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## **Bathymodioline mussel dominated Miocene whale fall from Italy**

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## 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 vesicomimid 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 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 paretii* (Manzoni, 1879) in the light grey hemipelagic siltstones and marls outcropping in the Carpineti locality, stratigraphically above the odontocete specimen (Figure 1b-c), is more consistent with an outer shelf, or upper slope paleoenvironment. Fossil species of the genus *Mazettia* are commonly associated 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 are preserved as external moulds of articulated specimens, presumably preserved in life position as

they are preserved directly in contact with bones or teeth, or are concentrated in the closest sediments (Fig. 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 interpreted as a whale fall community in the sulphophilic stage, based on comparisons with modern and other fossil whale fall communities (Amano & Little, 2005; Amano et al., 2007; Baco & Smith, 2003; Goedert et al., 1995; Kiel & Goedert, 2006; Smith et al., 1989).

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 and Goedert, 2007) and which also have small specimens of thyasirids (*Thyasira xylochia* 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 Vesicomidae 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 were too small, or had not enough oil content to sustain these animals (Kiel & Goedert, 2006). The discovery of abundant vesicomid 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 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 vesicomysids 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 there was a regional pool of molluscs in the NW Pacific during the Miocene 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 (“*Calcarella lucina*”: Terzi et al., 1994; Fontana et al., 2004), but monospecific occurrences of vesicomid clams are also reported (?*Calypptogena* in Lucente and 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.

## 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. Holotype: MSNF IGF102221, external mould, left valve (Fig. 3a). Paratypes: MSNF IGF102222, external mould, left valve (Fig. 3b); MSNF 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  $17 \times 6$  mm, minimum size  $4.5 \times 1.5$  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* 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 in 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* has a more developed anterior margin than the first specimen figured by Sacco. Among the modern species, *A. apenninica* 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* is more elongated and has a narrower anterior margin than *A. pelagica* (Woodward, 1854) and *A. pacifica* (Dall, Bartsch & Rehder, 1938). It is also more elongated than *A. osseocola* Dell, 1987, and has irregular growth wrinkles, compared to the well-spaced and regular wrinkles of *A. osseocola*. *A. crypta* (Dall, Bartsch &

Rehder, 1938) and *A. longissima* (Thiele & Jaeckel, 1932) are much more elongated than *A. apenninica* and, in *A. crypta*, in contrast to *A. apenninica*, the anterior and the posterior margins are similar in height. *A. apenninica* differs from *A. iwaotakii* (Habe, 1958) by having a bow-shaped outline.

## Figure Captions

**Figure 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.

**Figure 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 2 cm; b: scale bar 5 cm.

**Figure 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 IGF 102224). **f.** Lucinidae indet. (MSNF IGF102225). a-e: scale bar 1 cm; f: scale bar 0.5 cm.

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## **References**

- Adams H. & Adams A. (1854). Description of a new genus of bivalve Mollusca. *Annals and Magazine of Natural History*, 2(14): 418.
- Amano K. (1984). Two species of Mytilidae (Bivalvia) from the Miocene deposits in Hokkaido, Japan. *Venus*, 43: 183-188.
- Amano K. & Little C.T.S. (2005). Miocene whale-fall community from Hokkaido, northern Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 215: 345-356.
- Amano K., Little C.T.S. & Inoue K. (2007). A new Miocene whale-fall community from Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 247: 236-242.
- Baco A.R. & Smith C.R. (2003). Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology, An Annual Review*, 41: 311-354.
- Barbieri R. & Cavalazzi B. (2005). Microbial fabrics from Neogene cold seep carbonates, Northern Apennine, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 227: 143-155.
- Bertolaso L., Garilli V., Parrinello D., Sosso M. & Dell'Angelo B. (2015). A new Miocene deep-sea chiton and early evidence for Teredinidae-sustained wood-fall communities. *Palaeontologia Electronica*, 18.2.41A: 1-15.

