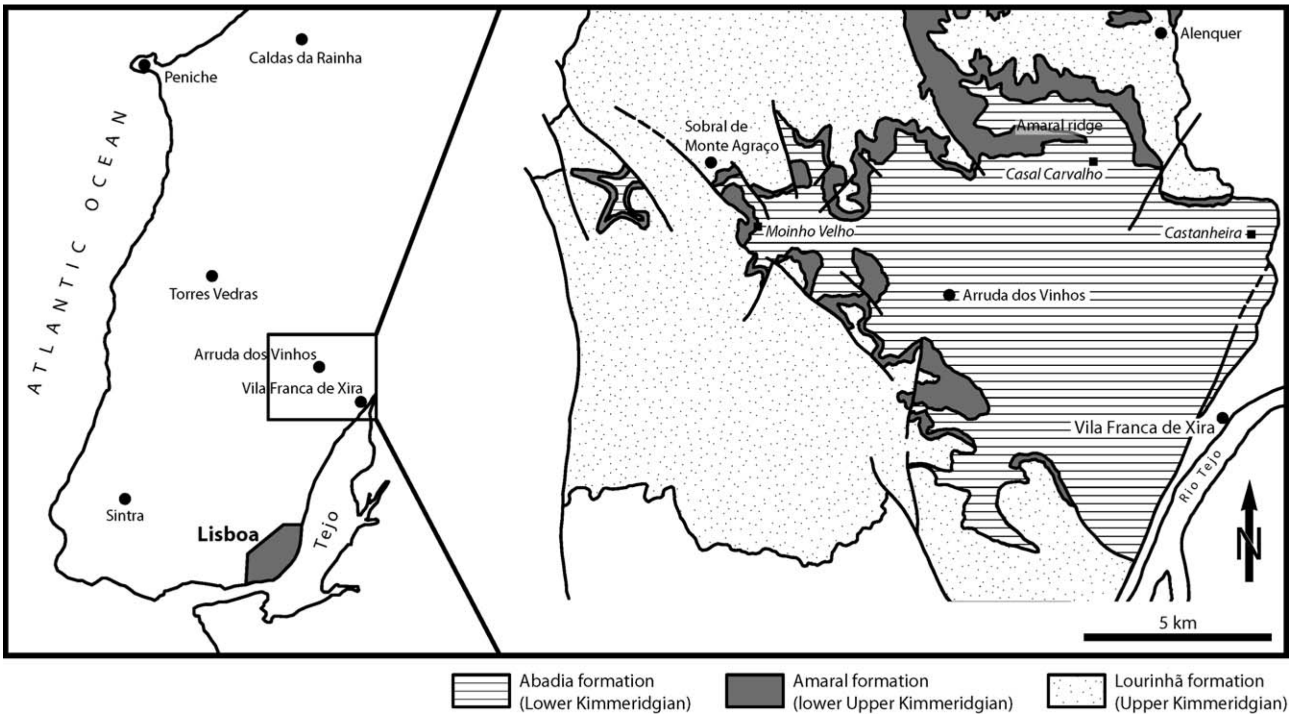

Fig. 1. Map of the central and southern part of the Arruda subbasin; collection sites are marked by black boxes (Moinho Velho, Casal Carvalho, and Castanheira). Modified and simplified after the official geological map 1:50 000, sheet Alenquer (Zbyszewski and Torre de Assunção, 1965).

Fig. 1. Carte géologique simplifiée de la partie centrale et méridionale du bassin d'Arruda ; gisements représentés par des carrés noirs (Moinho Velho, Casal Carvalho, Castanheira). Modifié d'après la carte géologique du Portugal 1 : 50 000, feuille Alenquer (Zbyszewski and Torre de Assunção, 1965).

the polyphyletic nature of some features previously considered to be characteristic and diagnostic for stromatoporoids such as astrorhizae and the possession of a calcareous skeleton. Such structures are now regarded as describing a grade of organisation rather than being of systematic value on a high taxonomic level (e.g. Vacelet, 1985; Wood, 1987; Wood and Reitner, 1986, 1988; Wood, 1991; Reitner, 1992). As a consequence, the validity of the class Sclerospongia has been doubted (e.g. Vacelet, 1985), and, based on similarities in spicule skeletons with non-calcifying Demospongiae and Calcarea, it was proposed that all coralline sponges were placed within the Demospongiae (e.g. Van Soest, 1984). A further complication in the systematics of fossil coralline sponges is the fact that some microstructural features have been identified as diagenetic (e.g. Wendt, 1984). In comprehensive works, R. Wood and J. Reitner critically examined some taxa of the coralline sponges and proposed a classification mainly based on the primary spicule skeleton (Wood and Reitner, 1986; Wood, 1987; Reitner, 1992). Reitner (1992) distinguishes four main types of secondary basal calcareous skeletons (crust, chaetetid, stromatoporoid, and sphinctozoid type) and points again to their convergent character. He (re-)defines the main groups of the Demospongiae according to the types and the presence of microscleres, but stresses the difficulties to classify coralline demosponges if microscleres are absent. It has to be noted that many Mesozoic coralline sponges with spicule pseudomorphs belong to this group (e.g. members of the Axinellida).

The aim of the present paper is to describe a new spiculate coralline sponge from the Upper Jurassic of Portugal and to discuss its microstructure and the possible systematical relationships to other coralline demosponges.

2. Geological framework, localities and material

2.1. Geological setting

The material is from the Upper Jurassic of central Portugal, in the surroundings of Arruda dos Vinhos (Fig. 1). Palaeogeographically, the Upper Jurassic sediments in this area belong to the Arruda subbasin, a half-graben which is part of the Lusitanian Basin (Leinfelder, 1986, 1993, 1994; Leinfelder and Wilson, 1998). An extensive sequence stratigraphic interpretation of the rift-related Upper Jurassic succession in the central Lusitanian Basin is given by Leinfelder and Wilson (1998).

2.2. Stratigraphic succession and facies

The Abadia Formation (Abadia beds; Lower Kimmeridgian; cf. Atrops and Marques, 1986) is widely exposed in the Arruda area (Fig. 1). It consists mainly of fine grained siliciclastics which formed a southwards prograding slope during the time of deposition. The Castanheira Member (?uppermost Lower Kimmeridgian) represents a reef limestone which formed on a submarine fan on the eastern margin of the subbasin (Leinfelder, 1986, 1994; Leinfelder and Wilson, 1998). The Serra Isabel unit is 30–40 m below the succeeding Amaral Formation. This unit is a carbonate-rich condensed interval with thrombolitic bindstones, with local abrupt change from siliceous sponge facies to high-diversity coral associations, and a thickness of up to 10 m; it can be related to a transgressive pulse during the *hypselocyclum* to *divisum* zone (Leinfelder, 1993; Leinfelder et al., 1993; Leinfelder and Wilson, 1998). The Abadia Formation is overlain by the Amaral Formation representing a shallow-water carbonate shelf facies. Two Members, the Corálico and Oólito, can be distinguished. The Amaral Formation is characterised by coral boundstones with abundant microbial crusts, interfingering with and mostly overlain by oolites. Rare ammonites indicate that the Amaral Formation may largely be dated as *acanthicum* zone (cf. Nose, 1995). The Lourinhã Formation (upper Kimmeridgian) consists mainly of red siliciclastics representing fluvial sediments. The Formation begins with the Sobral Member, representing prodelta marls with intercalations of oolitic sandstones and oolitic packstones (Leinfelder, 1986; Leinfelder and Wilson, 1998).

2.3. Localities and material

The first specimen of the new taxon described here was found by one of the authors during field work in 1991 (Schmid, 1992). Additional specimens were found by the authors in 1992. Altogether, five specimens were collected; thus, the genus must be considered as rare compared to other Upper Jurassic coralline sponges.

The material comes from three different localities (Fig. 1).

