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Bathymodioline mussel dominated Miocene whale fall from Italy

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KEY WORDS - Whale fall, Bathymodiolinae, Adipicola*, new taxa, Miocene, Northern Apennines, Cold seep.*

ABSTRACT - The bones of an unidentified odontocete from the Langhian Pantano Formation (~ 15 million years ago), found near the town of Carpineti (Reggio Emilia), Northern Italy, are associated with more than two hundred specimens of the bathymodioline mussel Adipicola apenninica *n. sp., rare specimens of* Thyasira *sp. and one Lucinidae indet. Based on comparisons with modern and other fossil whale fall communities, the fossil molluscs associated with the odontocete represent a whale fall community during the sulphophilic stage of the ecological succession. Our finding indicates the presence of chemosynthetic communities associated with organic remains in the proto-Mediterranean-Atlantic region at least from the middle Miocene. The previous connection of the Tethyan Realm with both the Atlantic Ocean and the Indo-Pacific, could have played a key role in the evolution and dispersal of bathymodiolins between the two regions.*

RIASSUNTO - [Whale fall italiana dominata da bivalvi della sottofamiglia Bathymodiolinae] *- Le comunità associate alle carcasse di balena (whale fall communities, wfc) ospitano bivalvi chemosintetici e altri metazoi specializzati che sfruttano l'acido solfidrico e il metano rilasciato nell'ambiente dalla decomposizione degli abbondanti lipidi presenti nelle ossa di balena. Comunità simili vivono associate alle sorgenti idrotermali (hydrothermal vents) e alle sorgenti di idrocarburi (cold seeps). Il registro fossile delle wfc è però limitato e nuovi dati sono essenziali per ricostruire la loro evoluzione. Qui viene segnalata una wfc associata ad ossa di un odontocete proveniente dalla Formazione di Pantano (Langhiano, ~ 15 milioni di anni fa), rinvenuta vicino al paese di Carpineti (Reggio Emilia). Le ossa sono associate ad oltre duecento esemplari di bivalvi chemosintetici della sottofamiglia Bathymodiolinae (*Adipicola apenninica *n. sp.), a rari esemplari di* Thyasira *sp. e ad un Lucinidae indet. Questo ritrovamento indica che comunità chemiosintetiche associate a vertebrati marini erano presenti nella regione proto-Mediterranea almeno dal Miocene medio. La somiglianza di* A. apenninica *n. sp. con specie fossili (*A. chikubetsuensis *[Amano, 1984]) ed attuali (*A. arcuatilis *Dell, 1995) dell'area indo-pacifica, suggerisce che la Tetide mediterranea, grazie alla sua connessione con l'Indo-Pacifico, possa avere svolto un ruolo importante nella dispersione dei Batimodiolinae e altre faune chemiosintetiche.*

INTRODUCTION

First discovered in 1987, when a chemosynthetic assemblage that unexpectedly resembled hydrothermal vent and cold seep communities was found associated with a balaenopterid skeleton in the deep sea off California (Smith et al., 1989), whale fall communities form around the carcasses of whales that after death sink to the sea bottom. Communities living at hydrothermal vents, cold seeps and organic falls, such as whale- and wood-falls, are characterized by the occurrence of highly specialized animals, such as vestimentiferan tube worms, bathymodioline mussels and vesicomyid clams that live in symbiosis with chemotrophic bacteria, which thrive on the abundant hydrogen sulphide and methane, and provide their hosts with nutrients (Dubilier et al., 2008). At whale falls, the hydrogen sulphide and methane are provided by the anaerobic decay of the whale bone lipids, which can sustain chemosynthetic assemblages from years to decades ("sulphophilic stage"; Baco & Smith, 2003).

The ecology of the associated fauna is increasingly well understood (see Smith et al., 2015 for a review). After almost thirty years from their discovery, whale falls have been studied on naturally occurring and artificially implanted carcasses in both the deep north and south Pacific, and in the north-east and south-west Atlantic Ocean. In contrast, systematic studies are lacking for the Mediterranean Sea, where knowledge of comparable communities is based only on occasional retrieval of whale bones by fishermen (Bolotin et al., 2005; Pelorce & Poutiers, 2009) and from the fossil record (Dominici et al., 2009; Danise & Dominici, 2014).

