



A new Miocene deep-sea chiton and early evidence for Teredinidae-sustained wood-fall communities

Luca Bertolaso, Vittorio Garilli, Daniela Parrinello, Maurizio Sosso, and Bruno Dell'Angelo

ABSTRACT

Deep-sea wood-falls are important biodiversity hot spots for insights on chemosynthesis-based communities. The study of deep-sea wood-fall-related palaeocommunities from the Neogene of north Italy shed light on interesting associations from the Miocene of Torrente Cinghio (Tortonian) and of Moncasale di Casina (Langhian). The most common components of this association are typical chemosynthetic/wood-fall molluscs, such as the gastropods *Homalopoma* sp. and *Pseudonina bellardii*, the bivalves *Idas* sp. and shipworms, and the chiton *Leptochiton lignatilis* n. sp., which belongs to a genus typical of recent sunken woods in tropical waters. The new species described is compared with other fossil and recent congeners, especially with those sharing the same kind of tegmental sculpture, fully covered with randomly or quincuncially arranged granules. An overview of the sunken wood-related chitons is provided. Surprisingly no taxa of the boring bivalves of the family Xylophagidae, whose species have been known to be fundamental for sustaining this kind of deep sea chemosynthetic ecosystem, were found in the studied site; however, other boring Teredinidae bivalves have been abundantly recovered. This suggests that, conversely to what has previously been observed on sunken wood communities, Teredinidae may be viewed as a counterpart for the maintenance of deep-sea wood-fall ecosystems.

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INTRODUCTION

Large nekton and wood-falls are important local resources of organic carbon in otherwise oligotrophic deep-sea environments. Recently an artificial deployment of a wood-fall in the Central Nile deep-sea fan delta in the Eastern Mediterranean (Bienhold et al., 2013) showed that, after only one year, the presence of wood on the seafloor led to the creation of lower oxygen and sulfidic conditions, prerequisites for colonization by specialized and/or opportunistic wood-fall fauna. As suggested by Distel et al. (2000), whale falls, wood-falls and other organic falls may provide important steps for the introduction of recent benthos to vents and seeps biota. Kaim et al. (2008) achieved similar conclusions for the fossil record, postulating the role of Mesozoic marine reptile carcasses as evolutionary and dispersal stepping stones. Moreover, studies by McClain and Barry (2014) on woods deployed on deep-sea bottoms have provided convincing estimates of how wood-fall environments may contribute to biodiversity.

Many observations on naturally sunken and deployed woods (e.g., Bernardino et al., 2010; Samadi et al., 2010; Heise et al., 2011) have highlighted the importance of factors such as wood type and size, position on wood logs, time after deployment, water temperature and depth in influencing the pattern of wood colonization, a situation analogous to that evidenced for whale falls (e.g., Lundsten et al., 2010).

The wood-boring bivalves of the family Xylophagidae Purchon, 1941 are the main colonizers of naturally and artificially sunken woods in deep water, usually in 400-3203 m (Turner, 2002; Voight, 2007, 2015). These bivalves have an important role in the initial degradation of the wood, as they transform the energy accumulated in the wood tissue into nutrients that are available for other animals (Turner, 1973, 1978). This transformation is accomplished by both the decomposition of woody material and the contribution of faecal pellets and larval stages that rain down to the sediment surface (Bernardino et al., 2010), setting up the best conditions for bacterial exploitation and for activating a chemosynthesis-based chain. The development of a chemically reducing habitat allows for the colonization of taxa capable of sustaining elevated concentrations of sulfide.

The drifting/floating wood may, however, be colonized by bivalves of the family Teredinidae Rafinesque, 1815. Some of these bivalves have been found alive in sunken wood retrieved from the deep sea (Turner, 1968; Nair and Saraswathy,

1971; McKoy, 1980; Pailleret et al., 2007; Saito, 2013; Voight, 2015 with other references therein), but it is still not clear how long they can survive at such depths or, at least, whether “the considerable time they may survive” (Turner, 1968) is enough for maintaining a chemosynthetic ecosystem. Evidence is likewise lacking for the possibility of teredinid larval colonization of deep-water wood-falls (Turner, 1968), because it has so far only been detected at shallow depths, from 7.6-25.9 m (Edmonson, 1962) to 60.9 m (Haderlie and Mellor, 1973), with increased settlement of some species at greater depths (Quayle, 1992 and references therein). Wood deployed on a 183-267 m deep bottom near the Bahamas, however, was recovered with two teredinid species (Heise et al., 2011).

Apart from the boring bivalves, other specialized, opportunistic molluscs may colonize sunken wood on deep bottoms, whereas colonizers at shallow sites are unspecialized species that are normally present in the background fauna (Santhakumaram and Sneli, 1984; Berg et al., 1987). For example, several taxa in the class Polyplacophora Gray, 1821 (i.e., chitons), particularly in *Lepidopleurida* Thiele, 1909, may colonize sunken wood in deep waters. Chitons are closely related to, and in some cases specialized for, this kind of substrate especially in tropical waters. Documentation of chitons in the fossil record that are related to wood-fall ecosystems are generally rare, however, thus making the origin of their possible specialization on wooden substrates, as well their phylogenetic relationship, a matter of debate.

Here we describe the first results of taxonomic and palaeoecological analyses of the invertebrate assemblages from some Italian Neogene deposits along the foothills of the northern Apennine Mountains, with special regard to molluscs from organic-rich marine palaeoenvironments. Specifically the goals of this work are to characterize the main molluscan species recovered from a wood-fall association, which is the first described Italian Miocene wood-fall deposit, and to provide preliminary discussion of the role of boring Teredinidae bivalves in the trophic structure of a deep-sea wood-fall community. Our report also includes the description of a new species of the chiton genus *Leptochiton* Gray, 1847.

