Shallow-water fossil whale falls from the Neogene of Italy

Journal:	*Lethaia*
Manuscript ID:	Draft
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Danise, Silvia; Plymouth University, Dominici, Stefano; Universita' degli Studi di Firenze, Museo di Storia Naturale
Keywords:	whale fall community, taphonomy, museum collection, Neogene, mollusc

For Peer Review

SCHOLARONE™
Manuscripts

Shallow-water fossil whale falls from the Neogene of Italy

Silvia Danise, Stefano Dominici

short title: Fossil shallow-water whale falls

For Peer Review

Twenty-five Neogene whales hosted in Italian museum collections and their associated fauna were analysed for evidence of whale fall community development in shallow water settings. Degree of bone articulation, completeness of the skeleton, and lithology of the embedding sediments were used to gather information on relative water depth, water energy, sedimentation rate and overall environmental predictability around the bones. Shark teeth and hard shelled invertebrates with a necrophagous diet in close association with the bones were used as evidence of scavenging. Fossil bone bioerosion, microbially-mediated cementation and other mollusc shells in the proximity of the remains informed on past biological activity around the bones.

The results are consistent with the hypothesis that shallow-water whale falls differ from their deep-water counterparts. Taphonomic pathways are more variable on the shelf and whale carcasses may not go through all steps of the ecological succession as recognized in the deep sea. Whilst the mobile-scavenger and the enrichment opportunistic stages are well represented, chemosynthetic taxa typical of the sulphophilic stage were recovered only in one instance. The presence of a generalist fauna among the suspension feeding bivalves and carnivore gastropods suggests that competitions rules out whale-fall specialists from shallow shelf settings.

Keywords: whale fall community; taphonomy; museum collection; Neogene; mollusc.

Silvia Danise [silvia.danise@gmail.com], School of Geography, Earth and Environmental Sciences, Plymouth University, Drake Circus, Plymouth, PL4 8AA, UK. Previous address: Dipartimento di Scienze della Terra, Università di Firenze, via La Pira 4, 50121, Firenze, Italy

Stefano Dominici [stefano.dominici@unifi.it], Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università di Firenze, via La Pira 4, 50121, Firenze, Italy

For Peer Review

Introduction

Whale fall communities are mostly known from deep water settings, where they pass through four stages of ecological succession and the whale organic matter is gradually consumed by a highly specialized fauna (Smith *et al.* 2002, Smith & Baco 2003). During the "mobile scavenger" stage, which lasts months to years, sharks, hagfish and other scavenging organisms remove flesh and soft tissues. Polychaetes, crustaceans and other opportunistic small-sized animals thrive on organic remains during the subsequent "enrichment opportunist" stage, which can last months to years. In the "sulphophilic" stage a complex community, lasting for decades, relies on the hydrogen sulphide produced by microbial consumption of the lipid-rich bones. During this stage, chemosynthetic bacteria, free living or in symbiosis within vesicomyid clams, bathymodiolin mussels and vestimentiferan tube worms, are at the base of a food web where organic matter is primarily produced by the oxidation of inorganic compounds. In the "reef stage", occurring after the depletion of the whale organic material, the skeleton is colonized primarily by suspension feeders exploiting hard substrata and flow enhancement (Smith *et al.* 2002). Some of the animals found at whale falls are restricted to vertebrate carcasses, such as the gutless bone-eating worm *Osedax* (Rouse *et al.* 2004; 2011), whilst chemosynthetic taxa are shared with other deep-sea reducing habitats, like hydrothermal vents and hydrocarbon seeps (Smith *et al.* 1989; Smith & Baco 2003; Dubilier *et al.* 2008).

Differently from the deep sea. on the shelf the sea floor is much more naturally enriched in organic carbon so that the organic input given by a whale carcass may represent an insignificant contribution to the nutrient budgets; taphonomic pathways are more complex than in the deep sea; and natural whale falls extremely rare (Smith 2006). Apart from anecdotal knowledge from rare natural occurrences (Smith 2006), modern data are available

For Peer Review

only from few experiments on artifically-sunken skeletons, performed so far in cold temperate seas (Dahlgren *et al.* 2006; Pavyluck *et al.* 2009; Glover *et al.* 2010). These studies suggest that successional stages develop also in shallow waters, with some differences with respect to the deep sea. In general, the carcasses are consumed by generalist mobile scavengers commonly living in the surrounding soft bottoms, and the rate of decomposition, expressed in terms of time taken to remove all the flesh, is significantly slower compared to deep-water analogues (Glover *et al.* 2010). The siboglinid worm *Osedax* is found also at shallow water whale falls (Glover *et al.* 2005; Dahlgren *et al.* 2006), as well as chemosymbiotic bivalves, although they are only known from rare reports not focusing on whale fall ecosystems (Marshall 1900; Wàren 1991) and from a recent study from an artificially implanted carcass in the North Sea (Danise *et al.* in press).

Similarly to marine biologists, palaeontologists have also been more focused on the evolution of deep sea chemosymbiotic ecosystems, especially molluscs. As a consequence, most of the published paleontological papers deal with deep water whale falls (Squires *et al.* 1991; Goedert *et al.* 1995; Amano & Little 2005; Nesbitt 2005; Kiel & Goedert 2006; Amano *et al.* 2007; Pyenson & Haasl 2007), with only a few exceptions (Dominici *et al.* 2009; Esperante *et al.* 2009; Danise *et al.* 2010).

Starting with the pioneering work of Schäfer (1972), palaeontologists working with large marine vertebrates have long shown interest on the serial biostratinomic processes that precede the final burial of the carcasses (Kauffman 1981; Martill 1985; 1987; Lancaster 1986), with a renewed interest after hearing the news from marine biologists, and proposing modern whale falls as viable analogues for the fossil record of Mesozoic reptiles (Hogler 1994; Martill *et al.* 1995; Reisdorf *et al.* 2012). Data collected during the excavation and recovery of a Pliocene fossil whale fall, at Orciano Pisano, Italy (Dominici et al. 2009), suggest that the taphonomic analysis of fossil marine vertebrates and their associated fauna

For Peer Review

can bring insights to the understanding of physical and biological processes at whale falls on a time scale not available in modern time series studies, and from the less known shallow environmental setting.