- Bienhold C., Pop Ristova P., Wenzhöfer F., Dittmar T. & Boetius A. (2013). How deep-sea wood falls sustain chemosynthetic life. *PLoS ONE*, 8, e53590.
- Bolotin J., Hrs-Brenko M., Tutman P., Glavic N., Kožul V., Skaramuca B., Lucic D. & Lucic J. (2005). First record of *Idas simpsoni* (Mollusca: Bivalvia: Mytilidae) in the Adriatic Sea. *Journal of the Marine Biological Association of the United Kingdom*, 85: 977-978.
- Borghi E. (2012). *Mazettia* (Maretiidae) un caratteristico echinoide del Miocene dell'Emilia-Romagna. *Notiziario Società Reggiana di Scienze Naturali*, 2012: 9-20.
- Borson S. (1825). Continuazione del Saggio di Orittographia Piemontese. *Memorie della Reale Accademia delle Scienze di Torino*, 29: 251-318.
- Bourillot R., Vennin E., Rouchy J.-M., Blanc-Valleron M.-M., Caruso A. & Durle, C. (2010). The end of the Messinian Salinity Crisis in the western Mediterranean: Insights from the carbonate platforms of south-eastern Spain. *Sedimentary Geology*, 229: 224-253.
- Cau S., Franchi F., Roveri M. & Taviani M. (2015). The Pliocene-age Stirone River hydrocarbon chemoherm complex (Northern Apennines, Italy). *Marine and Petroleum Geology*, 66: 582-595.
- Cavagna S., Clari P. & Martire L. (1999). The role of bacteria in the formation of cold seep carbonates: geological evidence from Monferrato (Tertiary, NW Italy). *Sedimentary Geology*, 126: 253-270.
- Cita M.B. (1976). Biodynamic effects of the Messinian salinity crisis on the evolution of planktonic foraminifera in the Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 20: 23-42.

- Clari P., Dela Pierre F., Martire L. & Cavagna S. (2009). The Cenozoic CH<sub>4</sub>-derived carbonates of Monferrato (NW Italy): A solid evidence of fluid circulation in the sedimentary column. *Marine Geology*, 265: 167-184.
- Clari P.A. & Martire L. (2000). Cold seep carbonates in the Tertiary of Northwest Italy: Evidence of bacterial degradation of methane. *In* Riding R. & Awramik S. (eds), *Microbial Sediments*. Springer, Berlin-Heidelberg: 261-269.
- Conrad T.A. (1849). Fossils from northwestern America. *In* Dana J.D. (ed.), *United States Exploring Expedition. During the years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes, U.S.N. Atlas. Geology, Volume 10: Philadelphia*.
- Conti S. & Fontana D. (1999). Miocene chemoherms of the northern Apennines, Italy. *Geology*, 27: 927-930.
- Conti S. & Fontana D. (2005). Anatomy of seep-carbonates: Ancient examples from the Miocene of the northern Apennines (Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 227: 156-175.
- Dall W.H., Bartsch P. & Reheder H.A. (1938). A manual of the recent and fossil marine pelecypod mollusks of the Hawaiian Islands. *Bernice P. Bishop Museum Bulletin*, 153: 1-233.
- Danise S. & Dominici S. (2014). A record of fossil shallow-water whale falls from Italy. *Lethaia*, 47: 229-243.
- Danise S., Dominici S. & Betocchi U. (2010). Mollusk species at a Pliocene shelf whale fall (Orciano Pisano, Tuscany). *Palaios*, 25: 449-456.
- Dautzenberg P. (1927). Mollusques provenant des campagnes scientifiques du Prince Albert Ier de Monaco dans l'Océan Atlantique et dans le Golfe de Gascogne. *Résultats des*

*campagnes scientifiques accomplies sur son yacht par Albert Ier Prince souverain de Monaco*, 72, 1-400.

Dela Pierre F., Martire L., Natalicchio M., Clari P. & Petrea C. (2010). Authigenic carbonates in Upper Miocene sediments of the Tertiary Piedmont Basin (NW Italy): Vestiges of an ancient gas hydrate stability zone? *Geological Society of America Bulletin*, 122: 994-1010.