Geological Setting and Stratigraphy of the Study Sites

The study sites are located in the domains resulting from a compressional tectonic regime, between the Adriatic-Apulian foreland structural

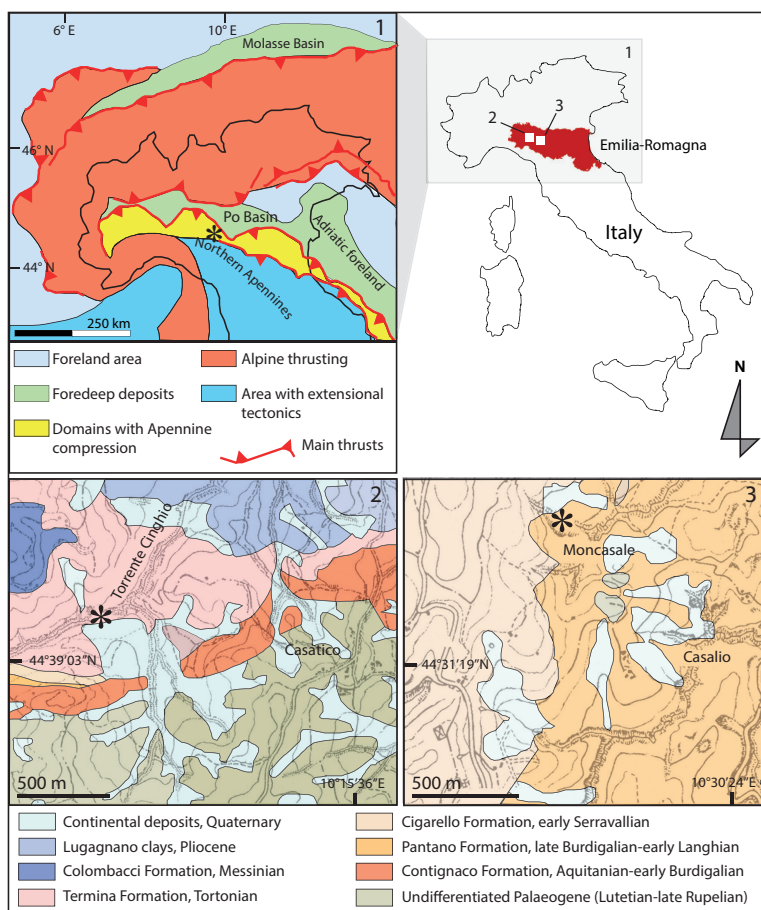


FIGURE 1. Location of the study area and of the Torrente Cinghio and Moncasale sites (asterisks) in the structural map (1) of northern Italy (modified from Scrocca et al., 2003) and in their respective geological setting (2-3) as modified from Papani (2002) and Di Dio and Zanzucchi (2005).

domain and the main thrust of the Northern Apennines (Figure 1.1), a rapidly migrating thrust belt developed mainly in Neogene times during the eastward roll-back of the subducting Adriatic plate (Scrocca et al., 2003).

Most of the studied material comes from the sediments of the Torrente Cinghio site (Figure 1.2). These sediments belong to the “Formazione del Termina” (Termina Fm) (Bettelli et al., 1989) that ranges from the late Serravallian to the late Tortonian, occasionally to the early Messinian (Miculan, 1992; Gasperi et al., 2005). In particular this site is middle to late Tortonian in age as the biozones MNN8a, MNN8b and MNN9 have been recognized (Fornaciari et al., 1996). The Termina Fm is a muddy unit at the end of a deepening-upward succession filling the Emilian basin, overlying coarser deposits of the Pantano Fm and the Cigarello Fm (Di Dio et al., 2005). Other material has been recovered near Moncasale di Casina (Reggio

Emilia, N Italy), in a gully situated on the left side of the “Fosso di Moncasale” (Figure 1.3). The lower and middle parts of the exposure belong to the Pantano Fm, aged late Burdigalian - Langhian (Amorosi et al., 1993). This material comes from sediment that contains *Praeorbulina glomerata circularis* Blow, 1956 (P. Miculan, personal commun., 1995), suggestive of the middle Langhian biozone MMi4b (Iaccarino and Salvatorini, 1982; Di Stefano et al., 2008), or, at least a middle-late Langhian age as this foraminifer does not occur in younger sediments (Ryan et al., 1979).

Chitons on Sunken Wood

Within the order Lepidopleurida, the families Ferreiraellidae Dell’Angelo and Palazzi, 1991, Nierstraszellidae Sirenko, 1992 and a part of Lepitochitonidae Dall, 1889 seem to have a close relationship with wood-falls, and many species are found in abundance on tropical sunken wood (Sig-

wart and Sirenko, 2012). On the basis of the strong similarity between the recent *Ferreiraella* Sirenko, 1988 (with most species living on sunken woods, Sigwart and Sirenko, 2012) and the Carboniferous *Glaphurochiton* Raymond, 1910, Sirenko (2004) suggested that wood-falls might have formed deep-sea habitats for chitons since the Middle to Late Palaeozoic when large woody plants first evolved on land (Wolff, 1979). Sirenko (2004) also inferred a post-Jurassic origin of the *Leptochiton* specialization on wood, later than the first occurrence of the family Leptochitonidae, a Carboniferous origin for Ferreiraellidae, and a late Mesozoic origin for *Nierstraszella* Sirenko, 1992. Proposals of ancient origins for deep-sea taxa should be treated cautiously, however, as well as the Palaeozoic origin of the specialization on wood substrates because their fossil record is not extensively known. In addition, *Glaphurochiton* was not found associated with fossil wood, but in black and dark shales assumed to be a palaeoenvironment rich in organic material (Kiel and Goedert, 2006a). The three families also have shell features that are generally interpreted as plesiomorphic so that it is difficult to pinpoint their origin in the fossil record.