Fossil cetaceans are abundant in Neogene shallow marine sediments of Italy, particularly in the central and northern regions of Piedmont, Emilia Romagna and Tuscany (Bianucci & Landini 2005; Bisconti 2009). Museum collections host specimens excavated from the 19th century, and for many of them information on the stratigraphic and taphonomic settings at the excavation sites is available (Cortesi 1819; Capellini 1865; Strobel 1881; Portis 1885; Caretto 1970; Sarti & Gasparri 1996; Chicchi & Scacchetti 2001). Notwithstanding not all the taphonomical data that can be gathered following a modern approach in the excavation of large fossil vertebrates are available when studying museum specimens, some useful information can be obtained. Different degrees of bone articulation, completeness of the skeleton, and lithology of the embedding sediments can give information on water depth, current intensity and rate of burial of the bones (Martill 1985; 1987; Lancaster 1986; Allison *et al.* 1991). Shark teeth in close association with the bones, which past researchers seem to have not missed (Bianucci *et al.* 2002), and hard shelled invertebrates with a necrophagous diet, occasionally reported in past excavations, testify scavenging. Fossil bone bioerosion, cementation, and hard shelled organisms in the proximity of the remains can inform on past biological activity around the bones at the micro and mesoscale (Martill 1987; Allison *et al.* 1991).

Building on the experience by Dominici *et al.* (2009), we propose here the analysis of twenty-five large fossil mysticetes hosted in northern and central Italian museum collections with the aim of aim of *(i)* reconstructing the course of whale-fall ecological succession in shallow water settings, and *(ii)* comparing it with modern and fossil data available from deep water whale fall communities.

For Peer Review

Geological setting

The twenty-five fossil mysticetes here under study (W1-W25, Table 1) come from two different paleogeographic domains of the Italian peninsula, the paleo-Adriatic and the paleo-Tyrrhenian domain, both related to the tectonic evolution of the northern Apennines. The northern Apennine fold-thrust belt was formed by collision between the European plate (Corsica-Sardinia block) and the Adriatic microplate (related to the African plate). The thrust imbrication includes the formation of an Upper Cretaceous–Cenozoic polyphase accretionary wedge characterized by the migration of the foredeep depocenters towards the foreland, actually located in the Adriatic Sea. Successively, during the Neogene, the Apennine thrust belt was interested by a NNE-migrating pattern, with a compressional regime in the front of the chain (palaeo-Adriatic domain) and extension in the hinterland area (palaeo-Tyrrhenian domain) (Carmignani *et al.* 2001).

For Peer Review

Specimens W2-W4 belong to the Pliocene Asti Basin, the North-Western extension of the paleo-Adriatic sea (Fig. 1). The basin is filled by a regressive sedimentary succession of circalitoral mudstones of Zanclean age at the base, followed by Piacentian shallow-marine sandstones (Ferrero & Pavia 1996; Polino & Clari 2003). Specimens W5-W16 come from the Pliocene portion of late Eocene to early Pleistocene satellite basins cropping out in the northern Apennines. These satellite, piggy-back basins are mostly filled by terrigenous, diachronuos deposits, originated during the NE migration of the Apennine thrust belt (Ricci Lucchi 1987). In particular, specimens W5-W13 come from the Castell'Arquato basin, whereas specimens W14-W16 are from the Pliocene Intra-Apenninic Basins of the Bologna and Modena Apennines.

Specimens W1, W17-W24 belong to the Pliocene portion of Neogene hinterland basins located on the Tyrrhenian side of the northern Apennines. They are part of the paleo-

Tyrrhenian domain and originated in the internal portion of the chain, when important extensional tectonic events were superposed upon existing compressional structures (Carmignani *et al.* 2001). The sedimentary fill of Tyrrhenian basins typically consists of Tortonian continental deposits at the base, covered by brackish, evaporitic, and marine sediments of Messinian to Pleistocene age (Bossio *et al.* 1992).

The Miocene fossil whale (W25) comes from the early filling of piggy–back basins of the Northern Apennines, belonging to the Epiligurid succession. It comes from the Monte Vallassa Formation, which ranges in age from the Serravallian to the Tortonian, and is an approximately 400 m thick sequence forming a marine transgressive cycle going from coastal settings to inner and outer shelf deposits (Bellinzona *et al.* 1971).

Materials and methods

During the excavation and the museum preparation of the Orciano Pisano fossil whale (W1) information on the taphonomy of the bones and the position of the associated macrofauna respect to the whale skeleton were recorded (Dominici *et al*. 2009; Danise *et al.* 2010). To evaluate the level of generality of the Orciano Pisano finding, Italian Neogene collections were surveyed for large more or less complete whale skeletons that could have hosted a whale fall community (n=25, including W1; Table 1). These include large skulls in the absence of postcranial bones (n=2) and articulated vertebral columns in the absence of the skull (n=3). We have not considered isolated bones, which were however abundant in some collections. For each specimen information on the taphonomy of the fossil bones and on the associated biota were collected (Table 2). Measured taphonomic data on the bones include (a) articulation and (b) completeness of the skeleton; preservation of (c) cortical bones and (d) vertebral processes; and (e) bone cementation. Information on the associated biota include the presence/absence of (f) shark teeth, (g) chemosynthetic bivalves, (h) encrusting epibionts and

For Peer Review

(i) other invertebrates associated with the bones, identified at the highest taxonomic level possible. Bone articulation was classified “high” when all the bones were preserved in anatomical position, showing true bone-to-bone relationships with adjacent elements of the skeleton; “medium” when the bones were slightly displaced from their original position and the original skeleton outline was still recognizable; “low” when the skeletons were completely disarticulated. Skeletal completes was classified “high” when all the main constituent of the skeleton were recovered (skull, jaws, arms, ribs, vertebrae); “low” when one or more skeletal element was missing. Cortical bone preservation was subdivided in “high”, “medium” or “low” if, respectively, the outer cortical bone was still in place, or it was partially removed or absent. Vertebral processes preservation was classified “high” when spinous processes were well preserved; “medium” when they were partially preserved; “low” when they were absent. Cementation was considered “high” when large part of the skeleton was enclosed in a carbonate concretion (*e.g.,* the whole thoracic region); “medium” if cements occurred in localized areas, otherwise “absent”. Encrusting epibionts were recorded if directly observed on the bone surface. Data on the presence/absence of shark teeth were considered reliable, since these fossils particularly attracted palaeontologists during excavations and have possibly never escaped recovery (see Bianucci *et al.* 2002). On the other hand, the absence of chemosymbiotic bivalves and other invertebrates from museum collections was interpreted as a missing datum (“n.d.”).

All these variables were recorded from different sources, including the direct observation of museum specimens, literature data on the excavations, oral interviews to people who directly participated to the digging operations. Additional data gathered from the literature concerned the age and the taxonomical classification of each fossil whale and the lithology of the embedding sediments.