Moinho Velho: Sample no. CSGP 4217. Slope 175 m southeast of the windmill “Moinho Velho” which is located 1.8 km southeast of Sobral de Monte Agraço and 500 m east of S. Quintino. A fauna containing corals and sponges weathering out from the marly sediments of the uppermost Abadia beds (Lower Kimmeridgian) was collected on a field beneath the steep face of the Moinho Velho plateau which is formed by limestones of the Amaral Formation. This faunal association is characterised by pharetronid sponges, stromatoporoids (e.g. *Dehornella*), and corals such as *Rhipidogyra* or microsolenids; thus, it can be regarded as typical for the uppermost Abadia beds (M. Nose, pers. comm.). It represents a middle-ramp setting (cf. Leinfelder et al., 1996) influenced by fine siliciclastic sediment input. This interpretation is further corroborated by the medium- to low-diverse microencruster association dominated by *Tubiphytes morronensis* and serpulids with some additional elements such as bryozoans (cf. Schmid, 1996; Leinfelder et al., 1994). This setting can be regarded as typical for the new genus described here.

Casal Carvalho: Sample no. BSP 2002 XIV 1. At windmill 100 m south of Casal Carvalho, 700 m southeast of the Amaral ridge. Abadia beds (Lower Kimmeridgian). Fauna dominated by corals and crinoids, resembling the Serra Isabel unit. Several metre-sized isolated limestone blocks with many corals and stromatoporoids, often encrusting, chaetetids, pharetronid sponges and microbial crusts.

Castanheira: Sample nos. BSP 2002 IV 2–4. Castanheira hill, 4.8 km northeast of Vila Franca de Xira. Several stromatoporoids, pharetronid sponges and stromatolitic crusts occur within numerous metre-sized limestone blocks, partly outcropping, partly isolated, which can be found between the top of the hill along the footpaths leading downwards in northwestern direction towards Casais do Burro. The Castanheira reef limestone (?uppermost Lower Kimmeridgian) is stratigraphically equivalent to the Serra Isabel unit.

The material is deposited within the collections of the Instituto Geológico e Mineiro, Lisbon (CSGP) and the Bayerische Staatssammlung für Paläontologie und Geologie, Munich (BSP).

3. Systematic part

Phylum PORIFERA Sollas, 1885.
Class DEMOSPONGIAE Sollas, 1885.
Subclass TETRACTINOMORPHA Lévi, 1953.
Order ?AXINELLIDA Lévi, 1953.
Genus ***Sobralispongia*** nov. gen.
Type species: *Sobralispongia densespiculata* nov. sp.

Derivatio nominis: From the small town Sobral de Monte Agraço, ca. 30 km north of Lisbon, which is situated near the type locality.

Diagnosis: Encrusting ?axinellid sponge with spicule skeleton dominated by styles and subtylostyles in a very dense plumose arrangement, with transverse spicule elements, ?aster-pseudomorphs may be present in certain areas; interspace between spicule columns tube-like; calcareous skeleton with microgranular or fibrous calcite, weakly developed due to the high density of spicule skeleton; primary mineralogy of calcareous skeleton probably high-Mg calcitic.

Sobralispongia densespiculata nov. gen. nov. sp.

Type specimens: Holotype (CSGP 4217) of Moinho Velho near Sobral de Monte Agraço, Central Portugal; paratypes: specimen BSP 2002 IV 2-4 of Castanheira and BSP 2002 IV 1 of Casal do Carvalho, all from the uppermost part of the Abadia Formation (?uppermost Lower Kimmeridgian).

Derivatio nominis: From densus (lat.) = dense, and spiculum (lat.) = small spine, referring to the extremely dense spicule skeleton.

Diagnosis: As for the genus.

Description: The holotype (CSGP 4217) is part of a complex facies sample consisting of different encrusting organisms (e.g. some pharetronids, corals, serpulids, *Tubiphytes morronensis*, bryozoans, and microbialite). *S. densespiculata* forms up to 7 mm thick crusts within and on the top of the specimen and covers nearly its whole surface (ca. 10 × 12 cm). The beautifully preserved sponge surface exhibits an irregular, meandroid calicle pattern with intercalated singular circular calicles (Fig. 2a, b). The thickness of the walls as well as the furrows in-between varies between 0.2 and 0.5 mm (mean value 0.3 mm for walls, 0.4 mm for furrows). The depth of the furrows is normally 0.4–0.5 mm.

In thin-section, vertical (= in growth direction) columns of spicule tufts alternate laterally with slightly darker tube-

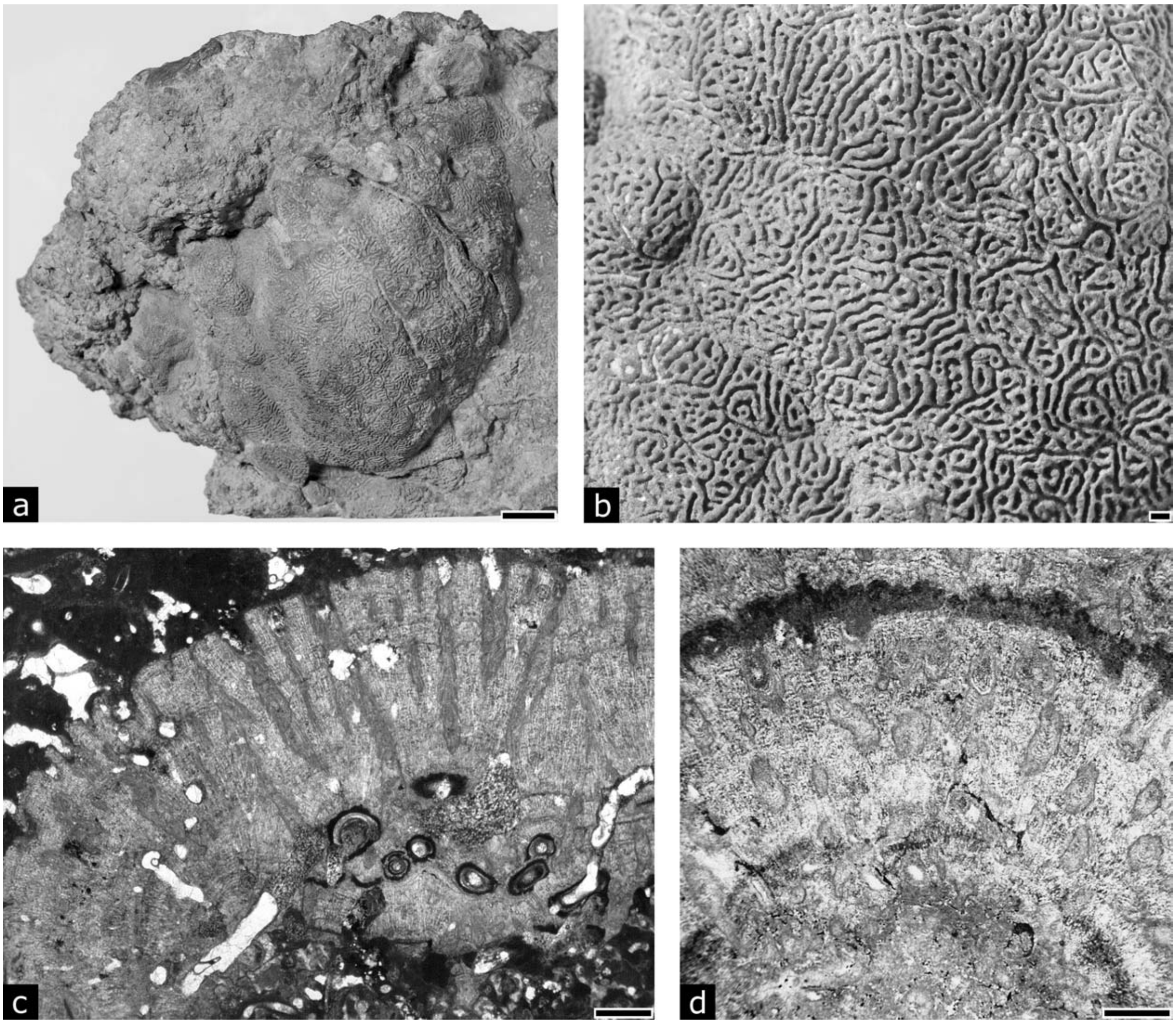

Fig. 2. *Sobralispongia densespiculata* nov. gen. and nov. sp.; holotype CSGP 4217. **a,** surface view on the central dome-shaped part; scale 10 mm. **b,** detail of figure 2a showing the meandroid and circular calicle pattern; scale 1 mm. **c,** longitudinal section with vertical spicule columns laterally alternating with darker tube-like interspaces; scale 1 mm. **d,** oblique section with distribution of darker tube-like interspaces within the skeleton; note the micritic rim in upper part indicating a growth interruption; scale 1 mm.