Fossil whale fall communities are recognized by the presence of hard-shelled invertebrates associated with the bones of cetaceans, secondarily by trace fossils (e.g., Higgs et al., 2012). Evidence is sparse so far, and comes from the late Eocene and Oligocene of the Olympic Peninsula, western Washington State, USA (Squires et al., 1991; Goedert et al., 1995; Nesbitt, 2005; Kiel & Goedert, 2006; Kiel, 2008), the middle Miocene of California, USA (Pyenson & Haasl, 2007), the middle Miocene of Hokkaido, Japan (Amano & Little, 2005; Amano et al., 2007), and the Pliocene of Italy (Dominici et al., 2009; Danise et al., 2010) and Spain (Esperante et al., 2009). Whale falls from Italy and Spain are associated with open marine deposits at shelf depths, whereas the other examples come from deep-water sediments. The study of these whale fall faunas, modern and fossil, has led to some interesting evolutionary case stories. For example, phylogenetic and molecular studies have shown that bathymodioline mussels living at organic falls have played a key role in the evolution and dispersal of this clade, acting as evolutionary stepping stones for the colonization of hydrothermal vents and seeps, and that this happened multiple times in the history of the taxon (Samadi et al., 2007; Lorion et al., 2013; Thubaut et al., 2013). Any

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new report is thus important inasmuch it adds a piece to a yet-unresolved puzzle. In particular, the hypothesis on the evolution and dispersal of bathymodiolins is largely based on modern data, and new fossil evidence is needed to test it. In this study we report on a new fossil whale fall community from Italy, and we show that chemosynthetic organic fall communities, dominated by bathymodioline mussels, were present in the proto-Mediterranean-Atlantic region in the middle Miocene.

MATERIAL AND METHODS

Fragmentary bones and teeth of a largely incomplete and unidentified odontocete and its associated bivalve fauna were collected near the town of Carpineti (Reggio Emilia), in Northern Italy (Fig. 1). The claystone succession hosting the specimen is about 20 m thick and monotonous, apart from a 1.5 m-thick interval richer in calcareous cement. It belongs to the Langhian Pantano Formation of the Epiligurid Bismantova Group (Roveri, 1966), forming part of the late Eocene to early Pleistocene satellite basins cropping out in the Northern Apennines. These basins are largely filled by terrigenous, diachronous deposits, originated during the NE migration of the Apennine thrust belt (Ricci Lucchi, 1987). The Pantano Formation is characterized by frequent lateral changes of facies and is commonly attributed to an inner shelf paleoenvironment dominated by litharenites (Roveri, 1966; Papani et al., 2002). However, the presence of the spatangoid echinoid *Mazettia pareti* (Manzoni, 1879) in the light grey hemipelagic siltstones and marls outcropping in the Carpineti locality, stratigraphically above the odontocete specimen (Fig. 1b-c), is more consistent with an outer shelf, or upper slope paleoenvironment. Fossil species of the genus *Mazettia* are commonly associated

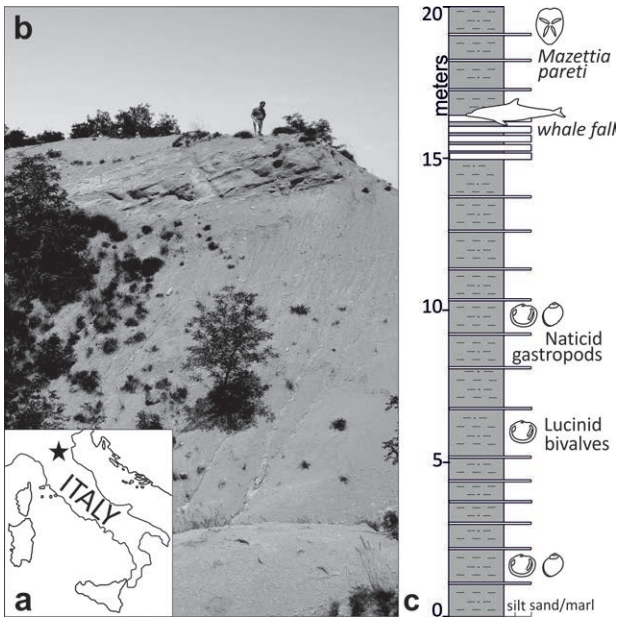

Fig. 1 - Location map and stratigraphic section. a) The Langhian toothed whale comes from Carpineti, Reggio Emilia (black star). b) Type locality of the Carpineti odontocete and associated *Adipicola apenninica* n. sp. c) Detailed stratigraphic section of the type locality.