For Peer Review

The studied fossil whales are hosted in the following museums: MGPT: Museo di Geologia e Paleontologia, Torino (TO); MPSC: Museo Paleontologico San Pietro in Consavia (AT); CMSNV: Civico Museo di Scienze Naturali di Voghera (PV), MPP: Museo Paleontologico Parmense (PR); MGC: Museo Geologico, Castell'Arquato (PC); MGCB: Museo "G. Capellini", Bologna (BO); MCRE: Musei Civici di Reggio Emilia (RE); MSNT: Museo di Storia Naturale e del Territorio, Università di Pisa, Calci (PI); MSNF: Museo di Storia Naturale, Firenze (FI); MCPG: Museo Civico di Palazzo Guicciardini, Montopoli in Valdarno (PI); CVB: Castello di Villa Banfi (SI); MCGA: Museo dei cicli geologici, Allerona (TR).

For Peer Review

Results

Taphonomy of twenty-five fossil whales

The twenty-five analysed specimens come from sandy sediments (52%) and mudstones (48%). 28% are fully articulated skeletons, 24% have the bones slightly displaced from their original position, 36% are disarticulated, and for the others (12%) no data are available (Fig. 2A, 4). Most of the disarticulated skeletons were embedded in sandstones (67%), and the others in mudstones. Well-articulated specimens come from sandstones in the 43% of the cases (Fig. 3A). In W22, which is a highly disarticulated skeleton, a bivariate orientation of the bones is observed (Fig. 4D). The specimen comes from a stratigraphic level characterized by silty sandstones and lay on a shell bed characterized by disarticulated and nestling bivalves which indicate reworking by bottom currents.

Half of the fossil skeletons are complete (Fig. 2A). Among incomplete skeletons four are acephalous, and two conserve only the skull (Table 1). 67% of low articulated specimens are also incomplete; whereas most of the well-articulated skeletons (86%) have a high degree of completeness (Fig. 3B).

More than half of the specimens preserve the external cortical bone tissue (60%), which is partially preserved or absent in the remaining 36% (Fig. 2A). Vertebral processes are pristine in the 32% of the fossil whales, partially damaged in the 24%, totally absent in the 20%, whereas there are no available data in the 24% (Fig. 2A, 5A-C).

The 20% of the studied specimens are highly cemented (Fig. 2A). The thoracic region, which includes cervical and thoracic vertebrae and the ribs, is the most interested by cementation (Fig. 5D). Highly cemented specimens have in most of the cases a good degree of cortical bone preservation (80%, Fig. 3D) and most of them come from muddy sediments. A medium degree of cementation was observed in the 36% of the specimens (*e.g.*, specimen in Fig. 5E, where isolated ribs are cemented). The others shows no cementation or no data are available (Fig. 2A).

Shark teeth associated with fossil bones are documented for the 40% of the studied fossil whales (40%) (Fig. 2B). They more frequently come from articulated skeletons (Fig. 3C). They are found directly in contact with the bones, as in W1 (see Fig. 1F in Dominici *et al.* 2009), or in the nearest sediments (Fig. 6A). The identified species are *Carcharodon Charcarias* (W1, W15, W17, W22), *Prionace glauca* (W1), *Carcharinus* cf. *brachyurus* (W22), *Odontapsis* sp. (W17), *Isurus oxyrhyncus* (W3), *Galeorhinus galeus* (W7), and *Galeorhinus* cf. *galeus* (W15).

Cemented epibionts directly attached to the external surface of the bones were found on the 44% of the specimens (Fig. 2B). They consist mostly of *Ostrea* specimens, with shells up to 10 cm in length (Fig. 6C-D), and balanid barbacles, solitary (Fig. 6B) or in clusters (Fig. 6E). Bioencrustation was recovered both from specimens from sandy and muddy sediments.

For Peer Review

No data are available for chemosymbiotic bivalves associated with the fossil bones, except for W1 (Fig. 2A, 6F), where more than twenty lucinids of the species *Megaxinus* cf. *incrassatus* were found directly in contact with the bones (Dominici *et al.* 2009) together with two small specimens of the bathymodiolin mussel *Idas* sp. (Danise *et al.* 2010). Other invertebrates were recovered in the 40% of the cases (Fig. 2B). In most cases data are available only on molluscs, but decapods are also reported (see W16 and W17, Table 1). Within the molluscs the most represented trophic category is the suspension feeders, including bivalves of the family Glossidae, Pectinidae, Veneridae and Mytilidae (Fig. 7, Table 1). Tens of specimens of *Glossus humanus* were found in life position next to intervertebral disks of W8 (Fig. 7A), and a few large specimens in contact with W1 bones (Dominici *et al.* 2009). Pectinids were associated with specimens W3, W5, W17, W20 and W21, and are represented by the species *Amusium cristatum, Chlamys opercularis* and *Chlamys* cf. *varia* (Fig. 7D). The venerid *Pelecyora brocchi* is associated with specimens W15 (Fig. 7C) and W24 (Fig. 7E). Unidentified mytilids are associated with W5 and W21, *Mytilus* sp. with W14 and *Modiolus* sp. with W16. Deposit feeders were found at W3 (*Aporrhais uttingeriana*, *Tellina compressa*) and W17 (*Aporrhais uttingeriana*, *Dentalium fossile*). Predatory carnivores are represented by naticid gastropods at W5, W15 and W20 (Fig. 6E, 7E), and by *Ficus* sp. (W14, Table 1). Among scavenging gastropods, nassarids were frequent (*Nassarius* spp.: W1; W3; W20).

Discussion

Biostratinomy of shelf-depth fossil whales

Since water depth correlates with several environmental parameters that are also factors controlling biostratinomic processes, such as bottom energy and sedimentation rate, water

For Peer Review

depth was roughly estimated from grain size of the sediments associated with the fossil whales. Muddy sediments settle in fact, on average, at greater depth than sandy sediments (Thorson 1957). According to this general rule, fossil whales excavated from sandstones were considered to come from shallower waters than those recovered from mudstones. A positive correlation between lithology and degree of skeletal articulation was observed (Fig. 3A), so that well-articulated specimens occur more frequently in muddy sediments, whereas disarticulated in sandstones, as also observed in a similar study on Jurassic marine vertebrates in the Lower Oxford Clay of central England (Martill 1985). This is consistent with conditions of lower bottom energy in the deposition of mudstones with respect to that of sandstones. As a consequence, in offshore areas with soft substrates and lower sedimentation rate marine vertebrate skeletons are preserved preferentially more articulated than in onshore position, where reworking before the final burial occurs more frequently.

From actualistic data is also known that disarticulation, especially if related to skeletal incompleteness, can be linked to carcass flotation after resurfacing (Allison *et al.* 1991). In shallow waters, floating carcasses resurfaced by the production of decay gasses in the abdominal cavity and within tissues, continue to decay. The removal of supportive soft tissues promotes the disarticulation of skeletal elements, so that the skull is usually the first part to be lost, and the mandibles are soon separated from the cranium (Schäfer 1972). Flotation in shallow waters may be prevented by scavenging if soft parts are stripped before decay, or by catastrophic burial, if a sufficient overburden of sediment is deposited on the carcass (Allison *et al.* 1991). Six of the fossil whales here under study, which miss either the trunk or the head, are good candidates as cases of re-flotation before final settling.