Fig. 2. *Sobralispongia densespiculata* nov. gen. et nov. sp. ; holotype CSGP 4217. **a,** vue supérieure de la partie centrale en forme de coupole ; échelle 10 mm. **b,** detail de la surface montrant l'arrangement méandroide et circulaire des tubes ; échelle 1 mm. **c,** section longitudinale avec piliers spiculaires verticaux alternants latéralement avec des espaces en forme tube (zones sombres) ; échelle 1 mm. **d,** section oblique montrant la distribution des espaces à forme tubulaire (zones sombres) dans le squelette ; à noter la zone micritique sombre dans la partie supérieure reflètant une interruption de croissance ; échelle 1 mm.

like interspaces (Figs. 2c, d and 3b). The spicules within the columns are densely packed and subparallel to slightly divergent, showing a plumose pattern sensu Reitner (1992) and Wood (1987). Spicules protrude into the tube-like interspaces generally with a larger angle (Fig. 3a, b). The spicules in the tufts are styles and subtylostyles. Some few spicules seem to have lateral spiny processes at the distal parts (Fig. 3g) which suggest an acanthostyle type. Despite the relatively similar form of these processes in all of these spicules, it cannot be excluded with certainty that super-imposed spicules may have caused this image in thin-section.

The spicule form is straight, slightly curved or, more rarely, undulating. Their length reaches generally 400 to 500 µm (maximum value 800 µm), the diameter varies between 15 and 30 µm. Apart from the general vertical direction, there are also some transversally oriented spicules of the same diameter as the vertical styles (Fig. 3b). Neighbouring spicules may be connected by horizontal elements which exhibit the same state of preservation like the spicules and are therefore considered as spicules (Fig. 3d). Ring-like elements of calcite with a micritic rim surrounding vertical styles also occur rarely (Fig. 3f). Besides the vertical and transversal monaxones, an accumulation of spherulitic spicules of 50 µm diameter may occur. The spherules differ in preservation from the styles by a slightly clearer calcite. This peculiar spicule type and its occurrence within the crust are better seen in specimen BSP 2002 IV 4 (see description below and Fig. 4).

The columns of spicule tufts may be bordered by a micritic rim which defines the limit between columns and interspaces (Fig. 3a–d, f). Its irregular, undulating form in longitudinal section points to a knobbly-like column surface. Fine convex micrite layers within columns indicate phases of growth

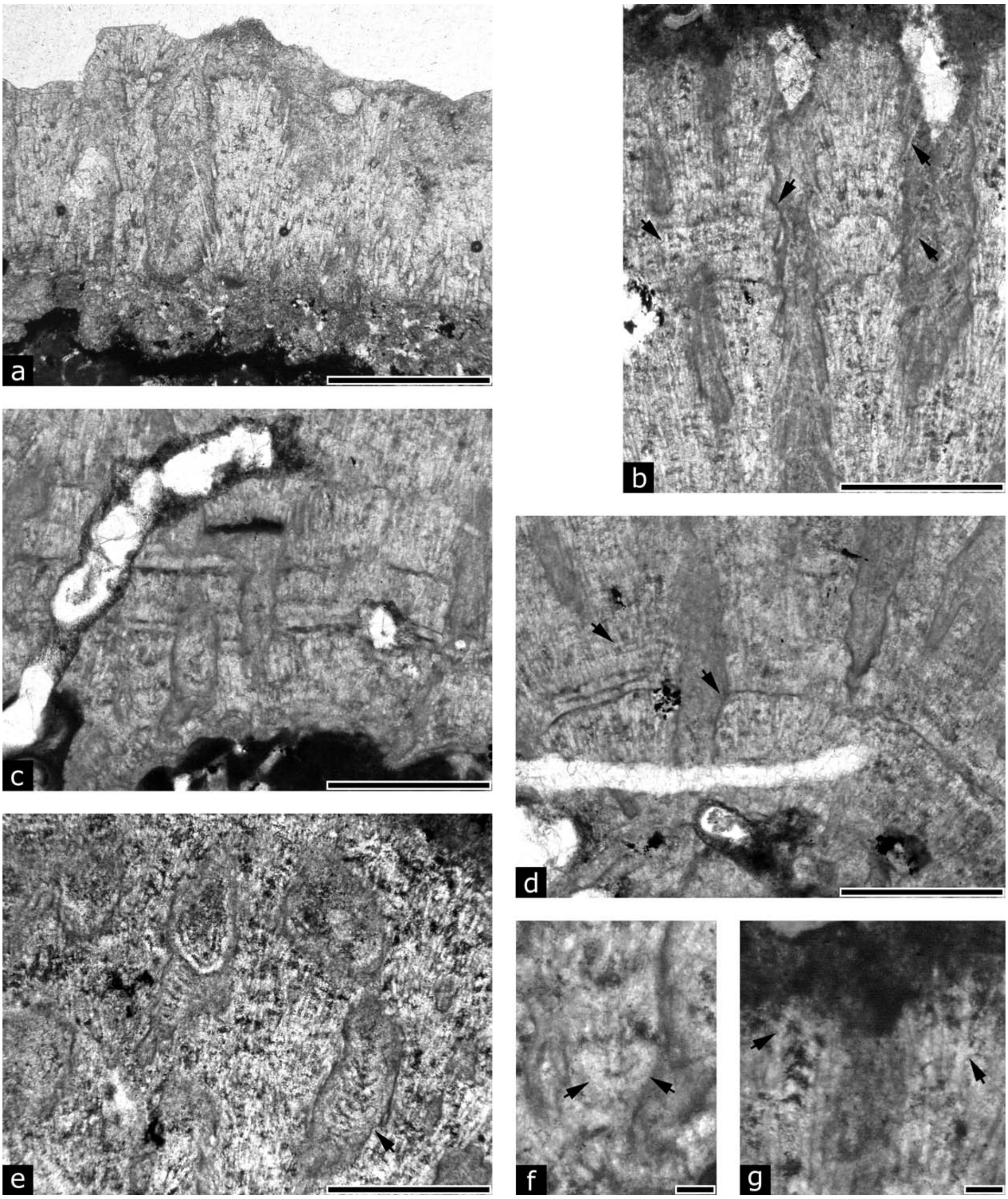

Fig. 3. *Sobralispongia densespiculata* nov. gen. and nov. sp.; holotype CSGP 4217. **a,** longitudinal section showing spicule columns with styles and subtylostyles, and tube-like interspaces; scale 1 mm. **b,** detail of densely packed spicule columns and interspaces; note the micritic rim (arrow in the mid part) bordering the spicule columns and indicating a knobby lateral surface of the columns; spicules within columns subparallel to slightly divergent, spicules protude with a larger angle into interspaces (right arrows); note also transverse spicules (left arrow); scale 1 mm. **c,** longitudinal section, horizontal micritic layers indicate growth stages of the calcareous skeleton; note convex micritic growth lines in single columns at the base of the crust; scale 1 mm. **d,** longitudinal thin-section; detail with micrite growth layers persistent across some neighbouring columns; note micrite layers proceeding along the edge of the columns down into the tubes reflecting the calcification surface and limit between living sponge and calcareous skeleton; scale 1 mm. **e,** oblique section, detail of figure 2d; note the tabulae of calcite with micrite rim filling the tube-like interspaces (arrow); scale 1 mm. **f,** longitudinal section with spicule tuft besides a tube at the right; note the ring structure sourrounding a vertical style (arrows); scale 100 µm. **g,** longitudinal section with acanthostyle-like spicules; scale 100 µm.

Fig. 3. *Sobralispongia densespiculata* nov. gen. et nov. sp.; holotype CSGP 4217. **a,** section longitudinale avec piliers spiculaires constituée de styles et de subtylostyles. Tubes entre les piliers de couleur sombre ; scale 1 mm. **b,** detail des piliers à spicules très denses ; le liseré micritique qui borde les piliers est bien visible (flèche au centre). Les bordures ondulantes reflètent la surface noduleuse des piliers ; spicules dans les piliers subparalleles à peu divergents ; spicules

and/or calcification of the calcareous basal skeleton (Fig. 3c, d). The growth of columns took place only in vertical direction (Fig. 5). A lateral growth by lateral accretion of spicule tufts of the single columns is of minor importance. Such micrite layers may be persistent across several neighbouring columns (Fig. 3c, d). However, they do not cross the tubes at the same horizon but proceed along the edge of the columns down into the tubes. This clearly mirrors the surface of the calcareous skeleton at the moment of calcification and indicates that calcification of the skeleton followed the actual morphology of the lower surface of the living sponge.

