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A highly diverse siliceous sponge fauna (Porifera: Hexactinellida, Demospongiae) from the Eocene of north-eastern Italy: systematics and palaeoecology

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A siliceous sponge fauna, consisting of more than 900 specimens, is described from an early Lutetian tuffite horizon in the Chiampo Valley, Lessini Mountains, north-eastern Italy. Thirty-two taxa (15 Hexactinellida, 17 Demospongiae) are determined and illustrated, belonging to 24 genera, two of which are new (*Rigonia* gen. nov. and *Coronispongia* gen. nov.). Among these, 10 new species are proposed: *Stauractinella eocenica* sp. nov., *Rigonia plicata* gen. et sp. nov., *Hexactinella clampensis* sp. nov., *Camerospongia visentinae* sp. nov., *C. tuberculata* sp. nov., *Toulminia italicica* sp. nov., *Coronispongia confossa* gen. et sp. nov., *Cavispongia scarpai* sp. nov., *Corallistes multiosculata* sp. nov. and *Bolidium bertii* sp. nov. Of the genera identified at Chiampo, 14 range back to the Cretaceous, three to the Jurassic and one to the Triassic, while six are still extant. The studied fauna shows affinities with sponges from the Eocene of Spain and the Cretaceous of Germany. The sponge fossils are uncompressed and bodily preserved, but the original siliceous skeleton is dissolved and substituted by calcite. Delicate attachments can be nevertheless documented: some sponges attached to a hard substrate by encrustation, while others were anchored on soft sediments by root-like structures. The presence of different modes of attachment suggests heterogeneous substrate conditions. Small, possibly young, sponges are recorded too. The sponge fauna is essentially autochthonous and lived in the middle-outer part of a carbonate ramp, where it formed clusters. This study extends the geographical and stratigraphical range of many sponge taxa, including *Camerospongia*, *Toulminia*, *Ozotrichelus* and *Bolidium*, previously documented only from the Cretaceous. The Recent calcified demosponge genus *Astrosclera* is reported here in the Cenozoic for the first time, having been reported previously in the Triassic only. Additionally, this study documents the second worldwide occurrence of the Recent sphinctozoan genus *Vaceletia* in the Palaeogene, formerly recorded exclusively in Australia.

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Keywords: Hexactinellida; Demospongiae; Eocene; Italy; palaeoecology

Introduction

Sponges are among the oldest extant multicellular animals. They appeared in the Precambrian and were already well established by the Cambrian, becoming major reef builders during the Palaeozoic and Mesozoic (Brunton & Dixon 1994; Wood 1998). Siliceous sponges play a significant role in marine ecosystems (Van Soest *et al.* 2012); for example, they contribute to the silicon cycle (Maldonado *et al.* 2005, 2010; Chu *et al.* 2011; Tréguer & De La Rocha 2013). However, little is known about the abundance and diversity of sponges in the geological past: due to the low preservation potential of many taxa, their fossil record is rather incomplete. Only sponges with a rigid skeleton, such as lithistids (demosponges with desmas), Hexactinosida and Lychniscosida (both representatives of Hexactinellida), and sponges with a massive calcareous

skeleton (a polyphyletic assemblage within demosponges and Calcarea), have a more or less continuous fossil record that is nevertheless inadequately studied, especially for the Cenozoic (Pisera 2006). For siliceous sponges (lithistids and hexactinellids), the fossil record is very rich in the Jurassic (e.g. Quenstedt 1877–8; Schrammen 1936, 1937; Leinfelder *et al.* 1993; Pisera 1997) and the Cretaceous of Europe (e.g. Schrammen 1910, 1912; Moret 1926; Reid 1958, 1959, 1961; Lagneau-Hérenger 1962). Many diverse sponge faunas are known from the Miocene of the Mediterranean area (e.g. Pomel 1872; Moret 1924; Brimaud & Vachard 1986a, b; Matteucci & Russo 2011 and references cited therein). Palaeogene sponges in contrast have a rather scarce record (Pisera 1999). Eocene bodily preserved sponge faunas are known from five areas. In Europe, Bartonian sponge faunas are known from Spain (Ebro and Pamplona Basin – Pisera &

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Busquets 2002; Astibia *et al.* 2014 and references cited therein) and France (Aquitanian Basin, Basque Country – d'Archiac 1846, 1850). In both cases hexactinellids are the dominant group, but lithistids occur in Spain as well. In North America, Bartonian sponges (hexactinellids, 'soft' demosponges, lithistids and calcareous sponges) have been reported from the Castle Hayne Formation, North Carolina, by Rigby (1981) and Finks *et al.* (2011). Late Paleocene–early Eocene sponge faunas were reported by Buckeridge *et al.* (2013), Kelly *et al.* (2003) and Kelly & Buckeridge (2005) from New Zealand, where hexactinellids are more abundant than lithistids. The Priabonian Pallinup Formation in south-west Australia also yields sponges, mostly lithistids (Pickett 1983; Gammon *et al.* 2000; Pisera & Bitner 2007 and references cited therein). In the late Eocene Oamaru diatomite in New Zealand there are isolated sponge spicules (Hinde & Holmes 1892; Edwards 1991).

Eocene siliceous sponges from the Chiampo Valley have been reported only by Menin (1972), Visentini (1994), Frisone, Fornasiero *et al.* (2014) and Frisone, Pisera & Preto (2014). Matteucci & Russo (2005) provided illustrations and preliminary determinations of 23 species. The poor knowledge of the Chiampo sponge fauna is in contrast with the richness of public collections in the museums of Vicenza and Venice and the University of Padua. These collections have never been studied or catalogued. The aim of the present study is to describe the taxonomy of the Chiampo sponges in order to shed a new light on the diversity of siliceous sponges of Eocene age. By assessing the sponge diversity of the Eocene of the Chiampo Valley, this study contributes to knowledge of sponge distribution through time, and provides new information on their role in Eocene marine ecosystems.

Geological setting

The study area is located in the eastern Lessini Mountains, a portion of the Prealps of north-eastern Italy, on the west side of Chiampo Valley (Fig. 1). The Lessini Mountains are a triangle-shaped tableland, and occupy some 800 km² in the western Venetian Region, at the transition between the Prealps and the Po Plain. They belonged to the Cenozoic Lessini Shelf, a resurrected carbonate platform with scattered reefs, lagoons, islands and volcanoes circumscribed northwards by lands and surrounded by deeper water marine settings (e.g. Bassi *et al.* 2008; A. Bosellini 1989; F.R. Bosellini & Papazzoni 2003). The studied sites were located within a NNW-trending extensional structure known as the Alpone-Agno or Alpone-Chiampo graben (e.g. Barbieri *et al.* 1982, 1991), bounded to the west by the Castelvero normal fault. The full extent of the graben is unknown because the outcrop area is truncated to the north and east. Zampieri (1995) proposed that the

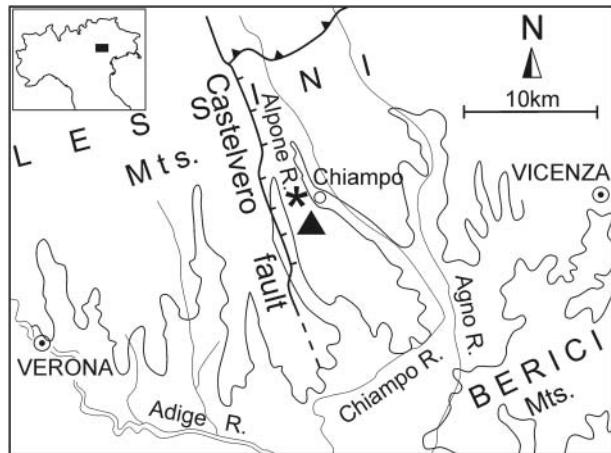


Figure 1. Location of the study area. Cengio dell'Orbo quarry is indicated with an asterisk, Lovara quarry with a triangle.

Alpone-Chiampo graben was 20 km wide and at least 35 km long. The area belongs to the Veneto Volcanic Province (VVP), identified by principally mafic and ultramafic rocks erupted during the Paleocene–Oligocene, mainly in submarine environments. Large volumes of mainly subaqueous volcanics and their penecontemporaneous reworking products (hyaloclastites and tuffites) accumulated in the graben. The eruptive centres of the eastern Lessini Mountains were aligned with the Castelvero fault (e.g. Piccoli 1966). Several magmatic pulses occurred, separated by periods of magmatic inactivity during which marine sedimentation took place (De Vecchi & Seda 1995 and literature therein). As a result of alternating volcanic activity and sedimentation, intercalated within volcanic rock successions as thick as 200 m are thick beds of limestone, locally called 'Chiampo limestone'. This unit was quarried until the 1990s as a building stone. It belongs to a lower–middle Eocene informal unit named 'Nummulitic limestone', widespread in the western part of Veneto (e.g. Fabiani 1915). This lithostratigraphical unit is not well constrained, and includes limestones with *Nummulites* of different ages and depositional settings (Bassi *et al.* 2013; Papazzoni *et al.* 2014). Beccaro *et al.* (2001) interpreted the 'Nummulitic limestone' of the studied sites as belonging to the outermost facies of a carbonate ramp and the volcaniclastic debris as transported by sediment gravity flows (debris flows and turbidites). In the study area, there is evidence of palaeocurrents: volcaniclastic sediments are often lens shaped with a channelized morphology (Martón *et al.* 2011), and transport sedimentary structures are visible in the field. Pelagic fossils (e.g. pteropods) are commonly found, and locally (Lovara quarry) there are accumulations of plankton and nekton fossils (e.g. planktonic foraminifera, shark teeth) (Beccaro *et al.* 2001). Volcaniclastic debris, tuffites or reworked tuff beds exhibit a faunal association more complete than usual. Some volcaniclastic levels are

extremely rich in very well-preserved fossils (e.g. three-dimensional crustaceans complete with appendages and ventral parts), that belong to several endemic species (e.g. Beschin *et al.* 1991; De Angeli & Garassino 2006). In a few sections, sponges constitute the most common macrofaunal element, especially in a relatively thin horizon of volcaniclastics within the ‘Nummulitic limestones’ of a few quarries on the western flank of the Chiampo Valley. Sponges are absent or rare in all other Eocene localities of the Venetian Prealps.

The sponge fauna described here comes from a horizon of tuffites and hyaloclastites, 50–200 cm thick (Fig. 2; Menin 1972; Agostini 1991; Visentin 1994; Matteucci & Russo 2005). The rock is typically a tuffite with arenaceous grain size, composed of rounded volcanic fragments, calcareous bioclasts and calcitic cement. The

volcanic clasts are strongly altered, with palagonitized glass in vesicles. The associated fauna is mainly composed of small benthic and planktonic foraminifera and larger foraminifera (e.g. Miliolidae, Rotalidae, *Nummulites*, *Discocyclina*). There are also crustaceans (decapods and ostracods), echinoids, bryozoans, molluses (gastropods, especially pteropods, rare cephalopods and bivalves), red algae and rare corals (e.g. Fabiani 1915; Schaub 1962; De Zanche 1965; Ancona 1966; Beschin *et al.* 1991; Fornasiero & Vicariotto 1997; De Angeli & Beschin 2010; Pacaud & Quaggiotto 2011). The bioclasts, especially larger benthic foraminifera, are often fragmented. This feature was also observed by Beschin *et al.* (1991) at Lovara Quarry. The age of the sponge horizon is Lutetian (Beccaro *et al.* 2001; Matteucci & Russo 2005). A preliminary analysis of calcareous nannofossils from the sediment surrounding the sponges (C. Agnini, pers. comm.) indicates that the investigated interval belongs to Zones CNE8–CNE9 (Agnini *et al.* 2014). This datum is likely correlative with the upper part of NP14–lower part of NP15 (Martini 1971) and CP12b–lower part of CP13 (Okada & Bukry 1980), which means early Lutetian.

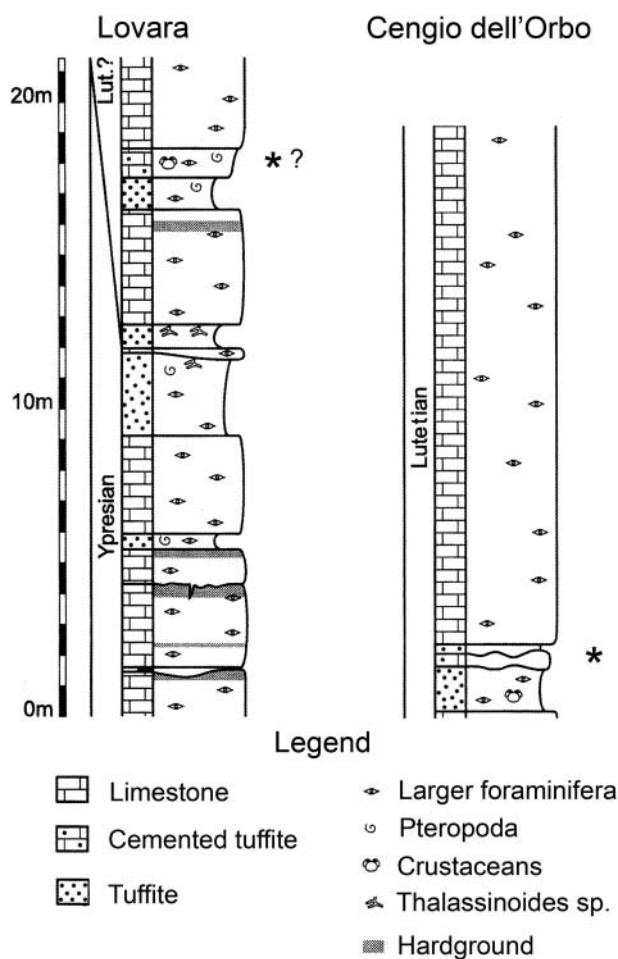


Figure 2. Simplified stratigraphical sections of Lovara and Cengio dell'Orbo quarries modified from Beccaro *et al.* (2001), with sponge-bearing horizons (asterisks). Facies codes are provided on the left of the stratigraphical column. The sponge-bearing horizon at Lovara quarry has a question mark as sponges were not found during fieldwork in this study. The data thus rely on labels of museum specimens and personal communications (Antonio De Angeli pers. comm.).

Material and methods

The studied sponge material comes from two adjacent quarries both located in the municipality of Chiampo (Vicenza): Cengio dell'Orbo: 45° 32' 25.56 "N, 11° 15' 44.47" E (called ‘Boschetto di Chiampo’ in Beschin *et al.* 1991; Beccaro *et al.* 2001 and other references); and Lovara: 45° 32' 11.87 "N, 11° 15' 58.92" E (part of which is named ‘Zanconato’ in, for example, Ancona 1966; Visentin 1994). The quarries have been closed since the 1990s and the sponge-bearing level is now inaccessible. A single small section (less than 3 m thick) that yielded only a few fossil sponges was found near Cengio dell'Orbo quarry.

The study material consists of more than 900 specimens, housed in six Italian public museums: Museo di Storia Naturale di Venezia (**MSNV**); Museo di Archeologia e Scienze Naturali ‘G. Zannato’, Montecchio Maggiore (**MCZ-PAL**); Museo Civico ‘D. Dal Lago’, Valdagno (**MCV**); Museo ‘Padre Aurelio Menin’, Chiampo (**MMC**); Museo di Geologia e Paleontologia dell’Università degli Studi di Padova (**MGP-PD** and **IG-PD**); and Museo Naturalistico Archeologico, Vicenza (**IG-VI**). Of the material studied, only 261 specimens were taxonomically useful. The others were either too poorly preserved or could not be adequately prepared. The study material was mainly collected by amateur palaeontologists between the 1960s and 1990s. The amateur palaeontologists frequently used mechanical preparation techniques to remove attached volcaniclastics, and therefore the sponge surface was often smoothed, destroying important characters of the outer surface (e.g.

rim around canal openings, small outgrowths, papillae). As methods of study depend on sponge preservation (Finks 2003b), the petrology of the specimens had to be investigated. Therefore, some specimens were etched in dilute acetic acid to reveal strongly calcified spicules. As the cement around the spicules is a carbonate too, the preparations chosen for the present study were polished hand sections and thin sections. In order to dissociate spicules from the entire specimen, various etching procedures were also tested on some sponge fragments, but none of them provided isolated spicular skeletons. The treatment of the sediment (method explained in Frisone, Pisera *et al.* 2014) also did not yield any spicules. Initially, spicules were searched for in each specimen under a binocular microscope. In some specimens with no evident megasclere on the surface, a polished section was prepared, and in many cases, a fused or articulated skeleton was recognized. Selected specimens were chosen for preparation of 52 thin sections, which confirmed that both the spicules and cement are made of calcite sparite. Veils of micrite and peloidal micrite always form coatings around spicules.

Reflected light observations on entire specimens were performed with a Leica MZ 125 optical binocular microscope. Thin sections were studied with petrographic microscopes, under transmitted optical (Leica DM EP T and Zeiss Axiophot) and fluorescent (Leica 5000B) light, all at Padova University. Classification and terminology for sponges generally follows Kaesler (2003, 2004), Hooper & Van Soest (2002) and Boury-Esnault & Rutzel (1997).

Systematic palaeontology

Phylum **Porifera** Grant, 1836

Class **Hexactinellida** Schmidt, 1870

Subclass **Hexasterophora** Schulze, 1886

Order **Lyssacinosida** Zittel, 1877

Family **Stauractinellidae** de Laubenfelds, 1955

Genus **Stauractinella** Zittel, 1877

Type species. *Stauractinella jurassica* Zittel, 1877, p. 60.

Stauractinella eocenica sp. nov.

(Fig. 3)

1972 Indeterminate sponge Menin: 68, pl. 6.

Diagnosis. Globular to compressed subglobular sponges with rounded terminal osculum. Spongocoel is divided by radial folds of the wall. Dermalia, atralia, gastralria are mostly pentactines while choanosomal megascleres are mostly diactines and hexactines.

Derivation of name. For the Eocene age of the type locality.

Material. Thirty-four specimens: MCZ-PAL 1377, 1378, 3734, 3740, 3743, 3793, 3795; MSNVE-22816, 22817, 22819, 22820, 22851, 22855, 22858, 22859, 22860, 22861, 22974, 22985, 22986, 23063, 23065, 23090, 23097; IG-PD 366219, 366220, 366221; MCV 266, 386, 387, 399; MMC 35, 37; IG-VI 272199.

Type specimens. Holotype: MCZ-PAL 3795. Paratypes: MCZ-PAL 3743, MSNVE-22974, IG-PD 366220, IG-PD 366221.

Type locality and stratum. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian volcanics.

Occurrence. Cengio dell'Orbo and Lovara quarries, Chiampo, Italy, Eocene, Lutetian.

Description. The holotype (MCZ-PAL 3795) is 9.1 cm high, 9.9 cm wide and 12.5 cm long. The smallest specimen (MSNVE-22855) is 2.1 cm high and 2.8 cm in diameter while the largest (MMC 35) measures 18 and 20 cm, respectively. Wall thickness varies from 1.35 to 4 cm. The osculum is generally rounded (Fig. 3A), ranging from 0.75 to 12 cm in diameter. Some specimens show on the external surface rounded canal openings of 4–6 mm in diameter (Fig. 3C). The external surface of some specimens is eroded so that the interior of the spongocoel is visible (Fig. 3B, C). The spongocoel is divided by radial folds of the wall forming large radial to irregular chambers that can be up to 9 cm long and 4 wide, visible on eroded specimens. Dermalia (Fig. 3D) are mostly pentactines. Their tangential rays are usually parallel to the sponge surface and are 2–8 mm long, while proximal rays are 1.6–4.0 mm long (Fig. 3D–F). Choanosomal megascleres are mostly diactines and hexactines. Their length is difficult to measure precisely as they are seen only in sections. Nevertheless, their dimensions are extremely variable, ranging from 2.4–4.8 mm for diactines, to 0.4–4 mm for hexactines and their other derivatives (Fig. 3G, H). Gastralria are pentactines, with four rays tangential to the spongocoel wall and the proximal ray towards the choanosome (hypogastralia). Proximal rays are 0.8–1.2 mm long (Fig. 3I).

Remarks. The genus *Stauractinella* is recorded mainly from the Upper Jurassic of Europe (e.g. Schrammen 1937; Pisera 1997). Reid (2004b) reported a Palaeogene–Neogene distribution but without references. Hinde (1884 [1883], pl. 5, figs 9, 10, 10a, 11) erected *S. cretacea* for isolated spicules from the Upper Cretaceous of England. In our material, morphology and spiculation are very similar to those of *S. jurassica* (illustrated in Quenstedt 1877–8, pl. 130, figs 17, 18). Moreover, in *S. jurassica* (Pisera unpublished) the spongocoel is divided by folds of the wall as in our specimens. Contrary to *S. jurassica*, our material lacks ‘breast-like’ outgrowths (Schrammen 1937), instead showing a smooth surface.

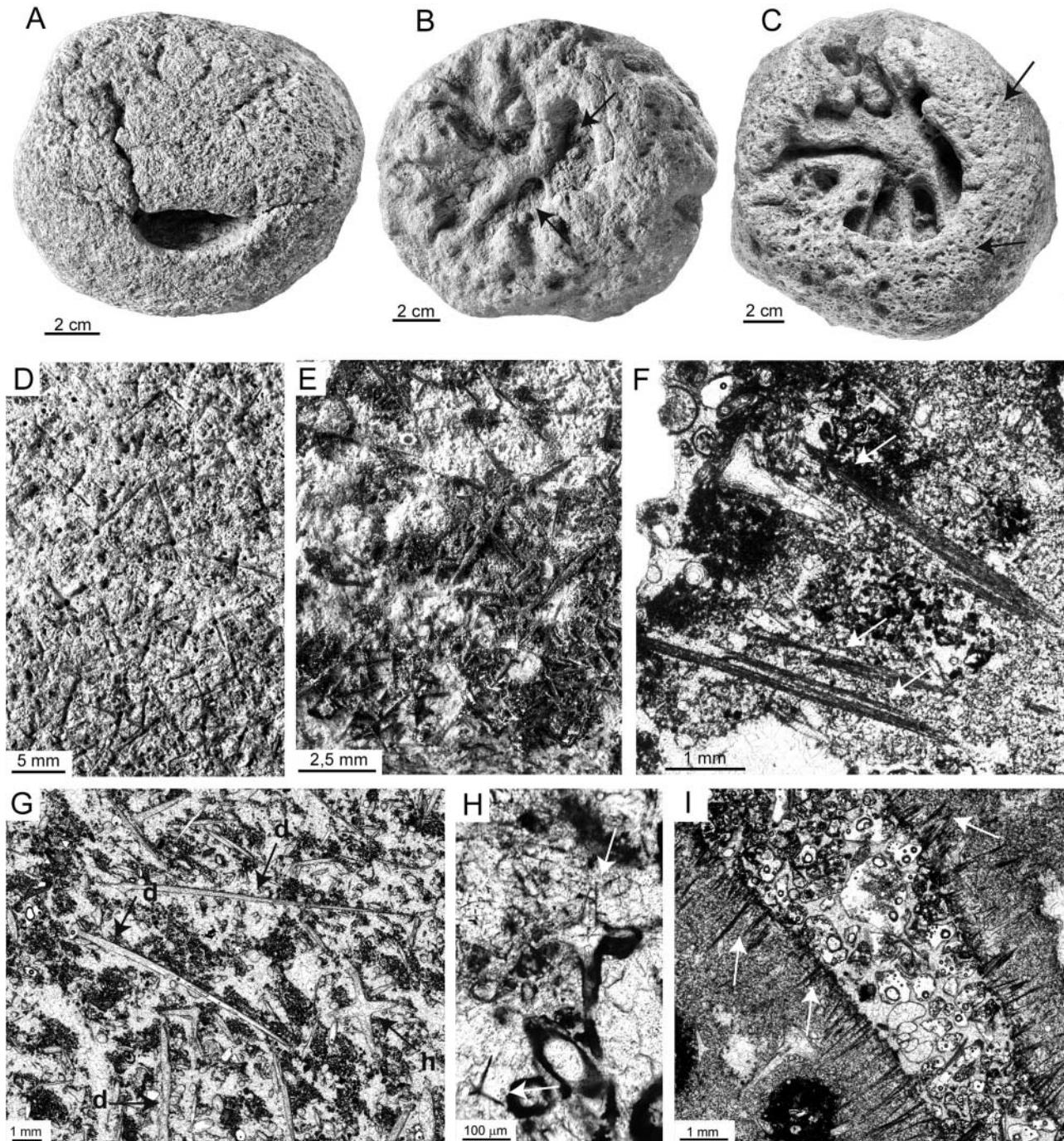


Figure 3. *Stauractinella eocenica* sp. nov. A, D, G, holotype MCZ-PAL 3795; B, paratype IG-PD 366221; C, MSNVE-22820 (photo B. Favaretto); E, paratype MSNVE-22974; F, I, paratype IG-PD 366220; H, paratype MCZ-PAL 3743. A, top view, subglobular shape and circular osculum; B, top view, the external membrane is completely eroded, the spongocoel is divided in chambers (arrows) by folds of the wall; C, top view, the external membrane is partially eroded and bears rounded canal openings (arrows), the spongocoel is visible; D, detail of external surface with imprints of pentactines (dermalia), tangential rays are parallel to the sponge surface; E, detail of external surface with pentactines; F, transversal thin section, dermalia proximal rays (arrows) are perpendicular to the sponge surface; G, longitudinal thin section, large diactines (d) and hexactines derivates (h); H, longitudinal section, various forms of hexactine and their derivates (arrows); I, transversal thin section, pentactines (hypogastralia) with proximal ray towards the choanosome (arrows).

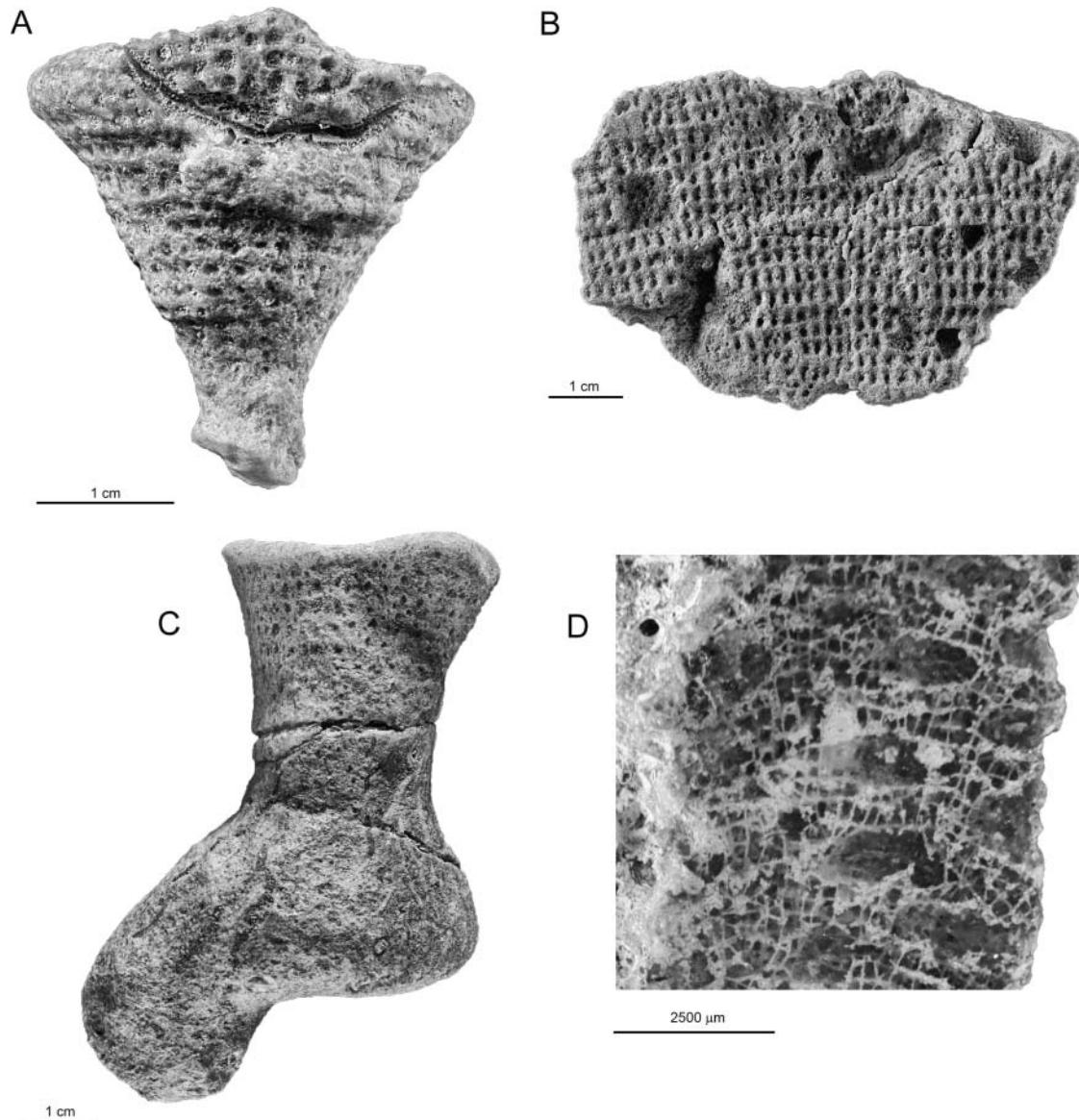


Figure 4. *Laocoetis patula* Pomel, 1872. **A**, lateral view of a conical specimen (MCZ-PAL 3711) with characteristic canal openings in quadrate arrangement; **B**, plate-like specimen (MCZ-PAL 3727) showing rectangular canal openings in quadrate arrangement; **C**, MSNVE–22891 lateral view showing a massive, tuberose base with some longitudinal canals; **D**, MSNVE–22869 longitudinal section showing mainly quadrate dictyonal meshes.