In cemented specimens, carbonate concretions probably precipitated by microbial processes linked to the decay of the whale organic matter, which favours carbonate precipitation increasing poor fluid alkalinity (Coleman & Raiswell 1993). Carbonate cements

For Peer Review

may form during early diagenetic processes when the bones are still close to the sediment-water interface (W25: Danise *et al.* 2013) or during late diagenetic processes (Kiel 2008). In both of these circumstances they serve as an indirect evidence of rapid burial, which covered the bones before all the organic matter was consumed. This is supported by the correlation between the degree of cementation and cortical bone preservation: highly cemented specimens show less signs of bone degradation that non-cemented once (Fig. 3D).

The abundance and diversity of shark teeth in close association with the bones indicates an interaction between pelagic sharks and whales. In the modern Mediterranean, cetaceans represent a significant component of the diet of large size white sharks, either through scavenging or predation on living animals (Mojetta *et al.* 1997). Considering the body size of Pliocene white sharks, Bianucci *et al.* (2002) hypothesized that active predation was possible only on small Mysticeti, as some cetotheriids and baleanids (*eg., Balaenula*), whereas in all other instances concerning larger specimens, the association with shark teeth must have been true scavenging. In the present dataset shark teeth are all associated with large specimens (7-10 m long), which can be considered positive evidence for scavenging. The correlation between high degree of articulation and occurrence of shark teeth (Fig. 3C) suggests that in shallow waters the action of scavengers is not intense enough to disarticulate whale carcasses and disperse their bones. This datum is in accordance with what observed from a modern shallow water study of a North Atlantic minke whale carcass at 125 m depth, which was consumed by sharks and haghfishes within 6 months without significant disarticulation (Dahlgren *et al.* 2006). It is important to note that no data are available on the presence and importance of hagfishes as taphonomic agents in the Mediterranean, modern or ancient.

Low degree of preservation of the cortical bone tissue, together with the loss of vertebral processes, suggest bioerosion both at the micro and mesoscale during exposition of

For Peer Review

the skeleton on the sea floor. At the microscale, bioerosion can be caused by heterotrophic bacteria, cyanobacteria, algae or fungi consuming the bones (Amano & Little 2005; Kiel 2008; Esperante *et al.* 2009; Shapiro & Splanger 2009; Danise *et al.* 2013). Microscale bioerosion so far has been mostly described by palaeontologists, and actualistic data are needed to better know the metabolism and the nature of the trace makers. At the mesoscale, an active bioeroder could have been the siboglinid worm *Osedax*, the most studied among bone consumers in modern shallow and deep water whale falls (Glover *et al.* 2005; Braby *et al.* 2007; Higgs *et al.* 2010), together with decapods, that can feed directly on fragile *Osedax*-laden lateral processes (Braby *et al.* 2007). Decapods are also among the more active scavengers at shallow sub-littoral, modern whale-fall sites (Glover *et al.* 2010) and are reported from three sites in our survey (W1, W16 and W17). *Osedax* trace fossils have been recognized so far in Oligocene whale and fish bones (Kiel *et al.* 2010; 2012) and in one isolated Pliocene whale bone from Orciano Pisano, from an ancient collection housed at the MSNF (Higgs *et al.* 2012).

Encrusting epifauna on the bones, especially oysters and balanids, are a good paleoecological indicator for oxygenated bottom waters and low sedimentation rates, depending on their size and concentration (Martill 1985). Lack of correlation between bioencrustation and lithology in our dataset, does not help to relate biological and physical processes. Instead, a one by one analysis of well-known encrusted skeletons and their associated sedimentary features, allows some important considerations. At W1 only one oyster was found attached to the bones, but the occurrence of other vertebrate remains in the same outcrop, of a laterally continuous shell bed and glauconite grains are all evidence of low sedimentation rates (Danise 2010). Many encrusting oysters and a lateral continuous shell bed are also associated with W16. This shell bed is in the middle part of a small-scale depositional sequence, corresponding to the maximum flooding interval (Danise 2010),

For Peer Review

thence also this case points to low sedimentation rate at the whale carcass. Scanty data are available for the highly encrusted W14. Finally, the excellent report of Giuseppe Cortesi, despite the whale skeleton is no longer available (W7), leaves little doubt that the whale carcass he studied in the early nineteenth century had been deposited at a starved bottom: "... *picciole ostriche, parecchie delle quali veggonsi tuttavia incollate sulle ossa medesime… Morì questo cetaceo in un mare permanente e tranquillo; e perciò rimase lo scheletro nella sua naturale disposizione*" ("many small oysters are still attached to the bones... This cetacean has died in a calm sea bottom, thence the skeleton has maintained its natural articulation": Cortesi 1819). Finally the size of the ostreids attached to the studied whales, up to 10 cm long, suggests that some specimens lay on the sea floor at least for 6-10 years (see Richardson 1993).

All of the above information helps framing the paucity of data concerning the chemosynthetic bivalves. As a conservative assumption positive conclusions cannot be drawn based on negative evidences. To this it must be added that chemosynthetic bivalves could have been present but overlooked during excavations aimed at freeing the whale skeleton from entombing sediments. Finally, very small chemosynthetic bivalves like Bathymodiolinae, which can only be observed under a binocular microscope (*e.g.,* Danise *et al.* 2010), can be easily overlooked upon during excavations, when these are not expressly designed at recovering the whole associated fauna. Nevertheless, large chemosynthetic bivalves, like at W1, must have been originally lacking in the best described cases of a fossil whale skeleton associated with molluscs (W3, W8, W14-W17), or they would have been reported.

Among heterotrophic molluscs, the abundant suspension feeders were possibly exploiting flow enhancement, similarly to encrusting epibionts mentioned in other instances

For Peer Review

(Martill 1986; Smith *et al.* 2002). Pectinids are the most frequent among suspension feeders in our dataset, and are also found associated with shallow water artificially implanted carcasses at 23-30 m in the North Sea (Glover *et al.* 2010). The unusual abundance or size of *Glossus humanus* and its proximity to large bones at two sites (W1, W8) might point to its special adaptation to high sulphide concentrations. However, the only available study on the biology and diet of this taxon (Owen 1953), adapted to very soft and calm mud bottoms, does not support this hypothesis. Nassaridae, found at three sites (W1, W3, W20), and abundant in some cases, are scavengers that might have fed directly on the whale flesh, as observed in modern examples (Glover *et al.* 2010). They could also have been secondarily active predators on polychaetes and small crustaceans, as they are known to do in the present (Britton & Morton 1994). Naticidae and Ficidae gastropods are predatory active carnivores present or abundant at many whale falls (W1, W5, W14, W15, W20); they could have preyed on soft bodied biota living around the whale carcasses, or on bivalves and crustaceans (see Taylor 1980).