Due to the very dense spicule skeleton, the calcareous basal skeleton is underdeveloped. No specific microstructure can be observed in transmittent and polarised light as it is known from other coralline sponges (e.g. spherulitic, fibrous, orthogonal, clinogonal; cf. Wendt, 1984; Wood, 1987). Even in regions of slightly lower spicule density and therefore more interspicule space, only microgranular calcite can be observed. The tube-like interspaces are also filled by microgranular calcite. Occasionally, they show tabulae-like structures consisting of clear transverse calcite elements delimited by micritic rims. These elements probably represent mineralised remains of former organogenous/collagenous tabulae (Reitner, 1992). In transverse section, the tube structures exhibit an outer zone of diffuse calcite and a fine micritic inner part which probably corresponds to the micritic rim bordering the spicule columns (Fig. 2d; cf. Fig. 4f).

Despite the absence of a definite microstructure of the calcareous skeleton, the preservation as microgranular calcite differs markedly from the neomorphic preservation of the former aragonitic scleractinian remains in the same sample. This points to an originally high-Mg calcitic calcareous skeleton of *Sobralispongia* rather than an aragonitic one. Some spicule pseudomorphs contain framboidal pyrite spherules (cf. Dieci et al., 1977; Kazmierczak, 1979; Wendt, 1984; Wood and Reitner, 1986; Wood, 1987), indicating a primary siliceous mineralogy of the spicules (Reitner, 1992: 55).

The other four specimens which are enclosed here within *S. densespiculata* generally share with the holotype the main characters such as the type and dimensions of the spicule skeleton, encrusting habit, surface pattern and microstructure of the calcareous skeleton. However, they differ in some details.

Specimen BSP 2002 IV 4 is a 3–5 mm thick crust of densely packed spicules (cf. Fig. 4e) on microbialite, coral fragments, serpulids and other encrusting organisms (Fig. 4a, b). Diameter (20–30 µm) and length (400 µm) of the vertical spicules are within the variation range of the spicules of the holotype. In transverse section, the tube-like structures consist of a darker micritic centre surrounded by a microgranular calcitic envelope (Fig. 4f). In addition to the vertical megascleres, spherical spicules of 50 µm mean diameter occur. In transmittent light, their form is round to slightly oval. These spicules are arranged in layers or globular concentrations above the vertical spicules, rarely also in basal parts of the *Sobralispongia*-crusts below a vertical spicule crust generation (Fig. 4b). Spherical and vertical spicules are generally separated by fine micritic layers indicating probably interruption of growth, but a continuous transition from vertical subtylostyles to adjacent spherules is also observed (Fig. 4c). It is remarkable that spherules which are situated directly above the megasclere skeleton are concentrated above the columns and rarely above the tubes (Fig. 4c, d). Tangential sections at the top of the colony clearly show that the spherical spicules are part of the *Sobralispongia* crust and do not belong to a different encrusting sponge species (Fig. 4g). The poor preservation does not allow an exact identification of the scleres. The generally rounded globular form excludes kidney-formed rhaxae. Rare spiny and irregular processes may indicate an aster-pseudomorph.

In surface view of the uppermost part of the crust, the superficially visible walls with embedded microscleres spicules are brownish calcitic whereas inter-wall spaces show distal sections of vertical styles within a milky-coloured calcitic matrix. A contrary impression is offered by a peel of the same tangential section. Here, the walls with microscleres are light coloured. In contrast, areas with the transverse crossed styles are slightly darker coloured (Fig. 4g).

Specimens BSP 2002 IV 2 and 3 from Castanheira with a 2.5 mm thick crust have a less pronounced meandroid surface pattern with more closed calicles (Fig. 6a), but exhibit generally the same microscopic structures with plumose arrangement of the monaxones (Fig. 6b, c). Diameter of the styles varies between 15 and 30 µm, the maximum length is 750 µm. In transverse section, the tube-like structures consist of a darker micritic centre surrounded by a fine calcitic envelope with a very fine radial ?fibrous structure. This is in contrast to the holotype which exhibits a microgranular microstructure.

The small specimen BSP 2002 IV 1 (diameter 3.3 cm) exhibits a slightly different surface pattern with discontinuous meandering walls. In thin-section, it shows the extreme densely arranged spicules exceptionally well (Fig. 6d). Furthermore, some spicules weathering out at the edge of the sample exhibit a smooth surface and clearly point to a style type rather than to an acanthostyle nature of the spicules. Diameter of the subtylostyles is 20–50 µm (maximum value at the proximal part), their length is about 500 µm (maximum

progressant dans l'espace à l'angle plus grand (flèche à droite) ; voir spicules transversaux (flèche à gauche) ; échelle 1 mm. **c**. section longitudinale avec horizons micritiques (flèches) indiquants des lignes de croissance du squelette calcaire ; à noter la convexité des lignes de croissance à la base des piliers ; échelle 1 mm. **d,** section longitudinale, détail avec lignes de croissance en micrite commune à plusieurs piliers adjacents ; à noter les lignes de micrite visibles le long des piliers et dans les tubes qui soulignent la surface de calcification ; échelle 1 mm. **e,** section oblique, détail de la Fig. 2d ; les tubes sont séparés par des tabulae préservées en calcite avec bordures micritiques (flèche) ; échelle 1 mm. **f,** section longitudinale avec faisceaux de spicules et un tube (à droite) ; à noter l'anneau en calcite entourant un style vertical (flèches) ; échelle 100 µm. **g,** section longitudinale avec mégasclères évoquant le type acanthostyle ; échelle 100 µm.