Dell R.K. (1987). Mollusca of the family Mytilidae (Bivalvia) associated with organic remains from deep-water off New Zealand, with revisions of the genera *Adipicola* Dautzenberg, 1927 and *Idasola* Iredale, 1915. *National Museum of New Zealand Records*, 3: 17-36.

Dell R.K. (1995). New species and records of deepwater Mollusca from off New Zealand. *Tuhinga*, 2:1-26.

Dominici S., Cioppi E., Danise S., Betocchi U., Gallai G., Tangocci F., Valleri G. & Monechi S. (2009). Mediterranean fossil whale falls and the adaptation of mollusks to extreme habitats. *Geology*, 37: 815-818.

Dubilier N., Bergin C. & Lott C. (2008). Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. *Nature Reviews Microbiology*, 6: 725-740.

Duperron S. (2010). The diversity of deep-sea mussels and their bacterial symbioses. In Kiel S. (ed.), *The Vent and Seep Biota: Aspects from Microbes to Ecosystems. Topics in Geobiology* 33: 137-167. Springer, Dordrecht,.

Esperante R., Muñiz Guinea F. & Nick K.E. (2009). Taphonomy of a Mysticeti whale in the Lower Pliocene Huelva Sands Formation (Southern Spain). *Geologica Acta*, 7: 489-505.

Fontana D., Conti S., Clari P. & Taviani M. (2004). Deep-sea fluid expulsion and related products in the Miocene foredeep and satellite basins of the northern Apennines, Italy. In

Proceedings 32<sup>nd</sup> International Geological Congress Field Guide Book P07, Florence, Italy. 16 pp.

- Fujiwara Y., Kawato M., Noda C., Kinoshita G., Yamanaka T., Fujita Y., Uematsu K. & Miyazaki J.-I. (2010). Extracellular and mixotrophic symbiosis in the whale-fall mussel *Adipicola pacifica*: A trend in evolution from extra- to intracellular symbiosis. *PLoS ONE*, 5, e11808.
- Giusti F., Mietto P. & Sbrana C. (2012). Il genere *Idas* (Mytilidae, Bathymodiolinae) in Mediterraneo, con la descrizione di quattro nuove specie. *Bollettino Malacologico*, 48: 122-135.
- Goedert J.L., Squires R.L. & Barnes L.G. (1995). Paleocology of whale-fall habitats from deep-water Oligocene rocks, Olympic Peninsula, Washington state. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 118: 151-158.
- Gustafson R.G., Turner R.D., Lutz R.A. & Vrijenhoek R.C. (1998). A new genus and five new species of mussels (Bivalvia, Mytilidae) from deep-sea sulfide/hydrocarbon seeps in the Gulf of Mexico. *Malacologia*, 40: 63-112.
- Habe T. (1958). Description of five new bivalves from Japan. *Venus*, 20: 173-180.
- Harzhauser M., Piller W.E., Steininger F.F. (2002). Circum-Mediterranean Oligo/Miocene biogeographic evolution - the gastropods' point of view. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 183, 103–133.
- Harzhauser M., Kroh A., Mandic O., Piller W. E., Göhlich U., Reuter M. & Bernin B. (2007). Biogeographic responses to geodynamics: A key study all around the Oligo–Miocene Tethyan Seaway. *Zoologischer Anzeiger*, 246: 241–256.