Stauractinella eocenica sp. nov. is similar in shape to representatives of the Recent genus *Pheronema* Leidy, 1868. Nevertheless, the family Pheronematidae Gray, 1870 is characterized by the prevalence of pentactines as choanosomal megascleres (Tabachnick & Menshenina 2002), while our material has mostly diactines and hexactines as choanosomal megascleres.

Order **Hexactinosida** Schrammen, 1903
Family **Craticulariidae** Rauff, 1893 (emend. Reid 1964)
Genus **Laocoetis** Pomel, 1872

Type species. *Laocoetis crassipes* Pomel, 1872, p. 93.

Laocoetis patula Pomel, 1872
(Fig. 4)

- 1872 *Laocoetis patula* Pomel: 95, pl. 2, figs 1–3.
1872 *Laocoetis obconoidea* Pomel: 97, pl. 1, fig. 1, pl. 1 ter, figs 3–5.
1901 *Craticularia patula* Pomel; Malfatti: 285, pl. 21, figs 6, 11, 12, pl. 22, figs 7–9.
1972 *Craticularia* sp. Menin: 65, figs 1–3.
2002 *Laocoetis patula* Pomel; Pisera & Busquets: 329, pl. 6, figs 3–6, pl. 11, figs 3–6.

2005 *Laocoetis patula* Pomel; Matteucci & Russo: 59, pl. 2, fig. 3a–c.

Material. Thirty specimens: MCZ-PAL 3711, 3713, 3727, 3744, 3745, 3746, 3747, 3749, 3782a; MSNVE-22869, 22871, 22883, 22897, 22898, 22899, 22936, 22938, 23009, 23012, 23013, 23014, 23015, 23016, 23017, 23018, 23019; MMC 20, 21, 22; MGP-PD 1072.

Occurrence. Cengio dell'Orbo and Lovara quarries, Chiampo, Italy, Eocene, Lutetian (Matteucci & Russo 2005; this study); Ebro Basin, Spain, Eocene, Bartonian (Pisera & Busquets 2002); Djebel Djambéida, Algeria, Miocene (Pomel 1872; Moret 1924); Maserna, Italy, Miocene (Malfatti 1901).

Description. Narrow to wide conical or plate-like sponge (Fig. 4A, B). The smallest specimen (MCZ-PAL 3744) is 1.1 cm high and 1 cm in diameter. The largest (MMC 22) is 16 cm in height and 18 cm in diameter. In some specimens, there is a massive, tuberose base (Fig. 4C) reaching 5.8 cm in height and 4.6 cm in diameter. Some superficial longitudinal canals (1 mm wide) are present on the base. Wall thickness is 4–6 mm. Canal openings are in craticulariid (quadrate arrangement) pattern on both surfaces. The external surface shows rectangular canal openings (0.8–1 × 1.5–2.00 mm, skeletal bridges 0.5–0.8 mm), while on the inner surface (when observable) they are rounded to elliptical (0.8–1.2 mm diameter or major axis); the horizontal skeletal bridges measure 0.5–2 mm. The skeleton is euretoid with mainly quadrate dictyonal meshes measuring 200–300 µm (Fig. 4D).

Remarks. As reported by Pisera & Busquets (2002), Pomel (1872) erected numerous species of his genus *Laocoetis* (= *Craticularia* Zittel, 1877) from the Miocene of Algeria based mostly on slight differences in general growth form. Moret (1924), however, did not take into account skeletal differences, and synonymized all Pomel's species into *Laocoetis crassipes* Pomel. Aside from shape differences, there are differences in basic skeletal structure among Pomel's species and differences in the shapes of canal openings on both surfaces. At least three different *Laocoetis* species were distinguished in Pomel's material by Pisera & Busquets (2002). One has round to elongated canal openings on both surfaces, another has canal openings on the outer surface with rectangular shapes and rounded canal openings on the inner surface, and the third has rounded canal openings on the outer surface and rectangular ones on the inner surface.

We assigned our material to *Laocoetis patula* Pomel, 1872 emended Pisera & Busquets (2002) because of the rectangular canal opening on the outer surface and the rounded to oval openings on the inner surface. Unfortunately, in many specimens internal canals opening are not observable, as the spongocoel is encrusted by sediment or poorly preserved. Nevertheless, the clear presence of

rounded canal openings on the inner surface of some specimens supported the assignment to *L. patula* with reasonable confidence. *Craticularia stellata* Lagneau-Hérenger, 1962, from the Lower Cretaceous of south-east France and north-east Spain, shows the same canal opening pattern: rectangular in the outer surface, rounded in the inner surface. Nevertheless, our material differs in general shape and spiculation from *C. stellata*, which has a cup-like or narrow cylindrical shape while our material is either cone-like or platy. *Craticularia stellata* shows spiny hexactines on canal openings of the outer surface. This feature was not observed in our material but, as spicules are strongly calcified, we cannot exclude that this is due to poor preservation. Additionally, some Chiampo specimens show rounded external pores, but we suspect that this could be due to abrasion caused by preparation. On the reverse of a few specimens, due to poor preservation, only the internal surface with rounded openings is visible, making the assignment uncertain. In fact, *Laocoetis crassipes* Pomel, 1872 is characterized by rounded canal opening on both surfaces. Moreover, the tuberose base, present in some specimens, is nearly identical in shape and in the longitudinal canals to *L. crassipes* (Pomel 1872; Moret 1924; Miocene of southern Spain: Ott d'Estevou & Térnier 1978; Pliocene of Sardinia, Italy: Matteucci 1989). Bulbose attachments are an adaptation to the substrate and do not have, in our opinion, a taxonomic value. The tuberose base observed in our material is also similar to those present in the species described by Malfatti (1901) from the middle Miocene of Emilia Romagna (northern Italy): *C. manzonii*, *C. globularis* and *C. ranzorei*. These species are no longer considered valid since Moret (1924) synonymized them with '*Craticularia crassipes*'. Regarding the Eocene, d'Archiac (1850) reported *Laocoetis samueli* from the Biarritz area (south-western Aquitaine Basin, Basque Country). The same species (that has oval canal openings both on the outer and inner surfaces) occurs in the Pamplona Basin (western Pyrenees) (Astibia *et al.* 2014). Finks *et al.* (2011) reported poorly preserved *Laocoetis* sp. cf. *L. crassipes* from Caste Hayne (North Carolina, USA). Pisera & Busquets (2002) reported *L. patula* from the Ebro Basin (Spain). In our material the 'hemispherical enlarged nodes' on the surfaces of the dictyonal skeleton reported by Pisera & Busquets (2002) were not observed, but this could be due to poor skeletal preservation.

Regarding the shape, there are fossil (e.g. Reid 1964; Pisera 1997) and Recent (e.g. Lévi 1986) *Laocoetis* species that are cone-like when small and then become more plate-like. The variety of shapes in the studied material can thus be interpreted to represent different ontogenetic stages. *Laocoetis* represents the longest living genus of Hexactinellida, ranging from the Late Jurassic to the Recent (Mehl 1992; Reiswig 2002a; Pisera & Tabachnick 2014).

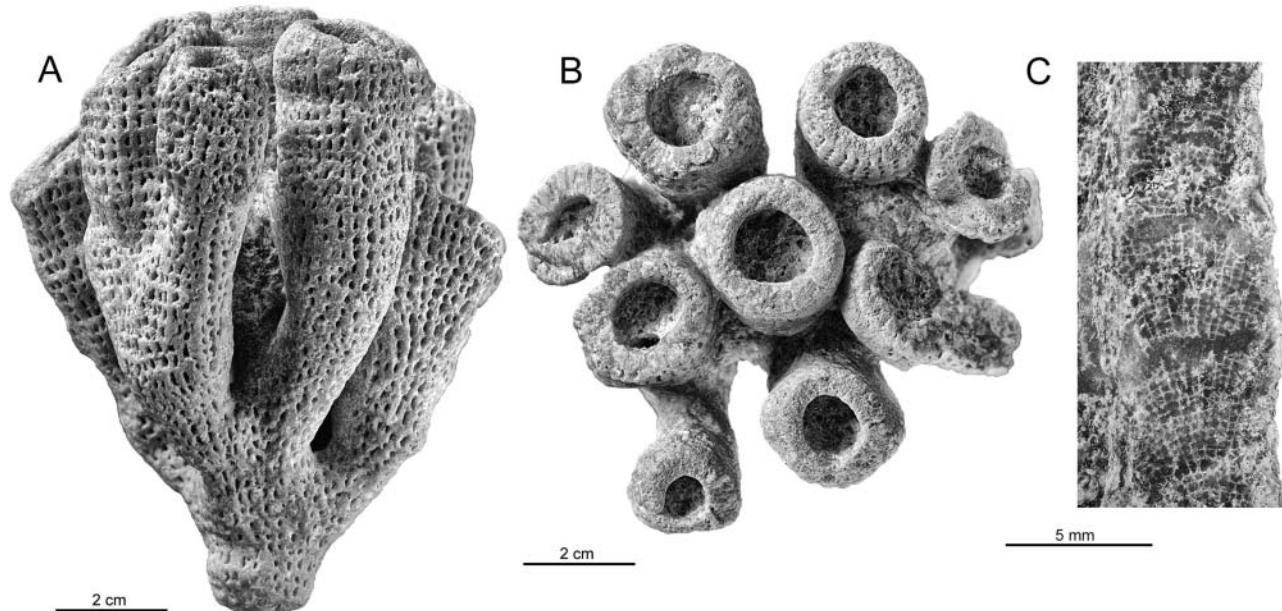


Figure 5. *Laocoetis ?emiliana* (Malfatti, 1901). **A**, lateral view of MSNVE-23020 with branched habitus and canal openings in quadrate arrangement (craticulariid pattern); **B**, top view of MSNVE-23020 with rounded tubes; **C**, detail of MSNVE-22903 showing quadrate dictyonal meshes and radial canals almost entirely crossing the sponge wall. Dictyonal strands are diverging toward both surfaces.

***Laocoetis ?emiliana* (Malfatti, 1901)**
(Fig. 5)

1901 *Craticularia emiliana* Malfatti: 285, pl. 20, figs 1–6, pl. 21, fig. 13, pl. 22, figs 1, 4.

2005 *Paracraticularia* sp. Matteucci & Russo: 59, pl. 2, fig. 5a, b.

Material. Four specimens: MSNVE-22903, 23010, 23011, 23020.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian (Matteucci & Russo 2005; this study); Maserna, Italy, Miocene (Malfatti 1901).

Description. Tubular-branched craticulariid up to 16.1 cm high and 12 cm in diameter (Fig. 5A) that is composed of three to nine cylindrical to subconical tubes (Fig. 5B) 1.3–3.5 cm in diameter. Rounded to subrounded terminal oscula are 0.7–1.8 cm in diameter. Wall thickness is 4–6 mm. Rectangular canal openings on outer surface are in quadrate arrangement and measure 0.7–0.8 × 1.5–2 mm. They are separated by skeletal bridges 1–1.5 mm wide (horizontally) and 1 mm high (vertically). Canal openings of the inner surface are rectangular as well, measuring 0.5 × 1.0–1.5 mm, and are separated by skeletal bands 0.5–1 mm wide horizontally, 1 mm wide vertically. Radial canals are 0.7–0.9 mm wide and cross almost entirely the sponge wall (Fig. 5C). The skeleton is euretid with mainly quadrate dictyonal meshes 200–399 µm in size, dictyonal strands diverging toward both surfaces.

Remarks. In describing *Craticularia emiliana* from the Miocene of Italy, Malfatti (1901) considered fragments of sponges that could correspond to singular tubes of our material. Nevertheless the external canal openings are mainly rectangular, while in the Miocene material they are subrounded. In our material, radial canals nearly completely cross the sponge wall, while in Malfatti's material they are shorter. The species was illustrated and preliminarily described by Matteucci & Russo (2005) as *Paracraticularia* sp. This genus, originally described by Schrammen (1937), was synonymized by Reid (2004b) with *Craticularia* Zittel, 1877. We agree with his opinion that the branching habitus has no taxonomic value at the genus level. Our material is very similar, in general morphology, to *Laocoetis fittoni* (Mantell, 1822), a species widespread in the Cretaceous of Europe (e.g. Hinde 1884 [1883]; Moret 1926). Świerczewska-Gładysz (2006, 2010) observed round canal openings on both surfaces, while in our specimens they are rectangular.

Family **Cribrospongiidae** Roemer, 1864
Genus **Guettardiscyphia** de Fromentel, 1860

Type species. *Guettardia stellata* Michelin, 1844, p. 121.

***Guettardiscyphia thiolati* (d'Archiac, 1846)**
(Fig. 6)

1846 *Guettardia thiolati* d'Archiac: pl. 5, fig. 15, pl. 8, figs 5, 6, non fig. 7.

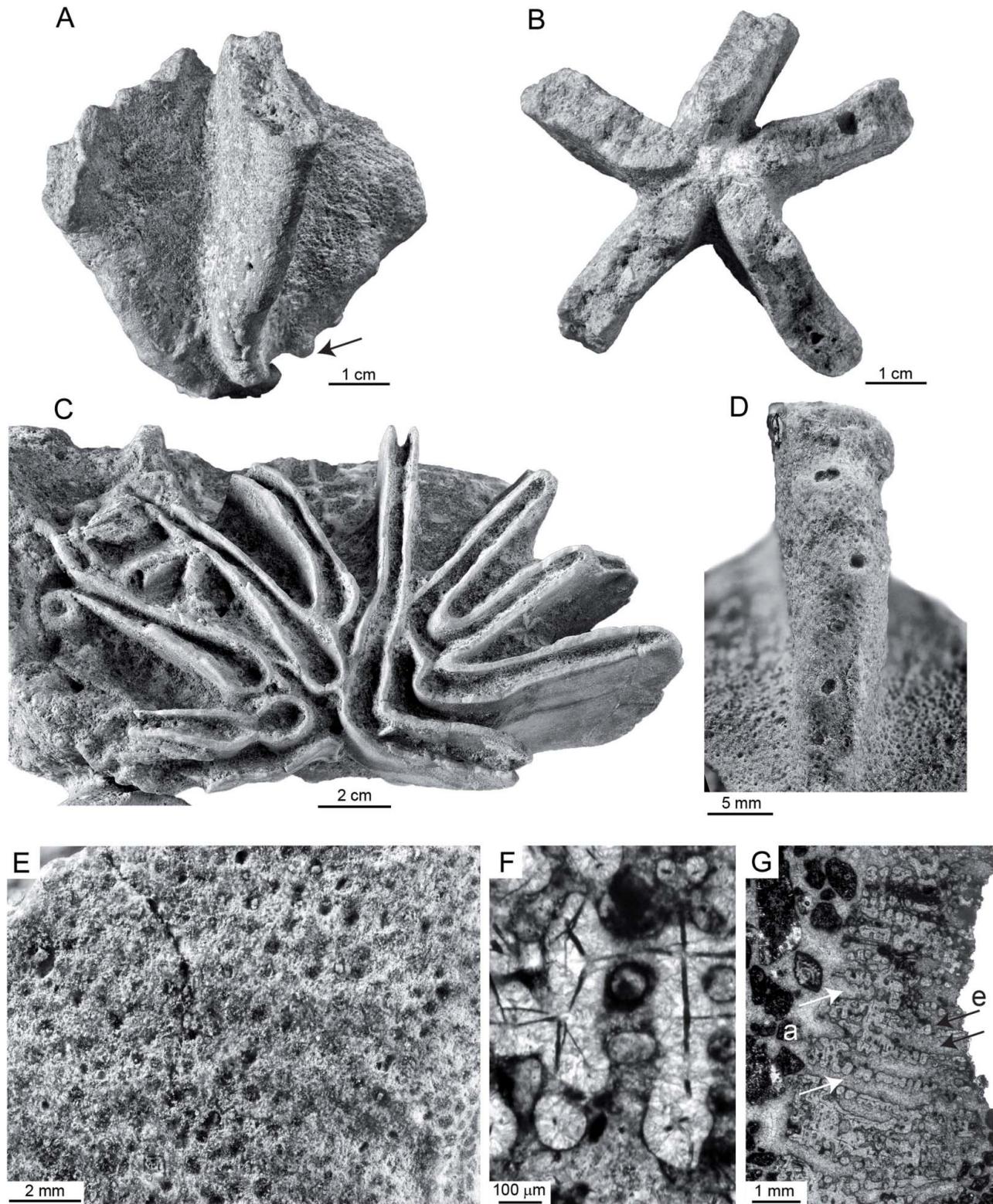


Figure 6. *Guettardiscyphia thiolati* (d'Archiac, 1846). **A**, MCZ-PAL 3786, lateral view, specimen with papilliform outgrowths (arrow) along the edges of the wings; **B**, MCZ-PAL 3786, top view showing a star shape; **C**, MCZ-PAL 3784b, plicate, irregular fins; **D**, MSNVE-22874 detail of wing's edge with papilliform outgrowths bearing small rounded oscula; **E**, MSNVE-23040 detail of a wing's external surface showing irregularly distributed canal openings; **F**, MCZ-PAL 3764, detail of the longitudinal thin section of a wing, with square to triangular meshes; **G**, MCZ-PAL 3764 detail of a transverse thin section, epiphyses (e) and aporphyses (a) perforate the sponge wall in opposite directions and generally terminate immediately below the opposite surface.

- 1850 *Scyphia quinquelobata* d'Archiac: 413, pl. 9, fig. 13.
 1925 *Pseudoguettardia thiolati* var. *gurbensis* Moret: 9, pl. 1, fig. 9.
 1972 *Guettardia* sp. Menin: 65, fig. 5.
 2002 *Guettardiscyphia thiolati* (d'Archiac); Pisera & Busquets: 337, pl. 7, figs 7–13, pl. 12, figs 1–3.
 2005 *Guettardiscyphia thiolati* (d'Archiac); Matteucci & Russo: 59, pl. 1, fig. 8a–c.

Material. Nineteen specimens: MCZ-PAL 3764, 3766, 3767, 3784b, 3786, 3787, 3803; MSNVE-22870, 22872, 22874, 22875, 22876, 23040, 23043, 23045, 23046, 23047, 23049, 23091.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian (Matteucci & Russo 2005; this study); Ebro and Pamplona basins, Spain, Eocene, Bartonian (Moret 1925; Pisera & Busquets 2002; Astibia *et al.* 2014); Aquitaine Basin, Biarritz, France, Eocene, Bartonian (d'Archiac 1846, 1850).

Description. Sponges with star cross section that are 4.6–8.8 cm high, 4.2–15.3 cm wide, 2.8–10.2 cm long, and usually composed of 5–6 wings. These wings are united in the lower part, but may be separate, forming elongated branches directed upward and outward, in the upper part (Fig. 6A, B). The largest specimen (MCZ-PAL 3784b) is 5.5 cm high, 15.3 cm wide and 8.5 cm long, and shows irregular fins instead of wings (Fig. 6C). Radial fins may be considered an adaptation to improve stability, due to large dimensions (Finks 2003a) (see 'Sponge autecology' below). Along the edges of the wings, there are papilliform outgrowths (4 mm in height) with rounded oscula 0.6–2 mm in diameter (Fig. 6A, D). The wings are 9–17 mm thick and have walls 2–7 mm thick. Canal openings on the outer surface are rounded to subrounded, 0.2–0.4 mm in diameter, either irregularly distributed (Fig. 6E) or in quincuncal arrangement. The skeleton is euretoid with node-to-node beam connection and regular meshes, from square (140–200 µm) to triangular (120–200 µm) (Fig. 6F). In transverse section, both canal systems (which can be interpreted as epirhyses and aporhyses *sensu* Reid 1963) perforate the wall in opposite directions and generally terminate immediately below the opposite surface (Fig. 6G).

Remarks. The presence of irregularly distributed canal openings on the external surface together with the pattern of canal systems supports the assignment to *Guettardiscyphia thiolati* (d'Archiac, 1846). The papilliform outgrowths observed in some specimens also complies with Reid's redefinition (1961, p. 743) of the genus *Guettardiscyphia* de Fromental, 1860 that includes occurrence of accessory parietal oscula along margins of flanges or branches.

The genus is widespread in the Cretaceous of Europe: United Kingdom (Reid 1961, 1968), Germany (e.g.

Schrammen 1910 as *Guettardia*), France (Lagneau-Hérenger 1962) and Czech Republic (Žitt *et al.* 2006). Within the material studied, some specimens may belong to either *Guettardiscyphia thiolati* (d'Archiac, 1846) or *Pleuroguettardia iberica* Pisera & Busquets, 2002, which are homeomorphic species/genera very similar in general morphology but belonging to different families, having different canalization patterns, i.e. Cribrospongiidae (cribospongiid or irregular pattern) and Craticulariidae (quadrangular, craticulariid pattern). This pattern is often disrupted in both genera, especially near parietal gaps, so assignment of poorly preserved/fragmentary material to either of the genera may be difficult (Pisera & Busquets 2002), and assignment is rather difficult without detailed study (Astibia *et al.* 2014). Matteucci & Russo (2005) assigned some specimens from Chiampo Valley to *Pleuroguettardia* sp. and *Pleuroguettardia* aff. *iberica*. The last species is also known from the Eocene of the Vic Marls Formation (Pisera & Busquets 2002).

?Family **Auloplacidae** Schrammen, 1912
 Genus **Rigonia** gen. nov.

Type species. *Rigonia plicata* sp. nov.

Diagnosis. Fan-shaped sponges, consisting of a thin, strongly plicated wall forming deep, narrow furrows and rounded ridges on one side. On the other side, a labyrinthine pattern of folds has large openings leading to the cavaedial spaces. The walls are perforated by deep, straight and closely spaced canals. The choanosomal skeleton has triangular meshes.

Derivation of name. In honour of Francesco Giuseppe Rigoni (Vicenza, Italy) who inspired this work.

Type locality and stratum. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian volcanics.

Remarks. Our material is similar in its fan-like shape to the tretodictyid *Ramalmerina* Brimaud & Vachard, 1986b from the Miocene of Spain, except for the lack of schizorhyses and the absence of oscula at branch bifurcations. In *R. fisheri* Brimaud & Vachard, 1986b (p. 426), dictyonalia form mainly rectangular and large meshes (700 × 200 µm), while in our material they are triangular and small (110–150 µm).

Our material shows morphological similarities to the poorly preserved ?*Auloplax* sp. from the Takatika Grit (Campanian–Danian), Chatham Islands, New Zealand (Consoli *et al.* 2009).

The genus *Auloplax* Schultze, 1904 was traditionally considered to belong to the family Tretodictyidae, but Reiswig (2002b) transferred it to Dactylocalyidae because it completely lacks schizorhyses. Reiswig & Kelly (2011, p. 136), in a study on Recent hexactinellids from New Zealand, proposed moving *Auloplax* Schulze,

1904 from Dactylocalycidae to the resurrected family Auloplacidae, presenting a new diagnosis for this monogenic family. This latter interpretation fits our material: body consisting of several vertical plates or fans composed of conjoined thin-walled tubes, which split with an acute angle and remain tightly connected side-by-side. Specifically, *Auloplax breviscopulata* Reiswig & Kelly, 2011 has a choanosomal skeleton with oval apertures similar to our material. Choanosomal skeleton beam length is comparable: approximately 110 µm for both genera. Nevertheless, there are fundamental differences in the skeleton framework between *Auloplax* and *Rigonia*: firstly, the wall of *Auloplax* has very shallow canalization, while in *Rigonia* it is deeply canalized; secondly, the choanosomal skeleton of *Rigonia* has mainly triangular meshes, while in *Auloplax* rectangular and polygonal forms are also common.

***Rigonia plicata* sp. nov.**
(Fig. 7)

Diagnosis. As for the genus.

Derivation of name. From the Latin ‘plicatus’ (= folded).

Type specimens. Two fragmentary specimens. Holotype: MSNVE–22980. Paratype: MCZ-PAL 3780.

Type locality and stratum. Cengio dell’Orbo quarry, Chiampo, Italy, Eocene, Lutetian volcaniclastics.

Description. Fan-shaped fragments 5–8.1 cm high, 4.7–10.3 cm wide and 3.1–3.6 cm long. The holotype (MSNVE–22980) is 8.1 cm high, 10.3 wide and 3.6 long. The wall is 1–1.2 mm thick and strongly plicated (Fig. 7E, F), forming 4–5 rounded ridges on one side, 7–10 mm wide, separated by deep narrow furrows (Fig. 7A, B). The other side shows a labyrinthine pattern of folds (6 mm wide) with rounded to elongated openings, 3–4 mm in diameter (Fig. 7C, D). Walls are perforated by closely spaced canals 0.25–0.35 mm in diameter, separated by skeletal bridges 0.15–0.25 mm wide (Fig. 7G). Canals are deep, straight and cross nearly the whole wall (Fig. 7H). The skeleton is composed of mainly triangular meshes, 120–140 µm in size from node to node (Fig. 7I).

Family Tretodictyidae Schulze, 1886
Genus *Anomochone* Ijima, 1927

Type species. *Anomochone expansa* Ijima, 1927, p. 269.

***Anomochone* sp.**
(Fig. 8)

Material. MCZ-PAL 3708, from Cengio dell’Orbo quarry.

Description. Fragment of a group of two branching tubular sponges 10.6 cm high, 4–4.1 cm in maximum diameter, with rounded (1.6 cm in diameter) to elliptical (2.5 × 0.9 cm in size) terminal oscula (Fig. 8A). On the external surface, irregularly distributed rounded to subrounded canal openings 1–2 mm in diameter are separated by skeletal bridges 0.5–2 mm wide (Fig. 8B). The sponge wall (9–14 mm in thickness) is deeply canalized, with cleft-like to labyrinthine cavities (schizorhyses) (Fig. 8C). The dictyonal skeleton has mainly triangular meshes 120–180 µm in size. The nodes are swollen (Fig. 8D).

Remarks. The presence of a euretid skeleton with schizorhyses supports assignment to the family Tretodictyidae. The occurrence of swollen dictyonal nodes strongly suggests affinity to some living genera: *Anomochone* Ijima, 1927, *Psilocalyx* Ijima, 1927 and *Cyrtaulon* Schulze, 1886 (Reiswig 2002b). The *Psilocalyx* body, however, is composed of small tubes (e.g. *P. nitidus* Schrammen, 1936), which are not present in our material. On the other hand *Cyrtaulon* lacks the central spongocoel. The skeleton of our specimen is very similar to that of *Anomochone* but with less plicate morphology. However, in the branching habit the studied specimen is similar to another tretodictyid, genus *Sclerothamnopsis* Wilson, 1904, but this genus lacks swollen nodes. *Sclerothamnopsis collina* Brimaud & Vachard, 1986b from the Miocene of southern Spain has a branching habit too, but the diameter of the branches is significantly smaller (10 mm) and the spiculation is unknown.

Genus *Hexactinella* Carter, 1885

Type species. *Hexactinella ventilabrum* Carter, 1885, p. 397.

***Hexactinella clampensis* sp. nov.**
(Fig. 9)

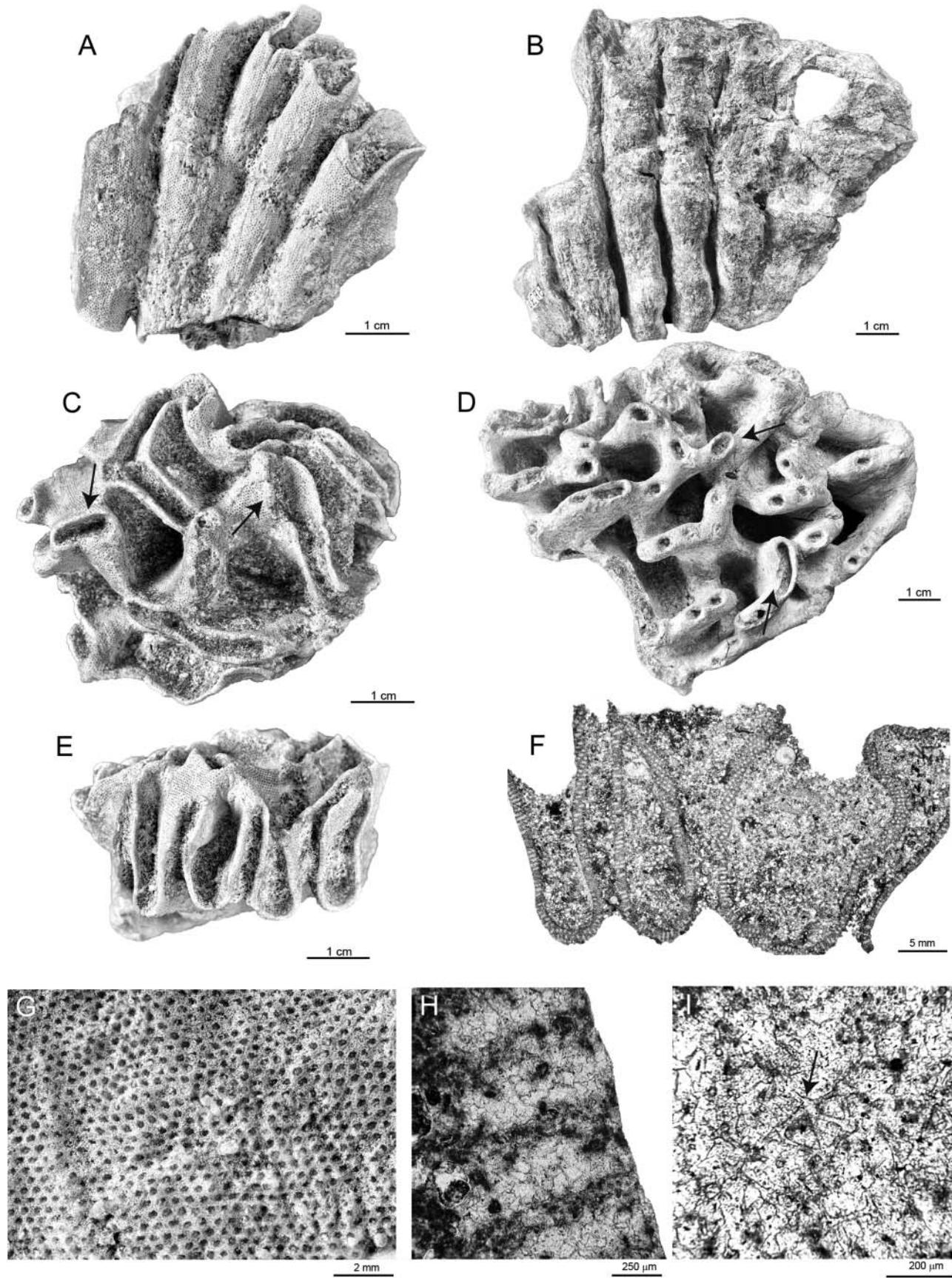
Diagnosis. Funnel- to plate-like *Hexactinella* with thick wall and irregular elliptical terminal osculum. On the external surface, subrounded canal openings are irregularly distributed. The dictyonal skeleton is euretid with mainly quadrate meshes.