One of Sirenko's (2004) main arguments for a phylogenetic association between the Palaeozoic *Glaphurochiton* and the extant *Ferreiraella* chitons living on sunken wood is the current known distribution of the latter. *Ferreiraella* only occurs along the tropical western and eastern coasts of the Pacific Ocean and extends into the Caribbean Sea, which corresponds loosely to the last remaining areas of the ancient Pantalassian coast.

The two established species in the genus *Nierstraszella*, *N. lineata* (Nierstrasz, 1905) and *N. andamanica* (Smith, 1906), are restricted to sunken wood habitats (Sigwart, 2009; Sigwart and Sirenko, 2012). The worldwide genus *Leptochiton* includes species living in a wide range of habitats, from intertidal to deep waters, even if a large number of deep-water species were found on sunken wood (Sigwart and Sirenko, 2012). This genus is well disseminated in the wood-falls from the W. Pacific (Pailleret et al., 2007; Samadi et al., 2010; Duperron et al., 2013; Sigwart and Sirenko, 2012) with a single species reported from wood-falls in the Caribbean Sea, *L. binghami* (Boone, 1928) (Gracia and Ardila, 2004; Sirenko, 2004; Sigwart and Sirenko, 2012), and a high species diversity in the Atlantic Ocean (Kaas and Van Belle, 1985) and the Mediterranean Sea (Dell'Angelo and Smriglio, 1999). A recent molecular phylogenetic study of Lepidopleurida (Sigwart et al., 2011) showed that

the genus is not monophyletic, *Leptochiton* and Leptochitonidae *sensu stricto* being restricted to North Atlantic and Mediterranean taxa. The results of that study also suggested the occurrence of two separate clades independently inhabiting sunken wood substrates in the southwestern Pacific.

There is a different trophic relationship with the wood substrate between Leptochitonidae and at least Nierstraszellidae. Sirenko (2004), studying the relationship between length of the digestive tract and content of food, regarded the "wood-fall related chitons" as detritivorous. This agrees with the analysis performed by Duperron et al. (2013) on *Leptochiton boucheti* Sirenko, 2001 and *Nierstraszella lineata* (Nierstrasz, 1905). Both species do not directly digest the wood, but instead feed on biofilms covering the decaying wood. These biofilms consist of microorganisms contributing to wood degradation and probably also suspended particulate organic matter derived from the downward flux of detritus. These two species also display associations with different bacterial partners. *Leptochiton boucheti* harbours *Mollicutes* Edward and Freundt, 1967 in regions of its gut epithelium, but has no abundant bacterium associated with its gills. Conversely, *Nierstraszella lineata* displays no dense gut-associated bacteria, but harbours bacterial filaments attached to its gill epithelium, related to the Deltaproteobacteria symbionts found in gills of the wood-eating limpet *Pectinodonta* Dall, 1882 (Zbinden et al., 2010; Duperron et al., 2013). *Nierstraszella lineata*, as a member of a family restricted to sunken wood, is likely better adapted to more anoxic conditions due to its gill-associated bacteria. *Leptochiton boucheti* is phylogenetically more proximate to an ancestral form not specialized on wood and may itself be more of a generalist, in agreement with the other members of "Leptochitonidae" whose diet has been studied. Another member of *Leptochiton*, *L. cf. assimilis* (Thiele, 1909), was recently found from sunken wood collected from the abyssal plain area off the Kuril-Kamchatka Trench (Schwabe et al., 2015) and seems to have similar feeding ecology to *L. boucheti*.

Further investigations are also needed within the more species-rich order Chitonida Thiele, 1909 to clarify the microhabitat and feeding ecology of its deep-water representatives as well as their potential specialized associations with a reducing environment or with a specialized substrate such as sunken wood. For example, *Tripoplax alba* Saito, 2013 from the East China Sea at depths of 576-611 m has been found living either on sunken

wood or dead shells generally together with *Calypptogena kawamurai* (Kuroda, 1943), a bivalve that is characteristically associated with chemosynthetic communities (Saito, 2013). Two other congeners are known from chemosynthetic environments off the Chilean coast, *Tripoplax balaenophila* (Schwabe and Sellanes, 2004) from a 240 m deep whale bone and *Tripoplax cowani* (Clark, 2008) from a methane seep area at a depth of 922 m (Schwabe and Sellanes, 2004, 2010). Examples of chitons linked to sunken woods are represented by two unidentified specimens of *Stenosemus* Middendorff, 1847 from the Solomon Islands (Sigwart and Sirenko, 2012) and by the unidentified specimens of Ischnochitonidae Dall, 1889 and Acanthochitonidae Pilsbry, 1893 from the Vanuatu Islands (BOA1 cruise, Samadi et al., 2010).

In spite of their considerable presence in recent wood-fall, chitons clearly associated with sunken wood are rare in the fossil records and are only represented by *Leptochiton* species. The oldest record is that of a “leptochitonid polyplacophoran” from a Poland Middle Jurassic sunken driftwood with no associated chemosymbiotic animals due to the absence of xylophagid boring bivalves (Kaim, 2011). *Leptochiton shapovalovi* Sirenko, 2013 from the Late Jurassic (Oxfordian) of Russia is another possible Jurassic xylophagous species. It shows a shape similar to recent xylophagous chitons and was found in clay with numerous pieces of fossil wood, together with a gastropod species associated with biotopes of sunken wood.

Cenozoic deep-water sediments in Washington State, USA, have produced fossil wood- and whale-fall communities, which occur in close geographic and stratigraphic proximity to cold seeps (Kiel and Goedert, 2006a, 2006b). Twenty-nine molluscs (excluding shipworms) were identified from 28 wood-fall communities from the Eocene to Oligocene, and a species attributed to *Leptochiton* was present in five of these communities (Kiel and Goedert, 2006a). Also, a single intermediate valve of an unidentified chiton was found in a wood-fall from the Eocene of the Lincoln Creek Formation in Washington State, USA (Kiel and Goedert, 2006b).

Our description of *Leptochiton lignatilis* n. sp. from the Miocene of Italy adds a further record to the scarce number of chitons in fossil wood-fall communities.