with epibathyal paleoenvironments (Smith & Gale, 2009; Borghi, 2012); a good modern analogue is the genus *Linopneustes*, found at depth of 70-570 m (Mortensen, 1950). The occurrence of the naticid gastropod *Tanea koeneni* (Sacco, 1891) and fragments of the nektonic, deep water dwelling cephalopod *Aturia* sp. (Teichert & Matsumoto, 2010), confirms this interpretation. Bivalves of the family Lucinidae, whose modern relatives are known to host chemosynthetic, sulphur-oxidizing bacteria (Taylor & Glover, 2006) are also common in the Carpineti hemipelagites stratigraphically below the odontocete, with abundant articulated individuals of *Megaxinus ellipticus* (Borson, 1825), *Lucinoma* cf. *borealis* (Linnaeus, 1767), and Lucinidae indet., occurring in association with rare small gastropods and solitary corals.

RESULTS AND DISCUSSION

More than 200 individuals of the bathymodioline mussel *Adipicola apenninica* n. sp. were found in association with the odontocete bones at the Carpineti locality. The mussels, which occur as external moulds of articulated specimens, are presumably preserved in life position as they are directly in contact with bones or teeth, or are concentrated in the closest sediments (Figs 2b, 3b), whereas they are absent from the surrounding strata. Rare specimens of *Thyasira* sp. (n=3) and Lucinidae indet. (n = 1) were also found in association with *A. apenninica* (Fig. 3).

The fossil molluscs associated with the Carpineti odontocete can be interepreted as a whale fall community in the sulphophilic stage, based on comparisons with modern and other fossil whale fall communities (Smith et al., 1989; Goedert et al., 1995; Baco & Smith, 2003; Amano & Little, 2005; Kiel & Goedert, 2006; Amano et al., 2007).

The dominance of bathymodioline mussels (*A. apenninica* n. sp.), and the rare occurrence of bivalves of the families Thyasiridae and Lucinidae, which are typical of sulphidic rich sediments (Dubilier et al., 2008), makes the Carpineti whale fall molluscan community very similar to that of late Eocene-Oligocene whale falls described from the Washington State, USA, the oldest whale fall communities known to date and which are similarly dominated by bathymodiolins (*Idas*? *olympicus* Kiel & Goedert, 2007) and which also have small specimens of thyasirids (*Thyasira xylodia* Kiel & Goedert, 2007, *Conchocele bisecta* [Conrad, 1849]) and lucinids (*Lucinoma*) (Goedert et al., 1995; Kiel & Goedert, 2006, 2007). Both occurrences are characterized by the absence of chemosymbiotic bivalves of the families Vesicomyidae and Solemyidae, which are instead typical of modern whale fall communities. Since the latter most heavily rely on sulphide for nutrition, it has been hypothesized that archaic whales where too small, or had not enough oil content to sustain these animals (Kiel & Goedert, 2006). The discovery of abundant vesicomyid clams in association with bones of a middle Miocene mysticete smaller than the adult individuals of any living mysticete species (ca. 3 meters), suggested that oil content, and not size, was an important factor for the development of a fully-developed association of the sulphophilic stage (Pyenson & Haasl, 2007). In our material, not knowing

