

A first glimpse on the taphonomy and sedimentary environment of the Eocene siliceous sponges from Chiampo, Lessini Mts, NE Italy

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ABSTRACT - *A diverse assemblage of bodily preserved sponges has been recovered from a lower Lutetian tuffite horizon in the Chiampo Valley, Lessini Mountains, Italy. The sponge assemblage is dominated by hexactinellids and lithistids. Using uniformitarian criteria, the composition of the assemblage suggests a water depth greater than 200 m. Sponges are often preserved in growth position including sponge clusters. Taphonomic processes facilitating sponge preservation include rapid burial of a living sponge community and early diagenetic calcification. Different modes of attachment suggest heterogeneous substrate conditions. The associated fauna, such as abundant pteropods in the matrix and in-situ preserved crinoids, confirms a rather deep-water environment. However, there are also common benthic elements of shallow-water origin. Although some of these elements show signs of transport, others, such as decapod crustaceans, do not. Moreover, trace fossils indicate high-energy environments. To reconcile these observations, we propose rapid, tectonically triggered sea-level changes.*

INTRODUCTION

Due to the low preservation potential of many taxa, especially those with organic skeleton, the fossil record of sponges is rather incomplete. Only sponges with a rigid skeleton, e.g., lithistids (demosponges with desmas), Hexactinosida and Lychniscosida (Class Hexactinellida) and sponges with a massive calcareous skeleton (polyphyletic demosponges and Calcarea), have a more or less continuous fossil record (Pisera, 2006). Moreover, the geological history of sponges is difficult to generalize, because of biases in the fossil record and uncertainties over identifying causal relationships (e.g., with regard to climatic changes; Muir et al., 2017).

The present study deals with a middle Eocene siliceous sponge assemblage from the Chiampo Valley, Lessini

Mountains, north-eastern Italy. The poriferan assemblage consists of 33 species: 15 hexactinellids and 18 demosponges (Frisone et al., 2016; Frisone & De Angeli, 2017). The sponges are three-dimensionally preserved but their originally siliceous spicules are replaced by calcite. Whereas the taxonomy of this sponge assemblage is now well understood, little is known about the environment in which these sponges lived. Sponge taxonomy, however, provides already some interesting hints; most relevant is that the most common extant relatives of the sponge taxa from the Lutetian of Chiampo inhabit rather deep waters today. Furthermore, the presence of different modes of attachment in the investigated specimens suggests heterogeneous substrate conditions. Small, possibly young sponges are present in the assemblage, as well as sponge clusters (Frisone et al., 2016).

Field sampling revealed hexactinellids to be strongly dominant over lithistids, thus suggesting a deep-water setting below 200 m water depth (Frisone et al., 2018). This interpretation is at odds with the traditional interpretation of a shallow-water environment in Chiampo (e.g., Fabiani, 1915; De Zanche, 1965), and hence with the notion that the “sponge assemblages developed in a shallow-water paleoenvironments” (Matteucci & Russo, 2011, p. 34).

In this study, we investigate the preservation, associated fauna and sedimentary context of the Chiampo sponges, in order to provide a better clue on their habitat. We also aim at a clarification of the taphonomic and diagenetic processes that led to the preservation of this unique sponge assemblage. Our hypothesis is that the sponges were fossilised in situ, in a deep-water setting, and buried alive.

GEOLOGICAL SETTING

The studied area is located in the eastern Lessini Mountains, a portion of the Prealps of north-eastern Italy, on the western side of the Chiampo Valley (Fig. 1). The

Lessini Mountains are a triangular-shaped tableland, which occupies some 800 km² in the western Venetian Region, at the transition between the Prealps and the Po Plain. They belong to the Cenozoic Lessini Shelf, a carbonate platform with scattered reefs, lagoons, islands and volcanoes circumscribed northwards by lands and surrounded by deeper water to the south and the east (e.g., Bosellini, 1989; Bosellini & Papazzoni, 2003; Bassi et al., 2008).

The studied 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 e.g., Ancona, 1966; Visentin, 1994). A single small outcropping section (less than 3 m thick) that yielded a few fossil sponges was logged and sampled in Via Motti, 45° 32’ 28.9” N, 11° 15’ 34.2” E, near the Cengio dell’Orbo quarry. The outcrop lies near the tip of the lens-shaped sponge-bearing tuffite horizon (Fig. 2). The studied sites are located within a NNW-trending extensional structure known as the Alpone-Agno or Alpone-Chiampo graben (Barbieri et al., 1982, 1991,