MATERIALS AND METHODS

Most of the studied material comes from an outcrop along the banks of the stream known as

Torrente Cinghio, 625 m from Case Cuccarello (Torrechiara, Langhirano, Parma, N Italy, Figure 1). It specifically comes from a massive dark grey claystone within a ca. 3 m thick succession on the right side of the stream. This layer, at 1.5 m over a characteristic lens of a bluish light grey bioturbated claystone of unknown lateral extent, contains few carbonized wood remains that are concentrated within a small lens-shaped feature (25 cm wide and up to 6-7 cm thick) surrounded by oxidized surfaces. This lenticular feature is interpreted as the “ghost” of the fossil sunken wood and gives an approximation of its size. This feature was sampled, washed and sieved (mesh sizes of 0.2, 0.5, 1.0, 2.0 mm), and all the organic remains were recovered. Particular attention was given to the mollusc remains for which a semiquantitative analysis was carried out, with emphasis on detecting species typical of wood-fall communities.

Further material is from the upper part of a 60-70 m thick succession cropping out in a gully on the left side of the “Fosso di Moncasale”, near Moncasale di Casina (Reggio Emilia, N Italy, Figure 1). This material comes from a lens-shaped mudstone that is within a body resedimented by slumping.

Morphological details of *Leptochiton lignatilis* n. sp. were preliminarily studied using a Cambridge S-360 scanning electron microscope (SEM) at the Dipartimento di Scienze della Terra dell’Università di Torino. Further in-depth analyses were performed using LEO 420 SEM.

Abbreviations

MGPT, Museo di Geologia e Paleontologia, University of Torino, Italy; MSNG, Museo Civico di Storia Naturale Giacomo Doria, Genova, Italy; MZB, Museo di Zoologia, University of Bologna, Italy; MZPD, Museo di Zoologia P. Doderlein, University of Palermo, Italy; NHMW, Natural History Museum Wien, Austria; ZISP, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia; BD, Bruno Dell’Angelo collection, Genova, Italy (will be deposited in MZB); LB, Luca Bertolaso collection, Reggio Emilia, Italy.

RESULTS

The Most Common Molluscs at the Study Sites

The analysis of the sample collected from the lens-shaped feature in the Torrente Cinghio deposit provided a relatively rich molluscan assemblage consisting of about 87 taxa, including 48 gastropods, 35 bivalves, five scaphopods and one chiton.

Among the most common species found were: 1) approximately 100 disarticulated valves of the new chiton species, *Leptochiton lignatilis* n. sp.; 2) almost 300 *Homalopoma* sp. and more than 250 *Pseudonina bellardii*, both gastropod species represented by a full growth series; 3) about 60 valves of the bivalve *Idas* sp. and, among the wood-boring bivalves, several palettes, tubes and valves of *Bankia* sp., *Psiloterodo* cf. *megotara* (Hanley in Forbes and Hanley, 1848) and *Teredotyra* sp.; and 4) more than 200 valves of an undetermined species still under study belonging to Teredinidae. The occurrence of other molluscs, including the gastropod *Alvania testae* (Aradas and Maggiore, 1844), the bivalve *Delectopecten* cf. *vitreus* (Gmelin, 1791) and the scaphopod *Entalina tetragona* (Brocchi, 1814) indicate a deep-sea epibathyal environment.

A less diverse assemblage was found in the sample collected from the Moncasale site, where fossils are generally poorly preserved. In this site, however, a similar community structure was detected, with the most significant taxa being teredinids, *Homalopoma* sp. and *Pseudonina bellardii*, all represented by a great deal fewer specimens.

Systematic Palaeontology

Class POLYPLACOPHORA Gray, 1821
Family LEPTOCHITONIDAE Dall, 1889
Genus LEPTOCHITON Gray, 1847

Type species. *Chiton cinereus* Linnaeus, 1767 *sensu* Montagu, 1803 (misapplication of name, subsequently designated by Gray, 1847) = *Leptochiton asellus* (Gmelin, 1791) (see Sirenko, 2001, p. 41).

Distribution. Worldwide; Upper Jurassic (Sirenko, 2013) - recent.

Leptochiton lignatilis n. sp. Dell'Angelo, Bertolaso and Sosso
Figures 2-4

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Type material. Holotype: MGPT-PU 108787 (tail valve, Figure 2.1-4); paratypes: MGPT-PU 108788 (head valve, Figure 2.6-7); MZB 32033 (intermediate valve, Figure 3.1-2, broken during preparation for SEM); MZB 32034 (intermediate valve); NHMW 2014/0451/0001 (intermediate valve, Figure 3.3-4); NHMW 2014/0451/0002 (tail valve, Figure 2.5); ZISP 2226 (intermediate valve); ZISP 2227 (intermediate valve); MSNG 57980 (one intermediate and one head valve); MZPD MAL-2074 (intermediate valve, Figure 2.8-9); MZPD MAL-2075 (head valve). MZPD MAL-2076 (fragment of intermediate

valve, Figure 3.5-8). These valves are from the Tortonian of Torrente Cinghio, Parma, Emilia Romagna, N Italy. Another paratype, MZPD MAL-2077 (fragment of intermediate valve, Figure 4.1-2), is from the Langhian of Moncasale di Casina, Reggio Emilia, Emilia Romagna.

Other material examined. 100 valves, most of them incomplete, from the Tortonian of Torrente Cinghio, in BD and LB.

Type locality. Torrente Cinghio, Parma, Italy; Miocene, Tortonian.

Type horizon. Dark grey claystone of the Termina Formation, Tortonian in age.

Etymology. The name *lignatilis* (relating to the wood) is from the Latin *lignum* (wood), with referring to the substrate linked to this species.

Distribution. *Leptochiton lignatilis* n. sp. is only known from the Miocene of northern Italy, particularly from the Tortonian of Torrente Cinghio (Parma), and from the Langhian of Moncasale di Casina (Reggio Emilia).