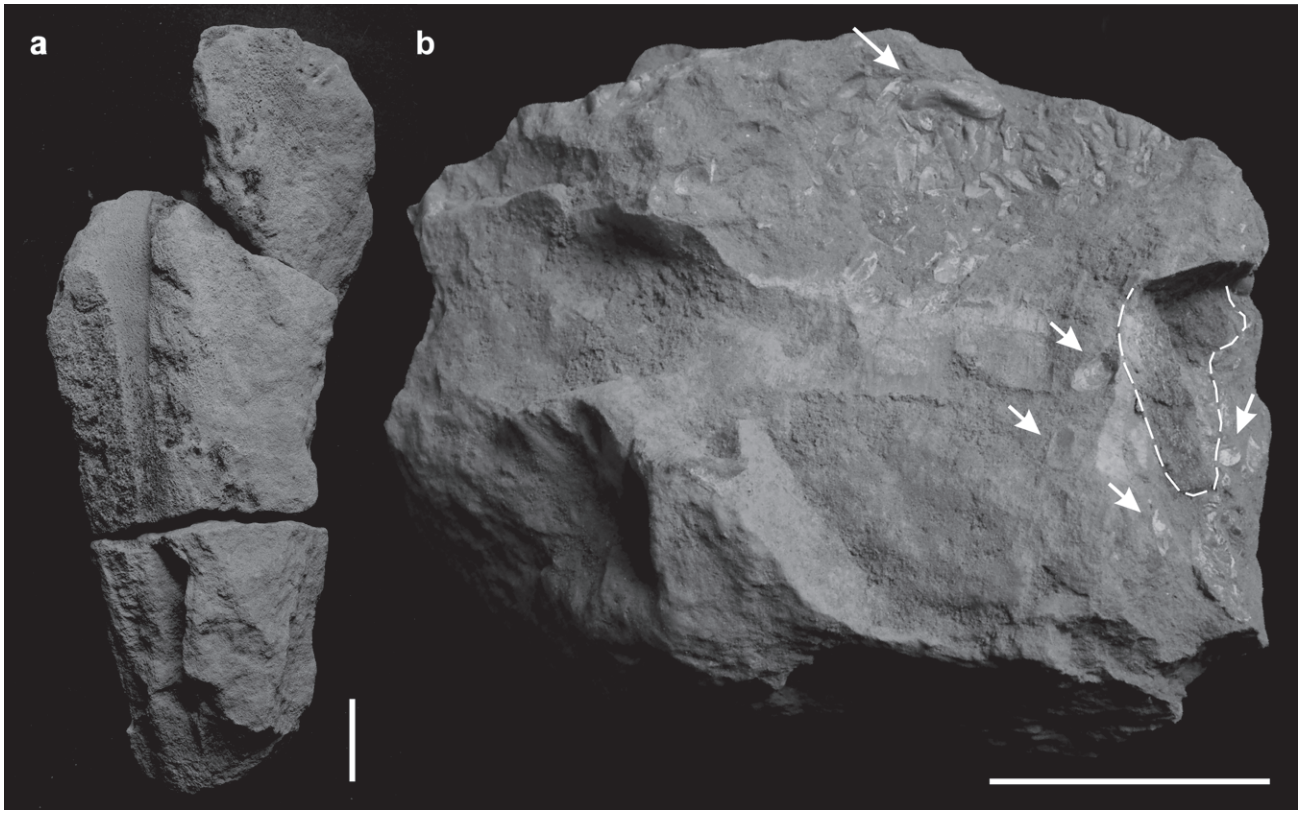

Fig. 2 - Carpineti toothed whale with associated chemosymbiotic bivalves. a) Postcranial bone of the unidentified toothed whale (MSNF IGF102219). b) *Adipicola apenninica* n. sp. (short arrows) concentrated around a bone fragment (dashed line) and in the surrounding sediment. Long arrow points to a well preserved left valve. a: scale bar corresponds to 2 cm; b: scale bar corresponds to 5 cm.

the exact size of the Carpineti odontocete, we suggest that the presence of a less diverse association with the bathymodioline mussels could also be linked to a temporally variable efflux of reduced compounds from the decaying bones. Modern bathymodioline species living at organic falls are in fact characterised by mixotrophic symbiosis (Fujiwara et al., 2010), a useful adaptation to cope with the highly variable environments that they experience (Duperron, 2010).

The Carpineti assemblage also differs from the Miocene whale falls from the Hokkaido region in Japan. The latter are also dominated by bathymodioline mussels of species *Adipicola chikubetsuensis* (Amano, 1984), but in association with vesicomyids and solemyids, as in typical modern whale fall communities (Amano & Little, 2005; Amano et al., 2007). Interestingly, these Japanese whale fall communities share genera and species with adjacent hydrocarbon seeps, suggesting that, during the Miocene, in the NW Pacific there was a regional pool of molluscs adapted to living at chemosynthetic sites and that could utilize compounds found at both seeps and whale falls (Amano et al., 2007).