The fate of a whale carcass on the shelf

Building on the recent experience of a fossil whale excavation aimed at recovering also all of the associated fauna and record available taphonomic evidences (W1: Dominici *et al.* 2009), the present study has shown that also museum specimens can be used to understand the taphonomy of shallow water whale falls and that insights bring substantial knowledge of interest for both palaeontologists and marine biologists.Furthermore, given the now abundant literature on the taphonomy of modern whales, the paleontological, ecosystem-level approach seems a promising way to gather a richer understanding also of the taphonomy of Mesozoic marine reptiles and other large marine vertebrates of the distant past.

Most of the natural occurrences of deep sea whale falls studied so far concern large and well-articulated carcasses, which have undergone all stages of whale fall ecological

For Peer Review

succession, and have been or are inhabited by large-sized shelled specialists, suggesting very similar taphonomic pathways (Allison *et al.* 1991; Naganuma *et al.* 1996; Goffredi *et al.* 2004; Lundsten *et al.* 2010). The ample variety of taphonomic states encountered in the Italian Neogene whale record, and in other sparse instances (*e.g.,* Esperante *et al.* 2009), suggests instead that in shallow marine bottoms the destiny of whale carcasses can be more variable than in the deep sea. Because of the wider ranges of variation of physical and biological factors, the way carcasses are recycled on the shelf can vary to a large degree.

After a dead whale sinks, its permanence on the sea floor will depend on the interplay between two main biological factors: the development of decompositional gasses and the rate of scavenging (Allison *et al.* 1991). If the process of soft tissue degradation is dominated by microbial decomposition and gas production, the carcass will easily resurface and become dismembered, leading to the final settlement of incomplete specimens. This has occurred in a minority of cases here under consideration, since the most studied specimens were complete (complete specimen here include those lacking the rostrum or the neurocranium, but with the two mandibles). This implies that most of the large whale falls analysed in this study that have made it to the fossil record, passed through the intense activity of scavengers and the rapid removal of abdominal soft tissues. Since gas production was not sufficient for buoyancy, the carcass had remained on the bottom where it had landed. The following course of transformation depended on sedimentation rates. Each carcass, whether complete or not, might have been exposed on the sea floor, interacting with the local ecosystem and subsequently becoming buried at any stage of development of a whale fall community.

Bioerosion and biota associated with the studied specimens suggest that most of them underwent an intense and prolonged biotic activity. We could recognize both the mobile scavenger stage and the enrichment opportunist stage on many shelf specimens, not differing

For Peer Review

from what occurs at deeper settings. Scavenging is testified by shark teeth or by shelled predatory invertebrates and the opportunist stage by the general downgrading of the bones or by rare traces of the bone-eating worm *Osedax*. Some specimens underwent a more prolonged exposure, pointing to sediment starvation, as testified by cemented epifauna resting on downgraded bones. The finding of bioincrustation on pristine bone suggests that successional stages can be intermingled and that taphonomic pathways can be complex, depending on the rapidity with which a part of the skeleton is exposed and for how long before final burial.

For Peer Review

Benthic taxa associated with the bones, mostly suspension feeding bivalves and carnivore gastropods, are common elements of other Neogene marine associations. Among these are the Pectinidae with their general adaptation to exploit enhanced flow conditions, and the Nassaridae, feeding on large food particles. This suggests that competition can be a possible factor ruling out whale-fall specialists from shallow shelf whale falls. The sulphophilic stage of whale falls was recognized only in one case, which coincides with the only excavation carried out so far on an ecosystem-level approach. Some evidences suggest that this stage on the shelf seldom involves larger chemosymbiotic molluscs like in deep sea sites. These evidences include *(i)* the only presence at the Orciano Pisano whale fall (W1) of infaunal lucinids and very rare bathymodiolins (Dominici *et al.* 2009; Danise *et al.* 2010) and the absence of other chemosymbiotic bivalves like vesicomyid clams; and *(ii)* the lack of chemosymbiotic taxa among all other shelled benthic invertebrates reported at other sites.

Conclusions

The taphonomic analysis of twenty-five large fossil mysticetes from the Italian Neogene gives new insights on the course of the whale fall ecological succession in shallow water settings.

(i) In shallow marine bottoms the destiny of whale carcasses can be more variable than in the deep sea, and the ecological succession more irregular.

(ii) The mobile scavenger stage at shelf depths, testified by shark teeth and possibly by shelled predatory invertebrates common around the bones of large specimens, is similar to the mobile scavenger stage in deeper settings.

(iii) The enrichment opportunist stage is indirectly attested by the general downgrading of the bones, exceptionally by traces of the bone-eating worm *Osedax*, and possibly by predatory active carnivores that preyed on soft bodied biota living around the whale carcasses.

(iv) The sulphophilic stage was recognized in only one instance; this was not probably just overlooked during the majority of past excavations, but it might have been altogether absent, especially at very shallow depths.

(v) The reef stage was testified by cemented epifauna resting on downgraded bones. Bioincrustation on pristine bone suggests that successional stages can be intermingled.

(vi) The presence of a generalist fauna among the suspension feeding bivalves and carnivore gastropods suggests that competition is a possible factor ruling out whale-fall specialists from shallow shelf whale falls.

For Peer Review

References

Allison, P.A., Smith, C.R., Kukert, H., Deming, J.W. & Bennett, B.A. 1991: Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the bathyal Santa Catalina Basin. *Paleobiology 17*, 78–89.

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.

Bellinzona. G., Boni. A., Braga,G. & Marchetti, G. 1971: Note illustrative della Carta Geologica d'Italia in scala 1:100.000, Foglio 71, Voghera. Servizio Geologico d'Italia, Roma, 121 pp.

Bianucci, G. & Landini, W. 2005: I paleositi a vertebrati fossili della Provincia di Pisa. *Atti della Società Toscana di Scienze Naturali, Memorie, Serie A 110*, 1–21.

Bianucci, G., Bisconti, M., Landini, W., Storai, T., Zuffa, M., Giuliani, S. & Mojetta, A. 2002: Mediterranean white shark-cetaceans interactions through time: a comparison between Pliocene and Recent data. *In* Vacchi, M., La Mesa, G., Serena, F. & Séret, B. (eds.): *Proceedings of the 4th European Elasmobranch Association Meeting, Livorno, ICRAM, ARPAT & SFI*, 33–48.