Diagnosis. Head valve semioval; intermediate valve rectangular, carinated, elevated; tail valve more than semicircular, mucro anterior. Tegmentum ornamented by irregularly arranged, well-separated roundish-subquadrangular granules.

Description. Holotype width (lateral) 3.5 mm, length (antero-posterior) 2.5 mm; maximum width 2.4 / 3.4 / 3.5 mm (head, intermediate, and tail). Head valve semioval (Figure 2.6), posterior margin widely V-shaped, slope concave. Intermediate valve broadly rectangular (Figure 3.1) with slightly rounded corners, carinated, anterior and posterior margins almost straight, apex indistinct, elevated (height/width 0.5), lateral areas scarcely differentiated. Tail valve more than semicircular (Figure 2.1), anterior margin convex, mucro anterior, not prominent, antemucronal slope convex, postmucronal slope a little concave just underneath mucro.

Sculpture of tegmentum formed by rather irregular elevated granules, of roundish shape (Figure 2.7), well separated from each other, irregularly arranged, except apex portion of head valve with concentric ridges. Granules become more irregularly elongate (Figure 3.5-6) towards the jugal area of intermediate valves, but always well separated, not coalescing. Each granule (diameter 40 to 50 μ m) bears a more or less central macroaesthete, and variable number of microaesthetes, two to four, up to five to six in more elongate granules (Figures 2.9, 3.6). Elongate granules can reach a maximum length up to 70 μ m.

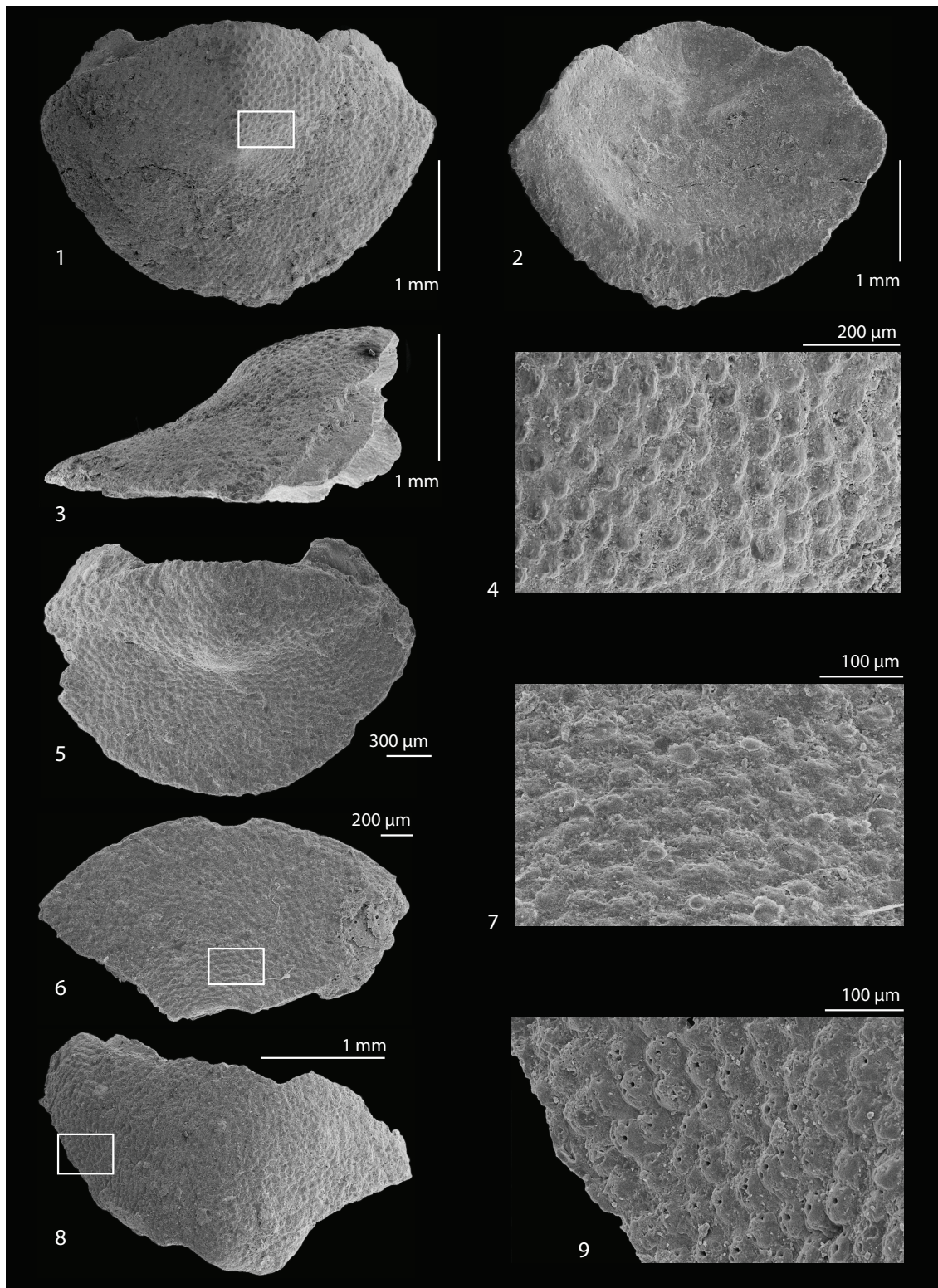


FIGURE 2. *Leptochiton lignatilis* n. sp. from the Miocene (Tortonian) of Torrente Cinghio (Parma, N Italy, type locality). **1-4.** Holotype, tail valve MGPT-PU 108787 in dorsal (**1**), ventral (**2**) and lateral (**3**) views, and close up (white rectangle in 1) showing sculpture (**4**). **5.** Paratype NHMW 2014/0451/0002, tail valve with a more protruding mucro. **6-7.** Paratype MGPT-PU 108788, head valve in dorsal view (**6**) and close up (white rectangle in 6) showing sculpture (**7**). **8-9.** Paratype MZPD MAL-2074, intermediate valve in dorsal view (**8**) and close up (white rectangle in 8) showing granules with aesthetes (**9**).