The Northern Apennines offer some well-studied examples of ancient cold seeps and the associated chemosymbiotic fossil communities (Conti & Fontana, 1999, 2005; Clari & Martire, 2000; Clari et al., 2009; Cau et al., 2015). Cold seeps were particularly common in the Apennine basins in Langhian/Serravallian and late Tortonian/early Messinian times (Ricci Lucchi & Vai, 1994), continuing into the Pliocene (Taviani, 2001; Barbieri & Cavalazzi, 2005; Cau et al., 2015). Although well studied for their structural, sedimentological, petrographical and geochemical characteristics (Cavagna et al., 1999; Peckmann et al., 2004; Barbieri & Cavalazzi, 2005; Conti & Fontana, 2005; Clari et al., 2009; Dela Pierre et al., 2010), the macro-invertebrate faunas of the Apennine cold seeps are poorly described, with only determinations at high taxonomic levels being usually available (Taviani, 1994; Taviani, 2001; Lucente & Taviani, 2005; Sami & Taviani, 2015). There are exceptions (e.g., Moroni, 1966), but these studies unfortunately predate the modern understanding of vent and seep biotas. Middle Miocene cold seeps of the Northern Apennines were dominated by large lucinid bivalves ("Calcari a Lucina": Terzi et al., 1994; Fontana et al., 2004), but monospecific occurrences of vesicomyid clams are also reported (?*Calyptogena* in Lucente & Taviani, 2005). None of the cold seep faunas studied so far in the Apennines are comparable to the assemblage occurring at the Carpineti whale fall, suggesting that, in contrast with the pattern in the Pacific Ocean, in the proto-Mediterranean-Atlantic region in the Miocene there was no species in common between cold seep and whale fall habitats. However, small bathymodioline mussels, so common at Carpineti, are a recurrent component of wood fall communities worldwide since the Eocene (Kiel & Goedert, 2009), and are represented at epibathyal depths in the Mediterranean at least since the Tortonian (Western Emilia, Northern Apennines: Bertolaso et al., 2015), and up to now (Eastern Mediterranean: Bienhold et al., 2013).

The presence of bathymodioline mussels in the Northern Apennines since the Miocene confirms that the Tethyan Realm (sensu Harzhauser et al., 2002), as a connection between the Atlantic Ocean and the Indo-Pacific, played an important role in the evolution and dispersal of chemosynthetic taxa between the two regions (Taviani, 2011). In the lower Miocene, the Tethyan Realm was a large embayment linking the Atlantic and the Indian Oceans (e.g., Rögl, 1998; Harzhauser et al., 2007). Connections between the Tethyan Realm and the Indo-Pacific ceased to exist after the Burdigalian with a short-lived marine connection during the Langhian (Harzhauser et al., 2007). A gradual decline of faunistic similarities between the two regions starts to develop from the Burdigalian, with several representatives being still present during the Langhian in the newly-formed proto-Mediterranean-Atlantic region (Harzhauser et al., 2007). The morphological similarity between *Adipicola apenninica* n. sp. and the species *A. chikubetsuensis* (Amano, 1984) and *A. arcuatilis* Dell, 1995, found respectively at fossil and modern whale falls in the Indo Pacific region, would testify then for a species pool between the Tethyan Realm and the Indo Pacific. Molecular studies on modern taxa indicate that the diversification of the bathymodioline mussels was initiated in the early Miocene, and subsequent diversification of the clade occurred in the early to middle Miocene (Miyazaki et al., 2010). In alternative, bathymodioline radiation would have occurred earlier, from the Middle Eocene to Early Oligocene (Lorion et al., 2013). It is, in any case, important to highlight that, because of the high level of polymorphism in shell shape of mussel of the subfamily Bathymodiolinae, due to either allometric growth or environmental plasticity (Lorion et al., 2010), caution needs to be made in inferring evolutionary trends based solely on shell morphology.