Derivation of name. From ‘Clampus’, the Latin name of Chiampo.

Material. Five specimens. Holotype: MCZ-PAL 3804. Paratypes: MCZ-PAL 3725, 3728. Other material: MCZ-PAL 3729; MSNVE–22890.

Type locality and stratum. Cengio dell’Orbo quarry, Chiampo, Italy, Eocene, Lutetian volcaniclastics.

Description. Funnel- (Fig. 9A, E) to plate-like (Fig. 9H) sponge, 7.5–17 cm high, 5.1–12 cm wide, 3.5–9 cm long, with irregular elliptical terminal osculum (maximum diameter 2.5–7.5 cm) (Fig. 9B, D). The holotype (MCZ-



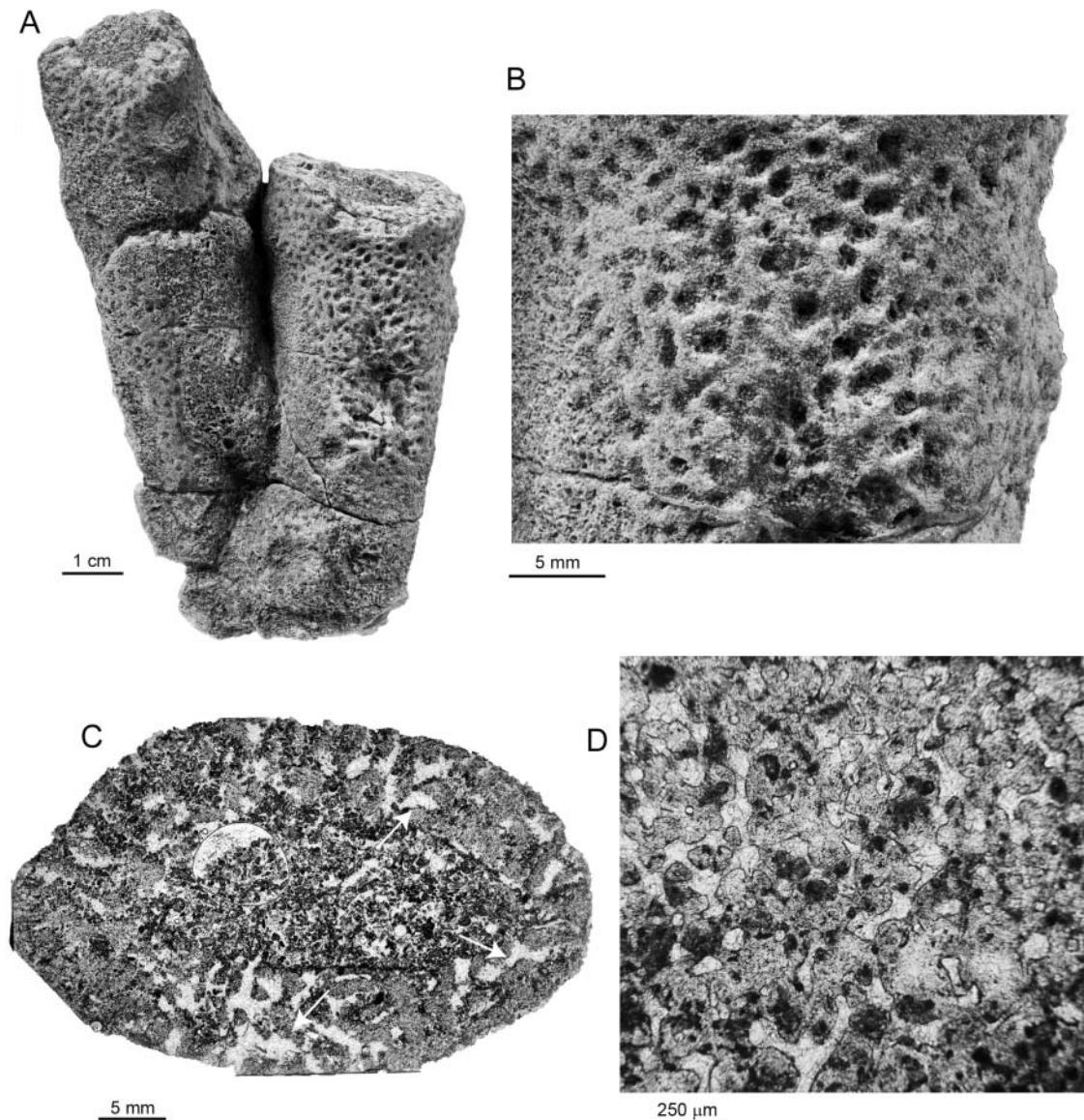


Figure 8. *Anomochone* sp. MCZ-PAL 3708. **A**, branching tubular sponge with rounded to elliptical terminal oscula; **B**, outer surface with rounded to subrounded irregularly distributed canal openings; **C**, transverse thin section of a branch, with deep, labyrinthine canals (schizorhyses) (arrows); **D**, detail of transverse thin section showing a dictyonal skeleton with swollen nodes and mainly triangular meshes.

PAL 3804) is 17 cm high, 12 cm wide and 9 cm long. The wall thickness is 9–17 mm. On the external surface, irregularly distributed subround canal openings (Fig. 9C, I), 0.7–2.0 mm in diameter, are separated by skeletal bridges 0.5–1.5 mm wide. The dictyonal skeleton is euretid with mainly quadrate meshes 120–180 µm wide (Fig. 9G),

deeply canalized and with cleft-like to labyrinthine cavities (schizorhyses) (Fig. 9F).

Remarks. In the study material there are both nearly complete specimens and platy fragments. We interpreted the latter as fragments of larger sponges. Actually, as in

Figure 7. *Rigonia plicata* gen. et sp. nov. **B**, **D**, MSNVE-2298, holotype; **A**, **C**, **E–I**, MCZ-PAL 3780, paratype; **A**, **B**, side view of fan-shaped fragments composed of rounded ridges divided by deep and narrow furrows; **C**, **D**, opposite side view with labyrinthic pattern of folds with rounded to elongated openings (arrows); **E**, upper view and (**F**) transverse thin section showing the strongly plicated wall; **G**, detail of wall structure with closely packed canals; **H**, detail of the wall with deep, straight canals as seen in thin section; **I**, transverse thin section. The skeleton is composed of mainly triangular meshes (arrow).

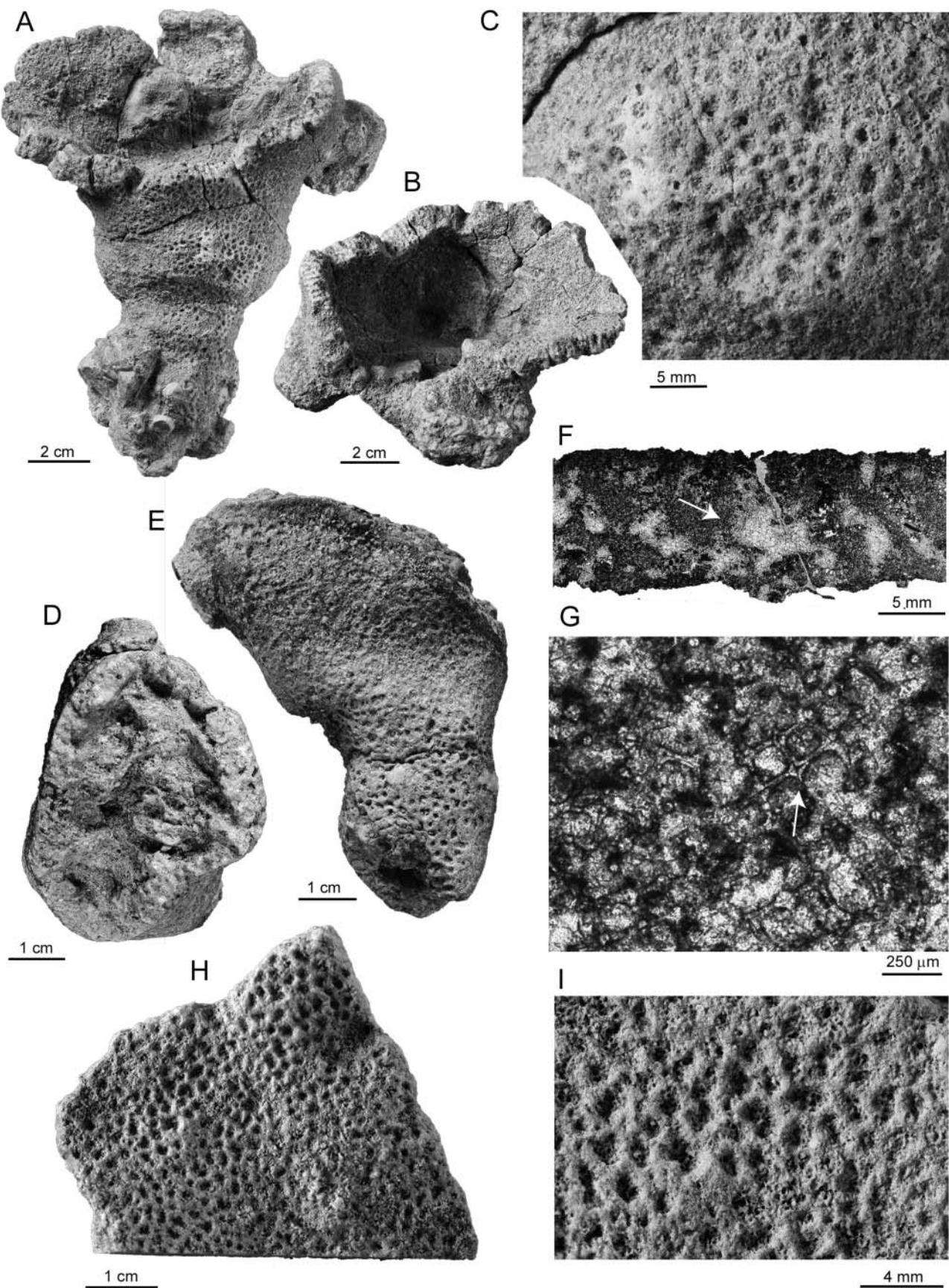


Figure 9. *Hexactinella clampensis* sp. nov. **A–C**, holotype, MCZ-PAL 3804; **D, E**, paratype, MCZ-PAL 3728; **F–I**, paratype, MCZ-PAL 3725. **A, E**, lateral view of funnel shape specimens; **B, D**, top view with irregular elliptical terminal oscula; **H**, platy specimen; **C**, irregularly distributed subrounded canal openings; **F**, longitudinal thin section of the sponge wall with schizorhyses (arrow); **G**, detail of a thin section: dictyonal skeleton with qudrate meshes (arrow).

many hexactinellids, smaller individuals of this species could have a funnel-like shape that later became platy. Certain hexactinellid sponges, such as the Recent species *Tretocalyx polae* Schulze, 1901, have an initial funnel-like habit that is subsequently modified through an increase of size by peripheral growth, so the internal surface becomes everted (Reid 1964). The platy fragments are similar to those of *H. calolepsis* Brimaud & Vachard, 1986b from the Miocene of southern Spain. This species differs from *H. clampensis* in having rounded canal openings, and larger skeletal bridges and dictyonal meshes. The studied specimens differ also from another platy species, the Eocene (Bartonian) *H. informis* Pisera & Busquets, 2002 from the Ebro Basin (Spain). *Hexactinella clampensis* has a thicker wall, larger skeletal bridges and a more regular subrounded shape of canal openings. *Hexactinella informis* is in fact characterized by irregular or polygonal canal openings, which are not observed in our material.

Order Lychniscosida Schrammen, 1903
Family Calldictyonidae Zittel, 1877
Genus *Callicylix* Schrammen, 1912

Type species. *Callicylix farreides* Schrammen, 1912, p. 302.

Callicylix eocenicus Pisera & Busquets, 2002
(Fig. 10)

?1993 *Plocoscyphia* (sic) *roemerii* Raffi & Serpagli: 69, pl. 2.37, fig. a.
2002 *Callicylix eocenicus* Pisera & Busquets: 342, pl. 10, figs 8, 9, pl. 14, figs 3, 4.
cf. 2005 *Centrosia* cf. *viquensis* Matteucci & Russo: 57, pl. 1, figs 4, 5.
2005 *Callicylix* aff. *eocenicus* Matteucci & Russo: 57, pl. 1, fig. 3.

Material. Thirty-two specimens: MCZ-PAL 3710, 3714, 3778, 3784a, 3788, 3789; MSNVE-22821, 22822, 22824, 22825, 22826, 22827, 22829, ?22830, 22831, 22834, 22835, 22837, 22838, 22839, 22840, 22841, 22842, 22831, 23057, 23058, 23087, 23094, 23095; IG-VI 272203, 272230; IG-PD 366225.

Occurrence. Cengio dell'Orbo and Lovara quarries, Chiampo, Italy, Eocene, Lutetian (Matteucci & Russo 2005; this study); Ebro basin, Spain, Eocene, Bartonian (Pisera & Busquets 2002).

Description. Ovoid to globose sponges (Fig. 10A, B) that are 3.6–12.7 cm high, 4.0–12.4 cm wide and 3.3–10.4 cm long. A possible young specimen (MSNVE-22830) is 2.4 cm high and 2 cm in diameter (Fig. 10C). The body is composed of anastomosing tubes and

lamellae. Tube openings range from subcircular (5–8 mm in diameter), to elongate (10–18 mm on the longer axis). The tube walls on the outer surface are 2–4 mm thick without an intradictyonal canal system (Fig. 10D). In cross section, the tube walls are either meandriform or anastomosing and form lamellae 4–6 mm thick, or bowl-shaped structures (Fig. 10E). Meshes of the dictyonal skeleton are rectangular (300–375 × 360–425 µm node to node) to quadrate (250–425 µm node to node), and have lychniscs (Fig. 10F).

Remarks. The studied specimens show two morphological varieties: one with more meandriform openings (Fig. 10A) and thinner walls, the other with mainly subcircular openings and generally thicker tube walls (Fig. 10B). These two morphotypes may belong to two different species. However, considering that one large specimen (MCZ-PAL 1380) shows both morphological features and wall thickness variability could also depend on fossil preparation, we regard them as conspecific. Traditionally, meandriform sponges have been classified as *Plocoscyphia* Reuss, 1846, but Reid (1962) clearly demonstrated that different sponges occur under this generic name (Pisera & Busquets 2002, p. 341). The studied specimens are homeomorphs of *Exanthesis* Regnard in Moret, 1926 and *Robinia* Finks, Hollocher & Thies, 2011, but they lack the labyrinthine canal system characteristic of these genera. The studied specimens are also morphologically nearly identical to *Callicylix farreides* Schrammen, 1912, but differ in the absence of a spongocoel. They show also affinities with genera *Brachiolites* Smith, 1848 and *Centrosia* Schrammen, 1912. In determining these specimens, we encountered problems of material preservation and difficult classification. Generally, calldictyonid sponges are poorly described in the literature and a revision of the family is needed. In fact, there are numerous fossil genera that are similar, and there are no clear-cut differences between them. Specifically, in our material the poor preservation and the lack of diagnostic characters (e.g. cortex, peripheral capsule, lychniscs sculptures) make the assignment difficult, if possible at all, in some cases.

Family Ventriculitidae Smith, 1848
Genus *Ventriculites* Mantell, 1822

Type species. *Alcyonium chonoides* Mantell, 1815, p. 402.

?*Ventriculites* sp.
(Fig. 11)

2005 *Ventriculites* sp. 1 Matteucci & Russo: 57, pl. 3, figs 6, 7a, b.

Material. One specimen: MCZ-PAL 1379.

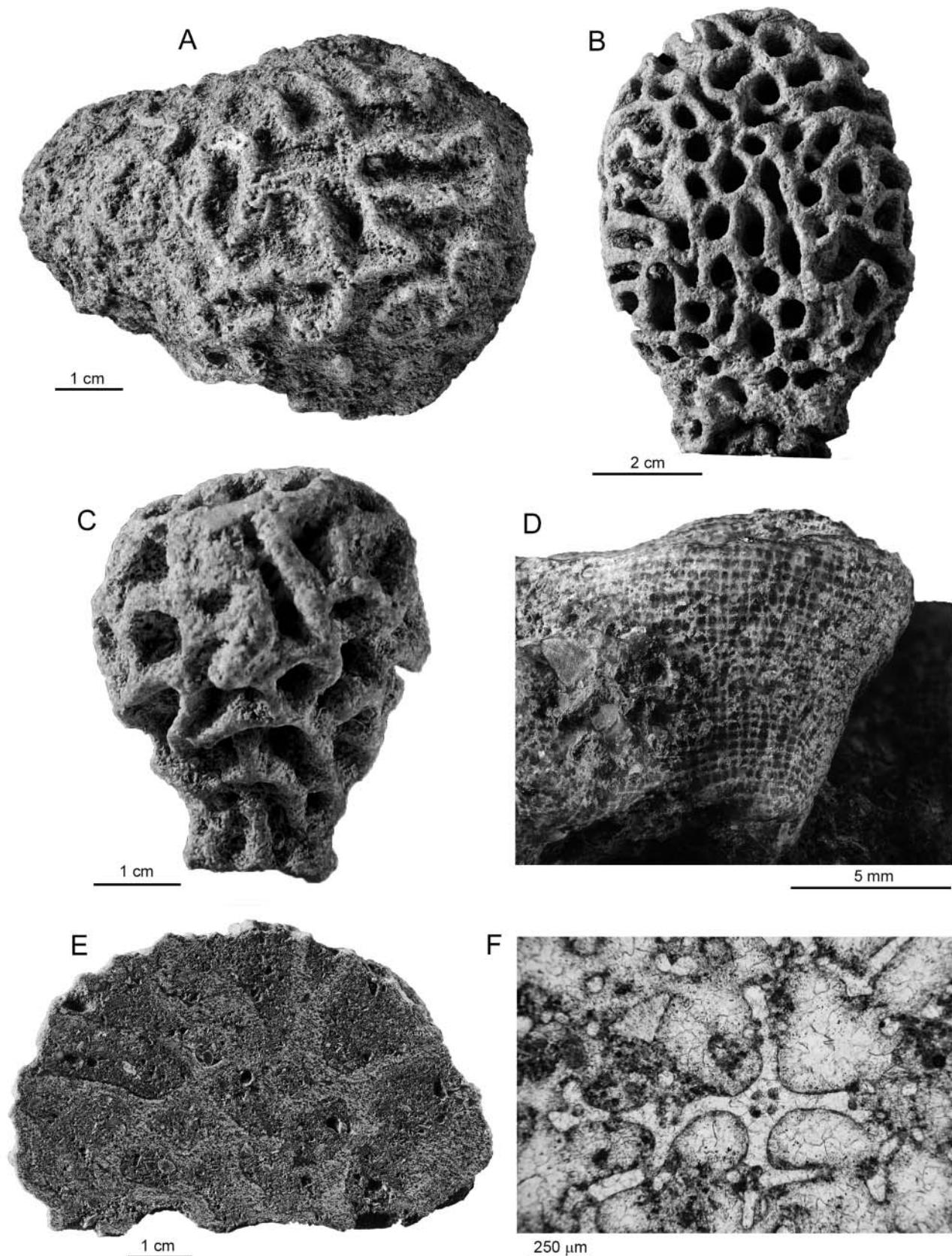


Figure 10. *Callicylix eocenicus* Pisera & Busquets, 2002. **A**, MCZ-PAL 3714, top view with dominant meandriform openings; **B**, MCZ-PAL 3789, top view with mainly subcircular openings; **C**, MSNVE-22830, young? individual; **D**, MCZ 3778-PAL, detail of the external surface without an intradictyonal canal system; **E**, MCZ-PAL 3710, longitudinal section with tube walls that are either meandriform or anastomosing, and forming pillars or bowl-shaped structures. Note the absence of a spongocoel; **F**, IG-PD 366225, lychniscs and quadratate meshes as seen in longitudinal thin section.

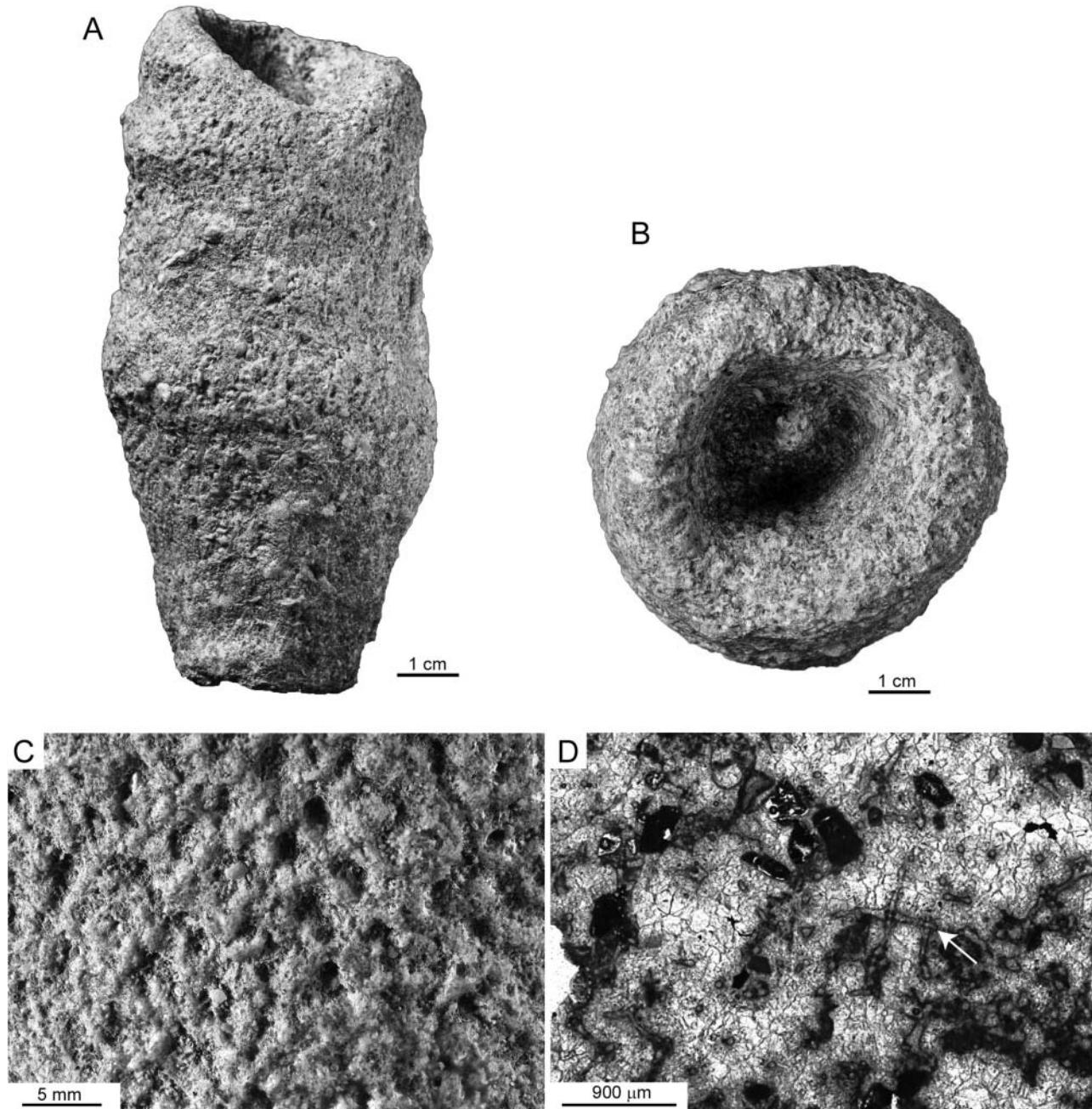


Figure 11. *?Ventriculites* sp. **A–D**, MCZ-PAL 1379. **A**, lateral view, individual with elongate conical shape; **B**, top view of the rounded terminal osculum; **C**, detail of the external surface with subrounded canal openings; **D**, thin section of a fragment from the base showing lychniscs (arrows).

Occurrence. Cengio dell'Orbo and Lovara quarries, Chiampo, Italy, Eocene, Lutetian (Matteucci & Russo 2005; this study).

Description. Elongate conical sponge (Fig. 11A), 12.5 cm high, 5.5 cm in diameter, with a rounded terminal osculum (Fig. 11B) 3.2 cm in diameter, and a wall thickness of 13 mm. On the external surface irregularly distributed subround canal openings occur (Fig. 11C), 1.6–2 mm in

diameter. The choanosomal skeleton has lychniscs (Fig. 11D) and mainly quadratic meshes, 300–400 µm (node to node) in size.

Remarks. The pattern of canal openings was difficult to observe due to problems in removing the embedding sediment. A thin section was prepared from the base of the specimen (to protect morphology), in which some lychniscs were observed but the internal canalization was not

seen. The genus *Ventriculites* is characterized by straight, unbranched canals that are perpendicular to the wall (e.g. Świerczewska-Gładysz 2012). These characters could not be observed in the studied material. As a consequence, the assignment is uncertain.

Due to the conical shape and large canal openings on the external surface, our material is similar to Cretaceous representatives of the genus. Many species, though, show more everted conical shapes and external furrows which are not observed in the studied specimen. The genus *Ventriculites* has a rich fossil record from the Cretaceous of Europe (e.g. Hinde 1884 [1883]; Lagneau-Hérenger 1962; Reid 1962, 1968; Świerczewska-Gładysz 2006, 2012; Olszewska-Nejbert & Świerczewska-Gładysz 2013). Pomel (1872) erected but did not illustrate three *Ventriculites*-like genera from the Miocene of Algeria: *Stelgis*, *Cladostelgis* and *Pleurostelgis*. Reid (2004c) synonymized these with *Ventriculites*. Another record (without illustration) of the genus is *Ventriculites poculum* Zittel from the Paleocene of Austria (Kühn 1930).

Family Camerospongiidae Schrammen, 1912
Genus *Camerospongia* d'Orbigny, 1849

Type species. *Scyphia fungiformis* Goldfuss, 1831, p. 218.

Camerospongia visentinae sp. nov.
(Fig. 12)

Diagnosis. Low-conical *Camerospongia* with a rounded to elliptical terminal osculum, around which a small elevated rim is present. The top surface is either flat or slightly inclined, and covered by a siliceous membrane. On the lateral surface, there are large rhomboidal to irregular canal openings, in quincuncial or irregular arrangement. The base may be supplied with a ledge.

Derivation of name. In honour of Marina Visentin, one of the first students of the Chiampo sponge fauna.

Material. Twenty-two specimens. Holotype: MCZ-PAL 3784c. Paratypes: MCZ-PAL 3712, 3775, 3781. Other material: MCZ-PAL 1382, 1385, 3715, 3779; MSNVE-22814, 22884, 22886, 22887, 22888, 22975, 23052, 23054, 23055; MCV 383, MGP-PD 1067, IG-VI 272204, 272232, 272237, from Cengio dell'Orbo and Lovara quarries.

Type locality and stratum. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian volcaniclastics.

Description. Low-conical sponges (Fig. 12A, D) that are 3.3–7.6 cm high, 4.7–12.9 cm wide and 3.6–9.8 cm long. The holotype (MCZ-PAL 3784c) is 3.9 cm high, 5.3 cm wide and 3.8 cm long. The conical spongocoel extends to the base of the sponge. The terminal osculum is elliptical, ranging from 1.0–1.3 × 2.3–6.2 cm in

dimension (Fig. 12B, C, E) to rounded 1.8–1.9 cm in diameter (Fig. 12F), and supplied with a narrow elevated rim 2–4 mm in height. The top surface of the sponge is covered with a smooth siliceous membrane. This membrane may also appear at the base of the sponge. The uppermost part of the sponge has a larger diameter than the rest, and forms an overhanging ledge over the lateral surface (Fig. 12A). The lateral surface of the sponge displays densely distributed, large, longitudinally elongated, rhomboidal to irregular canal openings that are 1.5–2.5 mm in diameter (Fig. 12G) and quincuncially or irregularly arranged. The base, when present, is encrusting, sometimes supplied with a ledge 3 mm wide (Fig. 12D). The sponge wall reaches up to 18–22 mm in thickness. The wall is pierced by large radial canals, 0.6–1.2 mm in diameter (Fig. 12H). The choanosomal skeleton has mainly quadrate meshes, with beams 400 µm (node to node) in length. On the external side of the sponge wall, beams are 300–500 µm long and meshes are more irregular in shape.