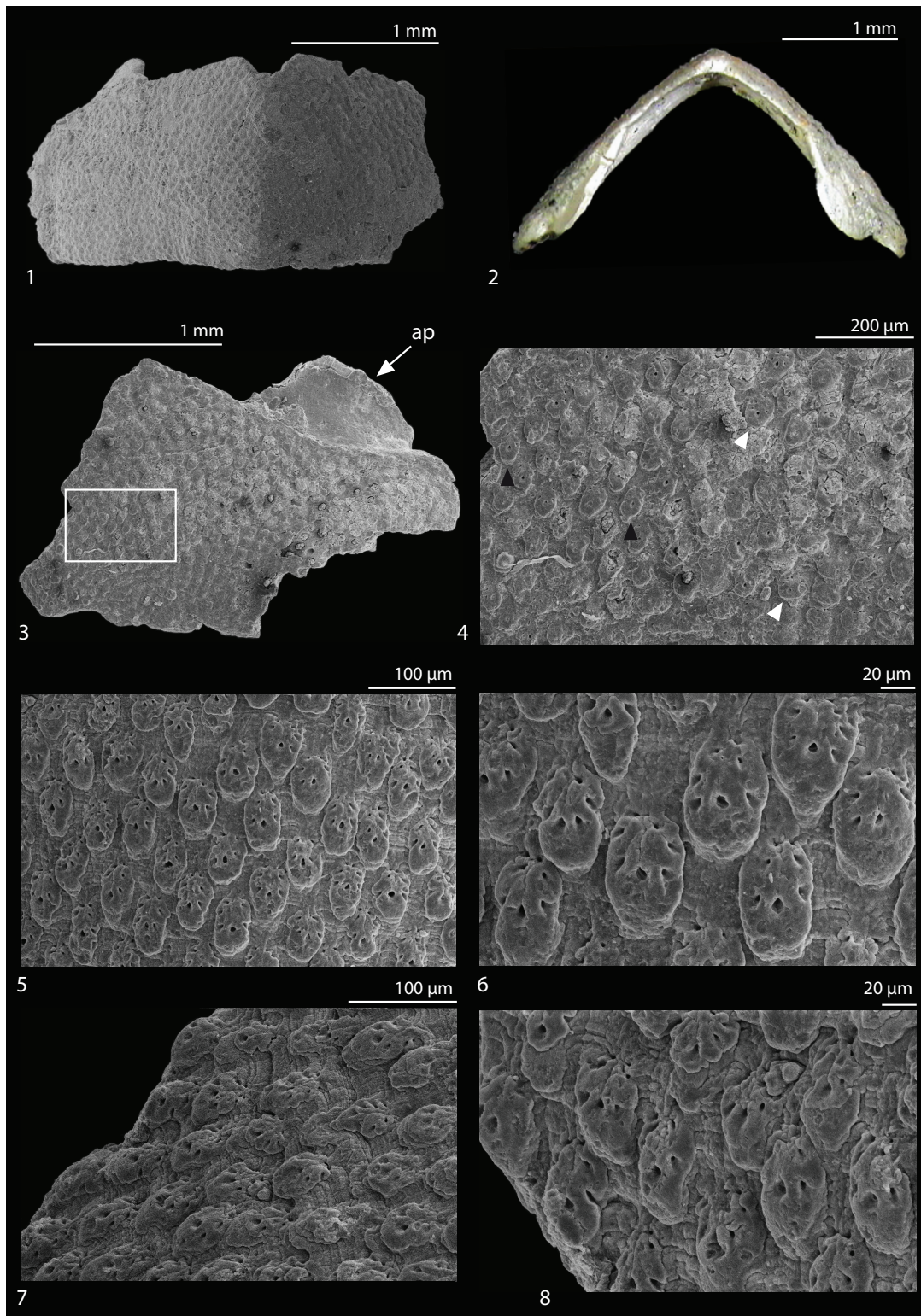


FIGURE 3. *Leptochiton lignatilis* n. sp., from the Miocene (Tortonian) of Torrente Cinghio (Parma, N Italy, type locality). **1-2.** Paratype MZB 32033, intermediate valve in dorsal (**1**) and profile view (**2**). **3-4.** Paratype NHMW 2014/0451/0001, fragment of a tail valve showing apophysis (ap in **3**) and close-up (white rectangle in **3**) showing variation in granule shape (**4**) from circular (white triangles) to elongate (black triangles). **5-8.** Paratype MZPD MAL-2076, detail of a fragment of an intermediate valve showing granule arrangement (**5**, **7**) and macro and microaesthetes (**6**, **8**).