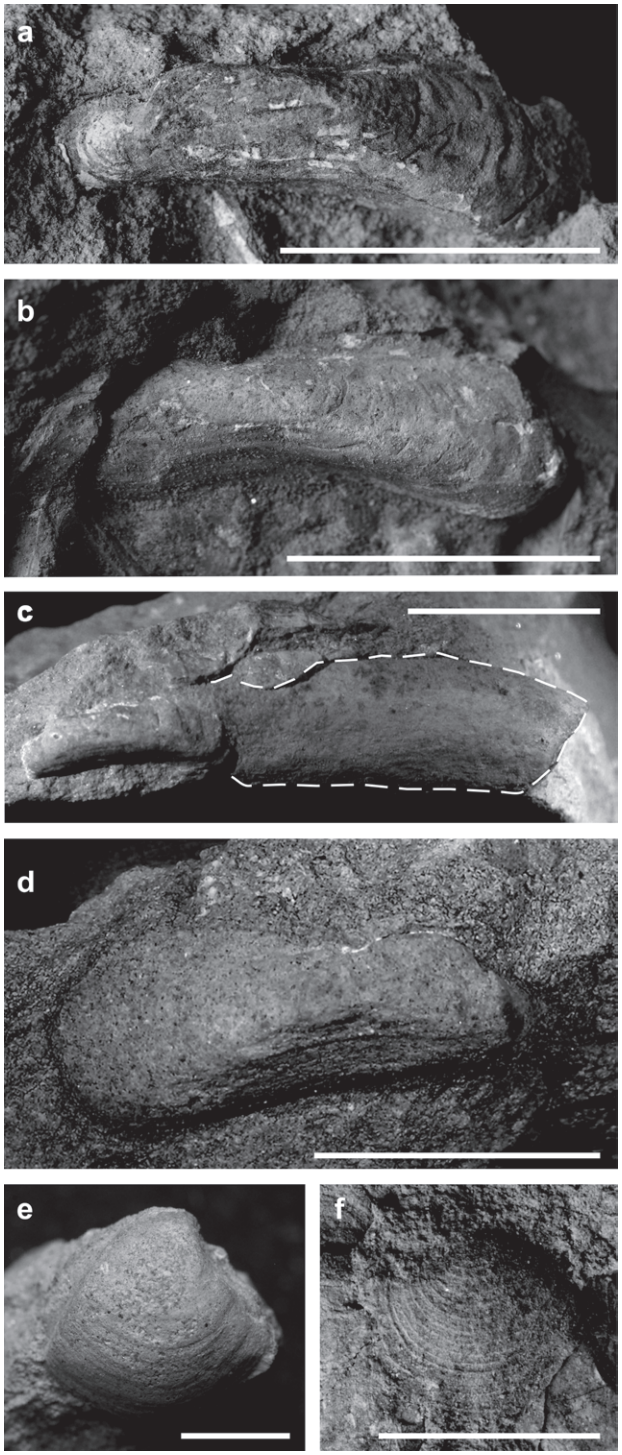

Fig. 3 - Chemosymbiotic bivalves associated with the Carpineti toothed whale. a) *Adipicola apenninica* n. sp., left valve, holotype (MSNF IGF102221). b) *A. apenninica* n. sp., left valve, paratype (MSNF IGF102222). c) *A. apenninica* n. sp., left valve, paratype (MSNF IGF102220) on a tooth (dashed line) of the fossil odontocete. d) *A. apenninica* n. sp., right valve, paratype (MSNF IGF102223). e) *Thyasira* sp. (MSNF IGF102224). f) Lucinidae indet. (MSNF IGF102225). a-e: scale bar corresponds to 1 cm; f: scale bar corresponds to 0.5 cm.

CONCLUSIONS

An assemblage of bivalves was found in close association with the bones of an unidentified odontocete at Carpineti, in Western Emilia (Langhian; Pantano Formation). This is dominated by the small bathymodioline bivalve *Adipicola apenninica* n. sp., interpreted by analogy with extant forms of the same subfamily as a chemosymbiotic form taking advantage of the sulphide present at the carcass. This interpretation is supported by the presence of other bivalves known to host chemosynthetic bacteria (Thyasiridae, Lucinidae). The Carpineti assemblage proves that whale fall communities have existed in the proto-Atlantic-Mediterranean region at least since the Langhian. This at the same time suggests that the Tethyan Realm, by forming a link between the Atlantic Ocean and the Indo-Pacific region, favoured the migration of chemosymbiotic invertebrates that use large organic falls as stepping stones.

APPENDIX

SYSTEMATICS

Family Mytilidae Rafinesque, 1815
Subfamily Bathymodiolinae Kenk & Wilson, 1985

Genus *Adipicola* Dautzenberg, 1927

Type species (monotypy): *Myrina denhami* H. & A. Adams, 1854 = *Modiolarca pelagica* Woodward, 1854, Recent, South Atlantic.

Remarks - The systematics of the genus is matter of debate. Some authors synonymize *Adipicola* with the genus *Idas* Jeffreys, 1876, claiming there are not enough morphological features to distinguish the two (Warén, 1991; Pelorce & Poutiers, 2009; Giusti et al., 2012). Others identify *Adipicola* as a distinct genus, and distinguish the two genera on the basis of differences in the morphological characters of the shells, like the crenulated area within the hinge, present in *Idas,* and absent in *Adipicola* (Dell, 1987, 1995), and differences in soft body anatomy of the demibranchs and the gills (Gustafson et al., 1998). Furthermore, biologists using molecular characters to recognise species within extant bathymodiolins (Lorion et al., 2010) distinguish between the two genera. Based on general shell morphology, and adopting the second opinion, we recognise *Adipicola* at Carpineti, keeping it distinct from *Idas*.