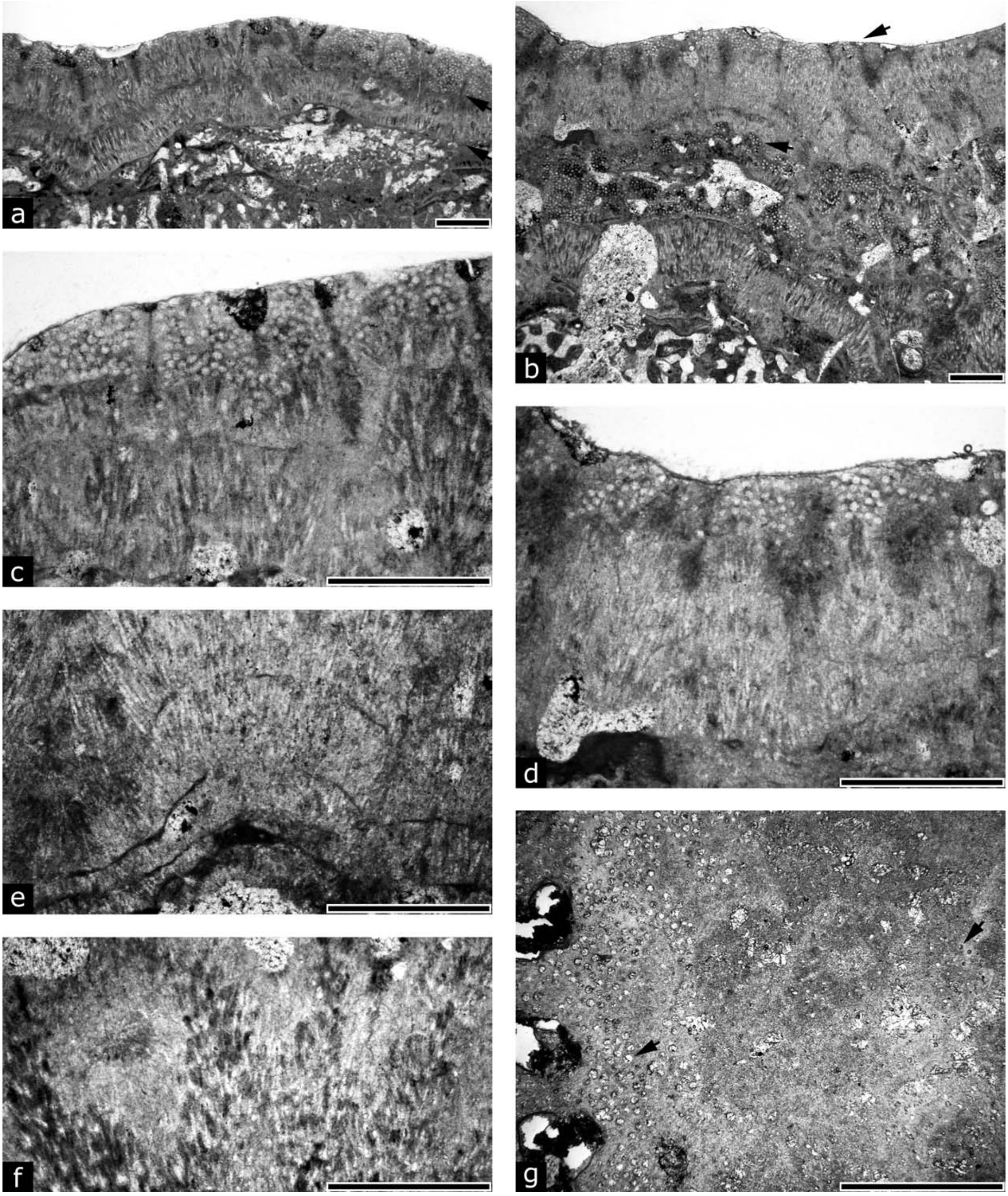

Fig. 4. *Sobralispongia densespiculata* nov. gen. and nov. sp., BSP 2004 IV 4; scale in all figures 1 mm. **a,** longitudinal thin-section BSP 2004 IV 4d; overview showing irregular base and inhomogeneity of growth in middle part of the crust; substrate in the lower part is a coral. **b,** longitudinal thin-section BSP 2004 IV 4 e, with layers of microscleres (?aster-pseudomorphs) at the base (lower arrow) and the top (upper arrow) of the megasclere spicule skeleton; tube-like interspaces darker; below base: coral colony. **c,** longitudinal thin-section BSP 2003 IV 4d; skeleton of monaxone spicules overlain by a layer of densely packed microscleres (?aster-pseudomorphs); note the continous transition between both spicule areas in the mid part of the figure, and a separation by a micritic layer in the left part. **d,** longitudinal thin-section BSP 2004 IV 4e; microscleres are mainly restricted to the top of the spicule columns which correspond to the walls on the sponge surface; darker areas are tube-interspaces. **e,** longitudinal thin-section BSP 2004 IV 4 e, with densely packed styles and micrite growth layers. **f,** oblique thin-section with transverse tube in the left; outer zone of tube with microgranular calcite, inner part micritic. **g,** transverse section of the uppermost part of the crust, peel BSP 2002 IV 4f; in the left part: light zone with microscleres (left arrow) corresponding to the superficially visible wall, darker areas with transverse sections of upper parts of vertical styles (right arrow).

Fig. 4. *Sobralispongia densespiculata* nov. gen et nov. sp., BSP 2004 IV 4 ; échelles 1 mm. **a,** section longitudinale, plaque mince BSP 2004 IV 4d ; vue d'ensemble du corps de l'éponge encroûtante avec base irrégulière et irrégularité de croissance dans sa partie médiane ; subtrat : corail. **b,** section longitudinale,

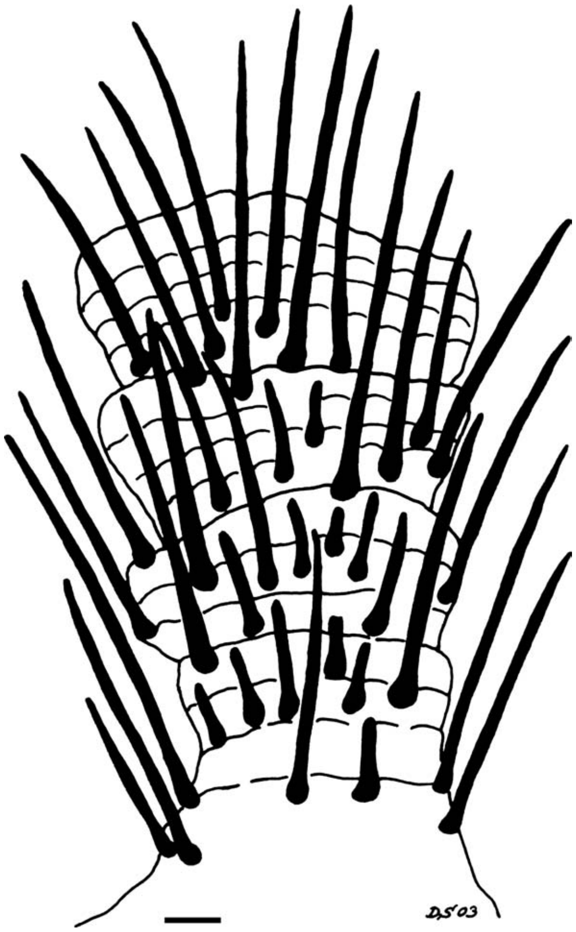

Fig. 5. Schematic view of a spicule column with subtylostyles. Micritic growth layers indicate an exclusively vertical growth of the calcareous skeleton; scale 100 μm.
Fig. 5. Représentation schématique d'un pilié constitué de faisceaux spiculaires à subtylostyles. Les lignes de croissance en micrite indiquent une croissance exclusivement verticale du squelette calcaire ; échelle 100 μm.

value 800 μm). Very well-developed are transverse elements consisting of 15–20 μm thick layers of clear calcite alternating with intercalated 20–25 μm thick micritic layers. Together with the radial spicule skeleton, these transverse layers form a net-like pattern (Fig. 6e, f).

The five specimens from the Kimmeridgian of Portugal display the same main features such as crustose habit, spicule type, spicule dimension, and density of spicules. They are therefore regarded as conspecific. Differences concern the presence of possibly aster-pseudomorphs which are observed in the holotype specimen and in specimen BSP 2002 IV 4. The specific occurrence of the spherulitic scleres which are restricted to zones above or below the areas of the normal vertical styles may explain the absence in the other specimens where such areas are not preserved or not positioned within the thin-section plane.

The calcareous skeleton exhibits the same microgranular calcitic microstructure in all specimens. Only in specimen BSP 2002 IV 2, the tube fillings show a very fine radial fibrous structure in transverse section.

There are differences in the surface pattern reaching from meandering or discontinuous meandering to the dominance of circular calicles. According to Reitner (1992) and Wood (1987), the development and structure of the calcareous skeleton is of generally low importance for the higher systematics and have only a functional character. The differences in the surface pattern may therefore be interpreted as ecophenotypic variation of one species rather than reflecting differences at species level. However, judging from the geological and palaeontological data of the localities where the specimens come from, it is not possible to conclude which ecological parameters may have caused the different surface morphologies. As far as we know, all specimens are associated with corals, pharetronid sponges, *Tubiphytes morronensis*, and other encrusting organisms and lived in similar environments.

4. Discussion and comparison with other genera

The definition of the genera and species of coralline demosponges is based on the features of the spicules and the calcareous skeleton. Most attention is focussed on the type and arrangement of spicules which are regarded as valuable features to separate taxa at genus and also at higher level. The features of the calcareous skeleton such as microstructure, inner organisation or primary mineralogy are considered to be of minor importance due to their convergent character but are used in combination with the spicule features to define genera and species (cf. Wood, 1987: Fig. 8). Comparing the Portuguese material with existing coralline sponge genera and species, we found some taxa which are similar in some aspects but do not share all the features with *S. densespiculata*.