Remarks. The investigated specimens differ from *Camerospongia fungiformis* (Goldfuss, 1831) in having a low-conical shape, a flat or slightly inclined – rather than convex – top surface, a ledge at the base, and large rhomboidal to irregular canal openings, in quincuncial or irregular arrangement. *Camerospongia tuberculata* sp. nov. has a cylindrical shape, low conical outgrowths and no ledge at the base. Although the genus *Camerospongia* has its roots in the Jurassic (Gaillard 1983; Pisera 1997), its fossil record is mainly from the Cretaceous of Europe: Germany (Schrammen 1912), Poland (Świerczewska-Gładysz 2010), Ukraine (Olszewska-Nejbert & Świerczewska-Gładysz 2012), France and Spain (Lagneau-Hérenger 1962), United Kingdom (Reid 1968). This study is the first record of *Camerospongia* for the Cenozoic. As a consequence, the last appearance of the genus can be moved forward to the Lutetian. Another camerospongiid, *Robinia striatopunctata* Finks, Hollocher & Thies, 2011, was described from the middle and upper Eocene of Castle Hayne Formation, North Carolina.

Camerospongia tuberculata sp. nov.
(Fig. 13)

Diagnosis. Cylindrical *Camerospongia* with a rounded terminal osculum. The lateral outer surface is covered with large low-conical outgrowths irregularly distributed.

Derivation of name. From the Latin adjective ‘tuberculatum’ (bearing tubercles).

Material. Seven specimens. Holotype: MSNVE-22973. Paratypes: MSNVE-22976, MCZ-PAL 3753. Other material: MCZ-PAL 3706, 3754; MSNVE-22907, 22916.

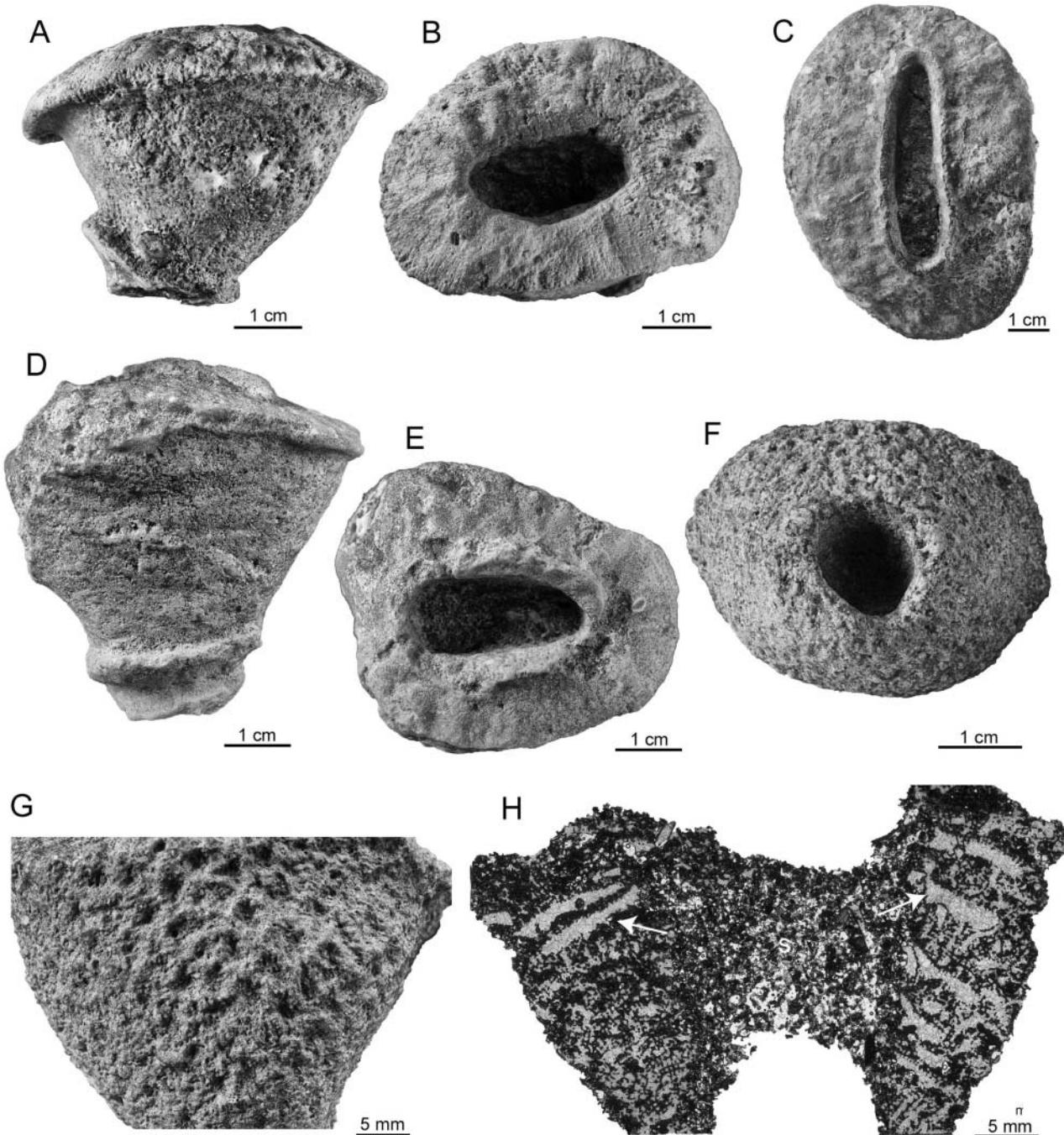


Figure 12. *Camerospongia visentinae* sp. nov. **A, B**, holotype, MCZ-PAL 3784c; **C**, MCZ-PAL 3775; **D, E**, paratype, MCZ-PAL 3712; **F–H**, paratype MCZ-PAL 3781. **A**, lateral view: see the low conical shape and the uppermost part of the sponge forming an overhanging ledge on the lateral surface; **B**, top view of an elliptical terminal osculum surrounded by a smooth membrane; **D**, lateral view showing the ledge at the base of the sponge; **C, E**, top views showing elliptical oscula around which a small elevated rim is present; **F**, top view of a rounded terminal osculum; **G**, detail of the lateral outer surface with irregularly distributed rhomboidal canal openings; **H**, longitudinal thin section, large radial canals (arrows) cross the sponge wall. A conical spongocoel(s) extends to the base of sponge.

Type locality and stratum. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian volcaniclastics.

Description. Cylindrical sponge slightly narrowing towards the base, 2.4–2.8 cm in diameter and 1.7–4.1 cm

high. The holotype (MSNVE–22973) is 2.5 cm in diameter and 3.5 cm high. The uppermost part of the sponge has a larger diameter than the rest and forms an overhanging ledge over the lateral surface (Fig. 13A, C). The terminal osculum is large and rounded (0.7–1.1 cm). The surface

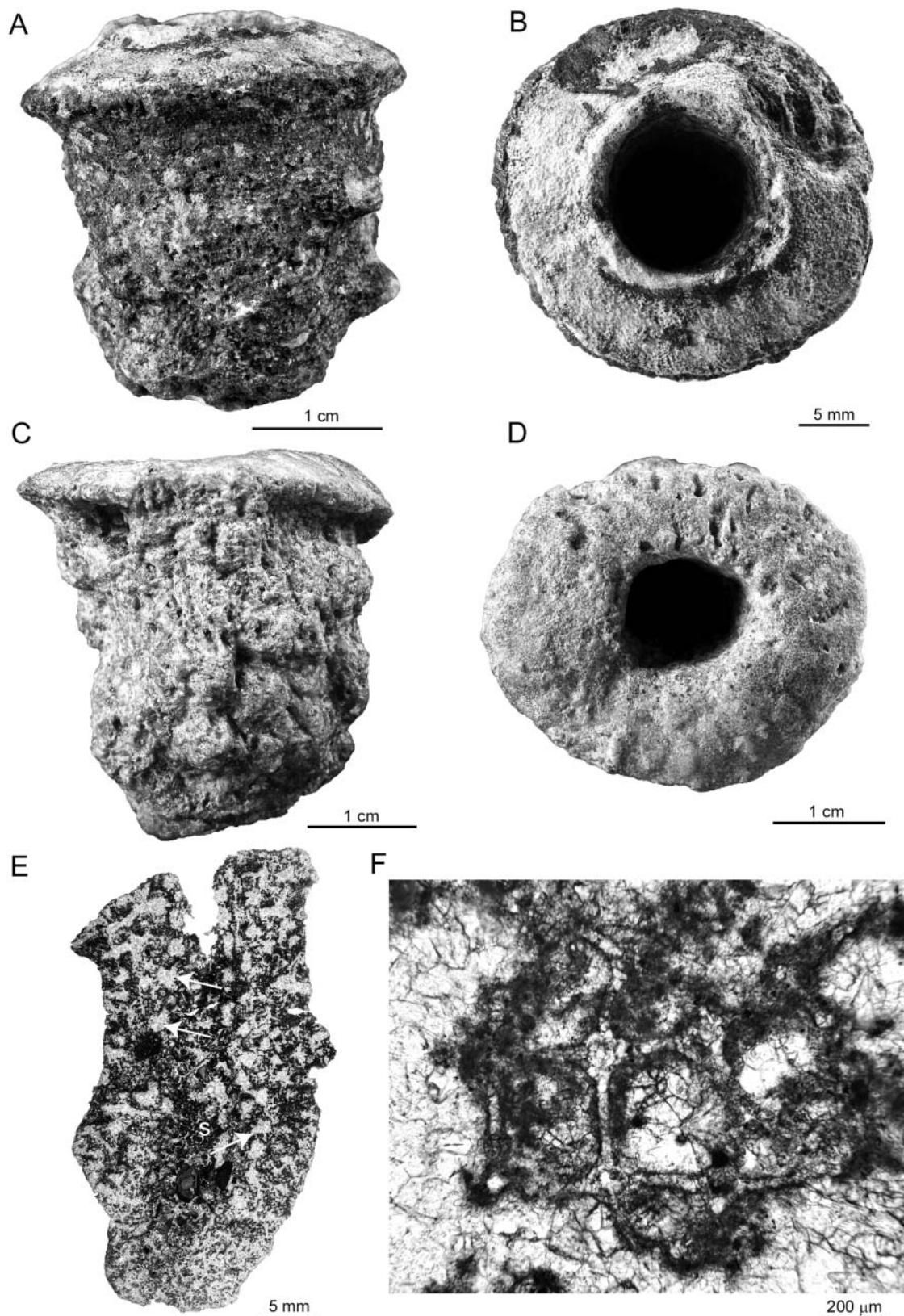


Figure 13. *Camerospingia tuberculata* sp. nov. **A, B**, holotype, MSNVE–22973; **C, D**, paratype, MSNVE–22976. **A, C**, lateral views showing cylindrical shape with an overhanging uppermost part and low conical outgrowths on the sides; **B, D**, top views showing the rounded terminal osculum surrounded by a finely porous membrane; **E**, MCZ-PAL 3753, longitudinal section showing the narrow and cylindrical spongocoel (s) running through the entire sponge and the radial canals (arrows); **F**, MCZ-PAL 3753 detail of thin section showing square meshes with lychniscs.

around the terminal osculum is flat and smooth, suggesting the original presence of a siliceous membrane (Fig. 13B, D). On the lateral surface there are outgrowths 4–5 mm in diameter and 3–4 mm tall. The spongocoel is narrow and cylindrical, running through the entire sponge. The canals are 0.8–1.6 mm in diameter (Fig. 13E). The skeleton has lychniscs with node-to-node connections and quadrate (200–300 µm) to rectangular (150 × 300 µm) meshes (Fig. 13F).

Remarks. The specimen resembles the Jurassic *Multiloqua fungiformis* (Goldfuss, 1833) in general shape, but *M. fungiformis* has hexactines, not lychniscs. The morphologically closest species is *Camerospongia elongata* Lagneau-Héranger, 1962 from the Cretaceous of France. Our specimens are different in having solid low-conical outgrowths, while *C. elongata* has large tubular openings. The type species *C. fungiformis* (Goldfuss, 1831) on the other hand differs strongly in shape, being biconical to hemispherical or pyriform, and generally being provided with a stalk. Yet the stalk is not always developed in *C. fungiformis* (e.g. Olszewska-Nejbart & Świerczewska-Gładysz 2013).

Genus *Toulminia* Zittel, 1877

Type species. *Cephalites catenifer* Smith, 1848, p. 286.

Toulminia italica sp. nov.

(Fig. 14)

Diagnosis. Narrow to irregularly conical *Toulminia* with a large and elliptical terminal osculum and sometimes a second lateral one. The wall is thick and composed of fused tubes that form low conical outgrowths with rounded ends on the lateral surface. On the external lateral surface, variably developed siliceous membrane showing horizontal concentric lines. The choanosomal skeleton has quadrate to rectangular meshes.

Derivation of name. From the Latin for Italy.

Material. Five specimens. Holotype: MSNVE–22972. Paratypes: MCZ-PAL 3800, MSNVE–22910. Other material: MCZ-PAL 3792, MGP-PD 1044.

Type locality and stratum. Cengio dell’Orbo quarry, Chiampo, Italy, Eocene, Lutetian volcanics.

Description. Narrow to irregularly conical sponge (Fig. 14A, F) that is 3.1–7 cm high, 1.7–3.1 cm wide and 2–4 cm long. The holotype (MSNVE–22972) is 4.6 cm high, 3.1 cm wide and 2.5 cm long. The terminal osculum is elliptical, 0.2–0.5 × 0.7–1.5 cm wide (Fig. 14C, E, H). Some specimens have a second osculum on one side (Fig. 14B) that is elliptical and up to 1 × 0.3 cm wide. The spongocoel is narrow and elliptical in cross section. The wall is up to 15 mm thick and composed of tubes that

are 3–5 mm in diameter. Low-conical lateral outgrowths 5 mm in diameter and 3–5 mm in height are present, and have rounded ends (Fig. 14A, F). An external siliceous membrane on the upper part of the sponge is developed in the holotype (Fig. 14C). The external surface of all specimens displays, at the sides, a characteristic originally siliceous membrane showing horizontal concentric lines (Fig. 14A, D, G). The choanosomal skeleton is composed of lychniscs. In transversal section, meshes of the dictyonal skeleton are quadrate (400–500 µm, node to node) to rectangular (400 × 500 µm).

Remarks. The smooth surface around the terminal osculum supports the assignment to the family Camerospongidae Schrammen, 1912 (see Reid 2004c), while the thick wall composed of tubes and the lateral outgrowths point to the genus *Toulminia* Zittel, 1877. As observed by Olszewska-Nejbart & Świerczewska-Gładysz (2012), all currently known species of *Toulminia* (see Mantell 1822; Smith 1848; Hinde 1884 [1883]; Schrammen 1912) differ in the development of the terminal ends of tubes. The type species *Cephalites catenifer* Smith, 1848, for example, shows horseshoe terminations, while *Toulminia polonica* Dunikowski, 1889 is characterized by rounded openings on terminations. Our material shows low conical outgrowths with blind rounded ends similar to those of *T. wollemanni* Schrammen, 1912 from the Cretaceous of northern Germany, but the latter are more elongated and never exceed 2–3 mm in diameter. This is the first record of *Toulminia* outside the Cretaceous. As a consequence the last appearance of the genus is now moved forward to the Lutetian (Eocene).

?Family *Diapleuridae* Ijima, 1927

Genus *Coronispongia* gen. nov.

Type species. *Coronispongia confossa* sp. nov.

Derivation of name. From the Latin *corona* (= crown) for the general shape.

Diagnosis. Conical to cup-shaped sponge composed of branching and radiating tubes, with a deep spongocoel. The dictyonal skeleton is lychniscosid, canalized and generally irregular. The canal openings on the outer surface are rounded to elongated.

Remarks. The assignment of this new genus to a family is a critical issue, as there are different points of view in the literature. In the *Treatise* (Reid 2004c), the only truly canalized lychniscosid family is Dactylocalycidae Gray, 1867. This family has a complex history and was traditionally considered to belong to the Hexactinosida. According to Reiswig (1991), Reid’s (1958, 1962) transfer to the Lychniscosida was surprising. Reiswig (1991, 2002c), who studied the problem in detail, returned the family to Hexactinosida due to the lack of lychniscs in the

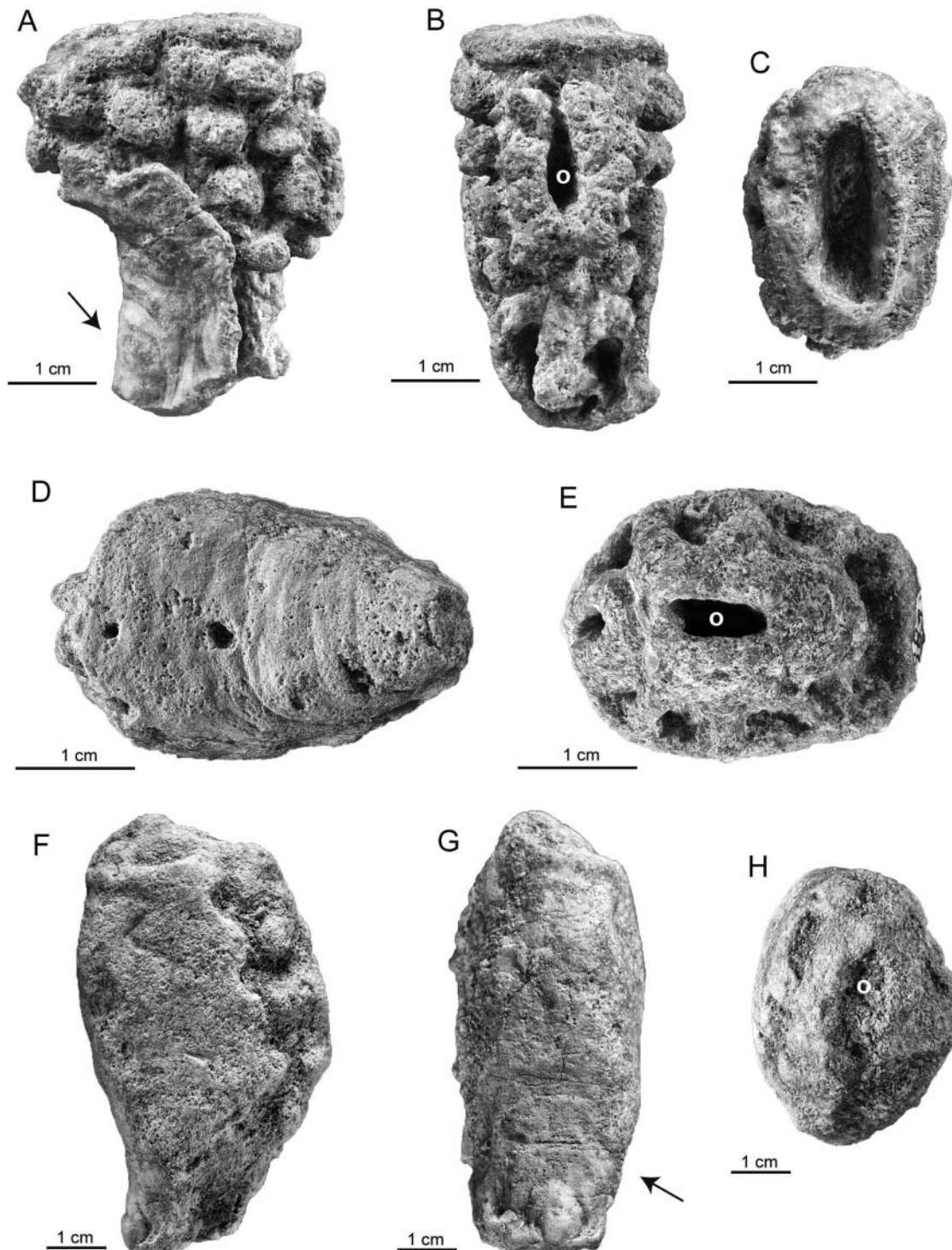


Figure 14. *Toulminia italica* sp. nov. **A–C**, holotype, MSNVE–22972; **D, E**, paratype, MSNVE–22910; **F–H**, paratype, MCZ-PAL 3800. **A**, side view, on the external surface conical outgrowths with rounded ends are visible, and an originally siliceous membrane with horizontal concentric lines at the base of the sponge is present (arrow); **B**, lateral view with a second lateral osculum (o); **C**, top view with an elliptical osculum surrounded by an originally siliceous membrane; **D**, lateral view showing an originally siliceous membrane with concentric lines; **E, H**, top views showing elliptical terminal oscula (o); **F**, lateral view, the originally siliceous membrane on the left side and the outgrowths with rounded end on the right side are visible; **G**, lateral view of the originally siliceous membrane with horizontal concentric lines (arrow).

dictyonal skeleton. Recent Lychniscosida include only two families: Aulocystidae and Diapleuridae (Reiswig 2002c). Taking into account the lack of loose spiculation and of many diagnostic characters – due to the poor preservation of our material – we tentatively locate the studied specimens in the Recent family Diapleuridae Ijima, 1927 (Reiswig 2002d). This decision is made on the basis of the similarity in skeletal canalization and the irregular framework of dictyonalia.

***Coronispongia confossa* sp. nov.
(Fig. 15)**

2005 *Brachiolites* sp. Matteucci & Russo: 57, pl. 1, fig. 2a, b.

Diagnosis. As for the genus.

Derivation of name. From the Latin *confossus* (= bearing holes), for the intradictyonal skeletal canals.

Material. Eight specimens. Holotype: MSNVE–22971. Paratypes: MSNVE–22979, MCZ-PAL 3783. Other material: MCZ-PAL 1381; MSNVE–23058; MCV 382, 385; MMC 16.

Type locality and stratum. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian volcaniclastics.

Occurrence. Cengio dell'Orbo and Lovara quarries, Chiampo, Italy, Eocene, Lutetian (Matteucci & Russo 2005; this study).

Description. Conical (Fig. 15A, C) to cup-shaped (Fig. 15F) sponges that are 5.4–9 cm high, 5.2–13.1 cm wide and 5.6–16 cm long. The holotype (MSNVE–22971) is 5.4 cm high and 6.5 cm in diameter. Wall is up to 30 mm thick. The wall is composed of a branching and anastomosing network of tubes 5–7 mm thick (Fig. 15A, C, F). The tubes circumscribe external cavedial spaces of approximately the same thickness. Tubes can be rounded at their ends (Fig. 15B, D). In the larger specimens, the wall is folded and fused to form a series of radial parietal tubes around the spongocoel (Fig. 15G). Radiating tubes are up to 15 mm wide and 40 mm long and have, distally, a circular opening (5–10 mm in diameter). The spongocoel is conical to cup shaped, and 3–6 cm deep. The dictyonal framework is irregular or, locally, with triangular to quadrate meshes (beams are 200 µm long, node to node). The intradictyonal canals are rounded (1–3 mm) to elongate (up to 5 mm in length) (Fig. 15E, H). The dictyonal skeleton is lychnicosid (Fig. 15I).

Remarks. Externally, *Coronispongia confossa* sp. nov. is extremely similar to the Cretaceous genus *Becksia* Schlüter, 1868, but *Becksia* is without an intradictyonal

canal system (e.g. Gasse *et al.* 1991) while *C. confossa* has rounded to elongated canals. Besides, the studied sponges are nearly identical in shape to the Recent hexactiniosid *Myliusia callocyathus* Gray, 1859. Nevertheless, our specimens show lychniscs and thus should be considered only homeomorphs of *M. callocyathus*. Homeomorphs are widespread among siliceous sponges, as shown by Reiswig & Wheeler (2002) in the case of the tortuous taxonomic history of the genus *Myliusia*. Our specimens are also very similar in shape to *Myliusia cancellata* Brimaud & Vachard, 1986b from the Miocene of Spain, but differ in spiculation (in *Myliusia* there are no lychniscs). Brimaud & Vachard (1986b) doubtfully synonymized the species with *Tretostamnia favosa* Pomel, 1872 from the Miocene of Algeria, suggesting also a revision of the taxon that was briefly described by Pomel (1872, pp. 70–71, pl. 2 bis, fig. 1). Matteucci & Russo (2005) assigned some of their specimens to the lychnicosid genus *Brachiolites* sp. This assignment should be treated with caution for the reason that an intradictyonal canal system was observed, while *Brachiolites* generally lacks channels (Reid 1962, p. 34; Reid 2004c). This new genus differs from the most closely related genus *Cavispongia* in having a deep spongocoel and in lacking tightly packed tubes.

**Family Neoaulocystidae Zhuravleva, 1962
Genus *Cavispongia* Quenstedt, 1877–8**

Type species. *Spongites cylindrata* Quenstedt, 1843, p. 418.

***Cavispongia scarpai* sp. nov.
(Fig. 16)**

2005 *Becksia*(?) Matteucci & Russo: 57, pl. 1, fig. 1a, b.

Diagnosis. Conical lychnicosan sponge composed of vertically packed cylindrical branches with regular to irregular circular terminal oscula. The external surface is knobby. A small tubular stalk could be present. The dictyonal skeleton has quadrate meshes.

Derivation of name. Dedicated to the amateur palaeontologist Giancarlo Scarpa (Mestre, Italy).

Material. Eighteen specimens. Holotype: MSNVE–23003. Paratypes: MSNVE–22843, MCZ-PAL 3716, MCZ-PAL 3794. Other material: MCZ-PAL 3717, 3718, 3719; MSNVE–22844, 22845, 22846, 22847, 22849, 22987, 23004, 23005, 23006, 23007, 23008.

Type locality and stratum. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian volcaniclastics.

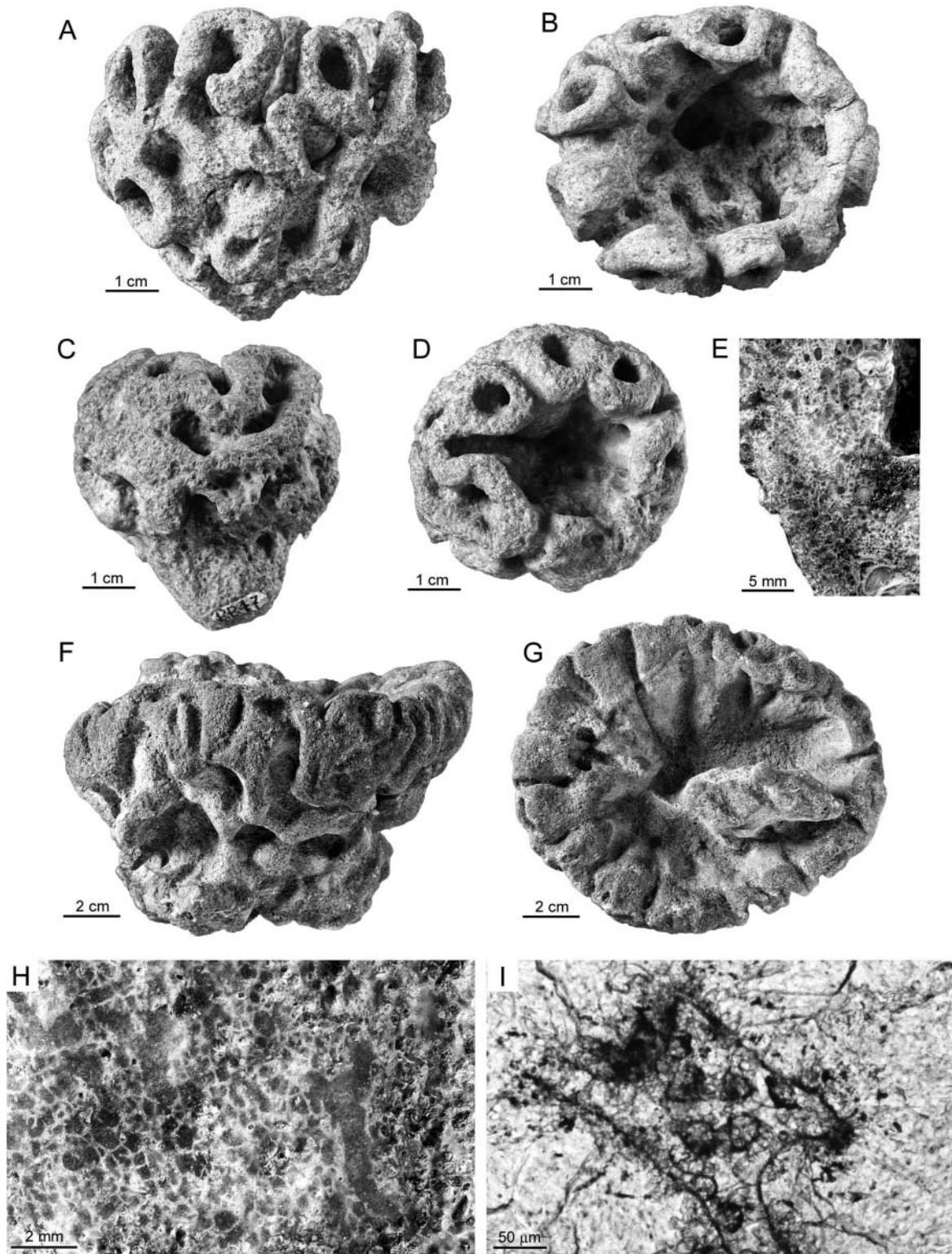


Figure 15. *Coronispongia confossa* gen. et sp. nov. **A, B**, holotype, MSNVE–22971; **C, D, E, I**, paratype, MSNVE–22979; **F–H**, paratype, MCZ-PAL 3783. **A, C, F**, lateral view, conical (**A, C**) or cup-shaped (**F**) sponges composed of branching and radiating tubes; **B, D**, top views of the deep spongocoel and circular openings of tubes; **E**, detail of a longitudinal section with rounded intradictyonal canals; **G**, top view, note the radial parietal tubes fused side by side around the spongocoel; **H**, detail of the upper surface of a parietal tube with elongated canal openings and the irregular skeletal framework; **I**, detail of a longitudinal thin section with a lychnisc.