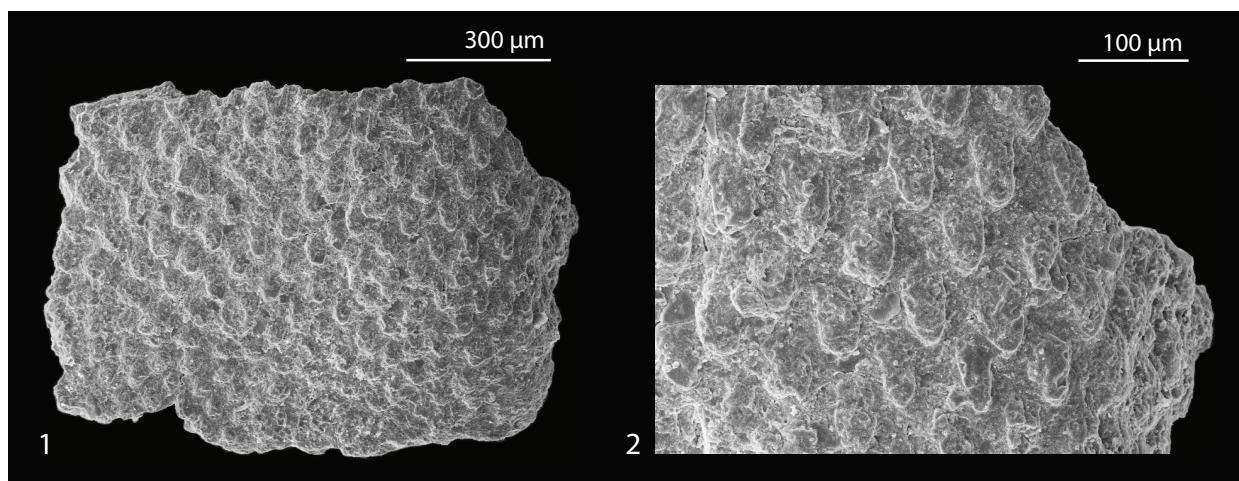


FIGURE 4. *Leptochiton lignatilis* n. sp., from the Miocene (Langhian) of Moncasale di Casina (Reggio Emilia, N Italy). 1. Paratype MZPD MAL-2077, dorsal view of a fragment of an intermediate valve. 2. Close-up of the specimen as in Figure 4.1 showing granules.

Articulamentum without insertion laminae (Figure 2.2). Apophyses small, triangular in intermediate valves (Figure 3.1, 3.3), more or less trapezoidal in tail ones (Figure 2.1, 2.3), widely separated by a large jugal sinus.

Remarks. In the material studied there are almost only small fragments of valves (of about 1-1.5 mm or less of width). Even though these fragmented valves have clearly visible tegmentum granules, in many cases it is not possible to identify them as head, intermediate or tail valves. Only 15 valves are complete or sufficiently complete.

The small fragment of the intermediate valve from Moncasale di Casina (Figure 4) has a sculpturing matching that of the material from Torrente Cinghio and is compatible with an attribution as *Leptochiton*. Considering the similarities of the sculpture, we provisionally consider this valve conspecific with the material from Torrente Cinghio.

Comparisons. The sculpture of *Leptochiton*'s tegmentum is fundamentally of two types, fully covered with randomly or quincuncially arranged granules, or with granules arranged in longitudinal striae in central and antemucronal areas (and both randomly/quincuncially or in radial striae on head valve, lateral and postmucronal areas).

For *Leptochiton* species known from sunken woods (Sigwart and Sirenko, 2012, table 2), 12 of 23 have a tegmental sculpture that is comparable with *Leptochiton lignatilis* n. sp. Five of them are less elevated, with a different shape of the tail valve and a subcentral mucro: *Leptochiton angustidens* Sigwart and Sirenko, 2012, *L. consimilis* Sigwart and Sirenko, 2012, *L. schwabei* Sigwart

and Sirenko, 2012, *L. deforgesii* Sirenko, 2001 and *L. vanbellei* Sirenko, 2001 (the latter with a slightly anterior mucro). Six others are also less elevated and also have a different shape of the tail valves and have a subcentral mucro, but they also differ in having the granules in the central areas more or less arranged in distinctive longitudinal rows: *Leptochiton benthedii* (Leloup, 1981), *L. rogeri* Sigwart and Sirenko, 2015 (new name for *L. clarki* Sigwart and Sirenko, 2012, see Sigwart and Sirenko, 2015), *L. longisetosus* Sigwart and Sirenko, 2012, *L. thandari* Sirenko, 2001, *L. vitjazi* (Sirenko, 1977) and *L. boucheti* Sirenko, 2001 (the latter with a slightly anterior mucro).

Leptochiton kurnilatus Kaas, 1985 is a carinated and elevated species comparable with *L. lignatilis* n. sp. (height/width 0.57 vs. 0.5), but differs by the different shape and profile of tail valves, with the posterior mucro at about three quarters of the valve length.

Only three *Leptochiton* species from the Mediterranean Neogene have the same kind of tegmental sculpture, fully covered with randomly or quincuncially arranged granules. *Leptochiton tavianii* Dell'Angelo et al., 2004 from the Pliocene of Estepona (Spain) differs in having the granules characterized by a fungiform section and arranged in a beehive structure; *L. salicensis* Dell'Angelo and Bonfitto, 2005 from the Pleistocene of Salice (South Italy) has sturdier yet dissimilar valves, which are evenly rounded (subcarinated in *L. lignatilis*), a less elevated tail valve with a subcentral mucro (anterior in *L. lignatilis*) and more polygonal granules. The Pliocene-recent *Leptochiton alveo-*

TABLE 1. Distribution and main characters of *Leptochiton lignatilis* n. sp., *L. alveolus* (M. Sars in Lovén, 1846) and *L. belknapi* Dall, 1878, allowing comparisons.

Distribution/taxonomic characters	<i>Leptochiton lignatilis</i> n. sp.	<i>L. alveolus</i>	<i>L. belknapi</i>
Stratigraphy	Miocene of Italy	Pliocene of Italy	-
Biogeography	-	Atlantic Ocean	Pacific and Indian Oceans
Valves	Thinner and fragile	Thinner and fragile	Thicker and sturdy
Tegmental granules	Irregular, rounded-subquadrangular shape	More regular, smaller and closely packed, rounded-oval shape	Larger and more widely spaced, oval to diamond-like in shape
Intermediate valves (IV)	Rectangular	Rectangular	Rectangular
IV back	Carinated	Arched	Carinated
IV anterior margin	Almost straight	Concave in the jugal area	Almost straight
IV posterior margin	Almost straight, apex not distinct	Almost straight, apex obsolete or poorly marked	Almost straight, obsolete or poorly marked
IV lateral areas	Not raised	Not raised	Little raised, distinctly marked by a diagonal depression
IV height/width ratio	0.50	-	0.36
Tail valve (TV)	More than semicircular	Semicircular	Semicircular to roughly triangular
TV anterior margin	Convex	Almost straight	Convex
TV mucro	Anterior	Central	Subcentral