Bisconti, M. 2002: An early Late Pliocene right whale (genus *Eubalaena*) from Tuscany (Central Italy). *Bollettino della Società Paleontologica Italiana 41*, 83–91.

Bisconti, M. 2007: A new basal balaenoperid whale from the Pliocene of Northern Italy. *Palaeontology 50*, 1103–1122.

For Peer Review

Bisconti, M. 2009: Taxonomy and evolution of the Italian Pliocene Mysticeti (Mammalia, Cetacea): a state of the art. *Bollettino della Società Paleontologica Italiana 48*, 147–156.

Borselli, V. & Cozzini, F. 1992: Il recupero di un cetaceo fossile in località Ponte a Elsa (Pisa). *Museologia Scientifica 8*, 9–22.

Bossio, A., Cerri, R., Costantini, A., Gandin, A., Lazzarotto, A., Magi, M., Mazzanti, R., Mazzei, R., Sagri, M., Salvatorini, G. & Sandrelli, F. 1992: I bacini distensivi neogenici e quaternari della Toscana. *76a Riunione estiva Società Geolologica Italiana, Guida alle escursioni*, 199–227.

Braby, C.E., Rouse, G.W., Johnson, S.B., Jones, W.J. & Vrijenhoek, R.C. 2007: Bathymetric and temporal variation among *Osedax* boneworms and associated megafauna on whale-falls in Monterey Bay, California. *Deep-Sea Research I 54*, 1773–1791.

Britton, J.C. & Morton, B. 1994: Marine carrion and scavengers. *Oceanography and Marine Biology: An Annual Review 32*, 369–434.

Capellini, G. 1865: Balenottere fossili del bolognese. *Memorie della Regia Accademia delle Scienze dell'Istituto di Bologna 4*, 3–24.

Capellini, G. 1905: Balene fossili toscane. III *Idiocetus guicciardinii*. *Atti della Reale Accademia delle Scienze dell'Istituto di Bologna, Serie 68*, 113–115.

Caretto, P.G. 1970: La balenottera delle sabbie plioceniche di Valmontasca (Vigliano d'Asti). *Bollettino della Società Paleontologica Italiana 9*, 3–75.

Carmignani, L., Decandia, F.A., Disperati, L., Fantozzi, P.L., Klingfield, R., Lazzarotto, A., Liotta, D. and Meccheri, M. 2001: Inner Northern Apennines. *In* Vai, G.B. &

For Peer Review

Martini, I.P. (eds.): Anatomy of an Orogen: the Apennines and adjacent Mediterranean basins. Springer press, 197–214.

Chicchi, S. & Scacchetti, M. 2001: Valentina - Balena fossile del mare padano. Civici Musei, Reggio Emilia, 31 pp.

Coleman, M.L. & Raiswell, R. 1993: Microbial mineralization of organic matter: mechanisms of self-organization and inferred rates of precipitation of diagenetic minerals. *Philosophical Transactions: Physical Sciences and Engineering 344*, 69–87.

Cortesi, G. 1819: Saggi geologici degli stati di Parma e Piacenza. Torchj del Majno, Piacenza, 165 pp.

Dahlgren, T.G., Wiklund, H., Källström, B., Lundälv, T., Smith, C.R. & Glover, A. 2006: A shallow-water whale-fall experiment in the north Atlantic. *Cahiers de Biologie Marine 47*, 385–389.

Damarco, P. 1995: Una curiosa combinazione: la balena e le conchiglie fossili. *Word Shells 15*, 26–28.

Danise, S. 2010. Modern and fossil shallow water whale fall communities. Unpublished PhD, Universita' degli Studi di Firenze, Italy. 178 pp.

Danise, S., Dominici, S. & Betocchi, U. 2010: Mollusk species at a Pliocene shelf whale fall (Orciano Pisano, Tuscany). *Palaios 25*, 449–556.

Danise, S., Cavalazzi, B., Dominici, S., Westall, F., Monechi, S. & Guioli, S. 2013: Fossil microbial ecosystem associated with a Miocene shallow-water whale-fall from Northern Italy. *Palaeogeography, Palaeoclimatololgy, Palaeoecology 317-318*, 13–26.

For Peer Review

Danise, S., Dominici, S., Dahlgren, T.G. & Glover, A.G. (in press). Molluscs from a shallow-water whale-fall and their affinities with adjacent benthic communities on the Swedish west coast. *Marine Biological Research.*

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 Review 6*, 725–740.

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.

Ferrero, E. & Pavia, G. 1996: La successione marina pre-villafranchiana. *In* Carraro, F. (ed.): Revisione del Villafranchiano nell'area-tipo di Villafranca d'Asti. *Il Quaternario 9*, 36–38.

Francou, C. 1994: Nelle terre del Piacenziano. Fondazione Cassa di Risparmio di Piacenza e Vigevano, Piacenza, 126 pp.

Glover, A.G., Kallstrom, B., Smith, C.R. & Dahlgren, T.G. 2005: World-wide whale worms? A new species of *Osedax* from the shallow North Atlantic. *Proceedings of the Royal Society of London B 272*, 2587–2592.

Glover, A.G., Higgs, N.D., Bagley, P.M., Carlsson, R., Davies,A.G., Kemp, K.M., Last, K.S., Norling, K., Rosenberg, R., Wallin, K., Källström, B. & Dahlgren, T.G. 2010: A

For Peer Review

live video observatory reveals temporal processes at a shelf-depth whale-fall. *Cahiers de Biologie Marine 51*, 375–381.

Goedert, J.L., Squires, R.L. & Barnes, L.G. 1995: Paleoecology of whale-fall habitats from deep-water Oligocene rocks, Olympic Peninsula, Washington State. *Palaeogeography, Palaeoclimatology, Palaeoecology 118*, 151–158.

Goffredi, S.K., Paull, C.K., Fulton-Bennett, K., Hurtado, L.A. & Vrijenhoek, R.C. 2004: Unusual benthic fauna associated with a whale fall in Monterey Canyon, California. *Deep-Sea Research I 51*, 1295–1306.

Higgs, N.D., Glover, A.G., Dahlgren, T.G.& Little, C.T.S. 2010: Using computed-tomography to document borings by *Osedax mucofloris* in whale bone. *Cahiers de Marine Biologie 51*, 401–405.

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.

Hogler, J.A. 1994: Speculations on the role of marine reptile deadfalls in Mesozoic deep-sea paleoecology. *Palaios 9*, 42–47.

Kauffman, G. 1981: Ecological reappraisal of the German Posidonienscheifer (Toarcian) and the stagnant basin model. *In* Gray J., Boucot A.J. & Berryw .B.N. (eds.): Communities of the Past. Hutchison Ross, Stoudsberg, Pennsylvania, 311–381.