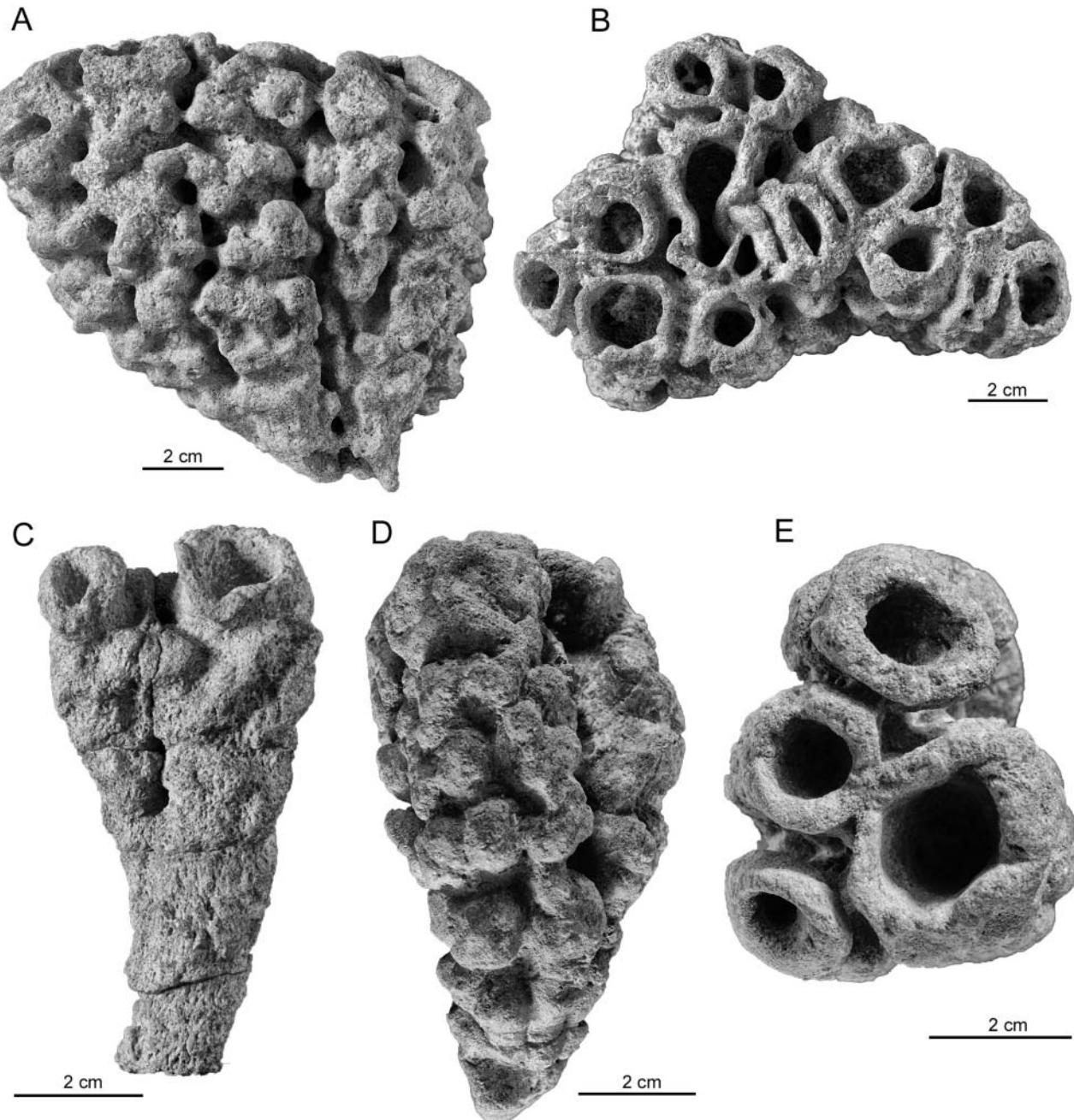


Figure 16. *Cavispongia scarpai* sp. nov. **A, B**, holotype, MSNVE-23003; **C**, paratype, MCZ-PAL 3794; **D, E**, paratype, MSNVE-22843 (photo: B. Favaretto). **A, C, D**, lateral views, showing the conical shape and the knobby external surface with meandering furrows; **B, E**, top views of the body composed of vertically packed tubes with regular to irregular circular terminal oscula; **C**, side view showing the tubular stalk at the base of the sponge.

Description. Conical sponge (Fig. 16A, C, D) 6.1–11.8 cm high, 4.1–14.5 wide and 2.4–9.5 cm long. The holotype (MSNVE-22003) is 11.8 cm high, 14.5 cm wide and 9.5 cm long. The body is usually composed of two to four (up to 12) cylindrical branches with generally circular terminal oscula 6–14 mm in diameter (Fig. 16B,

E), and wall 4–6 mm thick. The outer surface has rounded to roughly elongated knobs (Fig. 16A, D) 3–5 mm high, 6–8 mm wide and 9–21 mm long. The knobs are sometimes fused and separated by meandering furrows 3–6 mm wide. Some specimens show a small tubular stalk (Fig. 16C) 17 mm in diameter. The dictyonal

skeleton is preserved only in small sponge fragments. As a consequence only a few meshes could be observed. Meshes are mainly quadrate, beams are 300 µm long node to node.

Remarks. Matteucci & Russo (2005) identified with uncertainty this sponge as *Becksia* sp. In our material, the cylindrical tubes are mainly vertically packed while in *Becksia* sp. they are anastomosing. The general shape and knobby external surface are similar to *Mastospongia* Quenstedt, 1877–8 and *Trochobolus* Zittel, 1877. Diagnostic for these genera are the labyrinthine intradictyonal skeletal canals that were not observed in our material; however, this may be a preservational artefact. Yet features such as the general morphology, the body composed of vertically arranged tubes and the lateral surface with irregular outgrowths separated by meandriform furrows, suggest affinity with the Jurassic genus *Cavispongia* Quenstedt, 1877–8. In comparison with *C. cylindrata* Quenstedt, 1877–8 from the Upper Jurassic of the Swabian Alb (southern Germany) (see also Kolb 1910; Pisera 1997), our specimens show thicker walls of tubes and have generally larger size.

Class Demospongiae Sollas, 1885

Order Astrophorida Sollas, 1888

Remarks. Demosponges with desmas have been traditionally described as lithistid demosponges (from the order Lithistida Schmidt, 1870). Due to the fact that they have been found to be a polyphyletic group sharing just one common character that developed independently several times, i.e. the articulated choanosomal spicules called desmas, this taxon has been abandoned, and the families have been distributed mostly among Astrophorida and Spirophorida (Schuster *et al.* 2015). The term ‘lithistid sponges’ thus has no taxonomic significance, but exclusively a morpho-functional meaning.

Family Siphoniidae d’Orbigny, 1851

Genus *Siphonia* Goldfuss, 1826

Type species. *Siphonia piriformis* Hinde, 1884 [1883], p. 63.

?*Siphonia* sp.

(Fig. 17)

Material. Nine specimens: MCZ-PAL 3738; MSNVE-22811, 22810, 22894, 22988, 23000, 23096; IG-VI-272200, MGP-PD 1068.

Occurrence. Cengio dell’Orbo quarry, Chiampo, Italy, Eocene, Lutetian.

Description. Subglobular sponge (Fig. 17A–C) 4.1–8.3 cm in height, 4.2–7.5 cm in diameter, with a

wall 18–27 mm thick. A short stalk of 7–10 mm and a large terminal osculum 1–2 cm in diameter, surrounded by radial canals 1.5–2 mm wide and 10–35 mm long, characterize this taxon. On the outer surface, irregularly distributed rounded canal openings (Fig. 17D) 1–1.5 mm in diameter are present. Desmas are poorly preserved, probably smooth, tetraclasses (Fig. 17E).

Remarks. The typical stalked and subglobular habitus, the presence of a shallow central depression and the rounded canal openings on the outer surface support assignment to the genus *Siphonia* Goldfuss, 1826. The piriform shape appears in different ‘lithistid sponges’, e.g. *Scytalia curta* Moret, 1926 (with rhizoclasses desmas) and *Melonella radiata* (Quenstedt) (didymoclasses). Our specimens resemble also in shape another tetracladine, *Phyllocladia* Schrammen, 1924. *Siphonia* and *Phyllocladia* differ in the ectosomal spicules, which are not preserved in our material. As a consequence, the assignment of our specimens to *Siphonia* is tentative. Menin (1972) and Visentini (1994) already reported the presence of *Siphonia* sp. in the Lovara and Cengio dell’Orbo quarries. Catullo (1856) reported *Siphonia* from the Cretaceous and Eocene of north-eastern Italy, but recently Matteucci & Russo (2011) demonstrated that none of the specimens described by Catullo belong to siliceous sponges. Manzoni (1882) reported a doubtful *Siphonia* from the Miocene of northern Italy.

Genus *Rhoptrum* Schrammen, 1910

Type species. *Rhoptrum scytaliforme* Schrammen, 1910, p. 104.

?*Rhoptrum* sp.

(Fig. 18)

Material. Two fragmentary specimens: MCZ-PAL 3732, 3742.

Occurrence. Cengio dell’Orbo quarry, Chiampo, Italy, Eocene, Lutetian.

Description. Subcylindrical to cylindrical sponge fragments (Fig. 18A, B) that are 4.2–4.5 cm in diameter, with wall 13–20 mm thick and a central spongocoel 1.5–2.5 cm in diameter. Rounded canal openings 0.7–2 mm in diameter are irregularly distributed on the external surface. The choanosomal skeleton shows radial and longitudinal canals 0.5–1 mm wide (Fig. 18C), and is composed of tetraclass desmas (Fig. 18D), probably smooth, that are up to 450–569 µm in size.

Remarks. This sponge strongly resembles in shape the Cretaceous tetracladine genus *Rhoptrum*. It also shows affinities to another Cretaceous tetracladine, *Phymatella* Zittel, 1878. These two genera are very similar in general shape, canalization and canal opening pattern. The main

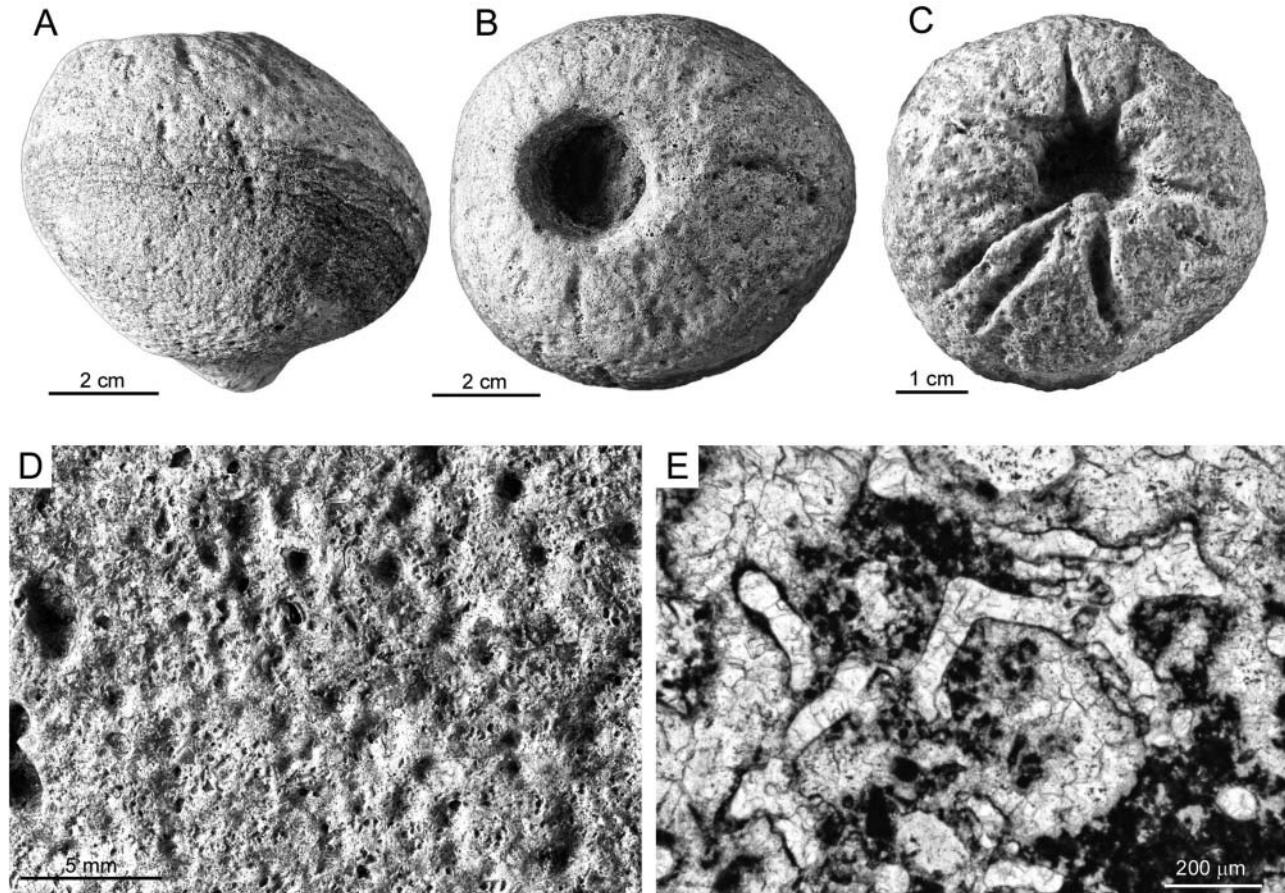


Figure 17. ?*Siphonia* sp. A, B, D, E, MCZ-PAL 3738; C, MSNVE-22810 (photo: B. Favaretto). A, lateral view, note the subglobular shape and the small stalk; B, C, upper views showing radial canals around large rounded terminal oscula; D, detail of the outer surface with poorly preserved rounded canal openings; E, detail of a longitudinal thin section with poorly preserved tetraclynes.

difference is in ectosomal spicules, which are not preserved in our material. As a consequence the assignment is uncertain. On the other hand, *Phymatella* is characterized by a tubular spongocoel with lateral chambers (e.g. Schrammen 1912; Świerczewska-Gładysz 2006) which are not visible in our material.

Family Corallistidae Sollas, 1888
Genus *Corallistes* Schmidt, 1870

Type species. *Corallistes typus* Schmidt, 1870, p. 22.

***Corallistes multiosculata* sp. nov.**
(Fig. 19)

Diagnosis. Club- or double club-shaped sponge. Numerous small circular oscula are found on the flat or slightly convex top; the lateral surface is finely porous. The base is an encrusting disc. The desmas are strongly arched and tuberculated dicranoclynes.

Derivation of name. For the many oscula (in Latin) on the top of the sponge.

Material. Twelve specimens. Holotype: MSNVE-22912. Paratypes: MCZ-PAL 3705, 3755. Other material: MCZ-PAL 3756, 3762; MSNVE-22911, 22913, 22914, 22991, 22994; MGP-PD 1069, 1070.

Type locality and stratum. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian volcanics.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian.

Description. Small club- (Fig. 19A) or double club-shaped (Fig. 19D) sponge 2.3–5 cm high, 1.1–4.3 cm wide and 1.2–1.8 cm long. The holotype (MSNVE-22912) is 3.9 cm high, 1.8 cm wide and 1.5 cm long. On the top, numerous circular oscula are present (Fig. 19B, E) which are 1–1.5 mm in diameter and 1–2 mm apart from one another. The lateral surface is finely porous with rounded canal openings

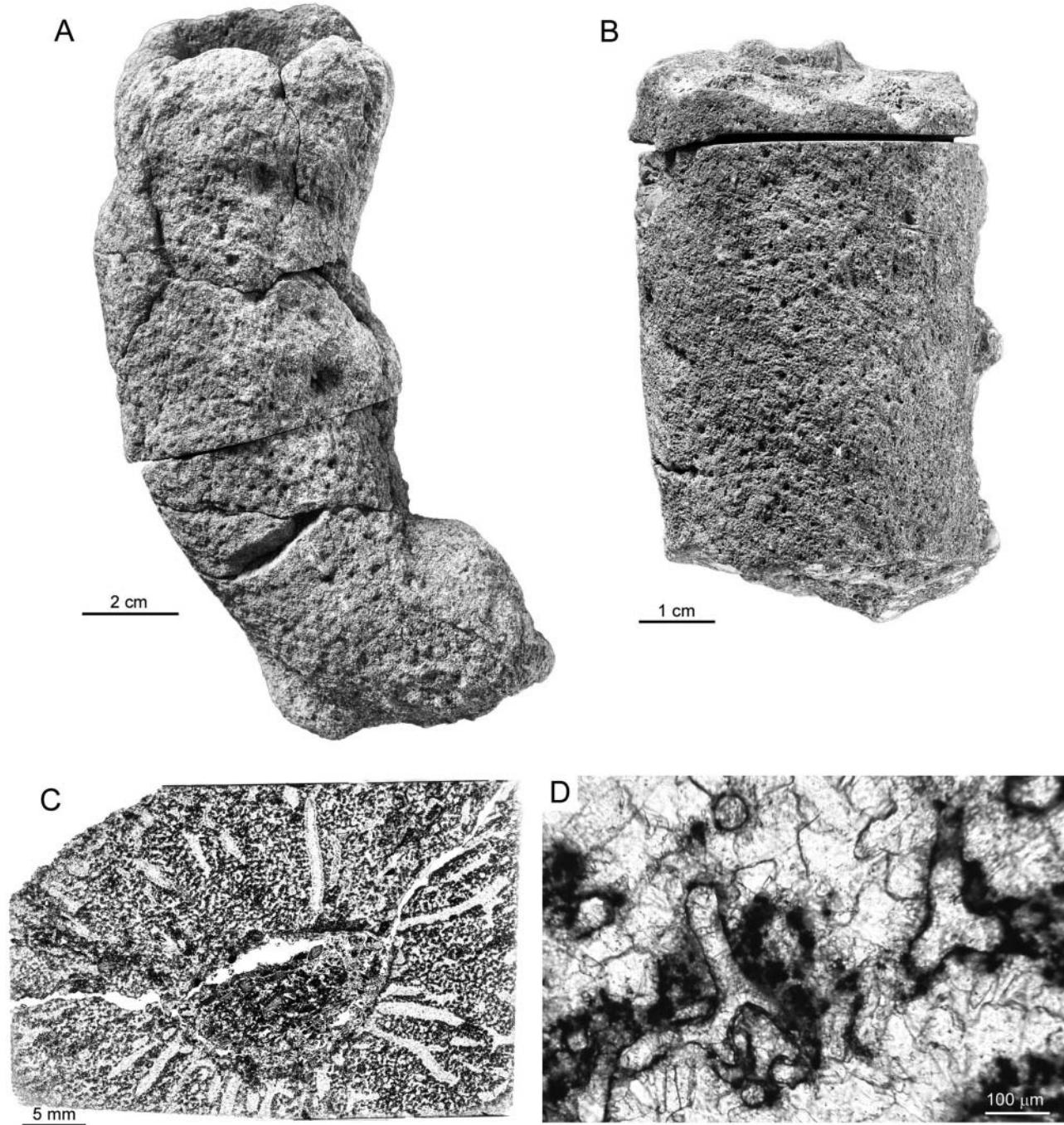


Figure 18. ?*Rhoptrum* sp. **A, C, D**, MCZ-PAL 3742; **B**, MCZ-PAL 3732. **A, B**, lateral view of cylindrical fragments with irregularly distributed rounded canal openings on the external surfaces; **C**, transverse thin section showing the thick wall and the large radial canals; **D**, detail of (C) with poorly preserved tetraclynes.

measuring 0.3 mm in diameter (Fig. 19D). A basal encrusting disc up to 2 cm in diameter is sometimes present (Fig. 19A). In cross section, vertical canals 0.8–1 mm in diameter are seen that lead to the openings visible on the top surface (Fig. 19C). Desmas are dicranoclynes 120–200 µm in size (Fig. 19F). Some

fragments of monaxial spicules (Fig. 19G) 200–400 µm in length, 20 µm wide were also observed. Because these spicules were observed in thin section only, they could be genuine monaxial – oxeas, strongyles or styles (tips are not clearly visible) – or fragments of triaene rhabdomes.

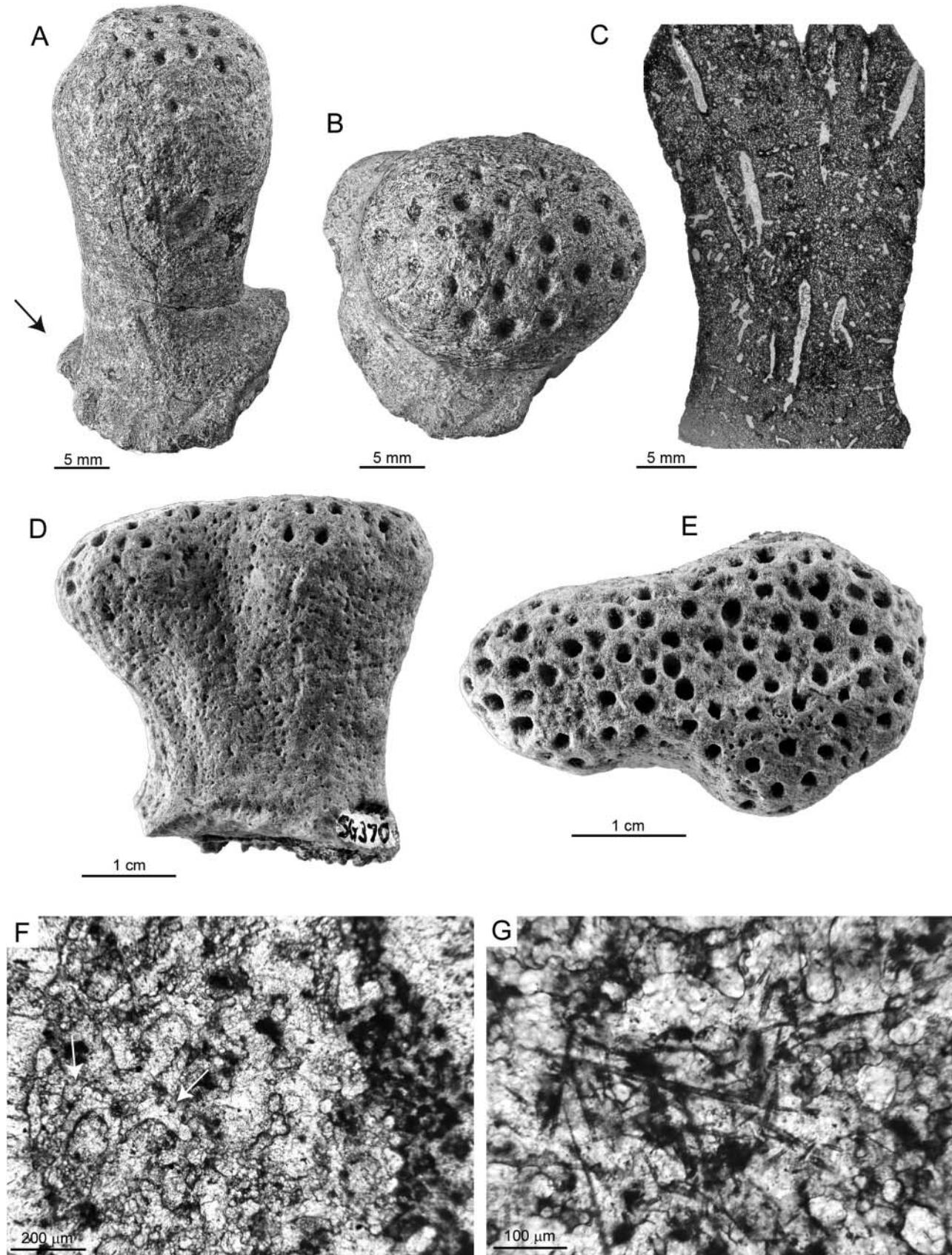


Figure 19. *Corallistes multiosculata* sp. nov. **A, B**, holotype, MSNVE–22912; **C, D, E, G**, paratype, MCZ-PAL 3705; **F**, paratype, MCZ-PAL 3755. **A**, club-shaped sponge with encrusting base (arrow); **B, E**, top of the specimens with numerous small rounded oscula; **C**, longitudinal thin section with vertical canals; **D**, double club-shaped sponge with slightly convex top and finely porous external membrane; **F**, detail of longitudinal thin section with dicranoclonies desmas (arrowheads); **G**, detail of the top part of (C) with desmas and monaxial fragments.

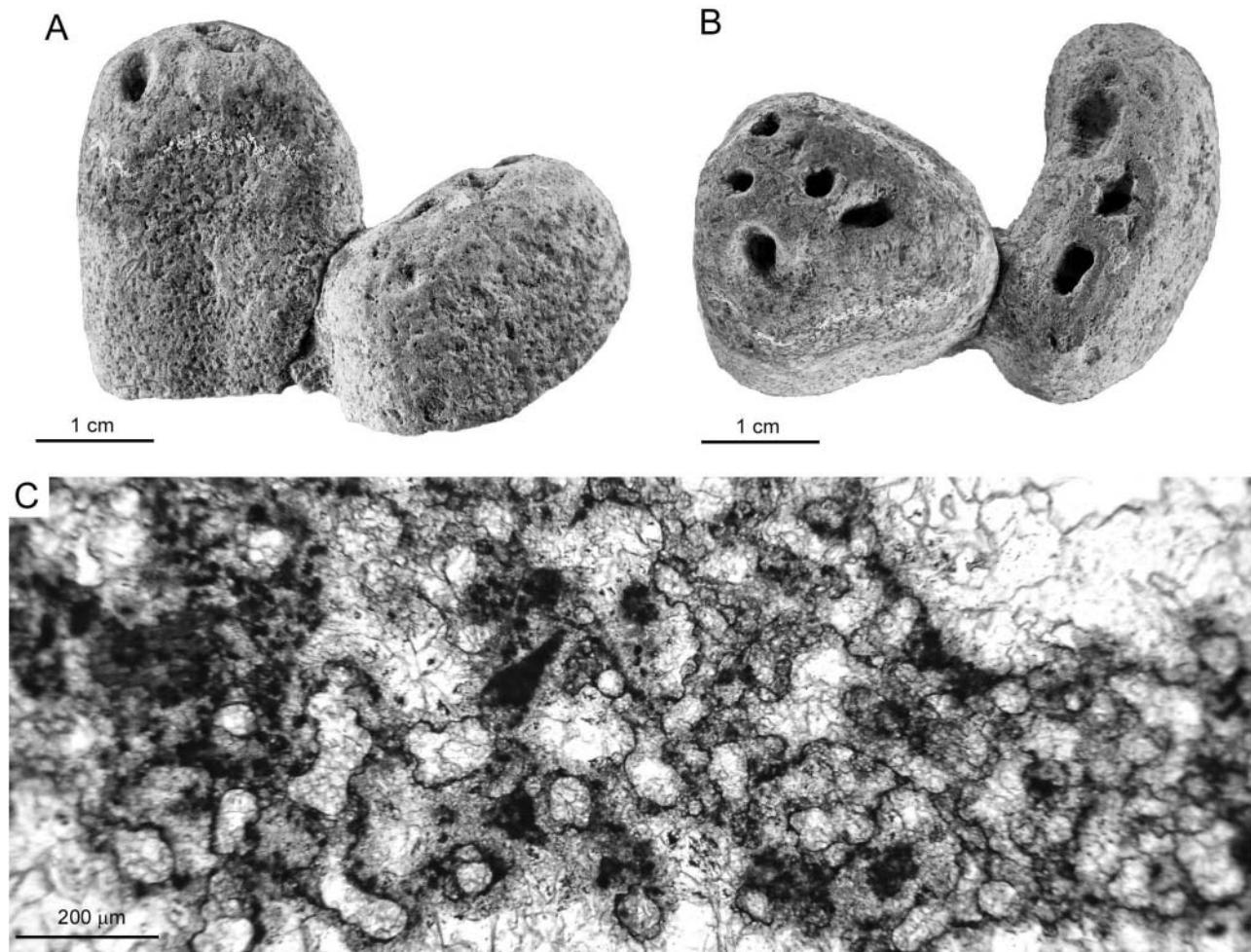


Figure 20. ?*Corallistes* sp. A–C, MCZ-PAL 3707. A, lateral view of the sponge composed of two subglobular parts; B, top view with rounded to elliptical oscula; C, detail of a longitudinal thin section, showing poorly preserved tuberculate desmas.

Remarks. This sponge is very close in shape and oscula organization to *Meta* sp. (Pomel, 1872), synonymized without figures by Moret (1924) with *Stichophyma ovoidea*. Pomel did not illustrate spicules, but *Stichophyma* has rhizoclones, not dicranoclones. Shape and canal openings on the top are comparable with those of the Recent corallistid species *Neophrissospongia microstylifera* (Lévi & Lévi, 1983) from New Caledonia. Our species differs morphologically from the type species *C. typus* which has a cup or vase shape.

?*Corallistes* sp.
(Fig. 20)

Material. One specimen: MCZ-PAL 3707.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian.

Description. Subglobular sponge 2.8 cm high, 4.9 cm wide and 3.1 cm long. The body is composed of two

subglobular parts (Fig. 20A), with respectively three and five oscula on the top. The oscula are rounded (2 mm in diameter) or elliptical (2–3 × 4–5 mm), and separated by 2.5–3 mm (Fig. 20B). In cross section, vertical canals of 2.2–2.4 mm in diameter open on the top surface. Desmas are poorly preserved, tuberculate, and 40–60 μm thick, and resemble dicranoclones (Fig. 20C).

Remarks. Desmas are too poorly preserved for a more precise assignment, and their size could not be measured due to poor preservation. The specimen is similar to *Corallistes multiosculata* sp. nov., from which it differs in general shape and larger, less numerous oscula. The specimen is also similar in general shape and oscula organization to *Meta gregaria* Pomel, 1872. Nevertheless, Pomel's species is elongate, while our material has a subglobular shape.