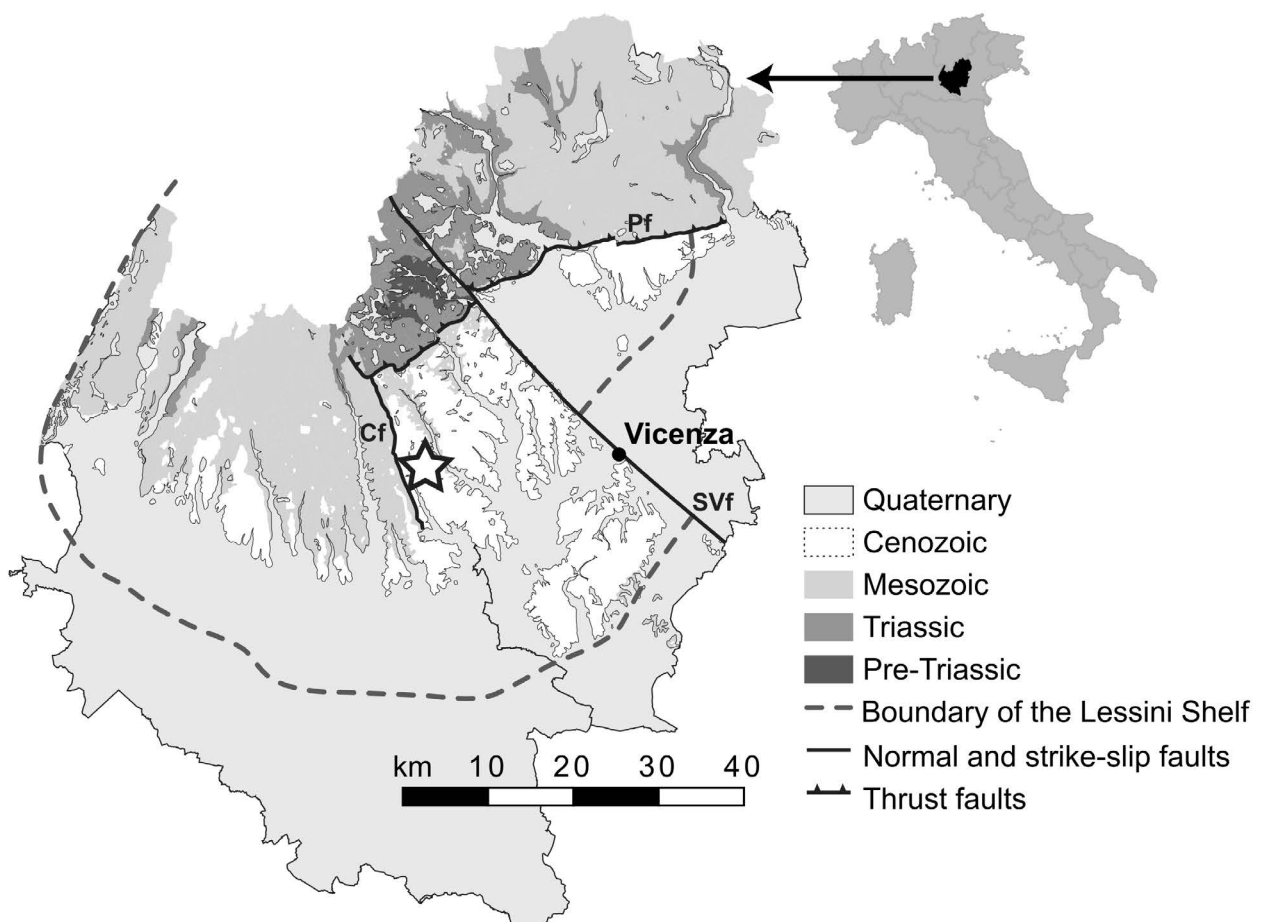


Fig. 1 - Simplified geological map of the study area (Verona and Vicenza provinces, Northern Italy), modified from Frisone et al. (2018). Regione Veneto, Sezione Geologia e Georisorse, released under the Italian Open Data License 2.0 (<https://www.dati.gov.it/content/italian-open-data-license-v20>). Outline of the Lessini Shelf during the Eocene modified from Bosellini (1989). The sponge-bearing outcrop near Chiampo is indicated by the white star. Cf: Castelvero fault; Sv: Schio-Vicenza fault; Pf: Pedemontana thrust fault.

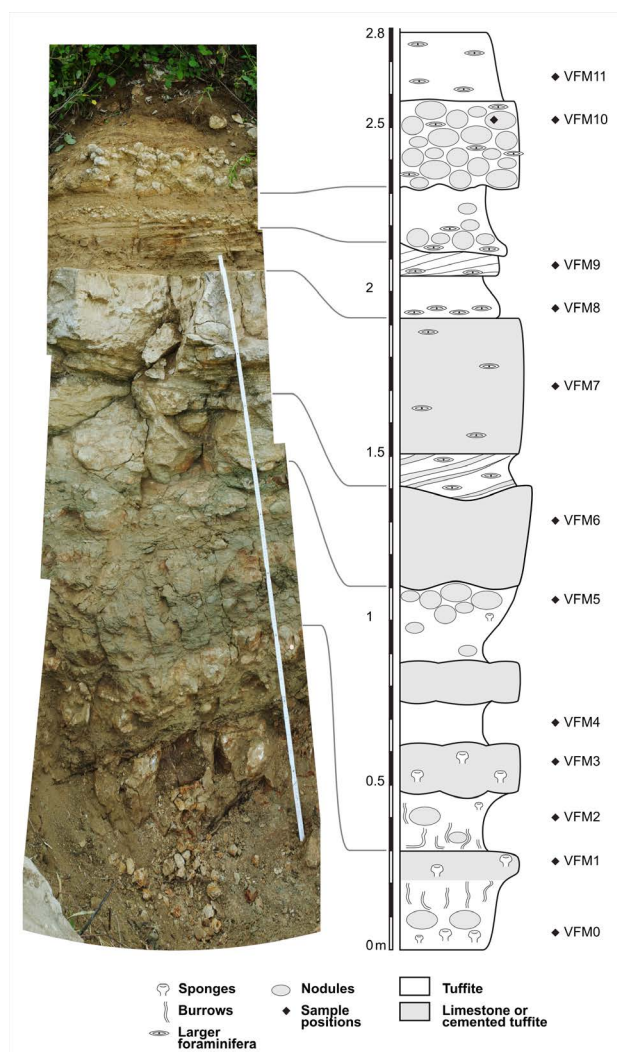


Fig. 2 - (color online) Field photomosaic and stratigraphic log of the Via Motti section. The wooden meter is 2 m long. The picture and log scales do not coincide perfectly because of perspective distortions of the photomosaic.

among others), bounded to the west by the Castelveto normal fault. Zampieri (1995) proposed that the Alpone-Agno graben developed in the South Alpine foreland as an extensional response to the active convergence between the European and Adriatic plates. It was about 20 km wide and at least 35 km long. The area belongs to the Veneto Volcanic Province, identified by principally mafic and ultramafic rocks erupted during the Paleocene-Oligocene. Large volumes of mainly subaqueous volcanics and their contemporaneous reworking products (hyaloclastites and tuffites) accumulated in the graben. The eruptive centers in the eastern Lessini Mts were aligned with the Castelveto fault (e.g., Piccoli, 1966). This fault was active during the Eocene, controlling the accumulation of volcanics, their reworked products and the interlayered carbonates (Barbieri & Zampieri, 1992). As a consequence, the accumulation of volcanic and volcanoclastic products was maximal on the eastern, lowered block of the fault. Interlayered carbonates are also thicker on the eastern side of the block, which was subsiding faster. Several magmatic pulses were separated by periods of magmatic

inactivity during which marine sedimentation took place (De Vecchi & Sedeà, 1995, and references therein). The sedimentary intercalations are locally called “Chiampo limestone”. This unit was quarried until the 1990s for extracting building stone. It belongs to a lower to middle Eocene informal unit named “Nummulitic limestone”, which is widespread in the western part of the Veneto region (e.g., Fabiani, 1915). This lithostratigraphic unit is poorly constrained and still in need of revision. It includes limestones with nummulitids 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 a distal carbonate ramp, and the debris as transported by debris flows and turbidites. Several volcanoclastic horizons are intercalated within the “Nummulitic limestone”. Some of these horizons are rich in very well-preserved fossils, including three-dimensionally preserved crustaceans complete with appendages and ventral parts (e.g., De Angeli & Garassino, 2006; Beschin et al., 2016). Beccaro et al. (2001) interpreted these tuffitic horizons as belonging to different stratigraphic levels with limited lateral extension. Other authors consider the fossil-bearing volcanoclastics horizons as one continuous unit, also known as “*Lophoranina* tuff” (sensu Beschin et al., 1991; see also Matteucci & Russo, 2005). The name derives from *Lophoranina marestiana* (König, 1825), a decapod crustacean that is common in this horizon.

Volcanoclastic sediments often have a lens shape and channelised morphology (Márton et al., 2011) and sedimentary structures, such as high-angle cross bedding, are sometimes visible in the field. Pelagic fossils (e.g., pteropods) are common and locally (Lovara quarry) there are accumulations of planktic and nektonic fossils (e.g., planktic foraminifera, shark teeth; Beccaro et al., 2001). In Cengio dell’Orbo and Lovara quarries, in a single horizon of volcanoclastics enclosed in the “Nummulitic limestone”, sponges represent the most common macrofaunal element (Matteucci & Russo, 2005). Outside of the Chiampo Valley, bodily preserved sponges are absent in the Eocene of the Southern Alps (Frisone et al., 2016). Isolated spicules of Demospongiae were reported (Frisone et al., 2014b) from the Bartonian of Monte Duello, Montecchia di Crosara, Lessini Mts (Verona, Italy).

The sponge assemblage investigated here originates from a 50-200 cm thick horizon of tuffites and hyaloclastites in the Lovara and Cengio dell’Orbo quarries (Menin, 1972; Visentin, 1994; Matteucci & Russo, 2005; Frisone et al., 2016). The rock is a tuffite, composed of rounded volcanic fragments, calcareous bioclasts and calcitic cement. The volcanic clasts are strongly altered, with palagonitised glass in vesicles. The associated fauna is mainly composed of smaller benthic, planktic and larger foraminifera. There are also crustaceans (decapods and ostracods), echinoderms, bryozoans, mollusks (especially pteropods, and other gastropods, and rare cephalopods and bivalves), red algae and rare corals (this study and Fabiani, 1915; Schaub, 1962; De Zanche, 1965; Ancona, 1966; Beschin et al., 1991, 2016; Fornasiero & Vicariotto, 1997; De Angeli & Beschin, 2010; Pacaud & Quaggiotto, 2011; Frisone et al., 2016). The bioclasts, especially the 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; Frisone et al., 2016).