Kiel, S. 2008: Fossil evidence for micro- and macrofaunal utilization of large nektonfalls: examples from early Cenozoic deep-water sediments in Washington State, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology 267*, 161–174.

For Peer Review

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 B 273*, 2625–2631.

Kiel, S., Goedert, J.L., Kahl, W.-A. & Rouse, G.W. 2010: Fossil traces of the bone-eating worm *Osedax* in early Oligocene whale bones. P*roceedings of the National Academy of Science, USA 107*, 8656–8659.

Kiel, S., Kahl, W.-A. & Goedert, J.L. 2012: Traces of the bone-eating annelid *Osedax* in Oligocene whale teeth and fish bones. *Paläontologische Zeitschrift 87*, 161–167.

Lancaster, W.C. 1986: The taphonomy of an archaeocete skeleton and its associated fauna. *Proceedings of GCAGS Symposium*. Montgomery Landing Site, Marine Eocene of central LA, 119–131.

Lundsten, L., Paull, C.K., Schlining, K.L., McGann, M. & Ussler III, W. 2010: Biological characterization of a whale-fall near Vancouver Island, British Columbia, Canada. *Deep Sea Research I 57*, 918–922.

Marshall, J.T. 1900: On a Brtish species of *Myrina*, with a note on the genus *Idas*. *Journal of Malacology 7*, 167–170.

Martill, D.M. 1985: The preservation of marine vertebrates in the Lower Oxford Clay (Jurassic) of central England. *Philosophical Transactions of the Royal Society B 311*, 155–165.

Martill, D.M. 1987: A taphonomic and diagenetic case study of a partially articulated ichthyosaur. *Palaeontology 30*, 543–555.

For Peer Review

Martill, D.M., Cruickshank, A.R.I. & Taylor, M.A. 1995: Speculations on the role of marine reptile deadfalls in Mesozoic deep−sea paleoecology: comment. *Palaios 10*, 96–97.

Mojetta, A., Storai, T. & Zuffa, M. 1997: Segnalazioni di *Carcharodon carcharias* in acque italiane. *Quaderni della Civica Stazione Idrobiologica di Milano 22*, 23–38.

Naganuma, T., Wada, H. & Fujioka, K. 1996: Biological community and sediment fatty acids associated with the deep-sea whale skeleton at the Torishima Seamount. *Journal of Oceanography 52*, 1–15.

Nesbitt, E.A. 2005: A novel trophic relationship between cassid gastropods and mysticete whale carcasses. *Lethaia 38*, 17–25.

Owen, G. 1953: On the biology of *Glossus humanus* (L.) (*Isocardia* cor Lam.). *Journal of the Marine Biology Associaiton, UK 32*, 85–106.

Pavlyuk, O.N., Trebukhova, Y.A. & Tarasov, V.G. 2009: The impact of implanted whale carcass on Nematode communities in shallow water area of Peter the Great Bay (East Sea). *Ocean Science Journal 44*, 181–188.

Polino, R. & Clari, P.A. 2003: Carta Geologica d'Italia alla scala 1.50000, Foglio 157. Torino, Apat Dipartimento Difesa del Suolo.

Portis, A. 1885: Catalogo descrittivo dei Talassoterii rinvenuti nei terreni terziari del Piemonte e della Liguria. *Memorie della Reale Accademia delle Scienze di Torino 37*, 247–365.

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.

For Peer Review

Reisdorf, A.G., Bux, R., Wyler, D., Benecke, M., Klug, C., Maisch, W.M., Fornaro, P. & Wetzel, A. 2012: Float, explode or sink: postmortem fate of lung-breathing marine vertebrates. *Palaeobiology and Palaeoenvironments 92*, 67–81

Ricci Lucchi, F. 1987: Semi-allochthonous sedimentation in the Apenninic thrust belt. *Sedimentary Geology 50*, 119–134.

Richardson, C.A., Collis, S.A., Ekaratne, K., Dare, P. & Key, D. 1993: The age determination and growth rate of the European flat oyster, *Ostrea edulis*, in British waters determined from acetate peels of umbo growth lines. *ICES Journal of Marine Science 50*, 493–500.

Rouse, G.W., Goffredi, S.K. & Vrijenhoek, R.C. 2004: *Osedax*: Bone-eating marine worms with dwarf males. *Science 305*, 668–671.

Rouse, G.W., Goffredi, S.K., Johnson, S.B. & Vrijenhoek, R.C. 2011: Not whale-fall specialists, *Osedax* worms also consume fish bones. *Biology Letters 7*, 736–739.

Sarti, C. & Gasparri, F. 1996: La balenottera Pliocenica di Gorgognano (Pianoro, Bologna). *Bollettino della Società Paleontologica Italiana 35*, 331–347.

Scabelli, 1843: Di una balena, di un delfino e molte conchiglie cavate dai colli del piacentino. Tipografia vescovile tedeschi, Piacenza.

Schäfer, W. 1972: Ecology and palaeoecology of marine environments. Chicago, University of Chicago Press, 568 ppF.

Shapiro, R.S. & Spangler, E. 2009: Bacterial fossil record in whale-falls: Petrographic evidence of microbial sulfate reduction. *Palaeogeography, Palaeoclimatology, Palaeoecology 274*, 196–203.

For Peer Review

Smith, C.R. 2006: Bigger is better: The role of whales as detritus in marine ecosystems. *In* Estes J. (ed.): Whales, Whaling and Ocean Ecosystems. Berkeley, University of California Press, 284–299.

Smith, C.R. & Baco, A.R. 2003: Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology: an Annual Review 41*, 311–354.

Smith, C.R., Kukert, H., Wheatcroft, R.A., Jumars, P.A. & Deming, J.W. 1989: Vent fauna on whale remains. *Nature 341*, 27–28.

Smith, C.R., Baco, A.R. & Glover, A. 2002: Faunal succession on replicate deep-sea whale falls: time scales and vent-seep affinities. *Cahiers de Marine Biologie 43*, 293–297.

Squires, R.L., Goedert, J.L. & Barnes, L.G. 1991: Whale carcasses. *Nature 349*, 574.

Strobel, P. 1881. Iconografia comparata delle ossa fossili del gabinetto di Storia Naturale dell'Università di Parma. Libreria Editrice Luigi Battei, Parma. 32 pp.

Taylor, J.D. 1980: Diets and habitats of shallow water predatory gastropods around Tolo Channel, Hong Kong. *In* Morton B. (ed.): The Malacofauna of Hong Kong and Southern China. Hong Kong University Press, Hong Kong, 163–180.