Order Sphaerocladina Schrammen, 1924
Family Vetulinidae von Lendenfeld, 1903
Genus *Ozotrachelus* de Laubenfels, 1955

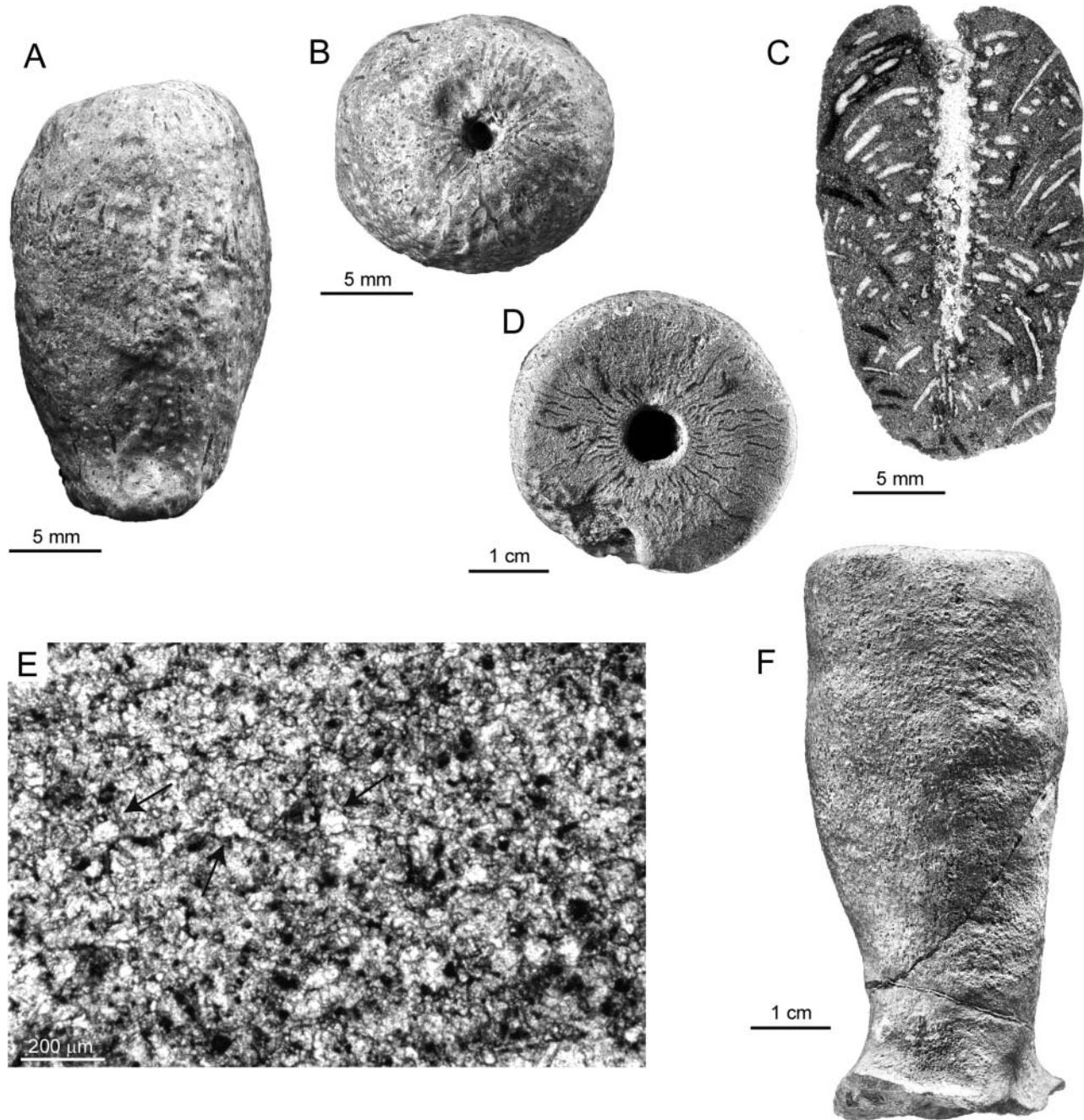


Figure 21. *Ozotrachelus conicus* (Roemer, 1841). A, B, C, E, MCZ-PAL 3761; D, F, MSNVE–22982. A, lateral view of a sponge with conical shape, rounded top and small canal openings on the outer surface; B, D, top views, showing canals radiating from the margins of rounded terminal oscula; F, lateral view of a sponge with conical shape, flat top and encrusting base; C, longitudinal thin section showing a cylindrical spongocoel and canals oriented obliquely downward; E, detail of (C) with spheroclynes desmas (arrows).

Type species. *Pachytrachelus expectatus* Schrammen, 1910, p. 174.

***Ozotrachelus conicus* (Roemer, 1841)**
(Fig. 21)

?1841 *Cnemidium conicum* Roemer: 4, pl. 1, fig. 10.
?1864 *Eudea tuberosa* Roemer: 25, pl. 10, fig. 3.

?1864 *Stellispongia?* *conica* Roemer: 49.
?1878 *Spongites conicus* (Roemer); Quenstedt: 374, pl.

133, fig. 3.

1910 *Pachytrachelus conicus* (Roemer); Schrammen: 171, pl. 24, fig. 1.

2004a *Ozotrachelus conica* (Roemer); Reid: 272, pl. 173, fig. 2i, j.

Material. Sixteen specimens: MCZ-PAL 3761; MSNVE-22932, 22982; MGP-PD 1045, 31431; MMC 1–8, 17–18; IG-VI 272202.

Occurrence. Sudmerberg and Petersberg, Germany, Cretaceous, Coniacian/Santonian (Schrammen 1910). Cengio dell’Orbo and Lovara quarries, Chiampo, Italy, Eocene, Lutetian (this study).

Description. Conical to cylindrical (Fig. 21A, F) sponges with rounded or, rarely, flat top, 1–7.4 cm high, 1.5–3.5 cm in diameter. An encrusting base may be present (Fig. 21F). The terminal osculum is rounded, 0.2–0.5 cm in diameter, and the wall is 6–19 mm thick. Radial canals are present on the top surface and run from the osculum margin to the top edge (Fig. 21B, D). The external surface has small (0.2–0.3 mm in diameter) rounded canal openings. The spongocoel is narrow, deep and cylindrical. Canals run horizontally or bend downward (0.3–0.7 mm wide) toward the sponge wall (Fig. 21C). Desmas are sphaeroclines (Fig. 21E), with 3–5 clones, approximately 200 µm in length (arm to arm).

Remarks. Our specimens are identical to *Pachytrachelus conicus* illustrated in Schrammen (1910). Some larger specimens that may belong to the same species show a flat top and cylindrical shape, but the type of desma is unrecognizable. The larger specimens seem more similar to *Phyllodermia houzeti* Ott d’Estevou, Termier & Termier, 1981 from the Miocene of southern Spain that have tetraclynes. Another morphologically similar species is *Cucumaltina placocephalus* Brimaud & Vachard, 1986a from the Miocene of southern Spain; however, this has rhizocline desmas. All the studied specimens are conical/cylindrical in shape, display radiating furrows on the top, and have a central rounded osculum and a deep, narrow spongocoel. Nevertheless, without well-preserved desmas, we cannot completely reject the idea that our material belongs to a different taxon. This is particularly true for the larger, cylindrical specimens. The species was reported previously only from the Upper Cretaceous of Germany. As a consequence, the range of the species is extended to the Lutetian (Eocene).

Order uncertain

Remarks. The systematic position of both Recent and fossil demosponges with rhizocline desmas is a matter of debate (Schuster *et al.* 2015): Recent sponges with rhizoclynes show affinities to Spirophorida (due to presence of sigmaspore microscleres in many taxa), but their relation to Astrophorida remains unclear.

Family **Azoricidae** Sollas, 1888
Genus **Bolidium** Zittel, 1878

Type species. *Amorphospongia palmata* Roemer, 1864, p. 55.

***Bolidium bertii* sp. nov.** (Fig. 22)

Derivation of name. Dedicated to the amateur palaeontologist Bruno Berti (Venice).

Diagnosis. Massive compound sponge, with lobated branches arising from a common, encrusting base. Various small, rounded oscula at the top of each branch. Two systems of canals are present, one vertical and larger, the other subhorizontal, finer and more meandriform. Desmas are rhizoclynes with rounded lumps.

Material. Three specimens. Holotype: MSNVE-22815. Paratype: MCZ-PAL 3769. Other material: MSNVE-23001.

Type locality and stratum. Cengio dell’Orbo quarry, Chiampo, Italy, Eocene, Lutetian volcaniclastics.

Description. Massive, large sponge 7–8.3 cm high, 10.9–16.2 cm wide and 8–15 cm long, composed of lobate branches (Fig. 22A, B) 2–3.4 cm thick and 2.5–6 cm long. The holotype (MSNVE-22815) is 8.3 cm high, 16.2 cm wide and 15 cm long. On top, various small, rounded oscula are present (Fig. 22C), 2–3 mm in diameter. The distance between oscula is 2–5 mm. Two systems of canals are seen in cross section, one vertical with canals 1.4–1.6 mm in diameter and the other subhorizontal and more meandriform, with canals 0.24–0.80 mm wide (Fig. 22D). Desmas are rhizoclynes 200–250 µm in length, covered with rounded lumps (Fig. 22E, F).

Remarks. Although the general morphology, shape of desmas and small oscula at the top of each branch fit with *Bolidium* descriptions, we were not able to observe in our material small pores on the external surface, probably due to inadequate preparation.

The compound shape, with *Jereica*-like branches arising from a common base and numerous small oscula on the top, is similar to *Polyierea dichotoma* Roemer, 1864 (p. 36, tab. 14, fig. 1) from the Late Cretaceous of northwest Germany, but this species has tetraclyne desmas. The exhalant system is very similar to that of *Jereica* Zittel, 1878, but our material is different because oscula are widely spaced, while in *Jereica* sp. they are closer and more numerous.

Rhizoclynes of the Cretaceous species *B. arbustum* Hurcewicz, 1968 are similar to those of *Jereica polystoma* (Roemer, 1864). Also similar are their arrangement in strands and the exhalant part. Because of these common features, Hurcewicz (1968) suggested a close relationship between *Bolidium* and *Jereica*. Schrammen (1910)

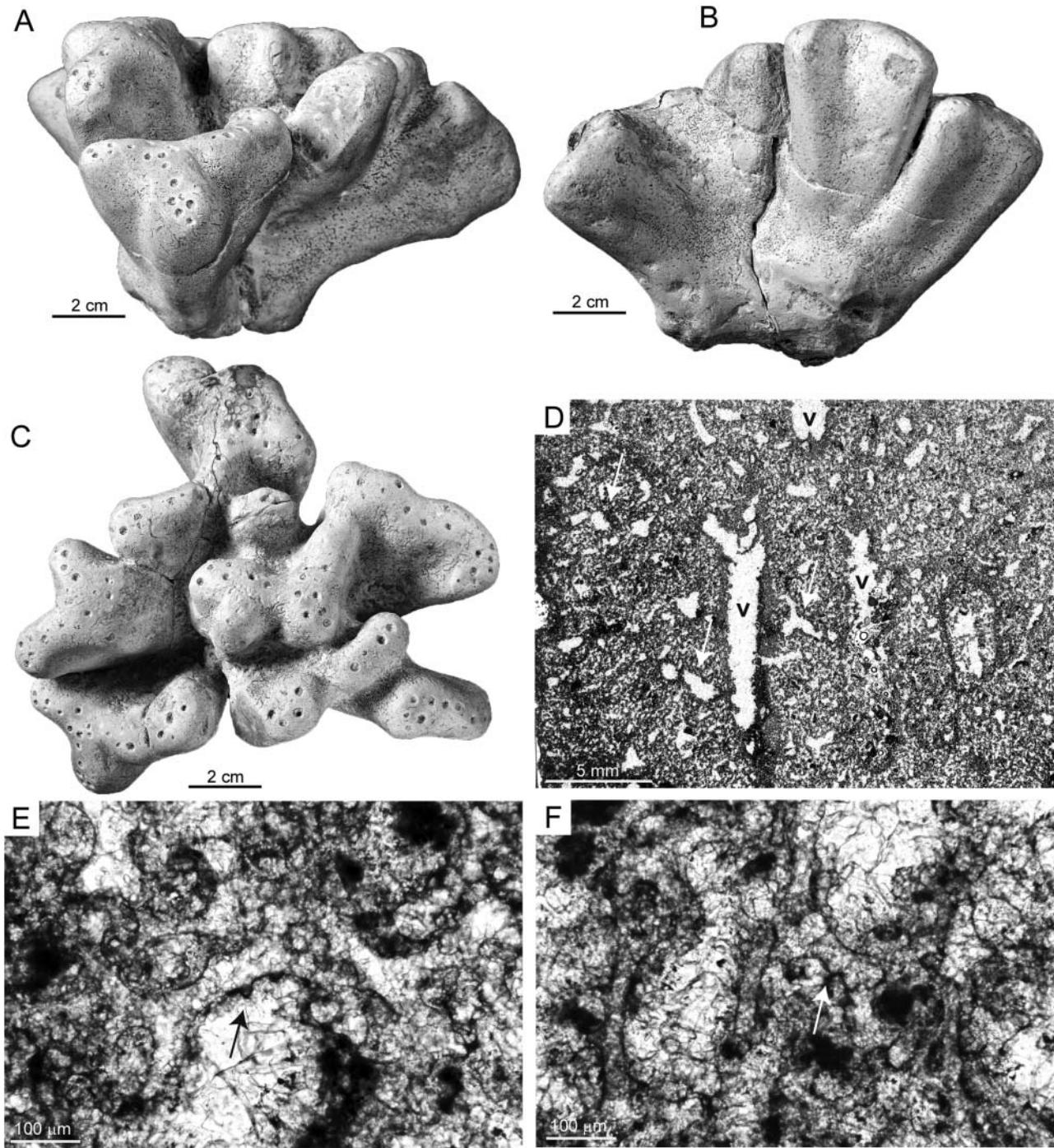


Figure 22. *Bolidium bertii* sp. nov. A–C, holotype, MSNVE–22815; D, E, F, paratype, MCZ–PAL 3769. A, B, side views of the massive sponge composed of lobate branches and having an encrusting base; C, top view of the lobate branches with numerous small rounded oscula; D, longitudinal thin section showing larger vertical canals (v) and smaller subhorizontal meandriform canals (arrows); E, F, detail of (D) showing rhizoclines with rounded lumps (arrows).

reported *B. palmatum* (Roemer, 1864) from the Cretaceous of Germany but without illustration.

This genus is known only from the Cretaceous of Europe: Germany (Roemer 1864; Zittel 1878; Schrammen 1910), Poland (Hurcewicz 1968) and Greece (Mermighis & Marcopoulou-Diacantoni 2004). This is the first record

of *Bolidium* from the Cenozoic and thus the range of the genus is extended to the Lutetian (Eocene).

Genus *Stachyspongia* Zittel, 1878

Type species. *Siphonocoelia spica* Roemer, 1864, p. 30.

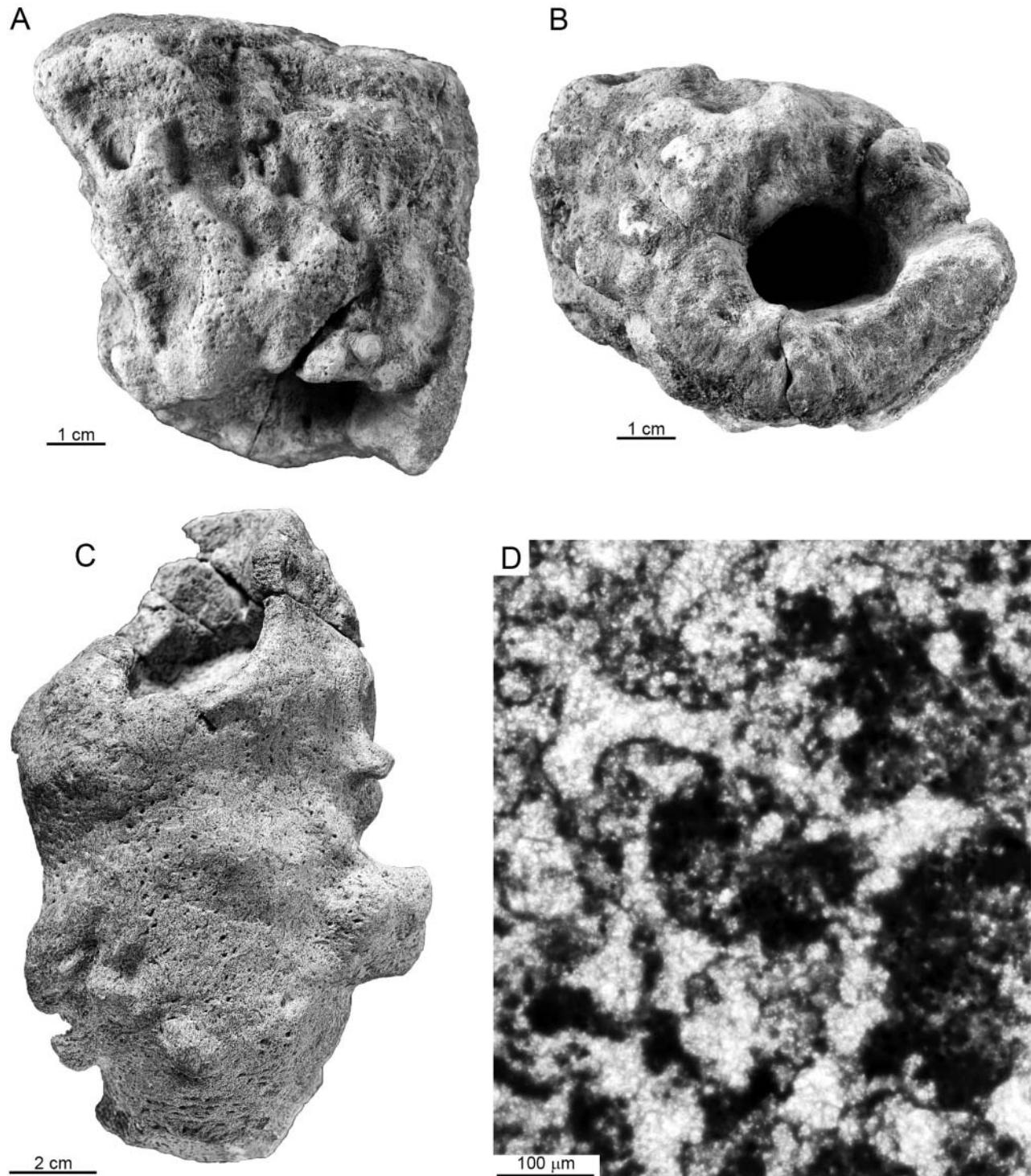


Figure 23. *Stachyspongia* sp. **A, B, D**, MCZ-PAL 3733; **C**, MSNVE-23022. **A, C**, lateral view showing the conical to subcylindrical shape, the irregular outgrowths, the irregularly distributed canal openings; **B**, top view of the circular osculum showing the thick sponge wall; **D**, detail of a longitudinal thin section with rhizoclone desmas.

***Stachyspongia* sp.
(Fig. 23)**

Material. Four specimens: MCZ-PAL 3733, MSNVE-23022, 22806, MMC 19 from Cengio dell'Orbo and Lovara quarries.

Occurrence. Cengio dell'Orbo and Lovara quarries, Chiampo, Italy, Eocene, Lutetian.

Description. Conical to sub-cylindrical sponge (Fig. 23A, C), 6–15 cm in height and 6–8.4 cm in diameter. The spongocoel is deep, tubular or slightly conical,

running throughout the sponge. A circular osculum is present (Fig. 23B), 3–4 cm in diameter. The wall thickness is 17–20 mm. The majority of the specimens bear, on the outer surface, irregular to cylindrical outgrowths (Fig. 23B, C) 6–12 mm high and 9–14 mm wide. Irregularly distributed canal openings, 0.4–0.5 mm in diameter, are situated on the outer surface. The skeletal framework is compact with radial canals (0.3–0.4 mm in diameter), and is composed of rhizoclone desmas (Fig. 23D).

Remarks. Due to the poorly preserved desmas, attribution below the genus level is not possible. The studied material shows thinner walls, and generally fewer and less developed outer surface outgrowths than other *Stachyspongia* species. The genus includes three species: *S. tuberculosa* (Roemer, 1864), *S. ramosa* (Quenstedt, 1877–8) and *S. spica* (Roemer, 1864), and is reported from the Cretaceous of Germany (Roemer 1864; Quenstedt 1877–8; Zittel 1878; Schrammen 1910), southern England (Hinde 1884 [1883]), France (Moret 1925), Spain (Lagneau-Hérenger 1962) and Poland (Hurcewicz 1968). There is only one dubious record of *Stachyspongia neoclavellata* (Chapman & Crespin, 1934) from the Eocene of Western Australia, but the Australian species is considerably smaller (5 cm in length, 2 cm in maximum width) than our material. The specimens illustrated by Chapman & Crespin (1934) and de Laubenfels (1953) have a ramosae (one is ‘H-shaped’) and elongated habitus that is not observed in our material. Pickett (1983) synonymized *S. neoclavellata* with the tetracladine ‘*Discodermia retepora*.

Genus *Jereopsis* Pomel, 1872

Type species. *Jereopsis inaequalis* Pomel, 1872, p. 178.

Jereopsis clavaeformis (Pomel, 1872) (Fig. 24)

1872 *Jerea clavaeformis* Pomel: 162, pl. 4, fig. 2.
1872 *Jerea acerra* Pomel: p. 167, pl. 18, fig. 3.
1924 *Jereica clavaeformis* (Pomel); Moret: 12, pl. 1, fig. 5, pl. 2, figs 2, 3, text-fig. 1 cum syn.
1986a *Jereopsis inaequalis clavaeformis* (Pomel); Brimaud & Vachard: pl. 7, fig. 7, pl. 8, fig. 4.
?2005 *Jereopsis(?) cf. clavaeformis* (Pomel); Matteucci & Russo: 59, pl. 1, fig. 9a, b.

Material. One specimen: MSNVE–22981.

Occurrence. Cengio dell’Orbo and Lovara quarries, Chiampo, Italy, Eocene, Lutetian (Matteucci & Russo 2005; this study); Djebel Djambeida and Beni bou Mileuk, Algeria, Miocene (Pomel 1872; Moret 1924); Pliego, Sorbas, Tercia, south-east Spain, Miocene (Ott d’Estevou *et al.* 1981; Brimaud & Vachard 1986a).

Description. Short, cylindrical sponge (Fig. 24A), 4.5 cm in height and 4 cm in diameter. It has a shallow, bowl-like terminal depression (Fig. 24C), 1 cm in diameter. No central spongocoel is present but a bunch of vertical canals occur which open in the terminal depression with small rounded openings (diameter 0.5 mm). There is another system of irregularly radial canals that open on the outer surface with rounded, irregularly distributed openings (Fig. 24B). Desmas are rhizoclones (Fig. 24D).

Remarks. Our specimen is identical in shape and terminal depression to *Jerea acerra* Pomel, 1872. The specimen illustrated by Matteucci & Russo (2005) shows on the external surface elongated outgrowths not observed in our material. The side canal openings have an irregular shape in their material while they are rounded in the material studied here. The general shape of our specimen is also similar to that of *Moretispongia micropora* Lagneau-Hérenger, 1962 from the Aptian (Cretaceous) of Spain, but our specimen lacks the typical rimmed canal openings on the sides. The exhalant system is very similar to a Recent rhizomarine from New Caledonia, *Jereicopsis graphicophora* Lévi & Lévi, 1983. *Jereopsis clavaeformis* (Pomel, 1872) was previously recorded from the Miocene only. The first occurrence of genus *Jereopsis* in the Eocene, suggested by Matteucci & Russo (2005), is thus here confirmed.

Family Scleritodermatidae Sollas, 1888

Genus *Verruculina* Zittel, 1878

Type species. *Chenendopora aurita* Roemer, 1864.

Verruculina ambigua (Pomel, 1872) (Fig. 25)

1872 *Pleurophyma ambigua* Pomel: 137, pl. 5 ter, figs 2, 3.
1924 *Verruculina ambigua* (Pomel); Moret: 15, pl. 2, figs 4, 4'.
1981 *Verruculina ambigua* (Pomel); Ott d’Estevou, Termier & Termier: 69, pl. 7, figs 4, 5, figs 6, 7?
1986a *Verruculina ambigua* (Pomel); Brimaud & Vachard: 309, pl. 4, figs 1–3.

Material. Seven specimens: MCZ–PAL 3802, MSNVE–22922, 22908; MMC 12, 13, 14, 15.

Occurrence. Cengio dell’Orbo and Lovara quarries, Chiampo, Italy, Eocene, Lutetian (this study); Djebel Djambeida and Beni bou Mileuk, Algeria, Miocene (Pomel 1872; Moret 1924); Pliego, Sorbas, Tercia, south-east Spain, Miocene (Ott d’Estevou *et al.* 1981; Brimaud & Vachard 1986a).

Description. Discoidal to cup-like (Fig. 25A) sponge, 3.2–7 cm in diameter. The wall thickness is 5–7 mm. The upper surface has numerous raised, rounded canal

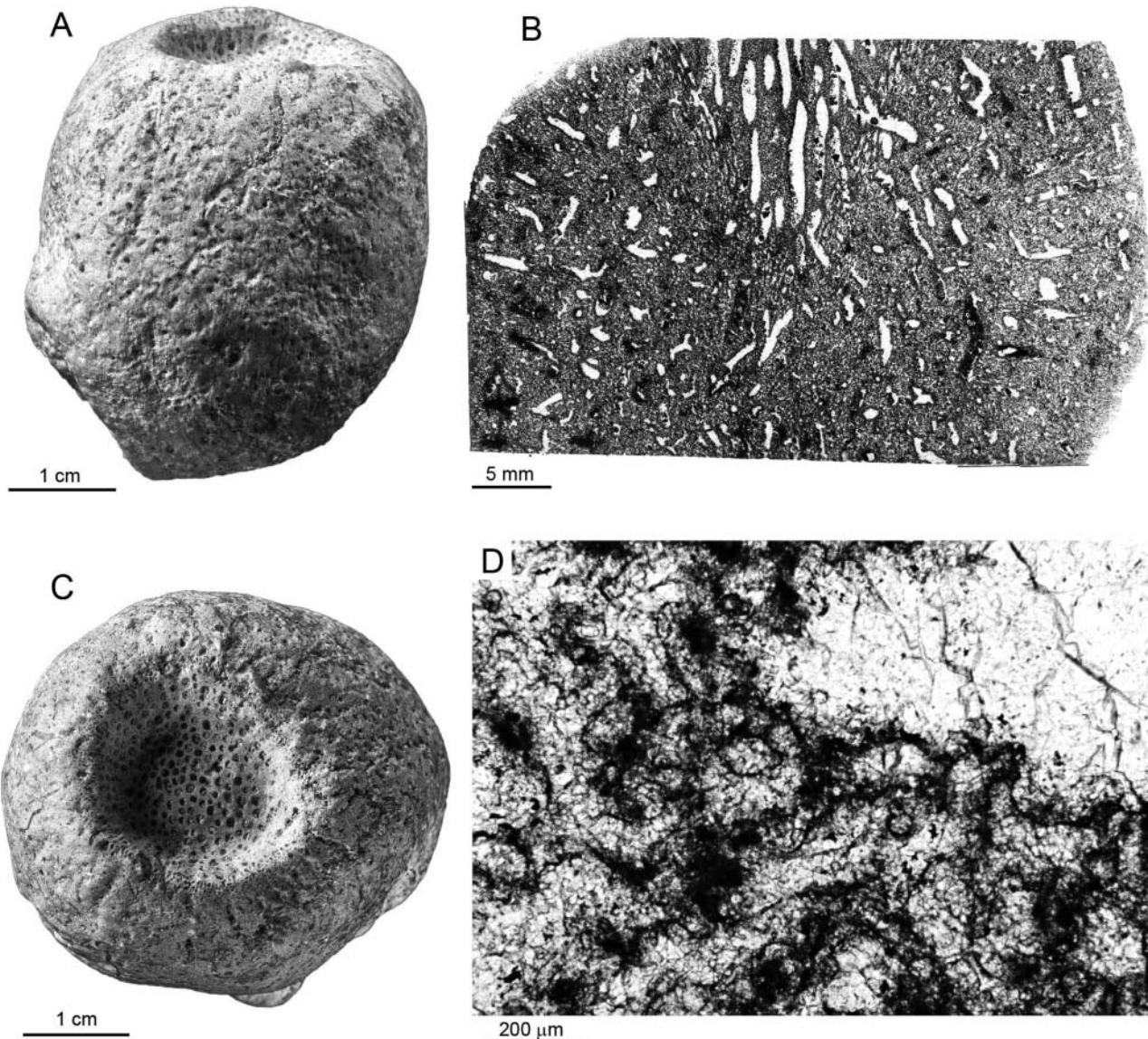


Figure 24. *Jereopsis clavaeformis* (Pomel, 1872), MSNVE–22981. **A**, lateral view showing the short cylindrical shape; **B**, longitudinal thin section showing the larger vertical canals and the smaller and shorter radial canals; **C**, top view of the shallow, bowl-like terminal depression with rounded canal openings; **D**, detail of (**B**) with rhizoclone desmas.

openings (Fig. 25B), irregularly distributed and 0.5–0.7 mm in diameter. The distance between canal openings is 2–3 mm. In thin section, a dense skeleton of heavily calcified desmas (Fig. 25C) was observed, but their shape was unrecognizable.