MATERIALS AND METHODS

The sponge 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). The study material was mainly collected by amateur paleontologists between the 1960s and 1990s.

Our study focuses on sponge assemblage and associated fossils and sediments from the Lovara and Cengio dell’Orbo quarries. As these quarries are abandoned and the sponge-bearing horizons are inaccessible, we have had to rely mainly on specimens that were collected with different approaches, by different people, at different times (e.g., Frisone et al. 2014a; Frisone & Favaretto, 2017). Although in Lovara and Cengio dell’Orbo quarries there are various volcanoclastic horizons, only one horizon yielded sponges (see geological setting and Matteucci & Russo, 2005). In Museum collections only seldom the horizon is defined in the specimens’ labels. For the purpose of the study, we selected collections that were clearly identified in the label as coming from the sponge horizon only. Thin sections, washings and smear slides from samples of Via Motti outcrop were prepared at the Università degli Studi di Padova. Eleven thin sections were analysed also with fluorescent light microscopy. Selected specimens of sponges were chosen for preparing 52 thin sections. The thin sections were studied with petrographic microscopes, under transmitted optical (Leica DM EP T and Zeiss Axiophot) and fluorescent (Leica 5000B) light, all at the Università degli Studi di Padova. At the end of 2013, clearing work resulted in the accumulation of debris from the Lovara and Cengio dell’Orbo quarries. Fossil sponges were visible on the surface of the debris heap, which was selected for a quantitative bulk surface sampling (Frisone et al., 2018). From 2014 to 2017 specimens appearing on the surface were randomly picked for one hour per sampling event. This prolonged sampling campaign allowed us to collect 365 additional sponge specimens that were studied by Frisone et al. (2018).

Associated macro- and micropaleontological content

Specimens from three Museum collections were used for the study of the associated fauna, named after their collectors: Berti (Museo di Storia Naturale di Venezia, Venice), Lovato (Museo di Archeologia e Scienze Naturali “G. Zannato”, Montecchio Maggiore) and Rossi (Museo di Geologia e Paleontologia dell’Università degli Studi di Padova). All the studied specimens from these museum collections come from the sponge-bearing level at Cengio dell’Orbo quarry. Moreover, samples from Via Motti section, near Cengio dell’Orbo quarry (section acronym

VFM) were collected to prepare ten washing residues and eleven smear slides.

Calcareous nannofossil biostratigraphy [C. Agnini]

For calcareous nannofossil analysis, raw sediments were processed to prepare standard smear slides (Bown & Young, 1998). A total of 12 samples from the Via Motti section were examined under a Zeiss light microscope at 1250× magnification. Calcareous nannofossils were determined using the taxonomy proposed by Aubry (1984, 1988, 1989, 1990, 1999) and Perch-Nielsen (1985). We adopted the zonal scheme of Agnini et al. (2014) for regional to global correlations.

Calcareous nannofossils are generally rare in the investigated samples and we thus decided to perform counts on a standardised area of 9 mm² (three traverses; modified after Backman & Shackleton, 1983) in order to check the presence of marker species.

Planktic foraminifera [V. Luciani]

Planktic foraminifera were analysed in washed residue (> 63 and < 500 µm fraction). A total of 11 samples from Via Motti section (VFM0 to VFM9 and VFM11) were observed under a stereoscopic microscope for planktic foraminiferal content. Planktic foraminifera were determined using the taxonomic criteria of Pearson et al. (2006). For the biostratigraphic attribution, we adopted the zonal scheme by Wade et al. (2011) with the modification proposed by Luciani & Giusberti (2014).

Crinoids [M. Roux & L. Giusberti]

Crinoids were picked up under the stereomicroscope from the residues of the > 500 µm fraction obtained from the tuffite horizon of Cengio dell’Orbo quarry (Lovato collection). Most of the specimens (more than one hundred ossicles) were obtained from the residues provisionally labelled as MCZ 1, 6 and 7. Preliminary observations were carried out under the stereomicroscope and SEM.

RESULTS

Sponge preservation

Sponge skeletons and spicules are replaced with calcite. The space between spicules is often partially filled by clotted peloidal micrite. A veil of micrite and peloidal micrite forms coatings around spicules (Fig. 3a). At least two cement generations grew on the spicular skeleton and on clotted peloidal micrite: a cloudy early cement is followed by a second generation of clear mosaic spar (Fig. 3b). Spicules and cement spar are not fluorescent, while the axial canals of spicules (when present) are slightly fluorescent. Clotted peloidal micrite is brightly fluorescent. Sometimes, a fluorescent thin veil was observed around spicules (Fig. 3d). Small (2-10 µm) pyrite crystals and framboids of pyrite are common and associated with clotted peloidal micrite of lithistid sponges (Fig. 3e). Generally, volcanoclastic grains are not observed in sponge spicules meshes and internal canals (that can be up to 1 mm) but only in the spongocoel, when present. This feature is observed both in hexactinellid (e.g., *Camerospongia visentinae* Frisone et al., 2016, *C.*