- Higgs N.D., Little C.T.S., Glover A.G., Dahlgren T.G., Smith C.R. & Dominici S. (2012). Evidence of *Osedax* worm borings in Pliocene (~3 Ma) whale bone from the Mediterranean. *Historical Biology*, 24: 269-277.
- Jeffreys J.G. (1876). New and peculiar mollusca of the *Pecten*, *Mytilus* and *Arca* families, procured during the Valorous Expedition. *Annals and Magazine of Natural History*, 4: 424-436.
- Kenk V.C. & Wilson B.R. (1985). A new mussel (Bivalvia, Mytilidae) from hydrothermal vents in the Galapagos Rift zone. *Malacologia*, 26: 253-271.
- Kiel S. (2008). Fossil evidence for micro- and macrofaunal utilization of large nekton-falls: Examples from early Cenozoic deep-water sediments in Washington State, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 267: 161-174.
- Kiel S. & Goedert J.L. (2006). Deep-sea food bonanzas: early Cenozoic whale-fall communities resemble wood-fall rather than seep communities. *Proceedings of the Royal Society of London (B: Biological Sciences)*, 273: 2625-2632.
- Kiel S. & Goedert J.L. (2007). Six new mollusk species associated with biogenic substrates in Cenozoic deep-water sediments in Washington State, USA. *Acta Palaeontologica Polonica*, 52: 41-52.
- Linnaeus C. (1767). *Systema naturae*. Editio duodecima, reformata. Tomus I. Pars II. L. pp. 533-1327. Salvius, Holmiae (Stockholm).
- Lorion J., Buge B., Cruaud C. & Samadi S. (2010). New insights into diversity and evolution of deep-sea Mytilidae (Mollusca: Bivalvia). *Molecular Phylogenetics and Evolution*, 57: 71-83.

- Lorion J., Kiel S., Faure B., Kawato M., Ho S.Y.W., Marshall B., Tsuchida S., Miyazaki J.-I. & Fujiwara Y. (2013). Adaptive radiation of chemosymbiotic deep-sea mussels. *Proceedings of the Royal Society (B: Biological Sciences)*, 280: 20131243.
- Lucente C.C. & Taviani M. (2005). Chemosynthetic communities as fingerprints of submarine sliding-linked hydrocarbon seepage, Miocene deep-sea strata of the Tuscan–Romagna Apennines, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 227: 176-190.
- Manzoni A. (1879). Gli echinodermi fossili dello Schlier delle colline di Bologna. *Denkschriften der kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe*, 39, 149-164.
- Miyazaki J.-I., Martins L. d.O., Fujita Y., Matsumoto H. & Fujiwara Y. (2010). Evolutionary process of deep-sea *Bathymodiolus* mussels. *PLoS ONE*, 5: e10363.
- Moroni A. (1966). Malacofauna del “Calcare a *Lucina*” di S. Sofia (Forlì). *Palaeontographia Italica*, 60: 69–87.
- Mortensen T. (1950). A monograph of the Echinoidea. Volume 5(1): 432 pp. C.A. Reitzel, Copenhagen.
- Nesbitt E.A. (2005). A novel trophic relationship between cassid gastropods and mysticete whale carcasses. *Lethaia*, 38: 17-25.
- Papani G., De Nardo M. T., Bettelli G., Rio D., Tellini C. & Vernia L. (2002). Note Illustrative della Carta Geologica d’Italia alla scala 1:50.000, Foglio 218, Castelnovo ne’ Monti. 144 pp. Servizio Geologico d’Italia, Firenze.
- Peckmann J., Thiel V., Reitner J., Taviani M., Aharon P. & Michaelis W. (2004). A microbial mat of a large sulfur bacterium preserved in a Miocene methane-seep limestone. *Geomicrobiology Journal*, 21: 247-255.

- Pelorce J. & Poutiers J.-M. (2009). Une nouvelle espèce de Bathymodiolinae (Mollusca, Bivalvia, Mytilidae) associée à des os de baleine coulés en Méditerranée. *Zoosystema*, 31: 975-985.
- Pierre C., Caruso A., Blanc-Valleron M.-M., Rouchy J. M. & Orzsag-Sperber F. (2006). Reconstruction of the paleoenvironmental changes around the Miocene–Pliocene boundary along a West–East transect across the Mediterranean. *Sedimentary Geology*, 188–189: 319-340.
- Pyenson N.D. & Haasl, D.M. (2007). Miocene whale-fall from California demonstrates that cetacean size did not determine the evolution of modern whale-fall communities. *Biology Letters*, 3: 709-711.
- Rafinesque C.S. (1815). *Analyse de la nature: or Tableau de l'univers et des corps organisés*. 244 pp. Palerme.
- Ricci Lucchi F. (1987). Semi-allochthonous sedimentation in the Apenninic thrust belt. *Sedimentary Geology*, 50: 119-134.
- Ricci Lucchi F. & Vai G.B. (1994). A stratigraphic and tectonofacies framework of the “calcarei a *Lucina*” in the Apennine Chain, Italy. *Geo-Marine Letters*, 14: 210-218.
- Rögl F. (1998). Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums in Wien*, 99: 279–310.
- Roveri E. (1966). Geologia della sinclinale Vetto-Carpineti (Reggio Emilia). *Memorie della Società Geologica Italiana*, 5: 241-267.
- Sacco F. (1891). I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte VIII. Galeodoliidae, Doliidae, Ficulidae e Naticidae. *Memorie della Reale Accademia delle Scienze di Torino*, (Serie 2), 41: 225-338.