Meandripetra zardinii from the Upper Triassic of the Southern Alps is very similar in outline and surface morphology. The genus and species was first described by Dieci et al. (1977) and included there within the family Ceratoporel-

plaque mince BSP 2004 IV 4 e, avec zones à microsclères (?aster-pseudomorphes) à la base (flèche au milieu) et au sommet (flèche au sommet) du squelette à mégasclères ; à noter la couleur sombre des tubes verticaux entre les faisceaux spiculaires ; subtrat : corail. **c,** section longitudinale, plaque mince BSP 2004 IV 4d ; squelette de monaxones recouvert de microsclères (?aster-pseudomorphes) très dense ; à noter la transition graduelle de la zone à monaxones à la zone à microsclères dans la partie médiane ; à gauche : séparation des deux zones par une mince couche de micrite. **d,** section longitudinale, plaque mince BSP 2004 IV 4e ; les microsclères sont restreints au sommet des piliers spiculaires qui correspondent ici au parois visibles à la surface de l'éponge ; les zones sombres correspondent aux tubes. **e,** section longitudinale, plaque mince BSP 2004 IV 4 e, avec styles très denses et lignes micritiques de croissance du squelette calcaire. **f,** section oblique, plaque mince BSP 2004 IV 4 e, avec section transversale d'un tube (à gauche) ; zone extérieure du tube en calcite microgranulaire, zone interne en micrite. **g,** section transversale de la partie sommitale du corps de l'éponge, peel BSP 2002 IV 4f ; à gauche : zone claire avec microsclères (flèche à gauche) correspondant aux parois visibles à la surface de l'éponge ; zone sombres avec sections transversales des mégasclères verticaux (flèche à droite).

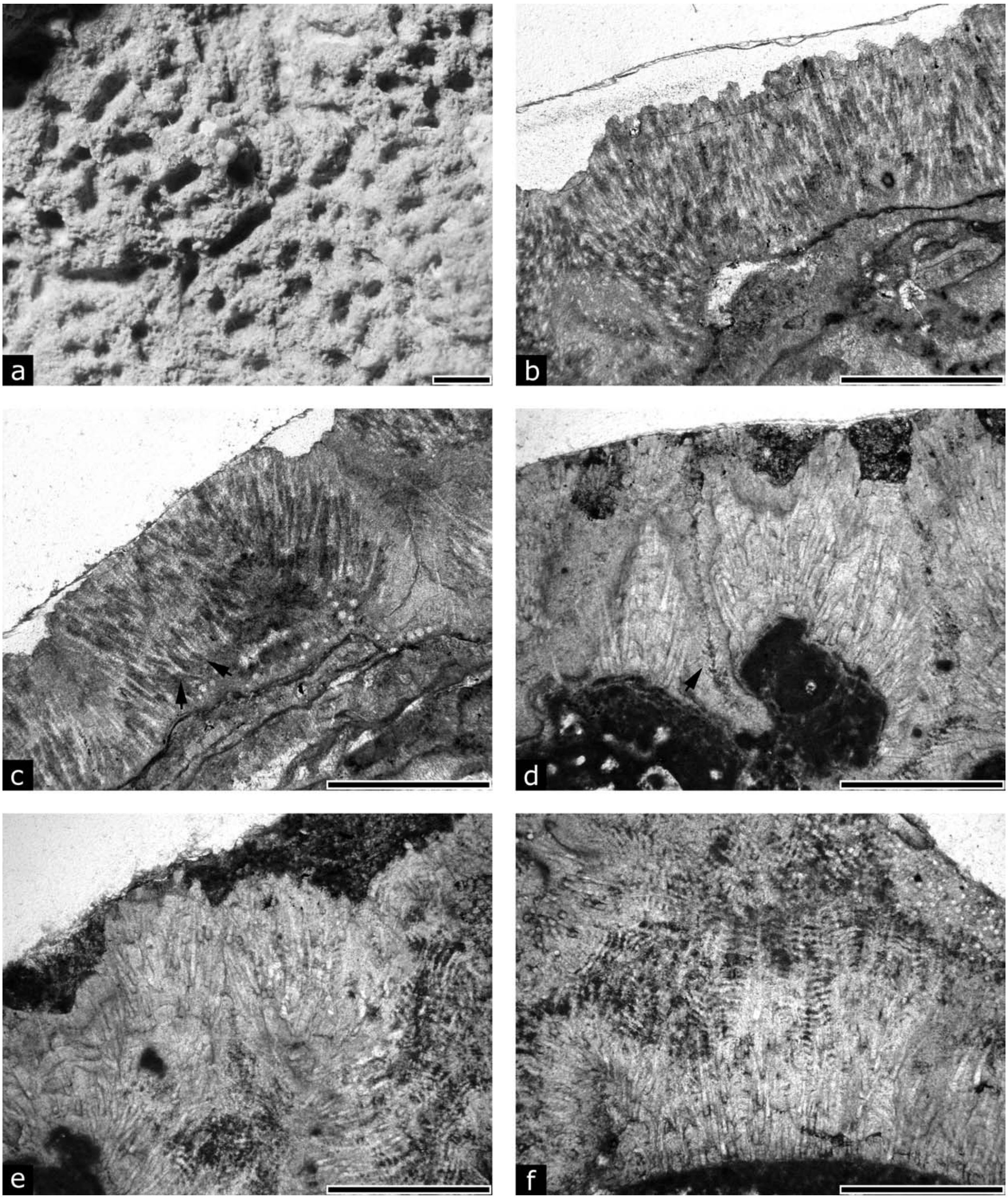

Fig. 6. *Sobralispongia densespiculata* nov. gen. and nov. sp.; all scales 1 mm. **a,** surface view of specimen BSP 2002 IV 3 with dominantly circular calicles; note densely packed spicules in the walls visible in tangential section as small points. **b,** longitudinal thin-section, BSP 2004 IV 2 d, with transversely crossed tube in the left; note the microgranular filling of the tube with an inner micritic part. **c**. longitudinal thin-section, BSP 2004 IV 2 d, with plumose structure of single spicule tufts (arrows). **d,** longitudinal section, BSP 2004 IV 1b, with densely packed spicule tufts; areas between spicule tufts filled with diagenetically orthogonal calcite (secondary calcite skeleton) (arrow). **e,** longitudinal section, BSP 2004 IV 1b; dense spicule skeleton with convex growth layers in single columns (arrow); in the right: former transverse organogenous tabulae preserved with clear calcite rimmed by micrite. **f,** same thin-section as figure 6e; transverse calcitic elements of former organogenous tabulae build a net-like structure together with the spicule skeleton.

Fig. 6. *Sobralispongia densespiculata* nov. gen. et nov. sp. ; échelles 1 mm. **a,** vue supérieure du spécimen BSP 2002 IV 3 dominée par des tubes circulaires ; à noter la grande densité des spicules dans les parois, visibles comme des points en section transversale. **b,** section longitudinale, plaque mince BSP 2004 IV 2b ; avec tube en section transversale (à gauche) ; à noter le remplissage microgranulaire et, au centre, micritique du tube. **c,** section longitudinale, plaque mince BSP 2004 IV 2b, avec structure plumeuse des faiseaux spiculaires (flèches). **d,** section longitudinale, plaque mince BSP 2004 IV 1b, avec faisceaux spiculaires très dense ; zones entre les faisceaux remplies par de la calcite orthogonale diagénétique (correspondant au squelette calcaire secondaire) (flèche). **e,** section