lus (M. Sars in Lovén, 1846) is characterized by the tegmentum covered with pronounced, neatly separated, rounded to oval granules, more or less distinctly quincuncially arranged on all the valves surface, the lateral areas indiscernible from the central areas and arched intermediate valves (see Kaas, 1981 for a detailed description). This deep-water chiton, and secondarily the distinct *Leptochiton belknapi* Dall, 1878 (Wu and Okutani, 1984), are the most comparable species to *L. lignatilis* n. sp. Differences between these species are summarized in Table 1. The specimen reported as “*L. alveolus*” from Eocene-Oligocene cold-seep limestones of the Olympic Peninsula, Washington (Goedert and Campbell, 1995; Squires and Goedert, 1995; Peckmann et al., 2002) has not been considered for this comparison because its specific and even generic assignment remains an open problem (Schwabe and Sellanes, 2010). However, geographic and stratigraphic separation of this specimen from *L. lignatilis* n. sp. allows considering them as different species.

DISCUSSION AND CONCLUDING REMARKS

Preliminary results of studies on several Neogene deep-sea wood-fall deposits from Emilia (N Italy) suggest that each of the molluscan assemblages has a highly distinctive biota (Bertolaso, personal observation). However, all of these assemblages are characterized by a taxonomic

composition comparable to those observed in analogous modern environments. More generally, in the chemosynthetic communities, there is broad overlap in community composition at generic and higher taxonomic ranks. In contrast, the unique biodiversity of each assemblage at lower (species/genus) taxonomic ranks appears to be mostly related to the depositional depth. These observations support the hypothesis that deep-sea wood-falls are a mixture of endemic and generalist taxa, and their composition may be related to the depositional setting as suggested by Kiel and Little (2006) for deep-sea seep molluscs as well as to the palaeogeographic dynamics that changed the Miocene Proto-Mediterranean-Atlantic Region to the recent Mediterranean basin (Harzhauser et al., 2002).

The most abundant molluscs in the studied samples from the Torrente Cinghio are *Pseudonina bellardii* (Michelotti, 1847) and *Homalopoma* sp. The former belongs to a typical deep-sea genus of the Neogene wood-falls (Bertolaso and Palazzi, 1994). The latter belongs to Colloniidae Cossmann, 1917, a typical family from late Mesozoic-recent chemosynthesis-based communities (e.g., Kiel, 2008; Gill et al., 2005; Kaim et al., 2009; Sasaki et al., 2010; Gracia et al., 2012), and is the same species as found in other Miocene wood-falls from northern Italy (Bertolaso, personal observation). Two other remarkable occurrences, both represented by a significant number of specimens, contribute to detailing a palaeoenvironmental

framework. The first, *Leptochiton*, is a typical wood-fall genus in deep waters. The second is *Idas* Jeffreys, 1876, a typical bivalve from chemosynthetic environments, common in wood-fall communities since the Eocene (e.g., Kiel and Goedert, 2006b; Pailleret et al., 2007; Bienhold et al., 2013). This four-taxa assemblage illustrates a typical wood-fall molluscan association in deep-sea chemosynthetic ecosystems. The deep environmental setting is supported by the occurrence of other species, such as the scaphopod *Entalina tetragona* and the scallop *Delectopecten* cf. *vitreus*. All the chiton material found belongs to the new species described, *Leptochiton lignatilis* n. sp., representing a genus that is common on sunken wood in tropical recent waters. The fossil record *Leptochiton* from these assemblages, however, is quite sparse. Aside from the type locality, this species is known only from one incomplete intermediate valve (a small fragment) found at the Moncasale di Casina site. The only diagnostic character of this valve is the tegmental sculpture comparable to that observed in the material from Torrente Cinghio, thus suggesting a conspecificity. In the same site were rare valves of Teredinidae and some specimens of *Homalopoma* sp. and *Pseudonina bellardii*. This association points to the occurrence of a wood-fall community similar to that of Torrente Cinghio, but represented by scattered specimens displaced from their natural habitat.

It is noteworthy that no Xylophagidae, only Teredinidae (*Psiloteredo* Bartsch, 1922, *Teredothyra* Bartsch, 1921, *Bankia* Gray, 1842) boring bivalves were found in the fossil wood-fall association studied from the Torrente Cinghio. Likewise, only teredinid remains were found at the Moncasale di Casina site. As already discussed, xylophagid bivalves are known to have been a fundamental component in wood-fall settings hosting chemosynthetic communities since at least the Cretaceous. Their decomposing faecal pellets significantly increase the amount of sulphide around sunken wood (Kaim, 2011 and references therein). In the studied case, neither Teredinidae colonization of wood during a floating stage nor after sinking can be definitely determined. There is evidence, however, of a chemosynthetic community originating on the deep-sea floor in the presence of living Teredinidae: 1) the co-occurrence of *Idas*, a genus never found alive on floating woods; and 2) the presence of taxa that are typical of deep sea and wood-fall ecosystems and are represented by a full growth series, conditions that are possible in the wood-fall communities due to the ecological

role carried out by the xylophagous bivalves. Our studied material has unexpectedly implied a colonization of sunken wood by Teredinidae, not anticipated in previous literature. The central role for Teredinidae apparently did not hamper the development of a specialized fauna in a deep-sea reducing environment, analogous to xylophagid dominated assemblages. It could be hypothesized that Teredinidae species, at least in the Mediterranean area, were previously living in deeper waters and have only recently been replaced by Xylophagidae; however, only a quantitatively exhaustive dataset on Neogene deep wood-fall communities could endorse this hypothesis. Future studies on similar deposits/communities from Emilia Romagna (N Italy) will likely shed some more light on the role of Teredinidae in this kind of ecosystem.

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