Remarks. The surface of all studied specimens appears to have been smoothed by mechanical preparation. Although typical rhizoclones were not observed, and characteristic raised canal openings were visible in one specimen only (MCZ-PAL 3802), we attribute all specimens to *Verruculina ambigua* (Pomel, 1872) for the general shape, the dense skeleton with desmas, and the pattern of canal openings on the upper surface. The smaller specimens are

discoidal, while the larger ones are vase-shaped. This feature was observed by Ott d'Estevou *et al.* (1981) as well. The species has been found in the Miocene of Algeria (Pomel 1872; Moret 1924) and southern Spain (Ott d'Estevou *et al.* 1981; Brimaud & Vachard 1986a). This is the first record of the species for the Eocene. *Verruculina albanyensis* Chapman & Crespin, 1934, from the Eocene of Western Australia (see also Pickett 1983), differs from the studied material in having a thicker wall (8–9 mm), and larger (1.75 mm in diameter) and less numerous canal openings on the upper surface.

Family **Platyponiidae** Schrammen, 1924
Genus **Platyponia** Zittel, 1878

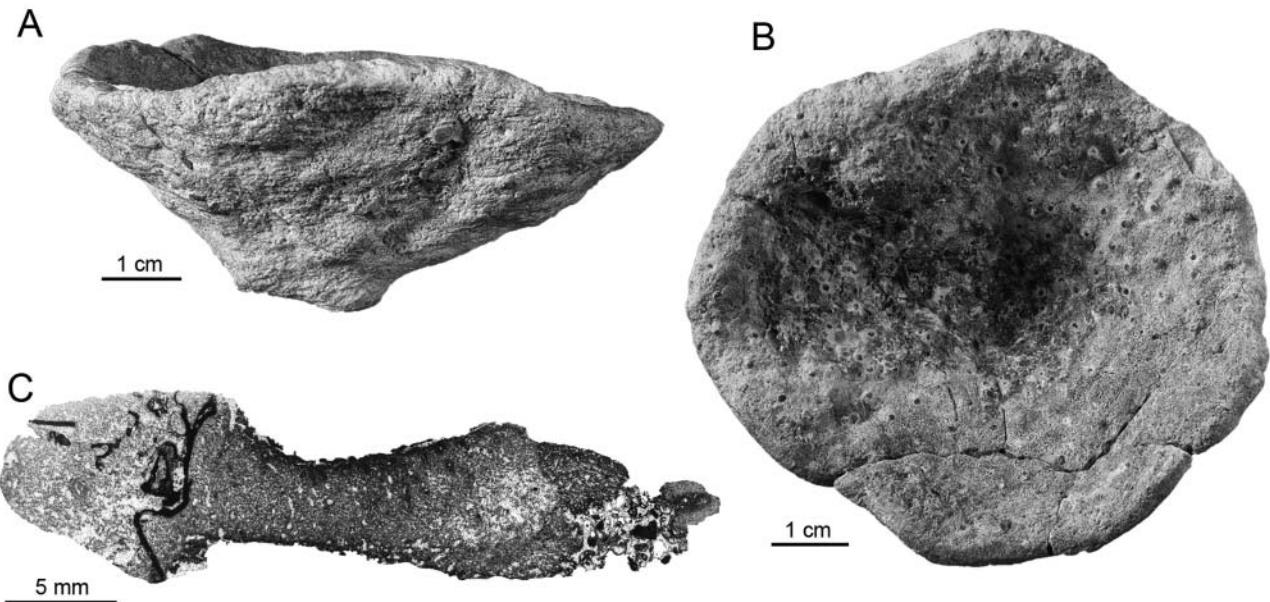


Figure 25. *Verruculina ambigua* (Pomel, 1872), MCZ-PAL 3802. **A**, side view showing the cup-like shape; **B**, top view with raised rounded canal openings; **C**, detail of longitudinal thin section with the dense, desma-bearing skeleton.

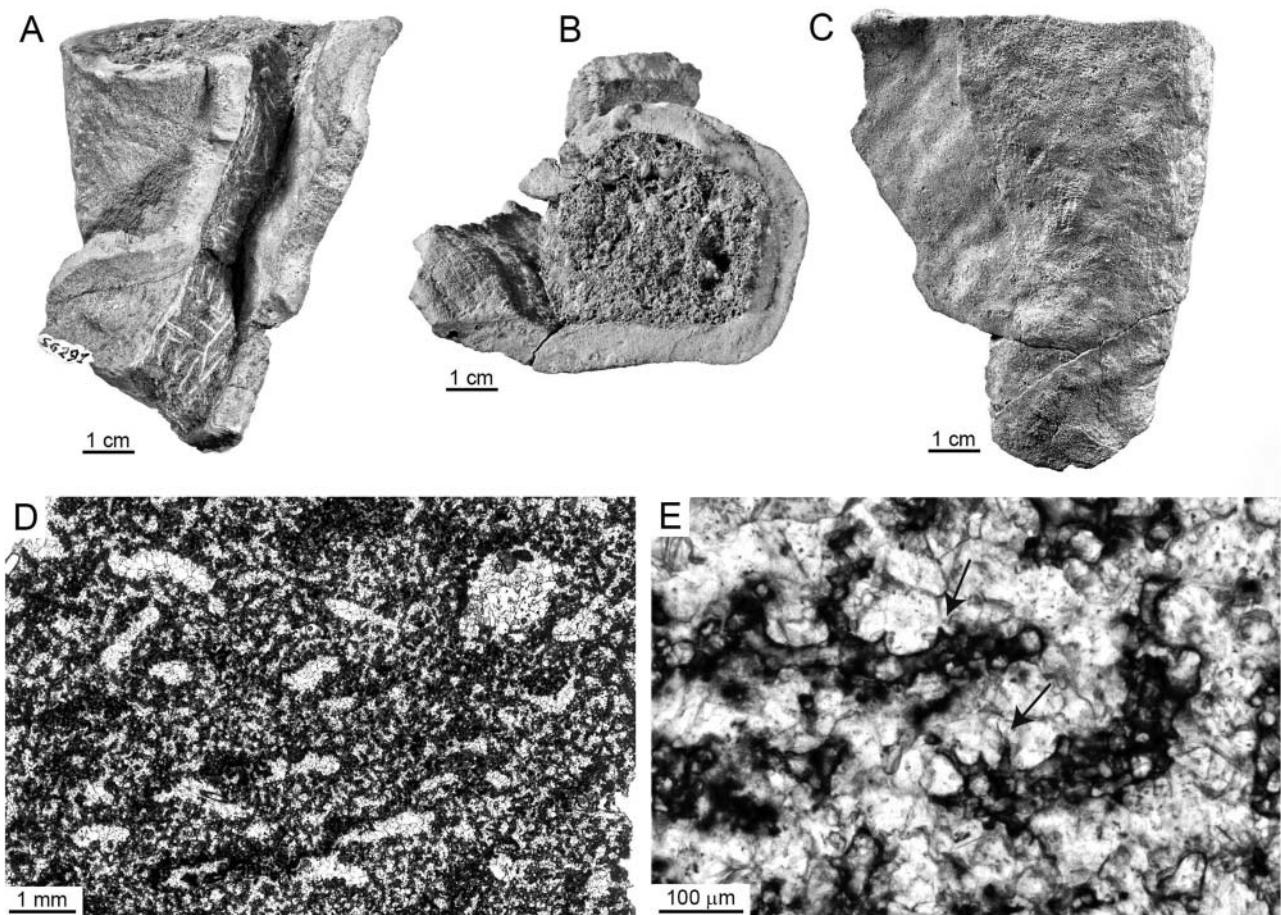
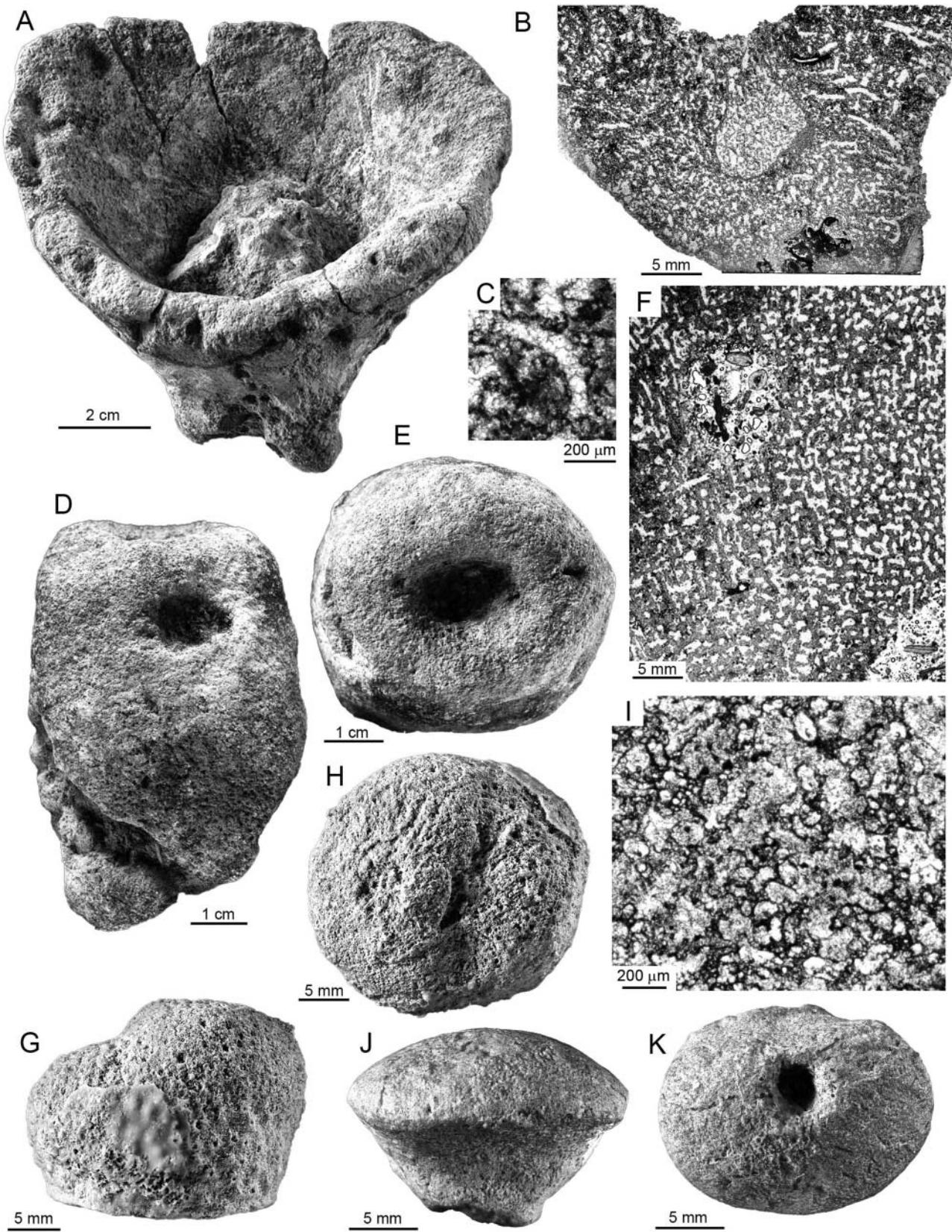


Figure 26. *Platychonia* sp. **A–C**, MCZ-PAL 3770; **D, E**, IG-PD 366222. Lateral (**A**) and top (**B**) views of a leaf-like specimen; **C**, detail of the upper surface with delicate pores; **D**, transverse thin section of the wall with the dense skeleton and small radial canals; **E**, detail of (**D**) with thorny rhizoclines (arrows).



Type species. *Spongites vagans* Quenstedt, 1858.

***Platychonia* sp.**
(Fig. 26)

Material. Two fragmentary specimens: IG-PD 366222, MCZ-PAL 3770.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian.

Description. Plate-like to leaf-like (Fig. 26A, B) sponge fragments 8.2 cm high, 4.1–6.8 cm wide and 2.7–4.7 cm long. Both surfaces are covered with delicate pores (Fig. 26C). The wall is 12 mm thick with small radial canals 0.22–0.36 mm in diameter (Fig. 26D). Thorny rhizoclines (Fig. 26E) 150–250 µm in length form a dense skeleton.

Remarks. The presence of rhizoclines, small canal openings on both surfaces, small radial canals and a leaf-like habitus support the attribution to the genus *Platychonia* Zittel, 1878. This is a typical Jurassic genus but it was reported also from the Eocene of Australia, with the species *Platychonia tertaria* Chapman & Crespin, 1934 (p. 117, pl. 11, fig. 22).

Unfortunately, the Australian species is poorly illustrated and preserved. The attribution to a rhizomorine lithistid is dubious as the desmas are described as globular and having “4 to 7 or more radiating arms” (Chapman & Crespin 1934, p. 117); thus, they could possibly be sphaeroclines. The leaf-like habitus is similar to that of other rhizomorine sponges: *Phlyctia expansa* and *Histiodia undulata* from the Miocene of Algeria, described by Pomel (1872) and revised by Moret (1924) and Pisera & Busquets (2002). Our material is different from *Phlyctia* in lacking the fibrous divergent skeletal structure, and from *Histiodia* in lacking external longitudinal furrows. In both Miocene genera, radial canals are missing. Another rhizomorine genus, *Chonellopsis*, has a very similar morphology but its canal openings are on the upper surface only (Schrammen 1937, p. 96), while the studied specimens show openings on both sides. Our material is comparable to the Cretaceous *Chonella tenuis* Roemer, 1864 (see Schrammen 1910, 1912), but it lacks the concentric growth lines, and the wall is thicker (12 mm in our material, 4–6 mm in *C. tenuis*).

Family uncertain
Indeterminate rhizomorine sp. A
(Fig. 27A–C)

Material. Three specimens: MCZ-PAL 3723, 3731; MSNVE-22992.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian.

Description. Vase-shaped and thick-walled (8–14 mm) sponge (Fig. 27A), 3–9 cm in height and 3.7–7.7 cm in diameter. Deep spongocoel. The surface is smooth, without canal openings. There are two systems of canals, one radial and larger, the other finer and meandritiform and descending from the top (Fig. 27B). Desmas are possibly rhizoclines (Fig. 27C).

Remarks. This specimen is left undetermined because it is poorly preserved. The habitus resembles that of the Jurassic rhizomorine genus *Hyalotragos* but the studied specimens lack the diagnostic vertical canals.

Indeterminate rhizomorine sp. B
(Fig. 27D–F)

Material. One specimen: MCZ-PAL 3736.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian.

Description. Cylindrical fragment (Fig. 27D) 7 cm high and 4.4 cm in diameter, having a thick wall. One large, circular osculum is present on the top (Fig. 27E). Rounded canal openings are visible in some parts of the surface. The skeleton framework is fibrous and composed of desmas that are possibly rhizoclines (Fig. 27F).

Remarks. Desmas are faintly visible in thin section. The skeleton framework is similar to that of *Phlyctia expansa* from Spain (Pisera & Busquets 2002), but this latter species is flat.

Indeterminate rhizomorine sp. C
(Fig. 27G–I)

Material. Three specimens: MCZ-PAL 3759, 3760; MSNVE-22928.

Figure 27. A—C, Indeterminate rhizomorine sp. A; A, C, MCZ-PAL 3731; B, MCZ-PAL 3723. A, lateral-top view of a vase-shaped sponge with a deep spongocoel; B, longitudinal thin section showing two systems of canals: one radial and larger, the other originating from the spongocoel, finer and meandritiform; C, rhizocline desma. D—F, Indeterminate rhizomorine sp. B, MCZ-PAL 3736; D, lateral view of a cylindrical shaped fragment; E, top view of the thick wall and circular terminal osculum; F, longitudinal thin section of the fibrous skeleton framework. G—I, Indeterminate rhizomorine sp. C, MCZ-PAL 3759; G, lateral view showing the subglobular shape and the rounded canal openings on the external surface; H, top view showing the faintly visible circular terminal osculum; I, detail of a longitudinal thin section with rhizocline desmas. J, K, Indeterminate rhizomorine sp. D, MSNVE-23032; J, lateral view of the ear-like shape sponge with encrusting base; K, top view of the rounded terminal osculum.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian.

Description. Subglobular sponge (Fig. 27G) 1.2–2.2 cm high and 2.3 cm in diameter. The terminal osculum is circular and shallow (Fig. 27H). No spongocoel was observed. On the external surface, rounded canal openings of 0.3–0.4 mm in diameter are found. Desmas are possibly rhizoclones (Fig. 27I).

Remarks. Due to the poor preservation of the material, the taxonomy of this sponge remains undetermined.

Indeterminate rhizomorine sp. D
(Fig. 27J, K)

Material. Eight specimens: MSNVE–23032, 22918, 22919, 22930, 22943, 22961; MGP-PD 1051, 1057.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian.

Description. Small, ear-like sponge (Fig. 27J) 1.1–1.9 cm in height and 1.4–2.5 cm in diameter. The base is encrusting, a central circular osculum 3.6 mm in diameter is seen (Fig. 27K) and the wall thickness is 6 to 10 mm. Small radial canals occur. Desmas may be tuberculated rhizoclones.

Remarks. Due to the poor preservation of the spicules, this taxon cannot be determined.

Indeterminate lithistid sp. A
(Fig. 28)

Material. One specimen: MCZ-PAL 3798.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian.

Description. Subglobular, massive sponge 3.8 cm high, 6 cm wide and 5.2 cm long. On the whole surface, numerous circular to elliptical oscula occur, 0.5–2.0 cm in diameter (Fig. 28A). The oscula have a 3–4 mm high rim (Fig. 28B). Short canals, 0.55–0.96 mm wide and 1.6–4.8 mm long, are present. A dense structure of completely calcified desma ghosts, outlined by peloidal micrite, has been observed in thin section.

Remarks. Our specimen is morphologically identical to the Upper Cretaceous *Discodermia gleba* Schrammen, 1910 (p. 98, tab. 15, fig. 2). Schrammen indicated a ‘chestnut’ size while our specimen is wider. Due to poor preservation, the type of desmas is not recognizable; thus, a taxonomic assignment is not possible.

Order **Agelasida** Hartman, 1980a
Family **Astroscleridae** Lister, 1900
Genus **Astrosclera** Lister, 1900

Type species. *Astrosclera willeiana* Lister, 1900, p. 459.

***Astrosclera* sp.**
(Fig. 29)

2005 *Pliobalia* [sic] (?) *vermiculata* Pomel; Matteucci & Russo: 59, pl. 3, fig. 1a, b.

Material. Three specimens: MCZ-PAL 3774, MSNVE–22893, 22805.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian.

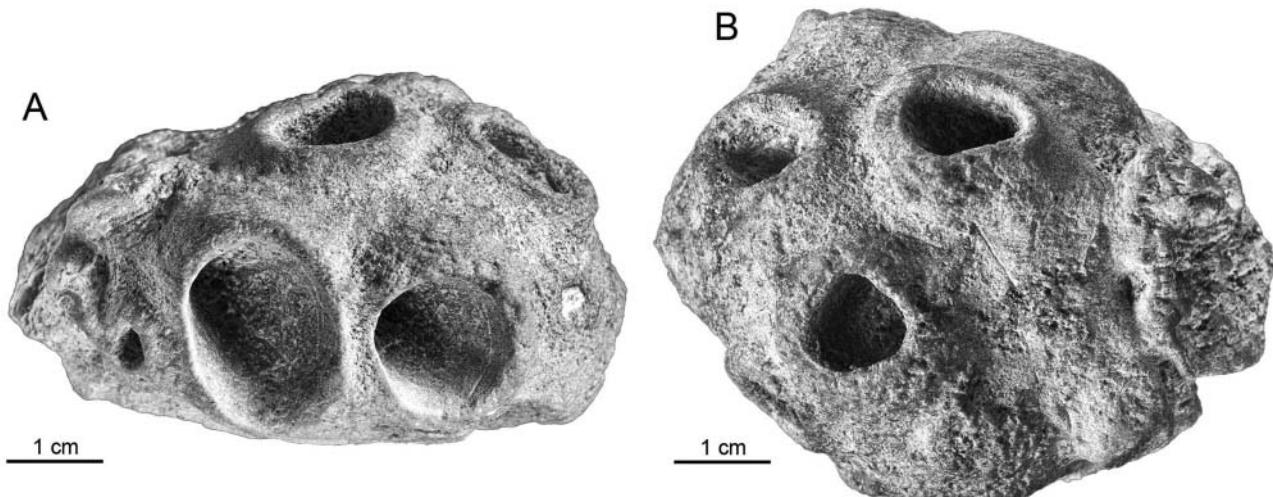


Figure 28. Indeterminate lithistid sp. A, MCZ-PAL 3798 **A**, lateral view of the sponge with subglobular shape, and large, circular and rimmed oscula; **B**, top view.

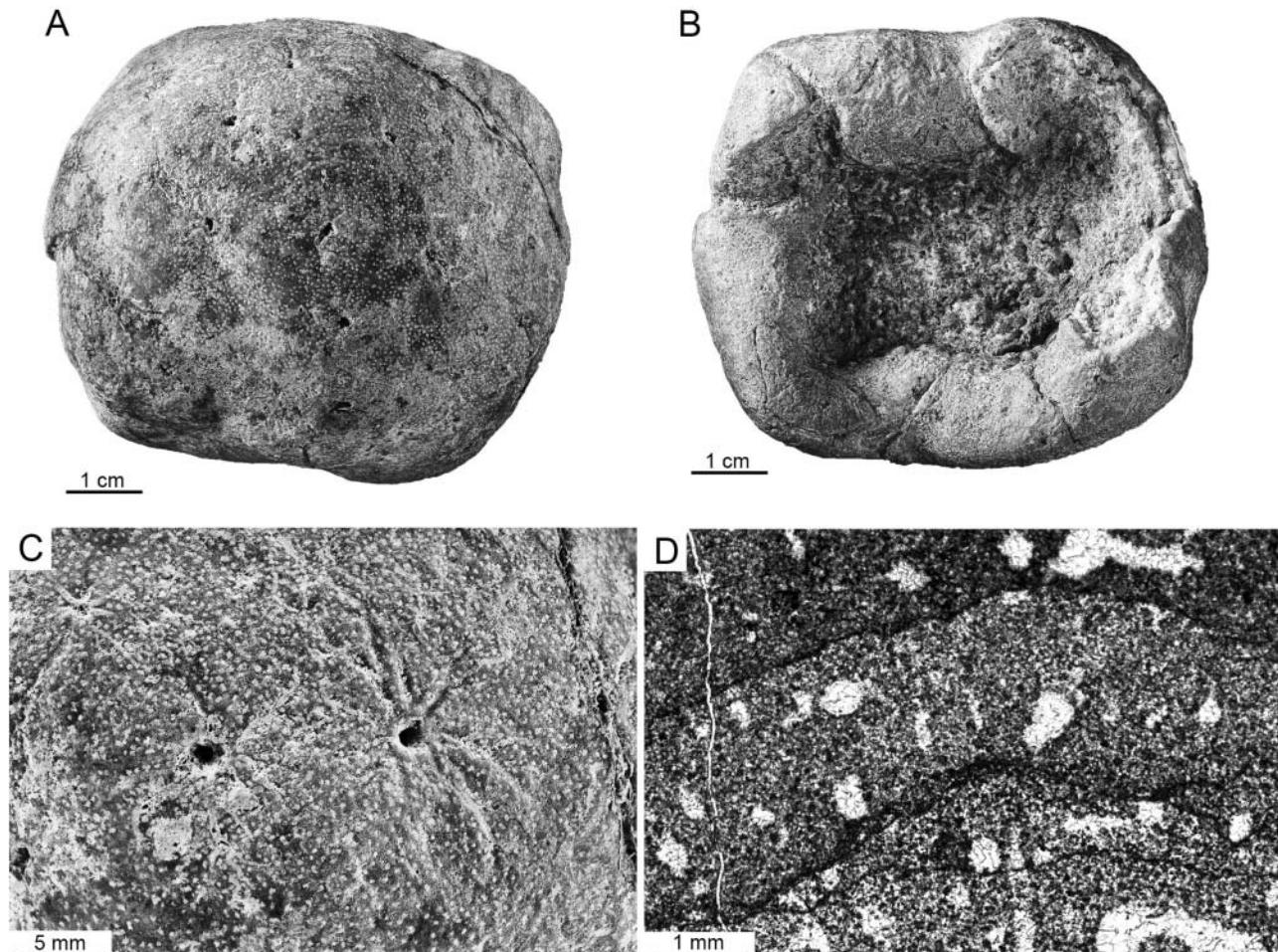


Figure 29. *Astrosclera* sp. **A–C**, MSNVE–22893; **D**, MCZ–PAL 3774. **A**, top view showing the subglobular shape **B**, bottom view showing the thick wall of the sponge; **C**, detail of (A) with small canal openings together with astrorhizae-like canals, i.e. larger openings surrounded by radial furrows; **D**, longitudinal thin section with spherulitic stratified structure.

Description. Subspherical lamellar sponge (Fig. 29A, B) 2.1–8.8 cm high and 4.5–11.2 cm in diameter. On the external surface, small canal openings together with rare astrorhizae-like canals – larger openings surrounded by radial furrows – can be observed (Fig. 29C). The wall thickness is 12 to 16 mm. The internal structure is spherulitic stratified, with spherulites approximately 100–130 µm in diameter (Fig. 29D). No spicules are visible.

Remarks. The upper surface of the studied specimens is very similar to that of *Pliobolia vermiculata* Pomel, 1872 described from the Miocene of Algeria, but the main canal openings and the radial furrows are less pronounced in our material. Nevertheless, the presence of a spherulitic microstructure together with astrorhizae-like canals on the external surface supports the assignment to genus *Astrosclera* (Vacelet 2002a and literature cited therein). The stratified internal structure observed in thin section can be interpreted as growth rings similar to those observed by Wörheide (1998). The lack of megasclere (e.g. diagnostic

verticillated acanthostyles) precludes determination at the species level. *Astrosclera* is regarded as a living fossil, with a first record in the Upper Triassic of Turkey (*A. cuiji* Wörheide, 1998) (Wörheide *et al.* 2002). The only Recent species, *A. willeyana*, is restricted to cryptic and light-reduced environments of the Indo-Pacific, with a depth range of 1–185 m (Hartman 1980b). *Astroscleridae* are the main representatives of the calcified demosponges (also known as ‘coralline sponges’) that were classified within class Sclerospongiae. This class was subsequently abandoned because it was shown to be polyphyletic (Van Soest & Hooper 2002 and literature cited therein). This is the first record of *Astrosclera* in the Cenozoic, which bridges the gap between the Triassic (hitherto the youngest known fossil) and the extant forms.

Order **Dictyoceratida** Minchin, 1900
 Family **Verticillitidae** Steinmann, 1882
 Genus **Vaceletia** Pickett, 1982

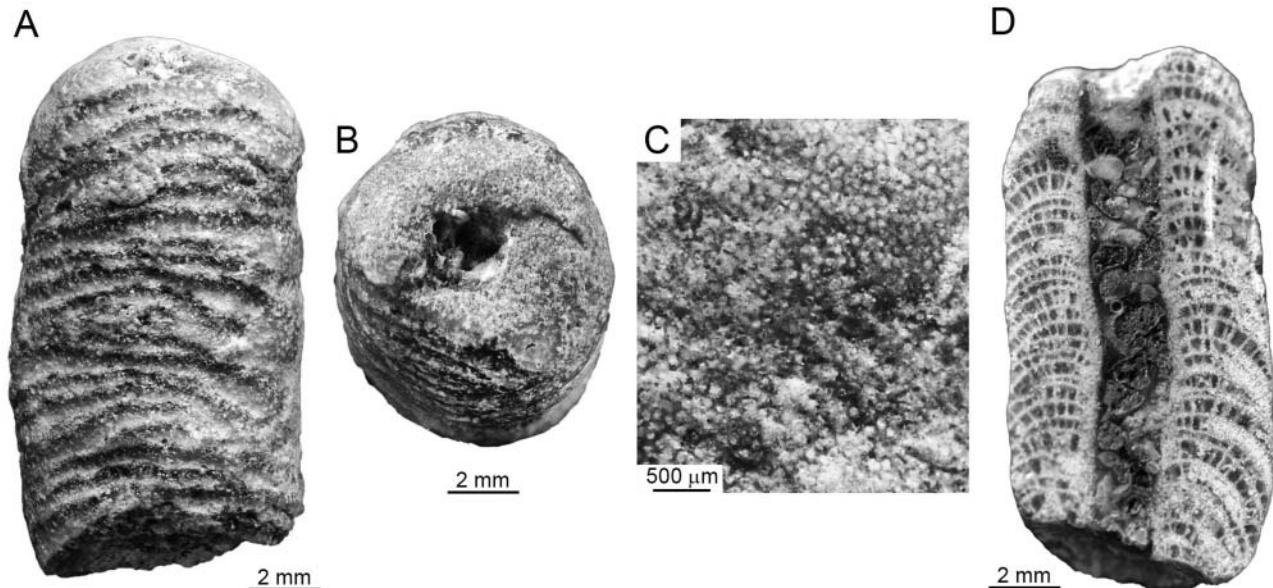


Figure 30. *Vaceletia progenitor* Pickett, 1982. A–D, MCZ-PAL 3763; A, lateral view showing the cylindrical shape, the domal upper face, the externally segmented body; B, top view of the circular terminal osculum; C, detail of the subpolygonal canal openings on the external surface; D, longitudinal section with the cylindrical spongocoel running for the full length of the specimen, and the sponge wall composed of annular, crescent-shaped chambers. Chambers are traversed by pillars.

Type species. *Neocoelia crypta* Vacelet, 1977, p. 509.

***Vaceletia progenitor* Pickett, 1982**
(Fig. 30)

1982 *Vaceletia progenitor* Pickett: 242, figs 2–6.

Material. Two fragments: MCZ-PAL 3763, MGP-PD 1056.

Occurrence. Cengio dell'Orbo quarry, Chiampo, Italy, Eocene, Lutetian (this study); Walpole and Esperance, south-west Australia, Eocene, Priabonian (Pickett 1982).