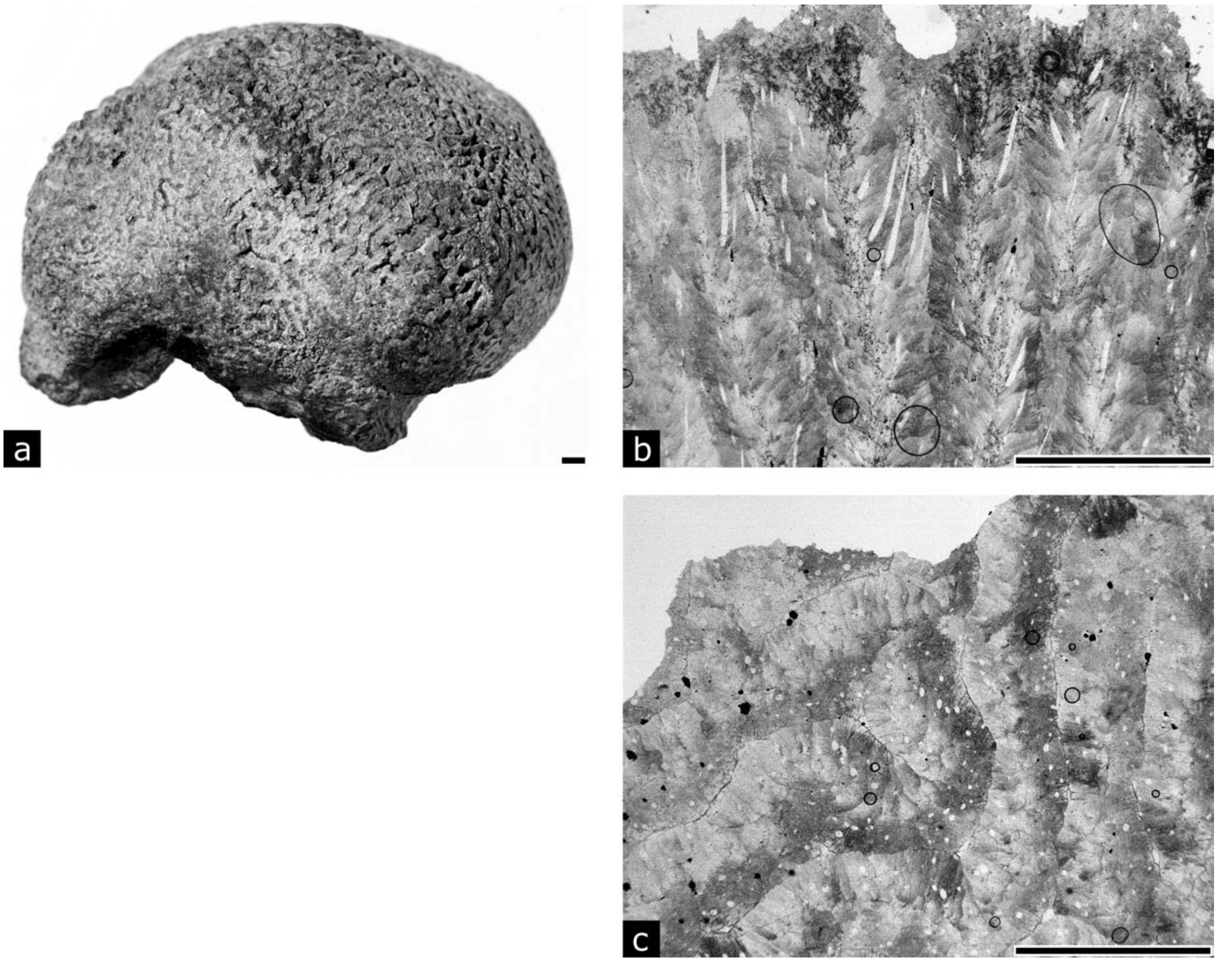

Fig. 7. *Meandripetra zardinii* Dieci et al. (1977), Cassian Formation, Upper Triassic. coll. Zardini Univ. Modena; scales 1 mm. **a**, surface view, holotype, no. 19094, showing meandroid calicle pattern of the calcareous skeleton very similar to *Sobralispongia*. **b**, longitudinal thin-section, paratype no. 19095 with plumose arrangement of styles. Note the clinogonal structure of the calcareous skeleton. **c**, transverse section, paratype, no. 19095; note the less developed density of styles compared with *Sobralispongia*.

Fig. 7. *Meandripetra zardinii* Dieci et al. (1977), Cassian Formation, Trias supérieur, coll. Zardini Univ. Modena ; échelle 1 mm. **a**, vue latérale de la surface, holotype n° 19094, voir l'arrangement de tubes méandroïde du squelette calcaire ressemblant à ceux de *Sobralispongia*. **b**, section longitudinale, plaque mince, paratype n° 19095, avec styles arrangés en forme plumeuse ; à noter la structure clinogonale du squelette calcaire. **c**. section transversale, paratype, n° 19095, à noter la densité des styles moins importante que chez *Sobralispongia*.

lidae. Particularly, *Meandripetra* has a similar meandroid surface pattern (Fig. 7a). However, this feature is of minor importance for the taxonomy as Dieci et al. (1977) already stated. They mention a similar pattern in *Blastochaetetes* which is a true chaetetid. Reitner (1992) and Wood (1987) also consider this character as convergent within stromatoporoid sponges. Microscopically, *Meandripetra* has similar monaxon spicules (styles) with comparable dimensions (Fig. 7b, cf. Table 1), but the density is less well-developed (Fig. 7b, c). As the original paper of Dieci et al. (1977) does not present thin-section figures, these features of the type material are reproduced here for comparison. Spherulitic microscleres like in *Sobralispongia* are not present in the thin-sections of the type material (no. 19094 and 19095, coll. Zardini, Univ. Modena), and tube-like interspaces are also absent. *Meandripetra* differs from *Sobralispongia* in having a penicillate (sensu Dieci et al., 1977; = clinogonal sensu Wendt, 1984) calcareous skeleton. The original mineralogy of the basal skeleton of *Meandripetra* is aragonite, that of *Sobralispongia* probably calcite which – apart from other differences – may point to a separation of both taxa. However, the relevance of mineralogy for taxonomy remains controversial. Reitner (1992) proposed a continuing existence of the genus *Murania* from the Triassic to the Cretaceous which implies that the genus had changed its mineralogy from aragonite (Triassic) to Mg-calcite (Jurassic-Cretaceous) according to the Sandberg cycles (Sandberg, 1983; see also Cuif and Gautret, 1991).

longitudinale, plaque mince BSP 2004 IV 1b ; squelette spiculaire dense avec lignes de croissance convexes dans quelques piliers (flèche) ; à droite : des tabulae d'origine organogène préservées en calcite claire avec bord micritique. **f,** idem ; les éléments transversaux en calcite reflètant des tabulae d'origine organogène forment, avec le squelette spiculaire, une structure réticulée.

Table 1
Characteristics of *Sobralispongia* specimens and two close axinellid genera, *Murania* and *Meandripetra*. Data and measurements for *Murania* from Reitner (1992); data and measurements for *Meandripetra* from Dieci et al. (1977) and own observations of the type material
Caractères des spécimens de *Sobralispongia* en comparaison avec ceux des deux genres axinellides voisins *Murania* et *Meandripetra*. Caractères et dimensions de *Murania* d'après Reitner (1992), ceux de *Meandripetra* d'après Dieci et al. (1977) et des observations personnelles du matériel type

	S. densespiculata				***Murania***	***Meandripetra zardinii***
	holotype (CSGP 4217)	2002 IV 2	2002 IV 1	2002 IV 4	(several species)	
Morphology/life habit	encrusting	encrusting	encrusting	encrusting	encrusting	encrusting
Surface pattern	meandroid calicles, rarely circular	circular calicles, rarely meandroid	discontinuous meandroid, rarely circular calicles	circular calicles, rarely meandroid	not described	meandroid calicles, rarely circular
Dimension of surface structures (WT wall thickness; FW width of furrows)	WT 0.30 mm (var. 0.20–0.50 mm); FW 0.40 mm (var. 0.30–0.50 mm)	WT 0.30 mm (var. 0.20–0.60 mm); FW 0.30 mm (var. 0.25–0.40 mm)	WT 0.35 mm (var. 0.25–0.40 mm); FW 0.25 mm (var. 0.15–0.25 mm)	WT 0.35 mm (var. 0.30–0.50 mm); FW 0.35 mm (var. 0.25–0.50 mm)	not described	WT 0.30–0.45 mm; FW 0.15–0.25 mm
Calcareous skeleton	spicule columns and tube-like structures	spicule columns and tube-like structures	spicule columns and tube-like structures	spicule columns and tube-like structures	spicule columns	spicule columns
Diameter of spicule columns	0.30–0.40 mm	0.20–0.40 mm	0.20–0.30 mm	0.40–0.90 mm	0.30 mm (var. 0.25–0.50 mm)	0.30 mm
Diameter of tube-like structures	0.45 mm (var. 0.15–0.60 mm)	0.50–0.60 mm (min. 0.20 mm)	0.30–0.30 mm	0.40 mm (var. 0.30–0.50 mm)	no tube-like interspace described	no tube-like interspace described
Structure of primary calcareous skeleton	microgranular	microgranular, fibrous	microgranular	microgranular, fibrous	fascicular/fibrous; partly orthogonal	penicillate = clinogonal
Megascleres	styles, subtylostyles	styles, subtylostyles	styles, subtylostyles	styles, subtylostyles	styles, subtylostyles	styles
Spicule length	maximum 800 µm	400–500 µm, maximum 750 µm	maximum 800 µm	400 µm, max 800 µm	150–220 µm (holotype), large species up to 1.1 mm	170–660 µm
Spicule diameter	15–20 µm	15–30 µm	20–50 µm	20–30 µm	30 µm (holotype), further species: var. 20–80 µm	20–35 µm
Spicule arrangement	plumose	plumose	plumose	plumose	plumose	plumose
Density of spicules	high	high	high	high	medium	low to medium
Microscleres	present, ?aster-pseudomorphs 40–50 µm	absent	absent	present, ?aster-pseudomorphs 40–50 µm	not described	absent
Mineralogy of calcareous skeleton	probably calcite	probably calcite	probably calcite	probably calcite	calcite or aragonite	aragonite