- Sacco F. (1898). I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte XXV. Spondilidae, Radulidae, Aviculidae, Vulsellidae, Pernidae, Pinnidae, Mytilidae, Dreissensiidae. 64 pp. Clausen, C., Torino.
- Samadi S., Quéméré E., Lorion J., Tillier A., von Cosel R., Lopez P., Cruaud C., Couloux A. & Boisselier-Dubayle M.-C. (2007). Molecular phylogeny in mytilids supports the wooden steps to deep-sea vents hypothesis. *Comptes Rendus Biologies*, 330: 446-456.
- Sami M. & Taviani, M. (2015). I calcari a *Lucina* e i gessi di Rontana. *Memorie dell'Istituto Italiano di Speleologia*, 2: 39-56.
- Smith A.B. & Gale A.S. (2009). The pre-Messinian deep-sea Neogene echinoid fauna of the Mediterranean: Surface productivity controls and biogeographical relationships. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 281: 115-125.
- Smith C.R., Glover A.G., Treude T., Higgs N.D. & Amon D.J. (2015). Whale-fall ecosystems: recent insights into ecology, paleoecology, and evolution. *Annual Review of Marine Science*, 7: 571-596.
- Smith C.R., Kukert H., Wheatcroft R.A., Jumars P.A. & Deming J.W. (1989). Vent fauna on whale remains. *Nature*, 341: 27-28.
- Squires R.L., Goedert J.L. & Barnes L.G. (1991). Whale carcasses. *Nature*, 349: 574-574.
- Taviani M. (1994). The “calcari a *Lucina*” macrofauna reconsidered: Deep-sea faunal oases from Miocene-age cold vents in the Romagna Apennine, Italy. *Geo-Marine Letters*, 14: 185-191.
- Taviani M. (2001). Fluid venting and associated processes. In Vai G. & Martini I.P. (eds), *Anatomy of an Orogen: the Apennines and Adjacent Mediterranean Basins*, Springer Netherlands: 351-366.

- Taviani M. (2011). The deep-sea chemoautotroph microbial world as experienced by the Mediterranean metazoans through time. *In* Reitner J., Quéric N.-V., Arp G. (eds), *Advances in Stromatolite Geobiology*, Springer, Berlin Heidelberg: 277-295.
- Taylor J.D. & Glover, E.A. (2006). Lucinidae (Bivalvia) – the most diverse group of chemosymbiotic molluscs. *Zoological Journal of the Linnean Society*, 148: 421-438.
- Taylor J.D. & Glover E.A. (2010). Chemosymbiotic Bivalves. *In* Kiel S. (ed.), *The Vent and Seep Biota: Aspects from Microbes to Ecosystems*. *Topics in Geobiology* 33: 107-135. Springer, Dordrecht.
- Teichert C. & Matsumoto T. (2010). The ancestry of the genus *Nautilus*. *In* Saunders W.B. & Landman N. (eds), *Nautilus*. Springer Netherlands: 25-32.
- Terzi C., Lucchi F., Vai G. & Aharon P. (1994). Petrography and stable isotope aspects of cold-vent activity imprinted on Miocene-age “calcarei a *Lucina*” from Tuscan and Romagna Apennines, Italy. *Geo-Marine Letters*, 14: 177-184.
- Thiele J. & Jaekel S. (1932). Muscheln der Deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition*, 21: 161-268.
- Thubaut J., Corbari L., Gros O., Duperron S., Couloux A. & Samadi S. (2013). Integrative biology of *Idas iwaotakii* (Habe, 1958), a ‘model species’ associated with sunken organic substrates. *PLoS ONE*, 8: e69680.
- Warén A. (1991). New and little known mollusca from Iceland and Scandinavia. *Sarsia*, 76: 53-124.
- Woodward S.P. (1851-56). *A manual of the Mollusca: or, a rudimentary treatise of recent and fossil shells*. 486 pp. J. Weale, London.