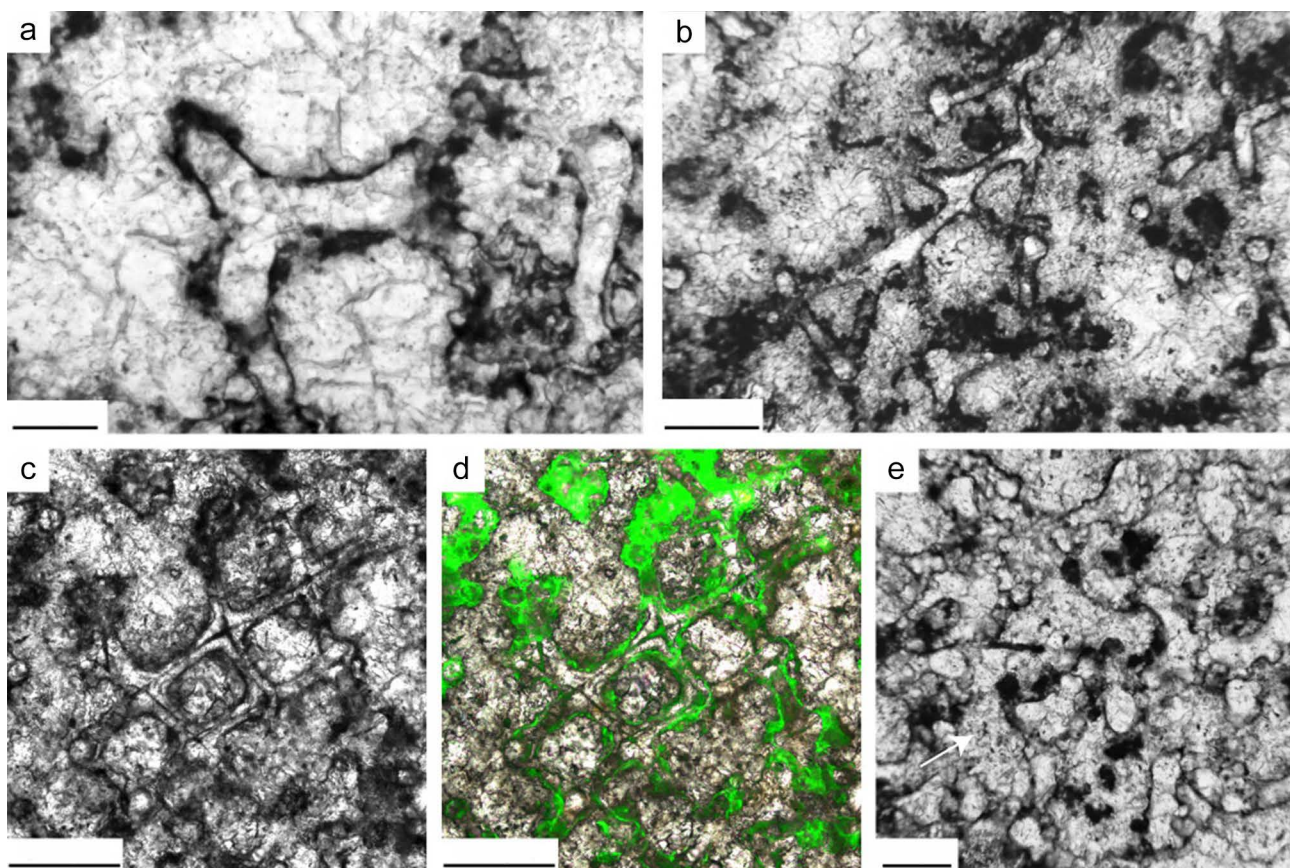


Fig. 3 - (color online) Thin sections of lithistid and hexactinellid sponges. a) Lithistid, with the space between spicules (desmas) partially filled by clotted peloidal micrite. A veil of micrite and peloidal micrite forms coatings around spicules (scale bar = 100 μ m). b) Hexactinellid. Two cement generations grow on the spicular skeleton and on clotted peloidal micrite: a cloudy early cement and then a second generation of clear mosaic spar (scale bar = 200 μ m). c-d) Hexactinellid sponge under optical (c) and fluorescent (d) light; in (d) spicules and cement sparite are not fluorescent while the infilling of axial canals of spicules is slightly fluorescent, and clotted peloidal micrite is bright fluorescent. There is also a fluorescent thin veil around spicules (scale bar = 200 μ m). e) Lithistid sponges with small (2-10 μ m) pyrite crystals and framboids (arrow) in association with clotted peloidal micrite (scale bar = 100 μ m).

tuberculata Frisone et al., 2016, *Hexactinella clampensis* Frisone et al., 2016 and *Anomochone* sp.) and lithistid demosponges (e.g., *Rhoptrum* sp. and *Corallistes multiosculata* Frisone et al., 2016) (Fig. 4).

Associated macro- and micropaleontological content of the embedding sediment

The embedding sediment is a sandy tuffite composed of rounded volcanic fragments, skeletal grains and calcitic cement (Fig. 5). The volcanic clasts are strongly altered, with palagonitised glass in vesicles (Fig. 5a). Pteropods are common in the sediment and clearly associated with the sponges. The association of sponges with other faunal elements is less clear. In the Via Motti section, the sponge-bearing sediment is bioturbated and includes distinct ichnofossils.

Ichnofossils [P. Monaco]

The ichnofossils are cylindrical and have average diameter of ca. 4 mm (Fig. 6). They cross both the sponge body and the embedding sediment. They belong to *Ophiomorpha nodosa* Lundgren, 1891, a trace of burrowing crustaceans (mainly callianassids). This ichnospecies is very common in coastal sediments; it has a branched form and externally a peloidal structure,

produced by the mucus of crustaceans to consolidate the tunnels. Peloids are concentrated only on the outer part of the trace, whereas the inside is smooth. *Ophiomorpha nodosa* develops in three dimensions, but often shows branched tunnels arranged horizontally or vertically, depending on the current regime and the amount of sands reaching in the coastal sea. *Ophiomorpha nodosa* prefers a high hydrodynamic regime and moderate sedimentation rates (e.g., Soria et al., 2014).

Crustaceans [A. De Angeli & C. Beschin]

Ten species of decapod crustaceans have been described so far from the sponge-bearing horizon in the Cengio dell'Orbo quarry (Beschin et al., 1988, 2016; De Angeli & Beschin, 2007): *Albunea cuisiana* Beschin & De Angeli, 1984, *Lessinipagurus boschettensis* Beschin et al., 2016 (Anomura), *Dromiopsis vicetinus* Beschin et al., 2016 (Dromioidea), *Antonioranina globosa* (Beschin et al., 1988), *Italianira punctulata* (Beschin et al., 1988), *Raniliformis ornata* De Angeli & Beschin, 2007, *Lophoranina marestiana*, *Notopoides exiguus* Beschin et al., 1988 (Raninoidea), *Liocarcinus priscus* Beschin et al., 2016 (Portunoidea), and *Palaeograpsus inflatus* Bittner, 1875 (Xanthoidea).

The decapods are generally three-dimensionally

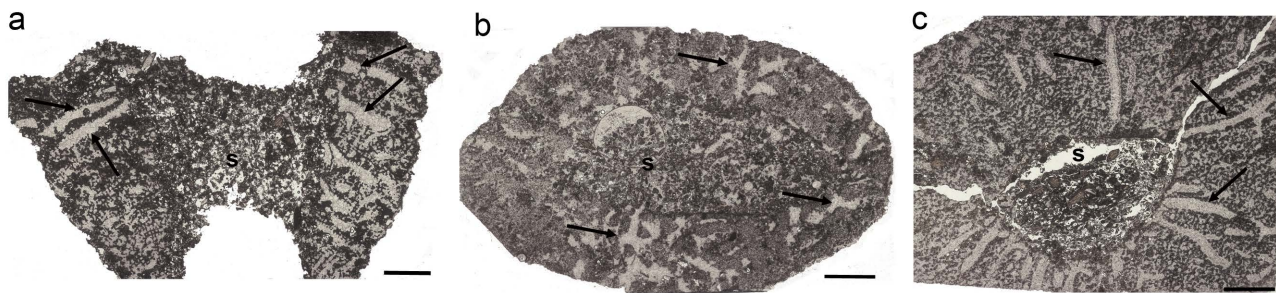


Fig. 4 - (color online) Thin sections showing specimens with large internal canals (arrows) devoid of sediment which is only observed in the spongocoel (s). a) Longitudinal thin section of *Camerospongia visentinae* MCZ-PAL 3712 with large radial canals. b) *Anomochone* sp. MCZ-PAL 3708 transverse thin section of a branch, with deep labyrinthine canals. c) *Rhoptrum* sp. MCZ-PAL 3742 transverse thin section showing large radial canals. Scale bars = 5 mm.

preserved and complete with appendages and ventral parts. They probably lived in the sediment like the extant *Raninoidea* (Bellwood, 2002). Other species, such as *Lessinipagurus boschettensis*, are hermit crabs of which only the claws have been found. None of the species described so far are compatible with the burrows of *Ophiomorpha nodosa* described above.

The crustacean *Lophoranina marestiana* that commonly occurs in the sponge horizon is related to the extant *Ranina ranina* (Linnaeus, 1758). This large “frog crab” lives in the subtidal zones of coasts of India, Indonesia, Vietnam, the Philippines, Hawaii and eastern Australia, hiding under the sediments (Baylon & Tito, 2012; Frantescu, 2013).