Adipicola apenninica n. sp.
(Fig. 3a-d)

Etymology - Species named after the Apennines Range, where it was found.

Diagnosis - Elongate modioliform shell, with a broad, rounded posterior margin and narrow anterior margin. Ventral margin from slightly to highly concave; ridge running from beak to posteroventral corner.

Type material - More than 200 specimens deposited at the Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze (MSFN). Holotype: MSNF IGF102221, external mould, left valve (Fig. 3a). Paratypes: MSNF IGF102222, external mould, left valve (Fig. 3b); MSFN IGF102220, external mould, left valve (Fig. 3c); MSNF IGF102223, external mould, right valve (Fig. 3d).

Type locality - Casella di Romagnano, 3.3 km east of the town of Carpineti, Reggio Emilia, Italy, off Strada Provinciale 7 (SP7). Coordinates: 44°27'27.60"N, 10°33'35.60"E.

Stratigraphic and geographic distribution - Middle Miocene, Langhian, Pantano Formation; known only from the type locality.

Description - Shell of small size (maximum measured size 17 × 6 mm, minimum size 4.5 × 1.5 mm), modioliform, elongate, inaequilateral, the anterodorsal and posterodorsal margins meeting at a broad angle. Umbo not very prominent, situated near anterior end, at one fourth of total shell length. Blunt ridge running from beak to posteroventral corner. Anterior margin narrow but slightly rounded, posterior margin rounded and more broadly expanded. Ventral margin from slightly to highly concave, giving a bow shaped outline to larger individuals. Surface smooth, except irregular growth increments. Hinge and interior of shell unknown.

Measurements of the holotype - Length 1.69 cm, width 0.38 cm.

Remarks - *Adipicola apenninica* n. sp. resembles *A. chikubetsuensis* (Amano, 1984) from the lower middle Miocene of Hokkaido, Japan, in the presence of a ridge running from the beak to the posteroventral corner and for the elongated outline (Amano, 1984; Amano & Little, 2005). *A. apenninica* n. sp. is however smaller in size, and has a less pronounced umbo and a sinuate, bow-shaped ventral margin, in contrast to *A. chikubetsuensis*, which has a ventral margin with a concavity in the mid position. Among the small mytilids reported from Italian Neogene deposits before the discovery of chemosynthetic ecosystems, *Modiola exbrocchii tauroparva* Sacco, 1898 from the Langhian of the Turin Hills can be included the present discussion. Sacco (1898) figured two specimens, one of which shows some of the characters of *Adipicola* (see Sacco, 1898, Plate XI, fig. 28; the specimen of fig. 29 probably belongs to *Modiola*, or possibly *Bathymodiolus*). *Modiola exbrocchii tauroparva* Sacco, 1898 lacks however a formal description and, in any case, *A. apenninica* n. sp. has a more developed anterior margin than the first specimen figured by Sacco. Among the modern species, *A. apenninica* n. sp. resembles *A. arcuatilis* Dell, 1995 from New Zealand, for the bow-shaped ventral margin, the elongated outline and position of the umbo toward the anterior margin, at around one fourth of the total shell length. *A. apenninica* n. sp. is however considerably smaller than the latter, which can be up to 30 mm in length, and has a much less developed anterior margin. *A. apenninica* n. sp. is more elongated and has a narrower anterior margin than *A. pelagica* (Woodward, 1854) and *A. pacifica* (Dall, Bartsch & Rehder, 1938). Is also more elongated than *A. osseocola* Dell, 1987, and has irregular growth wrinkles, compared to the well-spaced and regular wrinkles of *A. ossecola*. *A. crypta* (Dall, Bartsch & Rehder, 1938) and *A. longissima* (Thiele & Jaeckel, 1932) are much more elongated than *A. apenninica* n. sp. and, in *A. crypta*, in contrast to *A. apenninica* n. sp., the anterior and the posterior margins are similar in height. *A. apenninica* n. sp. differs from *A. iwaotakii* (Habe, 1958) by having a bow-shaped outline.

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