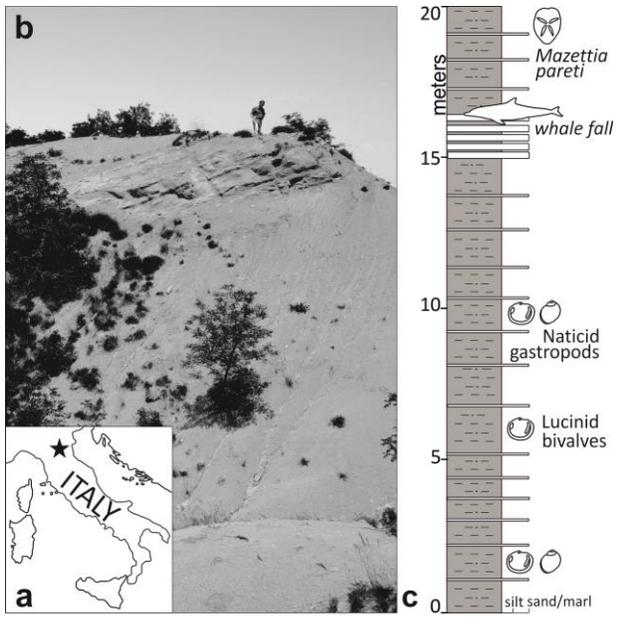


Figure 1

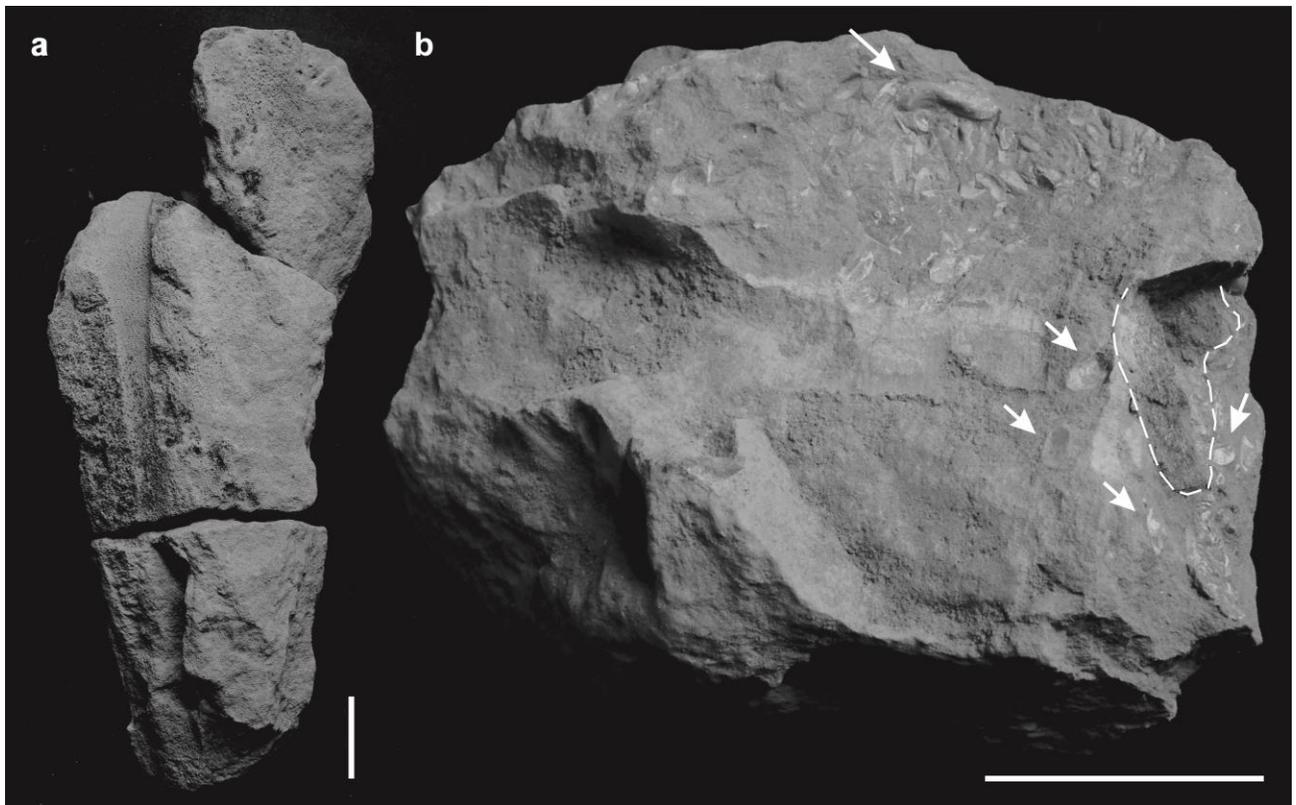