Pteropods [*P. Mietto* & *E. Quaggiotto*]

The sponge-bearing horizon in the Cengio dell’Orbo quarry is rich in pteropods (Fig. 7). In fact, the sedimentary matrix qualifies as a pteropod ooze. Pteropod shells are densely packed and found together with nautiloid larval shells, and yet unidentified micromollusks, resembling forms that currently live in circalittoral environments. From the micromollusks identified in the sponge matrix, the discovery of an undescribed species of *Thecopsella* Cossmann, 1888 (cf. Janssen, 2005) is noteworthy (MGP-PD 32335).

Whereas some pteropods could be identified at species level, other morphotypes are unknown from Paleogene sediments and largely represent new species.

Overall, there are at least 26 species-rank taxa, 13 of which belong to the Cavolinoidea and the remaining to the Limacinoidea (Tab. 1). Among the former there are nine new species, whereas among the latter five new species have been recognised so far. The Cengio dell’Orbo quarry pteropod assemblage has been recorded in other localities near Vicenza and consistently lies in the basal Lutetian (within the calcareous nannofossil Zone NP15; Beccaro, 2003). Although data are preliminary and poorly comparable with available literature, because of the presence of very little documented Praecuvierinidae and *Tibiella* Meyer, 1884 in Europe it seems that this assemblage shows greater affinity with those from North America than those from Central and Northern Europe.

Before the discovery of the Chiampo pteropods, the oldest known fossil pteropods from Italy were of Oligo-Miocene age (Bernasconi & Robba, 1982). In addition to the single Bayan (1870a) report, the discovery of pteropods in Eocene deposits in the Vicenza area (Beccaro

et al., 2001; Beccaro, 2003), and, in particular, in the Alpone-Agno graben is of particular significance. There, pteropods occur in lower Eocene to lower Oligocene volcano-arenitic, volcanopelitic, tuffitic and marly-clayey sediments. They are very frequent locally in the Ypresian-Lutetian interval, sporadic in the Bartonian, completely absent in the Priabonian and rare in the Rupelian.

Other mollusks [*S. Dominici*]

The benthic mollusk assemblage coming from the sponge-bearing horizon of Cengio dell’Orbo (called “Boschetto di Chiampo” as in Beschin et al., 1991; Beccaro et al., 2001; Rossi collection, Box C13, MGP-PD) indicates a neritic environment. Gastropods other than pteropods include *Pterynotus tripteroides* (Lamarck, 1822), *Eoconus* sp., *Volutilithes* cf. *frederici* (Bayan, 1870b), *Siphonalia* sp. and Buccinoidea indet., all of which are carnivores, implying a complex base level trophic web. Co-occurring bivalves are *Astarte* sp. and *Barbatia* sp. *Volutilithes frederici* has been recorded from the Lutetian (Cossmann & Pissarro, 1910-1913) and the Priabonian (Piccoli & Savazzi, 1983), whereas *Pterynotus tripteroides* is typical of the Lutetian. A Lutetian age is consistent with the chronostratigraphic distribution of the other taxa.

Calcareous nannofossils [*C. Agnini*]

Samples are virtually barren of nannofossils, except for VFM2, VFM3 and VFM4, where calcareous nannofossils are sporadically occurring. Marker species defining biohorizons used in the standard zonations of Martini (1971) and Okada & Bukry (1980) are not present in the study samples. Nevertheless, the presence of two specimens of *Nannotetrina cristata* (Martini, 1958) Perch-Nielsen, 1971 and the absence of specimens ascribable to *Sphenolithus furcatolithoides* Locker, 1967 indicate that the investigated interval belongs to Zones CNE8-CNE9 of 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) and thus the study samples are of early Lutetian age. This result is consistent with that reported by Beccaro et al. (2001) and Matteucci & Russo (2005) for the sponge horizon.

Planktic foraminifera [*V. Luciani*]

Some of the samples analysed are barren of planktic foraminifera or contain extremely rare specimens (VFM2,

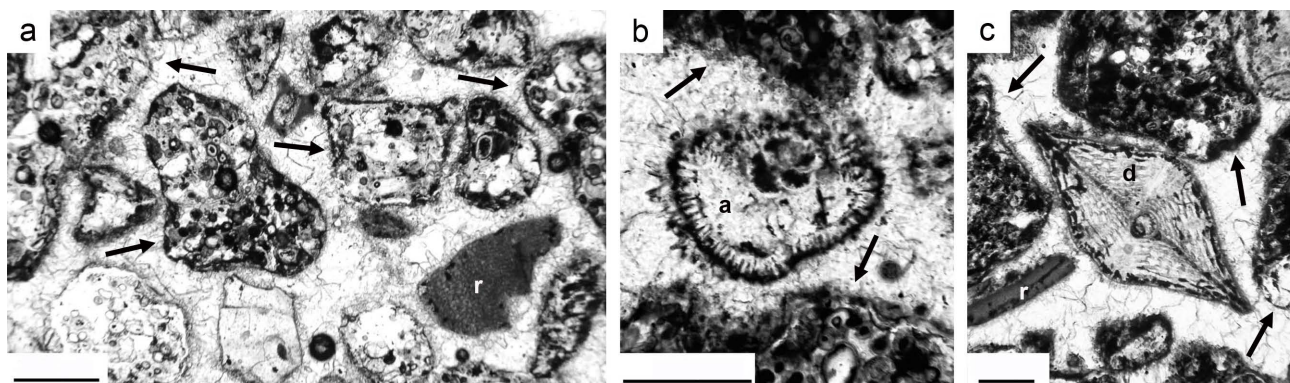


Fig. 5 - Thin sections of the tuffite surrounding the sponges. a) Rounded volcanic fragments (arrows), a red alga (r), and calcitic cement. The volcanic clasts are strongly altered, with palagonitised glass in vesicles. b) Volcanic clasts (arrows) and the planktic foraminifer *Acarinina* sp. (a). c) The larger foraminifer *Discocyclina* sp. (d), red algae fragment (r) and volcanic clasts (arrows). Scale bar = 200 μ m.

VFM6, VFM7). Other samples (VFM0, VFM1, VFM3, VFM4, VFM5, VFM8, VFM9, VFM11) comprise similar assemblages that include: *Acarinina bullbrookii* (Bolli, 1957), *A. cuneicamerata* (Blow, 1979), *A. mcgowrani* Wade & Pearson, 2006, *A. pentacamerata* (Subbotina, 1947), *A. primitiva* (Finlay, 1947), *A. punctocarinata* Fleisher, 1974, *Morozovella aragonensis* (Nuttall, 1930), *Morozovelloides bandyi* (Fleisher, 1974), *M. coronatus* (Blow, 1979), *M. crassatus* (Cushman, 1925), *Parasubbotina inaequispira* (Subbotina, 1953), *Subbotina hagni* (Gohrbandt, 1967), *S. linaperta* (Finlay, 1939), *S. roesnaesensis* Olsson & Berggren, 2006, *S. senni* (Beckmann, 1953), and *Turborotalia frontosa* (Subbotina, 1953).