Murania Kazmierczak, 1974, first described from the Lower Cretaceous of Poland, differs from *Sobralispongia* by its closely spaced columns with irregular polygonal cross-sections. Like in *Sobralispongia*, styles and subtylostyles of variable dimensions (Table 1) dominate the spicule skeleton, but in the type species *M. lefeldi* and other *Murania* species (cf. Reitner, 1992) the spicules are restricted to the axial zone of the columns. The primary calcareous skeleton is formed by clinogonal or orthogonal calcite in contrast to *Sobralispongia* where microgranular and, rarely, fibrous structures occur. The short, delicate calcareous processes as described by Kazmierczak (1974) from the upper surface are not present in the Portuguese specimens. In contrast to the Portuguese material, no tubes with tabulae have been described in *Murania*. Main differences consist in the presence of the aster-like microscleres, transverse spicule elements and ring-like structures around radial monaxones in *Sobralispongia*. *Sobralispongia* apparently has a more complex skeleton than *Murania*.

The hadromerid genus *Pachytheca* from the Devonian has similar radial tylostyle megascleres, but the tufts typically consist of few (five to six) spicules. In contrast to the other Hadromerida, no microscleres are known (Reitner, 1992). The calcareous skeleton displays a ceratoporellid (= chaetetid) architecture and differs clearly in this feature from *Sobralispongia*.

Within the Hadromerida, the genus *Calcisuberites* Reitner and Schlagintweit, 1990 from the Albian of Austria exhibits a similar tylostyle spicule skeleton, but is characterised by two different spicule sizes in the basal and, respectively, the uppermost part of the skeleton. The tylostyles are subradially arranged in small tufts of four to five spicules. The genus has a stromatoporoid-like calcareous skeleton (Reitner and Schlagintweit, 1990; Reitner, 1992). Microscleres are not mentioned.

The genus *Euzkadiella* Reitner, 1987 from the Cretaceous has a more complex architecture in having a plumose spicule skeleton of relatively large subtylostyles and oxes as well as transversely arranged smaller strongyle spicules which, together, form a reticulate pattern (Reitner, 1987, 1992). In contrast, the transverse elements of *Sobralispongia* consist of ?styles with the same size as the radial ones which connect single spicules only. A reticulate pattern as in *Euzkadiella* or its relative *Newellia* from the Carboniferous (Wood et al., 1989) as well as a stromatoporoid architecture with astrorhizae is not developed in *Sobralispongia*. According to Reitner (1992), *Euzkadiella* bears a spherulitic calcareous skeleton, thus also differing in this feature from *Sobralispongia*.

Dehornella Lecompte, 1952, possesses a densely packed plumose spicule skeleton from which spicules may project into the interskeletal space like in *Sobralispongia*. Both genera have irregular occurring tabulae within the tube-like interskeletal space which are enveloped by micritic rims and are interpreted as rests of previously organic tabulae (Reitner, 1992: 188). However, the type and the dimensions of the spicules as given by Wood (1987); Reitner (1992); Hudson (1960) for *Dehornella* clearly differ from the larger spicules in *Sobralispongia*. *Dehornella* has astrorhizae which are absent in *Sobralispongia*. Additionally, ?aster-like microscleres of *Sobralispongia* are not reported from *Dehornella*.

There is a large number of Portuguese coralline sponges which have been previously described from the Jurassic of Portugal by Dehorne (1917, 1920, 1922); Rosendahl (1985) and Termier et al. (1985a, 1985b). However, most of these taxa are stromatoporoids with astrorhizae (e.g. *Dehornella*, *Shuqraia*, *Actinostromaria*) or have a chaetetid architecture (e.g. *Blastochaetetes*, *Chaetetopsis*) and therefore cannot be confounded with *Sobralispongia*. Termier et al. (1985a, 1985b) describe the “sclerosponges” *Neuropora lusitanica* and the new genus *Periomipora*, which clearly differ from the present genus (e.g. by a chaetetid architecture, spherulitic and orthogonal microstructure).

5. Systematic position of *Sobralispongia*

The type of monaxone spicules (styles and subtylostyles) and their plumose arrangement around an organo-collagenous axis (“axial condensation”) are considered to be characteristics of the Axinellida (Reitner, 1992: 175; Wood, 1987: 50). Particularly some genera of the axinellid family Milleporellidae share the similar encrusting habit with *Sobralispongia*, the plumose structure of the spicule skeleton and comparable types of spicules (e.g. the genus *Murania*). However, these genera differ in detail from *Sobralispongia* (see above). Axinellid affinities are supported by irregularly occurring tabulae-like structures within the interspiculate skeleton (tubes) known from some axinellid genera (e.g. *Dehornella*). Also, the occurrence of transverse spicule elements does not contradict an axinellid attribution as it is realised within axinellid genera with a more complex architecture (e.g. *Euzkadiella*).

On the other hand, *Sobralispongia* bears some features which do not fit with the Axinellida: spicules with acanthostyle-like lateral processes in their distal parts do not agree with the axinellid family Milleporellidae sensu Wood (1987); Reitner (1992). They occur in the Agelasida with a particular form (verticellid acanthostyles) and in the Poecilosclerida (fide Reitner, 1992: 215, 231). As the true nature of the spicules is not very clear and a superposition of different spicules causing this acanthostyle effect in thin-section cannot be excluded, these spicules are not considered here for systematic assignment. Further material may verify the presence of acanthostyle-type spicules.

The spherulitic spicules of *Sobralispongia* with a diameter of 50 µm reach an unusually large size compared with microscleres in other coralline sponges. Similar sizes are mentioned from the Hadromerida (e.g. the genus *Calcistella*, *Chondrochaetetes*; cf. Reitner, 1992: 156 ff.). The concentration of these ?aster-pseudomorphs usually above the radial spicule columns could indicate that the microscleres where housed during the life of the sponge above the subtylostyle spicule skeleton and may generally have had a slim chance of incorporation into the calcareous skeleton. For this reason, the fossilisation of such microscleres was perhaps possible only in unusual favourable circumstances and may thus explain the rarity in the fossil documentation. According to Wood (1987: 50), microscleres are often absent in Axinellida. She particularly notes the absence of microscleres in the family Milleporellidae. Concerning the Axinellida, Reitner (1992) mentions only rhaphids from the Halichondrida which he, however, considers as not being true microscleres.

Another questionable element in *Sobralispongia* are ring structures of clear calcite around vertical styles (Fig. 3f). The rings are of the same thickness as the megascleres. A micritic rim is visible at the lower and upper edge of the rings which may be interpreted as organic matter that has caused the mineralisation. Thus the ring structures may reflect former organo-collagenous material around the vertical styles. We did not find any comparable features in other sponges and therefore cannot evaluate the taxonomic significance of this element.

Summarising the different facts, the Portuguese material cannot be included in one of the existing genera of coralline sponges. *Sobralispongia* has most features in common with taxa of the Axinellida, particularly the monaxone spicule type and the plumose architecture. These characteristics are considered by Reitner (1992) as "very weak" to define taxonomic groups, but for some practical reasons he includes most of the fossil material of this type within the Axinellida. The presence of ?aster-pseudomorphs clearly contradicts an assignment to this order. However, the differences in spiculation and architecture of the calcareous skeleton to taxa of the Hadromerida and other orders of the Demospongiae seem to be more significant. Despite these uncertainties, the Portuguese material is included here tentatively within the Axinellida. If this is true, the diagnosis of this taxon/order must be enlarged by the presence of ?aster-like microscleres.

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