Figure 2

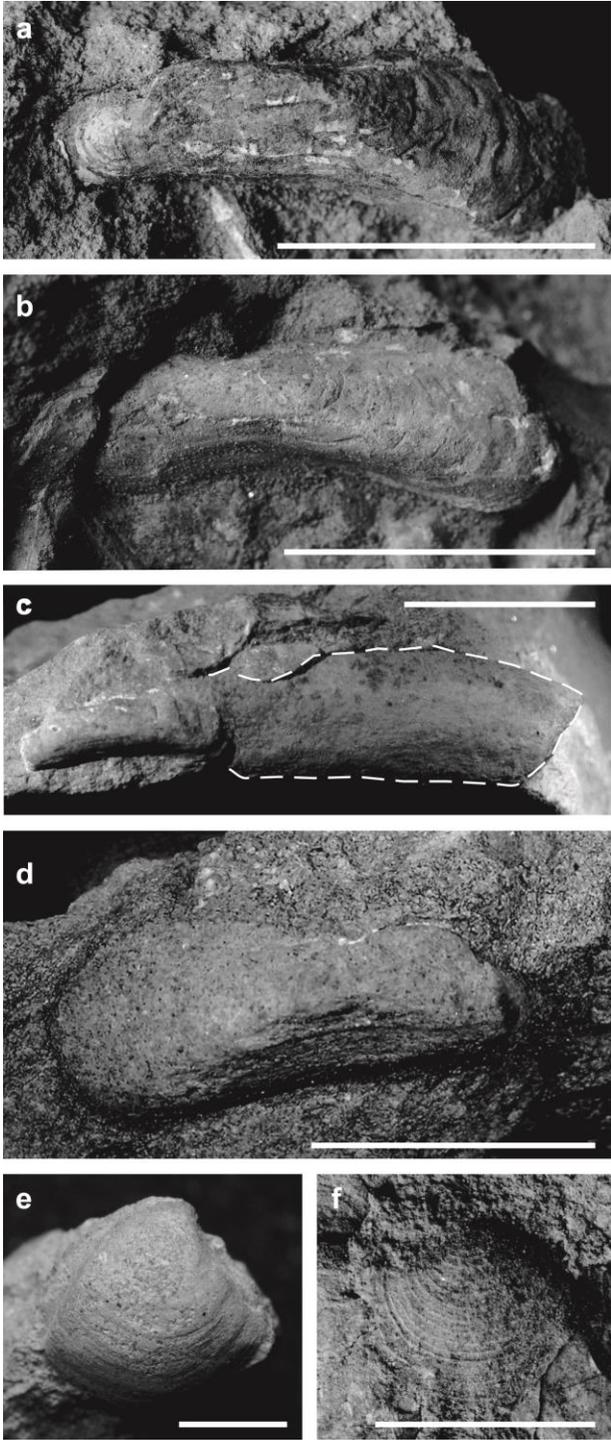


Figure 3