The occurrence of *Turborotalia frontosa* allows us to refer the samples analysed to the Zone E7b (Wade et al., 2011). The top of this zone was defined by Wade et al. (2011) based on the first appearance of *Guembelitroides nuttalli* (Hamilton, 1953). The latter species, however, proved to appear significantly earlier (Zone E5), albeit with rare specimens (rare occurrence) (Luciani & Giusberti, 2014), thus these authors proposed the common occurrence of *G. nuttalli* to identify the Lutetian Zone E8. The absence of this species in the study samples supports the attribution to Zone E7b. The base of *T. frontosa* is estimated to be ~ 550 kyr older than the primary event to identify the Ypresian/Lutetian boundary, that is the first

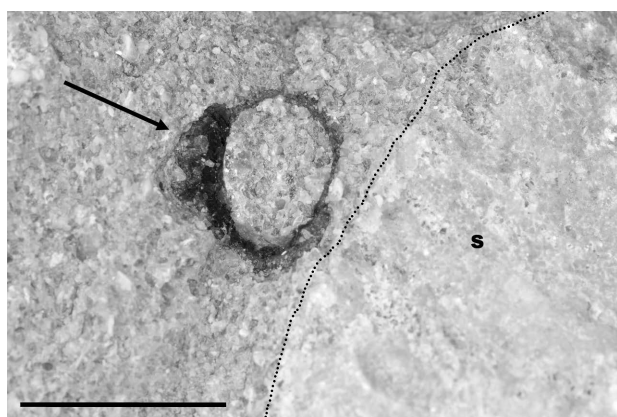


Fig. 6 - *Ophiomorpha nodosa* ichnofossils (arrow) crossing the embedding sediment near a hexactinellid sponge (s). Note the peloids concentrated at the margin of the burrow. Photo M. Bellanda. Scale bar = 1 cm.

appearance of calcareous nannofossil *Blackites inflatus* (Payros et al., 2009). Samples from Chiampo can be referred to the lower part of Lutetian Zone E7b, according to the calcareous nannofossil results.

Larger foraminifera [C.A. Papazzoni]

Abundant larger foraminifera were collected both in the Cengio dell'Orbo and the Lovara quarries. The material contains several isolated tests and some of them are naturally split, showing diagnostic equatorial sections. The preservation of the material is variable, sometimes excellent, with empty tests, sometimes with strongly recrystallised tests infilled by calcite. Moreover, even material from the same level is preserved with a variety of colors including reddish, greenish, and whitish gray. Some of the tests are badly broken or worn, suggesting transport and possibly in part reworking. The mixing of foraminifera coming from the shallow-water environment with pelagic elements such as pteropods and planktic foraminifera reinforces the case for resedimentation of this material. A preliminary survey of the larger foraminifera permitted to identify some index species, assigning both localities to the same biozones.

In the Via Motti outcrop, a sample from the base of the section (VFM 0) contains among others *Nummulites burdigalensis cantabricus* Schaub, 1981, *Assilina parva* (Douvillé, 1930), *Discocyclina pulchra pulchra* (Checchia-Rispoli, 1909), *Nemkovella strophiolata strophiolata* (Gümbel, 1870), and *Asterocyclina stellata adourensis* Less, 1987. This assemblage indicates the zones SB13 (higher part) to SB14 (Serra-Kiel et al., 1998), or the lower-middle Lutetian. The presence of *Nummulites burdigalensis cantabricus* should indicate the SB11 Zone, but the poor preservation of the material suggests reworking.

In the Lovara quarry the larger foraminiferal assemblage includes *Nummulites kugleri* Schaub, 1981, *N. maior* de la Harpe, 1883, *Assilina parva*, *Discocyclina pulchra pulchra*, *Nemkovella strophiolata strophiolata*, and *Orbitoclypeus varians angoumensis* Less, 1987. This assemblage also indicates zones SB13-SB14 (Serra-Kiel et al., 1998).

Corals [F.R. Bosellini]

Only two fragments of colonial scleractinian corals were observed in the studied collections, one ascribed

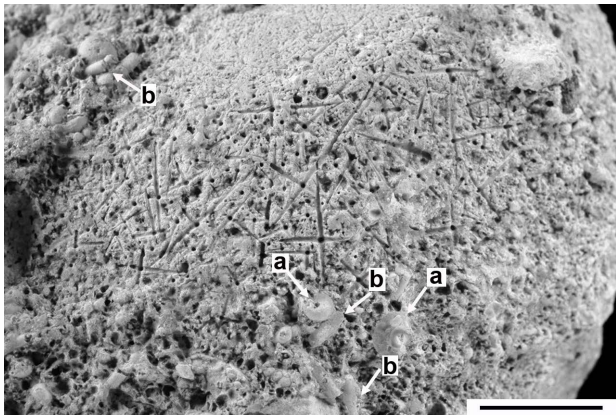


Fig. 7 - Detail of the external surface of the sponge *Stauractinella eocenica* Frisone et al., 2016 (IG-PD 366220) with imprints of pentactines spicules (dermalia). The sponge is associated with pteropods belonging to the Limacinidae (a) and Cuvierinidae (b). Photo S. Castelli. Scale bar = 1 cm.

to *Astrocoenia* sp. (Berti collection, Venice) and one to *Stylophora* sp. (MCZ-PAL 3739). These corals are inferred to have harbored photosymbionts, thus indicating a shallow water origin and transportation. The occurrence of the solitary coral *Heterocyathus* is also recorded from the Lovara quarry (Rossi collection, MGP-PD).

Crinoids [M. Roux & L. Giusberti]

The crinoid fauna from the Cengio dell'Orbo quarry (Lovato microfossil collection-MCZ-PAL) includes isocrinids, cyrtocrinids and rhizocrinids forming an exceptionally diverse fossil assemblage. Isocrinid stalk fragments consist of isolated thick columnals of small size displaying a diplocrinin-like articulation such as in *?Isocrinus archiaci* (Pasotti, 1929). Cyrtocrinids are represented by several calyces and numerous brachials of *Holopus spileccense* (Schlüter, 1878) and one calyx of *Cyathidium* sp. Abundant small aboral cups with globulous basals and flared radials belong to yet undescribed cyrtocrinid taxa. Several small encrusting disks might be attributed to these taxa, which presumably had a short thin stalk. Rhizocrinid columnals and aboral cups of two species of *Conocrinus*, of which one has long interradian projections and is close to *C. veronensis* (Jaekel, 1891), and one species of *Paraconocrinus* are frequent.

Conocrinus and *Paraconocrinus* are well-known in the Eocene foreland basins of the Pyrenees and Alps (Roux et al., 2019), as well as isolated columnals of *?Isocrinus archiaci* (Pasotti, 1929; Roux & Plaziat, 1978). *Holopus spileccense* is the single fossil species of the genus based on rare calyx described from the Spilecco Hill, near Bolca (Manni, 2005). In the reddish crinoidal facies of the Spilecco hills, rhizocrinid ossicles strongly predominate. The Cengio dell'Orbo site differs from other Eocene crinoidal assemblages in yielding three cyrtocrinid taxa represented by numerous ossicles, which are sometimes more frequent than rhizocrinid ones. Moreover, the assemblages include ossicles from different skeletal parts (attachment disks, columnals, calyces and brachials), frequently well-preserved despite some of them are fragile (*Holopus* brachials, interradian projections of *Conocrinus*

radials). This suggests a rapid in situ burial without hydrodynamic selection of the different kinds of ossicles.