Description. Cylindrical, externally and internally segmented (Fig. 30A, D) fragments 1.5 to 1.7 cm high and 0.7 to 1.3 cm in diameter. The domal upper surface bears a circular terminal osculum 1.8 mm in diameter (Fig. 30B). The spongocoel is cylindrical, 1.8 mm in diameter. The sides of the spongocoel have a continuous wall (endowall) 0.15–0.2 mm thick, running along the whole specimen. Sponge walls are 2–3 mm in thickness. Internally, the sponge consists of a series of annular, crescent-shaped chambers which extend throughout the full width of the sponge wall (Fig. 30D). They are 0.4–0.6 mm high and traversed usually by pillars 0.05–0.1 mm thick. Subpolygonal canal openings, 0.1 mm in diameter, occur on the external surface (Fig. 30C).

Remarks. Our material is morphologically almost identical to the specimens from Pallinup Siltstone of south-west

Australia (Eocene, Priabonian) described by Pickett (1982). Chambers are smaller in our specimens, and, curiously, more similar to the living species *Vaceletia crypta* (Vacelet, 1977) (Table 1) than to those of the Eocene of south-west Australia. In our material, pillars have a thickness intermediate between those of *V. crypta* and *V. progenitor*. The Australian specimens are branched, while we interpret our material as fragments of branches. The genus *Vaceletia* is the only Recent representative of the polyphyletic group ‘Sphinctozoa’, a grouping of chambered calcareous sponges. It has a chambered skeleton of aragonite and is devoid of spicules. It was shown by Wörheide (2008), on the basis of rDNA sequences of Recent *Vaceletia* sp., that this genus is closely related to the extant keratose demosponges of the order Dictyoceratida Minchin, 1900. This is the second record of *V. progenitor* from the Cenozoic and extends its geographical range to the northern hemisphere. The Australian record and the present one bridge the gap between the previously youngest known fossil sphinctozoans from the Late Cretaceous (e.g. *Vaceletia crustans* Reitner & Engeser, 1989, from Spain) and the extant forms.

Palaeoecological remarks

Mode of attachment. The mode of attachment of Recent sponges and the success of their settlement are largely determined by the type of substrate (mud, hard rock, shells, etc.). Some sponges attach to a hard substrate by

Table 1. Comparison of the biometric parameters of *Vaceletia crypta*, *V. progenitor* from Australia and *V. progenitor* from Chiampo. Measurements in mm (data from Pickett 1982 and this study).

Taxon	Branch diameter	Chamber height	Spongocoel diameter	Canal openings diameter	Pillar thickness	Endowall thickness
<i>V. crypta</i>	4	0.6	0.5–0.8	0.1	0.04–0.05	0.05
<i>V. progenitor</i> (Australia)	5.9–11.9	0.9–1.2	2.0	0.1	0.10–0.17	0.15
<i>V. progenitor</i> (Chiampo)	7–13	0.4–0.6	1.8	0.1	0.05–0.10	0.15–0.20

encrustation (e.g. basiphytous hexactinellid *Aphrocalistes*); others anchor on soft sediments by a basal spicule tuft (e.g. hexactinellid *Hyalonema*). In our material, some specimens of *Ozotrachelus conicus* and *Corallistes multi-osculata* (lithistids) show a basal subcircular disc, 2–3 cm in diameter (Fig. 31A, B). In Recent sponges, basal discs are associated with the presence of a hard substrate. In some specimens, such as the lithistid *Bolidium bertii* and some indeterminate rhizomorines, an encrusting base has been observed (Figs 22B, 27J). There is more direct evidence that the sponges studied were attached to a hard substrate at least in their initial life stages. Some specimens of hexactinellids and lithistids are still attached to larger foraminifera (Fig. 31F, G). Red algae and larger foraminifera (*Nummulites* sp.) were found incorporated in the skeletons of the sponges (Fig. 31H, I). In one case, a *Hexactinella* sp. was found encrusting red algal nodules (Fig. 31J). In other cases, small cavities (0.8–1.6 cm high, 0.7–1.6 in diameter; Fig. 31K) are found at the base of complete sponges that are interpreted as originally hard objects that dissolved during diagenesis, or were organic in nature and decayed leaving an empty space. Tuber-like or root-like basal structures were observed instead in some hexactinellids. Three specimens of *Laocoetis patula*, for example, show a tuber-like basal part that is 2.5–4.6 cm in diameter and 3.6–5.8 long (Fig. 31C, D). Delicate, root-like structures of 4–4.5 mm in diameter were observed in a specimen of *Guettardiscyphia/Pleurogettardia*, although their delicate tips are always broken (Fig. 31E). These basal structures differ from those of *Laocoetis*, because they are more delicate and smaller in proportion to the complete sponge body. As for the basal disc, these structures are also often lost after breaking off.

Sponge clusters

In spite of the fact that the material available for this study was collected decades ago, and thus it is now impossible to establish whether some of the sponges were found in life position, six slabs bearing numerous sponge specimens were found in museum collections (Fig. 32A, B). These sponge aggregates are mainly composed of hexactinellids (hexactinosan and lychniscosan), with the most abundant species being the lychniscosan *Callicylix eocenicus*. Other hexactinellids, such as *Camerospangia*

visentinae, *Guettardiscyphia/Pleurogettardia* and *Laocoetis patula*, were also identified. The individuals in these specimens apparently grew one on top of the other (Fig. 32E). We interpret these structures as natural sponge clusters that could not be transported en masse, and therefore infer that at least some of the sponges of Chiampo Valley were collected in life position.

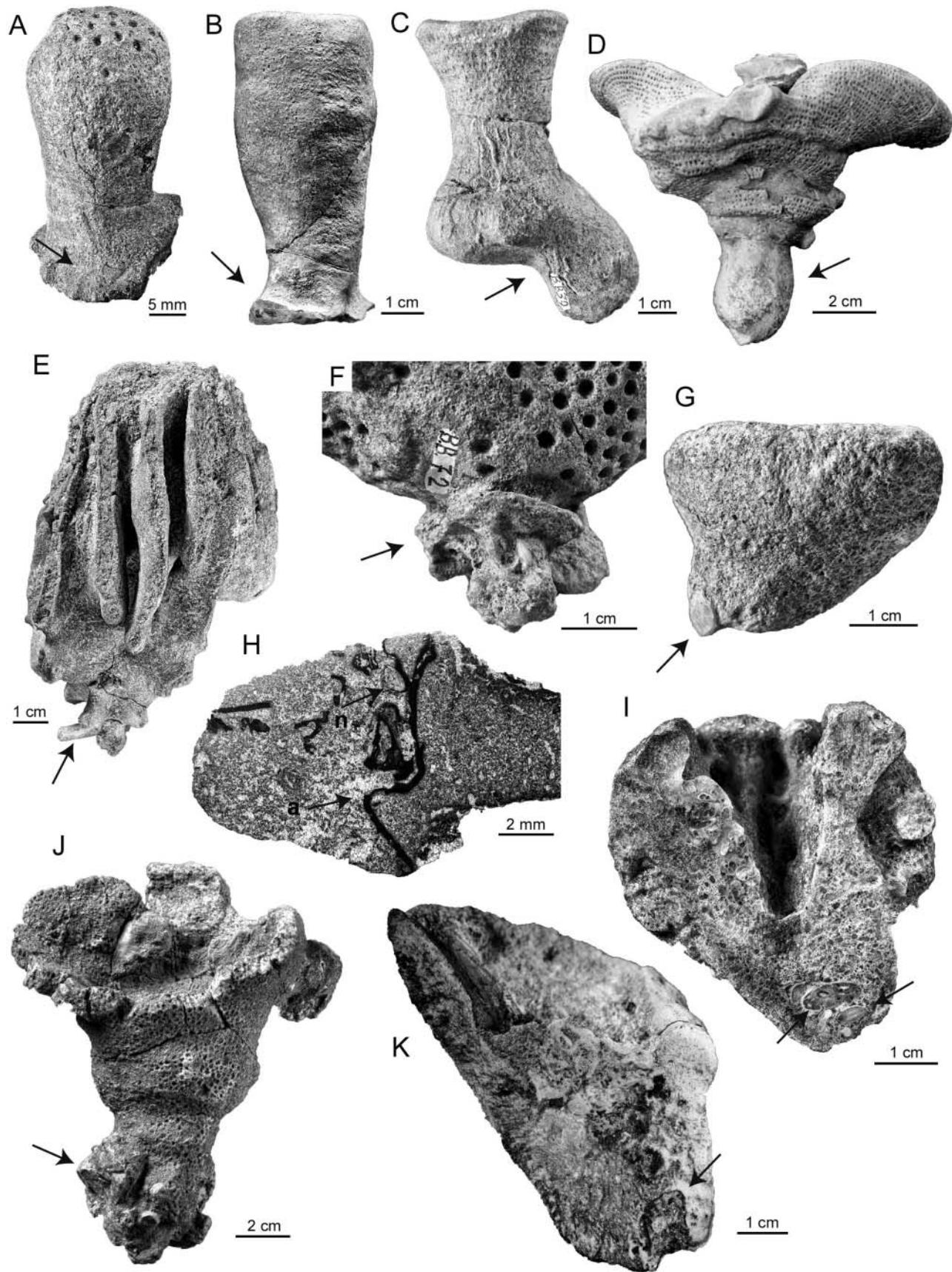
Small specimens

More than 150 specimens among the over 900 of this study are less than 3 cm high, some 1.5 cm or smaller. For the majority of these small specimens, taxonomic attribution was impossible due to the paucity of diagnostic features. Nevertheless, a few can be assigned to described taxa with reasonable confidence, including *Laocoetis patula* (Fig. 32C, D), *Stauractinella eocenica*, *Callicylix eocenicus* and *Toulminia italicica*. These taxa show a wide range in dimensions. Considering entire specimens only, the smallest specimen of *Toulminia* is half the size of the largest (height range 3.1–7 cm), the smallest specimen of *Callicylix* is one-third the size of the largest (3.6–12.7 cm), the smallest specimen of *Stauractinella* is one-eighth the size of the largest (2.1–18 cm) and the smallest specimen of *Laocoetis* is one-fourteenth the size of the largest (1.1–16 cm). Although we cannot exclude the possibility that many of the small specimens were adults, those for which a taxonomic assignment was possible and which belong to taxa represented by large-sized specimens should be considered young forms. We suspect that smaller specimens would have been recovered if the outcrops were accessible for unbiased sampling.

Discussion

Diversity of the sponge fauna and chrono-bio-geographical affinities

The Eocene Chiampo sponge fauna is highly diverse, and consists of 32 siliceous sponge taxa belonging to 24 genera. Among them, two genera (*Rigonia* and *Coronispongia*) and 10 species (*Stauractinella eocenica*, *Rigonia plicata*, *Hexactinella clampensis*, *Camerospangia tuberculata*, *C. visentinae*, *Toulminia italicica*, *Coronispongia*



confossa, *Cavispongia scarpai*, *Corallistes multiosculata*, *Bolidium bertii*) are described as new in the present work.

Fifteen species (47% of the total) belong to the class Hexactinellida, among which one (3%) belongs to the order Lyssacinosida, seven to Hexactinosida (22%) and seven to Lychniscosida (22%). Seventeen species belong to the class Demospongiae (53%), of which 15 are lithistids (47%) and two are non-lithistids (6%).

Among 261 identifiable specimens, the most abundant species is *Stauractinella eocenica*, followed by *Callicylix eocenicus*, *Laocoetis patula*, *Camerospomgia visentinae* and *Ozotrachelus conicus*. Seventy-four percent of the specimens belong to Hexactinellida, and 24% to Demospongiae. In terms of species diversity, the Shannon index (Hammer *et al.* 2001) is 2.966, which should be considered high in comparison with other marine invertebrate Eocene communities (cf. Veto *et al.* 2007; Pearson *et al.* 2008; Yamaguchi *et al.* 2014). Due to the fact that this study was based only on museum collections (collected mostly by amateur palaeontologists) a strong sampling bias is expected, so further statistical analysis would be unreliable. Nevertheless, judging from the presence of clusters, which are pristine sponge associations, the dominance of hexactinellids over lithistids appears to be a genuine feature of this fauna.

A critical comparison of Chiampo fossil genera with other fossil sponge faunas was performed based on selected papers for which the systematic palaeontology is well documented. Data quality in palaeospongiology is generally a serious problem: difficulties in taxonomic assignments, discontinuous fossil records, and preservational and collection biases (Hartman *et al.* 1980; Pisera 2004) make sponges less than ideal organisms for palaeobiological analyses. Despite this, but keeping in mind all the limitations mentioned above, we attempted to make a comparison of faunal composition at the generic level using a binary dissimilarity analysis (R Core Team 2014; software package ‘vegan’, Oksanen *et al.* 2014). We recorded the presence/absence of hexactinellid and demosponge genera in nine bodily preserved sponge faunas (see Online Supplemental Material). Only valid genera were considered (Kaesler 2004). Records of either indeterminate species or species identified only above the genus level were ignored. The two new genera described in this paper were ignored. As non-lithistid (soft)

demosponges have a low fossilization potential (Finks & Rigby 2003; Reid 2003; Pisera 2006), we interpret the absence of ‘soft’ demosponge in the Chiampo fauna as a taphonomical effect rather than a real feature of the faunal composition. As a consequence, we removed the ‘soft’ demosponge genera found in other faunas from the analysis. The cluster dendrogram resulting from this analysis (Fig. 33) clearly shows the affinity of the studied fauna with sponges from the Eocene of Spain and the Cretaceous of Germany. The three main clusters in the dendrogram can be interpreted as three major chrono-biogeographical groups: Eocene south-west Pacific faunas, Miocene Tethyan faunas and Cretaceous–Eocene Tethyan faunas.

Ancestors and extant descendants of the Chiampo fauna

Among the taxa identified in the Chiampo Valley fauna, some have ancestors in the Mesozoic. Three genera have their roots in the Jurassic: *Stauractinella*, *Laocoetis* (see Kaesler 2004) and *Ventriculites* (see Hérenger 1942). The genus *Astrosclera* was documented in the Triassic (Wörheide *et al.* 2002).

Six genera are still extant. Of these, four (*Laocoetis*, *Anomochone*, *Astrosclera*, *Vaceletia*) are recorded only in the Indo-Pacific Ocean, a fifth (*Hexactinella*) is also present in the Atlantic Ocean, and a sixth (*Corallistes*) is cosmopolitan and occurs also in the Mediterranean Sea (Van Soest *et al.* 2014).

Most extant descendants of Chiampo sponges live in rather deep waters. The only living *Laocoetis* species, *L. perion* Lévi, 1986 from the Southern Indian Ocean, is known from 250–750 m water depth at temperatures of 9 to 15°C (Lévi 1986; Tabachnick & Lévi 1997; Pisera & Tabachnick 2014). *Anomochone* has three valid Recent species: *A. expansa* Ijima, 1927 from Indonesia and eastern Australia; *A. globosa* Ijima, 1927 from Indonesia; and *A. furcata* Reiswig & Kelly, 2011 from eastern Australia. The two Indonesian species live at a water depth of 90 to 900 m (Ijima 1927; Reiswig & Kelly 2011), while the Australian species is found between 292 and 774 m. The 14 living valid species of the genus *Hexactinella* (see Van Soest *et al.* 2014) are distributed mainly in New Zealand waters and Japan, with some species in the Atlantic.

Figure 31. Attachment structures. **A**, encrusting basal disc (arrow) in *Corallistes multiosculata*, MSNVE–22912; **B**, *Ozotrachelus conicus* with basal disc (arrow), MSNVE–22982; **C**, *Laocoetis patula* with tuberose base (arrow), MSNVE–22891; **D**, *L. patula* with tuberose base (arrow), MMC 22; **E**, root-like structures (arrow) at the base of *Pleuroguettardia iberica*, MSNVE–22891; **F**, hexactinellid encrusting a cluster of larger foraminifera (arrow), MSNVE–22977; **G**, lithistid encrusting a larger foraminifer (arrow), MCZ-PAL 3723; **H**, thin section of a lithistid sponge showing a red alga (a) and a small nummulite (n) inside the body, MSNVE–22908; **I**, cross section of the lychniscosan sponge *Coronispongia confossa* showing nummulites (arrows) at the base of the body, MSNVE–22979; **J**, *Hexactinella clampensis* sp. nov. encrusting red algal nodules (arrow), MCZ-PAL 3804; **K**, lithistid sponge with a hole at the base (arrow) suggesting that the sponge encrusted an object that dissolved during diagenesis, MCZ-PAL 3731.

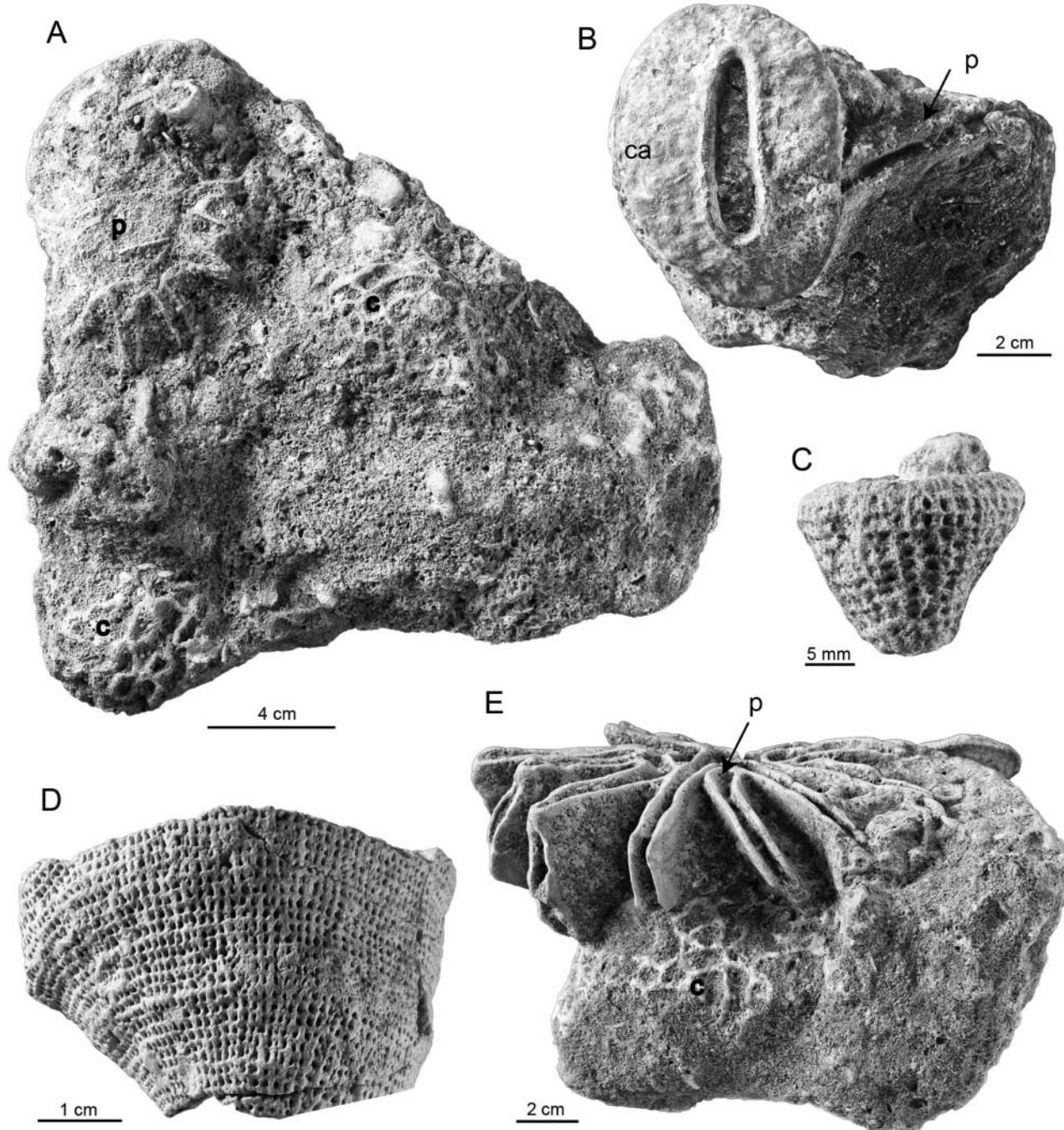


Figure 32. Sponge clusters and small specimens. **A**, sponge cluster with hexactinellids: *Callicylix eocenicus* (c) and *Pleuroguettardia/Guettardiscyphia* (p), MCZ-PAL 3785; **B**, cluster of the hexactinellids *Camerospongia visentinae* sp. nov. (ca) and *Pleuroguettardia/Guettardiscyphia* (p), MCZ-PAL 3775; **C**, young specimen of *Laocoetis patula*, MCZ-PAL 3745; **D**, fragment of large specimen of *L. patula* (photo: B. Favaretto), MSNVE-23012; **E**, *Pleuroguettardia* sp. (p) growing on *C. eocenicus* (c), MCZ-PAL 3784.

Hexactinella carolinensis Reiswig, Dohrmann, Pomponi & Woerheide, 2008 was sampled at 213 m depth off South Carolina, USA, and *H. divergens* Tabachnick, 1990 from 570–670 m in the south-east Atlantic. The New Zealand species of *Hexactinella* (Reiswig & Kelly 2011) have a depth range of 610–1248 m and also probably live attached to hard substrates. The genus *Corallistes* has 14

valid species today and a cosmopolitan distribution: Mediterranean Sea, Florida, Caribbean, Gulf of Mexico, Galapagos Islands, northern to southern coast of Brazil, Southern Africa (Natal Coast), South India and Sri Lanka, New Caledonia and Papua New Guinea, with a depth range of 90–640 m (Pisera & Lévi 2002; Van Soest *et al.* 2014). *Vaceletia* has only one Recent species, *V. crypta*

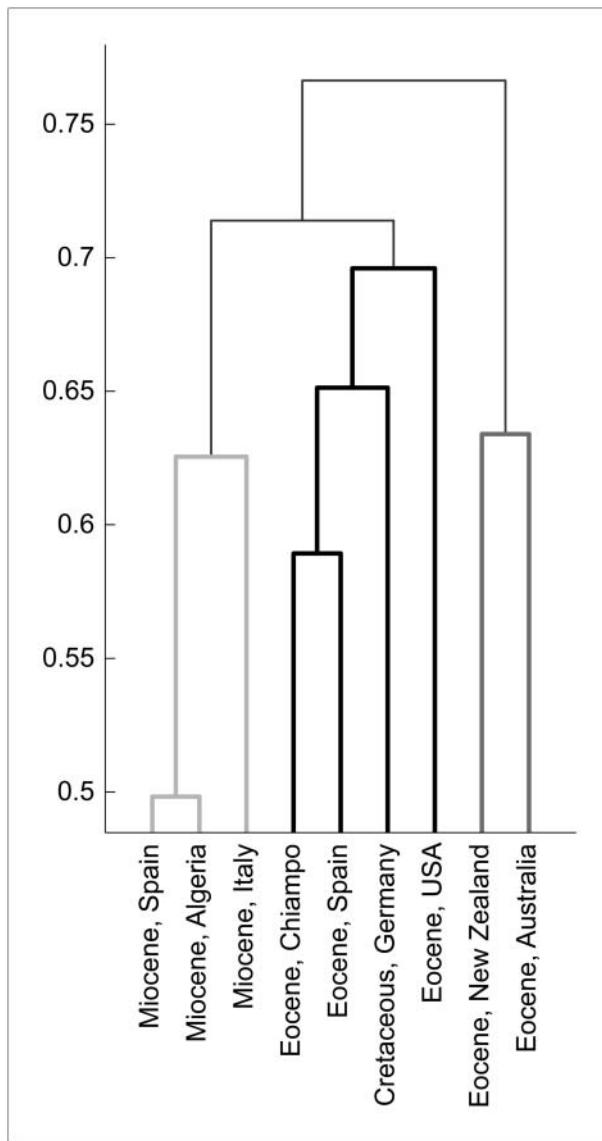


Figure 33. Cluster dendrogram showing the similarity of nine bodily preserved siliceous sponge faunas (Hexactinellida and Demospongiae genera) described in selected literature. See text and Online Supplemental Material for details.

(Vacelet, 1977) which lives in semi-closed cavities of coral reefs and bathyal environments of the Indo-Pacific, at 10–530 m water depth (Vacelet 2002b; Wörheide & Reitner 1996 and references cited therein). The only living species of *Astrosclera*, *A. willeyana* Lister, 1900, is distributed in the tropical Indo-Pacific and, as for *Vaceletia*, thrives in semi-closed microenvironments such as coral rubble, reef cavities, caves and deep cliffs, with a depth range of 1–185 m (Vacelet 2002a and references within).

In summary, the majority of living representatives of the studied Eocene sponges live in deeper shelf environments, which could also have been the setting for the Chiampo fauna. The presence of the lyssacinid *Stauracanthella* further strengthens this hypothesis. Recent

lyssacinids, with few exceptions, live in the bathyal or even the abyssal zone (e.g. Janussen *et al.* 2004; Van Soest *et al.* 2007; Janussen & Reiswig 2009), and this life environment is generally confirmed in the fossil record (e.g. Pisera & Busquets 2002; Świerczewska-Gładysz & Jurkowska 2013).

Beccaro *et al.* (2001) found that the sponge-bearing sediment of the Cengio dell'Orbo quarry exhibits sedimentary structures indicative of mass transport, in the context of an outer ramp sedimentary environment. Therefore, the sponge fauna, together with sedimentological evidence and the composition of the associated fauna (including planktonic foraminifera, pteropods, shark teeth: Beccaro *et al.* 2001), points to a middle-outer carbonate ramp depositional environment.

Sponge autecology

Despite the fact that our study material comes only from museum collections, the large number of examined specimens (more than 900) allows for some autecological considerations based on functional morphology.

Important insights can be obtained into the types of substrate on which the sponges lived. It is clear that some demosponges with desmas colonized a hard-bottom substrate. This is indicated by the presence of a basal disc, which today characterizes sponges from hard bottoms or attached to hard objects on a muddy substrate (Pisera 1997; Pomponi *et al.* 2001). The basal disc is lost in many specimens because the stalk is the most fragile part of the sponge. Tuber-like basal structures of some hexactinellids indicate anchorage in soft sediment, similar to the tuber-like basal part of the Jurassic hexactinellid *Cribrospomonia radicata* (Quenstedt) that was interpreted as a structure preventing the sponge from sinking into mud by creating buoyancy. The mass of the basal root structure keeps the sponge in an upright position (Krautter 1998). Root-like structures in hexactinellids are seldom reported in the literature (e.g. Reid 1958). Krautter *et al.* (2006) described similar basal structures in *Aphrocallistes vastus* and *Heterochone calyx*, in the only known Recent hexactinellid reef, off British Columbia. When these two species increase in size, they produce root-like outgrowths that can attach to hard objects such as rocks and sponge skeletons. Krautter *et al.* (2006) interpreted the production of outgrowths as an intrinsic mechanism to optimize stability by helping the growing sponge to keep an optimal life position. Accordingly, the delicate root-like basal structure of *Guettardiscyphia/Pleurogettardia* from Chiampo could have had a stabilizing function as well.

In summary, there is compelling evidence that most of the Eocene sponges of the Chiampo Valley colonized a hard substrate, at least in their early growth stages, while sponges with root-like tubers are rare in this fauna. Generally, sponge larvae need to settle on hard objects (e.g.

rocks, mollusc shells, rhodoliths) to begin metamorphosis (Bergquist 1978). In this process, they can form an envelope around hard objects (Krautter *et al.* 2006), and in later stages they can incorporate sediment and living organisms like foraminifera (Cerrano *et al.* 2007; Guibault *et al.* 2006). This explains the occurrence of small bioclasts completely enclosed in some of the Chiampo sponges. However, large/old specimens also retain structures indicative of a hard substrate. The presence of different modes of attachment in the Chiampo sponge fauna suggests heterogeneous bottom surface conditions. This feature was also well documented in the Miocene sponge fauna from southern Spain (Brimaud & Vachard 1985) in resedimented deposits.

A second group of observations testifies to the autochthonous nature of the Chiampo fauna, in which various growth stages are present with small and fully grown specimens being found together. The absence of size selection implies minimal influence of transport processes, and the abundance of small specimens indicates that reproduction must have been a frequent event (Klitgaard & Tendal 2001). Preservation of delicate encrusting bases, sponge clusters and the fact that sponges were reported in one site only strengthen the hypothesis that the studied sponge fauna is essentially autochthonous or parautochthonous, and most probably was rapidly buried.

Conclusions

The bodily preserved fauna from the Eocene of Chiampo Valley (northern Italy) is highly diverse, with 32 taxa that belong to 24 genera, including 10 new species and two new genera. It is dominated by siliceous sponges, most having solid skeletons (Hexactinosida, Lychniscosida and lithistid demosponges). The original siliceous skeleton of the sponges was dissolved and replaced by calcite. However, a veil of peloidal micrite is observed around skeletal elements which often permits the identification of spicules. A comparison of faunal composition at the generic level using a binary dissimilarity analysis shows the affinity of the Chiampo fauna with sponge faunas from the Eocene of Spain and the Cretaceous of Germany. The presence of the genera *Camerospomia*, *Toulminia* and *Bolidium* extends their last occurrences from the Cretaceous to the Eocene. Six extant genera live today in rather deep-water environments. The Recent calcified demosponge genus *Astrosclera* is reported here for the first time in the Cenozoic, and the second worldwide occurrence of the Recent sphinctozoan genus *Vaceletia* in the Palaeogene is also reported. The Chiampo Valley sponges colonized a mixed substrate, sometimes forming clusters. The sponge fauna is essentially autochthonous and inhabited the middle-distal portion of a carbonate ramp.

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Supplemental material

Supplemental material for this article can be accessed here: <http://dx.doi.org/10.1080/14772019.2015.1132015>

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