DISCUSSION

Sedimentary environment

The fossil content of the sponge-bearing tuffite horizon at Chiampo clearly represents a mixture of shallow and deep marine fauna. Some benthic elements (e.g., larger foraminifera and the rare fragments of colonial corals) are of shallow-water origin and have been likely transported into the deeper water environment where sponges were thriving. Some other benthic elements (e.g., decapod crustaceans, larger gastropods) are also of shallow water origin but do not show obvious evidence of transport. As an example, the crustacean *Lophoranina marestiana* is generally three-dimensionally preserved and complete with delicate appendages and ventral parts. Its association with the sponges is unclear.

The diverse crinoidal fauna suggests a heterogeneous seafloor. Rhizocrinids usually have branching roots penetrating soft sediment, whereas cyrtocrinids are attached on hard bottom by a distal stalk encrusting disk, or directly by the calyx base. Isocrinids frequently inhabit environments with irregular bottom including coarse sediment, pebbles and boulders (Tunnicliffe et al., 2016). Using the associated macrofauna and microfauna, Roux et al. (2006) evidenced that Eocene and extant stalked crinoids had about the same bathymetric distribution at depths greater than 100 m and similar ecophenotypic adaptive characters. In present seas, the shallowest known sites are 216 m for *Holopus* and 171 m for *Cyathidium* (Améziane et al., 1999). Dense *Holopus* populations were observed on vertical and overhanging walls at depths between 430 and 640 m in the Caribbean Sea (Syverson et al., 2015). A paleoenvironmental reconstruction based on a uniformitarian approach of the crinoid assemblage at Cengio dell'Orbo thus suggests a paleodepth greater than 170 m and likely more than 210 m.

Diversity analysis of random field sampling collections (Frisone et al., 2018) revealed that the sponge assemblage is dominated by hexactinellids. Using uniformitarian criteria, this suggests a water depth of more than 200 m. This interpretation is consistent with the paleodepth suggested by the crinoidal assemblage. The most common extant sponge taxa at Chiampo, e.g., *Laocoetis* (24.9% in bulk field sampling; Frisone et al., 2018) and *Hexactinella* Carter, 1885 (9.6%), inhabit rather deep water today. *Laocoetis perion* Lévi, 1986 is known from 250-750 m water depth in the Southern Indian Ocean (Lévi, 1986; Tabachnick & Lévi, 1997; Pisera & Tabachnick, 2014), whereas *Hexactinella* has a depth range of approximately 200-1200 m (Tabachnick, 1990; Reiswig et al., 2008; Reiswig & Kelly, 2011). The lyssacinoid *Stauractinella* is also expected to occur in this depth range. With a few exceptions, Recent lyssacinoids live in the bathyal or and even abyssal zone (e.g., Janussen et al., 2004; Van Soest et al., 2007; Janussen & Reiswig, 2009) and this environment is generally confirmed in the fossil record (among others e.g., Pisera & Busquets, 2002; Świerczewska-Gładysz & Jurkowska, 2013). Consistently, the abundant pteropods and planktic foraminifera in the sponge-bearing

Superfamilies	Families	Genera and species	Repository MGP-PD
Cavolinoidea	Creseidae	<i>Euchilotea elegans</i> Harris, 1894	32336
		<i>Creseis simplex</i> (Meyer, 1886)	32337
		<i>Creseis</i> Rang, 1828 sp. indet.	28455
	Praecuvierinidae	<i>Texacuvierina gutta</i> Hodgkinson in Hodgkinson et al., 1992	32338
		<i>Praecuvierina</i> aff. <i>lura</i> Hodgkinson in Hodgkinson et al., 1992	32339
	Cuvierinidae	<i>Bucanoides</i> Hodgkinson in Hodgkinson et al., 1992 n. sp.	28456
		<i>Ireneia</i> Janssen, 1995 sp. indet.	28454
		<i>Cuvierina</i> Boas, 1886 (2 sp. indet.)	28458-28459
		<i>Tibiella</i> Meyer, 1884 (4 sp. indet.)	28460 to 28463
Limacinoidea	Limacinidae	<i>Altaspiratella multispira</i> (Curry, 1982)	32340
		<i>Altaspiratella bearnensis</i> (Curry, 1982)	32341
		<i>Altaspiratella gracilens</i> Hodgkinson in Hodgkinson et al., 1992	32342
		<i>Currylimacina cossmanni</i> (Curry, 1982)	32343
		<i>Limacina angustana</i> (Gardner, 1951)	32344
		<i>Limacina davidi</i> Hodgkinson in Hodgkinson et al., 1992	32345
		<i>Limacina</i> aff. <i>gormanii</i> (Curry, 1982)	32346
		<i>Limacina</i> cf. <i>pygmaea</i> (Lamarck, 1805)	32347
		<i>Limacina</i> Bosc, 1817 (5 sp. indet.)	32348 to 32352

Tab. 1 - Preliminary composition of the pteropod fauna of Cengio dell'Orbo quarry, with reference to the systematics by Janssen (2012).

sediment indicate rather deep-water sedimentation. Our interpretation is at odds with the traditional interpretation of a shallow-water environment of Chiampo (e.g., Fabiani, 1915; De Zanche, 1965), and hence with the notion that the “sponge assemblages developed in a shallow-water paleoenvironments” (Matteucci & Russo, 2011, p. 34).

The material available for this study did not allow a sedimentological interpretation of the sedimentary environments: this work is mostly based on materials from previous collections, and the only available outcrop (Via Motti section) is too limited for a robust facies analysis. Nevertheless, previous works may be challenged in the light of the new data that have become available with the present study. The studied sites have been interpreted to represent an outer carbonate ramp (Beccaro et al., 2001) rather than a platform-reef-slope system, on the base of the faunal association dominated by foraminifera, and lacking reef-building organisms, except for the sponges. This interpretation accounts for the biotic association of both the “Nummulitic limestone” and the volcanoclastic horizons, which also both show evidence of reworking in debris and turbidity flows (Márton et al., 2011). The biotic association described here confirms this interpretation. The skeletal association of the “Nummulitic limestone” and of the tuffite horizons include abundant typical elements of Eocene Mediterranean, oligophotic middle ramps (e.g., Nebelsick et al., 2005), such as *Nummulites*, other larger foraminifera, and rhodoliths (Beccaro et al., 2001).

The occurrence of mass-transport deposits on a carbonate ramp depositional environment is not easy to explain. Such deposits should in fact not be easy to form on the gentle inclinations of a carbonate ramp. In such depositional systems, the mixing of shallow-water and deeper-water elements may be expected offshore of the middle ramp, especially for ramps that are distally steepened. There, the ramp may achieve a sufficient

inclination to trigger mass-transport processes (e.g., Mateu-Vicens et al., 2008). Furthermore, it cannot be excluded that reworked shallow-water sediment (i.e., sediment bearing abraded corals, red algae and larger foraminifera) may have originated outside of the Alpone-Agno graben, west of the Castelveto fault or at the footwall of other similar normal faults, and its deposition was triggered at the scarp of these active faults.

We thus propose the following paleoenvironmental setting for the sponge assemblage: 1) the setting was the distal, oligophotic to aphotic part of a distally steepened carbonate ramp (see also Beccaro et al., 2001; Márton et al., 2011); 2) the shallow-water fauna observed in the sponge-bearing horizon has been transported from the inner and middle ramp, or from outside the area of the Alpone-Agno graben, and redeposited in an outer ramp environment at substantially greater depths. Overall, heterogeneous substrate conditions are suggested both by sponges and crinoids. The occurrence of the trace fossil *Ophiomorpha nodosa* at Via Motti, usually interpreted as diagnostic for a high-energy, shallow waters, requires further investigation. Rapid sea-level changes, due to regional tectonics, may explain the close association of deep-water and shallow water tracers.

Taphonomy of Chiampo sponge fauna

There is evidence that the fossilisation process of the sponges of Chiampo involved bacterial activity. During early diagenesis, the precipitation of pyrite and peloidal micrite within the body of sponges could have been induced by the activity of sulfate reducing bacteria. The clotted peloidal carbonates are strongly fluorescent under UV light, and as UV fluorescence is induced mostly by unsaturated organic compounds, the fluorescence implies that organic matter has been incorporated during the precipitation of carbonate, possibly within a biofilm, and it is thus a microbial carbonate. The idea

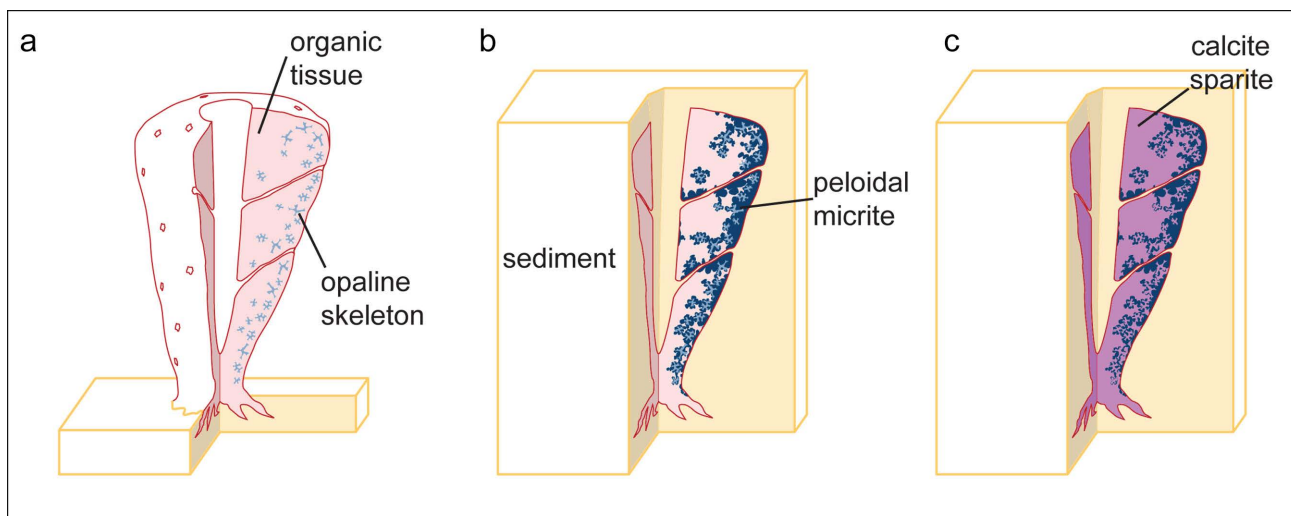


Fig. 8 - (color online) Schematic representation of taphonomic and diagenetic events (sponge anatomy is simplified). a) The living demosponge had an opaline skeleton and organic tissue. b) The sponge was buried very quickly by volcanoclastic sediments. Partial calcification of decaying tissue by sulfate-reducing bacteria produced clotted peloidal micrite. c) Complete solution of opaline skeleton and filling of interspicular and spicular voids by sparry calcite.

that micrite formation in sponges may be induced by microbial communities is widespread in the literature (e.g., Narbonne & Dixon, 1984; Brachert et al., 1987; Reitner, 1993; Warkne, 1995; Buckeridge et al., 2013). Calcification occurs within those portions of the sponge that are buried in the sediment and it is an in-vivo to early post-mortem process (Brachert, 1991; Neuweiler et al., 2007). Gaillard (1983) provided a scheme of this diagenetic process with different preservational stages. In the Upper Jurassic epicontinental limestones of central Europe sponges are preserved as calcareous “mummies”, where the entire specimens were preserved by very early precipitation of micrite by bacteria associated with decaying sponges (e.g., Brachert, 1991; Keupp et al., 1993; Pisera, 1997; Leinfelder, 2001). The Chiampo sponges seem to differ from calcareous “mummies” mainly because in the Chiampo sponge bodies the voids among spicules are mostly filled by sparite instead of micrite. Clotted peloidal micrite is present in the Chiampo sponges but not as abundantly as in Jurassic sponges. However, the microbial metabolisation of soft tissues of sponges seems to have been important for preservation in the studied case: spicules are only recognisable in thin section because they are coated by a thin veil of fluorescent micrite. This micrite is locally in continuity with patches of fluorescent clotted peloidal micrite and is thus most probably the product of microbial anaerobic metabolisation of the sponge soft tissue.

Preservation like that of the Chiampo sponges has been often reported, for example from the Eocene of Spain (Astibia et al., 2014) and New Zealand (Buckeridge et al., 2013). Other examples are from the Upper Cretaceous: hexactinellids from Ukraine (Świerczewska-Gładysz & Olszewska-Nejbert, 2013) and demosponges from Denmark (Madsen & Stemmerik, 2009). Bacteria could have also contributed to volcanic glass alteration. Palagonite is the first stable product of aquatic mafic glass alteration. Stronck & Schminke (2002) reported that microbial activity enhances the rate of dissolution of

volcanic glass by creating a local microenvironment as a result of the fluids of their metabolic products.

The fact that generally no sediment was found inside the sponge canals suggests that the sponges were buried alive, with their organic tissue still covering them. The presence of organisms testifying to different water depths in the embedding sediment (e.g., planktic and larger foraminifera together) is an evidence of resedimentation and confirms the facies analysis of Beccaro et al. (2001): the volcanoclastics of Lovara and Cengio dell’Orbo quarries were probably resedimented within the outer part of a carbonate ramp.

Based on the above observations, the following model of the taphonomic and diagenetic sequence can be proposed (Fig. 8):

1. The sponges are largely preserved in growth position (evidence documented in Frisone et al., 2016: delicate encrusting base, various ontogenetic stages, sponge clusters).

2. The sponges were rapidly buried alive, possibly by a gentle subaqueous volcanoclastic sediment flow (evidence: volcanic glass, no sediment in the sponges interspicular space and canals, mixed associated macro-micropaleontological content, siliceous membrane preserved in some specimens; this study and Frisone et al., 2016).

Partial calcification of decaying tissue by sulfate-reducing bacteria (evidences: clotted peloidal micrite, pyrite) occurred immediately after burial.

3. Complete dissolution of opaline skeletons, filling of interspicular and spicular voids by calcite sparite during burial.

CONCLUSIONS

Our work confirms the hypothesis that the Chiampo sponge assemblage was buried alive, at a water depth greater than 200 m and fossilised in situ. The fossilisation

of the sponges involved bacterial activity during early diagenesis calcification. We provide evidence that the associated fossils of the embedding sediment represent a mixture of shallow and deep marine fauna. Some benthic elements (corals, larger foraminifera) are of shallow-water origin and have been resedimented into the deeper water habitat of sponges and crinoids. Some other benthic elements (e.g., the decapod crustacean *Lophoranina marestiana*) are also of shallow water origin but do not show evidence of transport. Their association with the sponges is unclear. Pteropods and planktic foraminifera in background sediment indicate deep-water hemipelagic sedimentation whereas trace fossils suggest high-energy environments. Although further studies are needed to explain these controversial observations, we propose that rapid sea-level changes, due to regional tectonics, best explain all our findings.

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