Thorson, G. 1957: Bottom communities (sublittoral or shallow shelf). *Geological Society of America, Memoir 67*, 461–534.

Trevisan, L. 1941: Una nuova specie di Balaenula pliocenica. *Palaeontographia Italica 40*, 1–13.

Vai, G.B. 2001: Structure and stratigraphy: an overview. *In* Vai, F. & Martini, I.P. (eds.): Anatomy of an Orogen: The Apennines and Adjacent Mediterranean Basins. Springer press, 15–32.

For Peer Review

Warén, A. 1991: New and little known Mollusca from Iceland and Scandinavia. *Sarsia* *76*, 53–124.

For Peer Review

FIGURES

Fig. 1. Schematic geological map with the localities of recovery of the studied fossil whales. Modified from Vai (2001).

Fig. 2. Histograms summarizing results of the analyses on the twenty-five fossil whales. A. Taphonomic data: bone articulation, skeletal completeness, cortical bone preservation, vertebral process preservation, bone cementation. B. Biota associated with the bones: shark teeth, chemosymbiotic bivalves, encrusting epifauna,, other invertebrates. All data expressed in per cent. Error bars represent the standard error.

Fig. 3. Bar diagrams comparing some of the measured taphonomic and paleoecologic variables. A. Degree of bone articulation versus lithology of the embedding sediments. B. Bone articulation versus skeletal completeness. C. Bone articulation versus presence/absence of shark teeth. D. Changes in degree of cementation versus cortical bone preservation. vs: versus.

Fig. 4. Different degrees of skeletal articulation in the studied fossil whales. A. W10 with highly articulated bones and well preserved vertebral processes. B. Acephalous W18 in sandy sediments; ribs are in true position and vertebrae missing or displaced C. W16 in fine grained silty sandstones, with a medium degree of bone articulation; note the ribs in anatomical position whereas vertebrae are displaced. D. W22, highly disarticulated specimen; note the bimodal distribution of the bones.

Fig. 5. Different degrees of cortical bone preservation, vertebral process preservation and cementation. A. W1 with highly bioeroded vertebra and badly preserved compact bone tissue. B. W13 with partially preserved spinous processes and partially preserved compact bone. C. W11 with intact spinous processes and well preserved outer compact bone. D. Articulated

For Peer Review

skeleton with pristine costae, heavily cemented to thoracic vertebrae in unconsolidated muds (W17). E. Isolated ribs partially enclosed in a carbonate concretion.

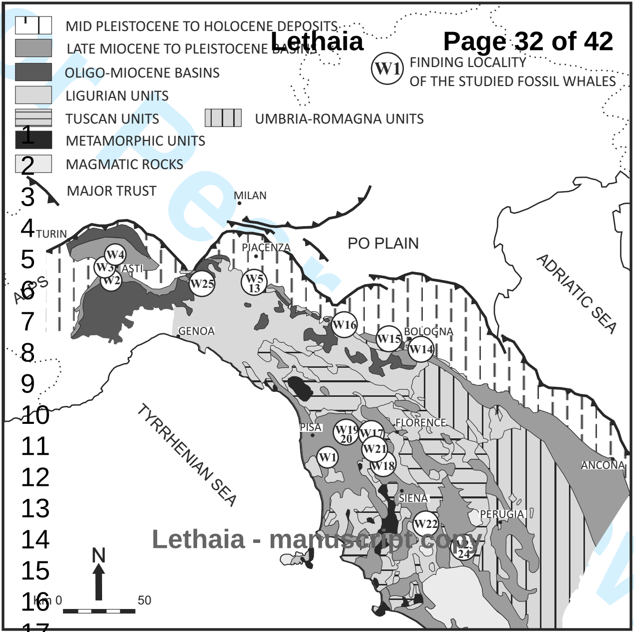
Fig. 6. Shark teeth, encrusting epifauna and chemosynthetic bivalves associated with fossil whale bones. A. W17 with *Carcharodon carcharias* tooth next to the bones. B. Large solitary balanid barnacle on one vertebral process (W22). C and D. Ribs and mandibles with encrusting oysters (W16). E. W11 encrusted with balanid barnacles and a small naticid gastropod next to them. F. Articulated specimen of the lucinid *Megaxinus* cf. *incrassatus* on the skull of W1.

Fig. 7. Molluscs associated with fossil whale bones. A. Three articulated specimens of *Glossus humanus* (arrows) next to intervertebral disks of a large whale (W8) embedded in muddy sediments B. Mytilid on one vertebra (W11). C. *Pelecyora brocchi ?* attached to a vertebra (W24). D. Mytilid (large arrow) and pectinid cf. *Chlamys varia* (small arrow) enclosed in the carbonate concretion around W21. E. *Pelecyora brocchi ?* (large arrow) and naticid gastropod (small arrow) on lumbar vertebra (W15).

Table 1. Information on the studied Neogene fossil whales. Hosting institution abbreviation and taphonomic variables explained in the text. Among incomplete skeletons, those with *are acephalous, those with “ preserve only the skull.

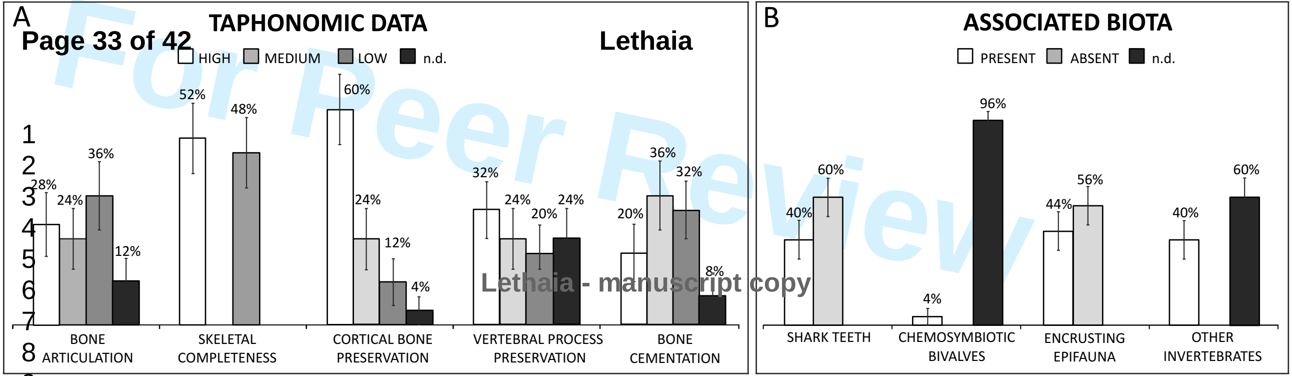
Table 2. List of the main taphonomic and paleoecologic variables considered in this study.

For Peer Review

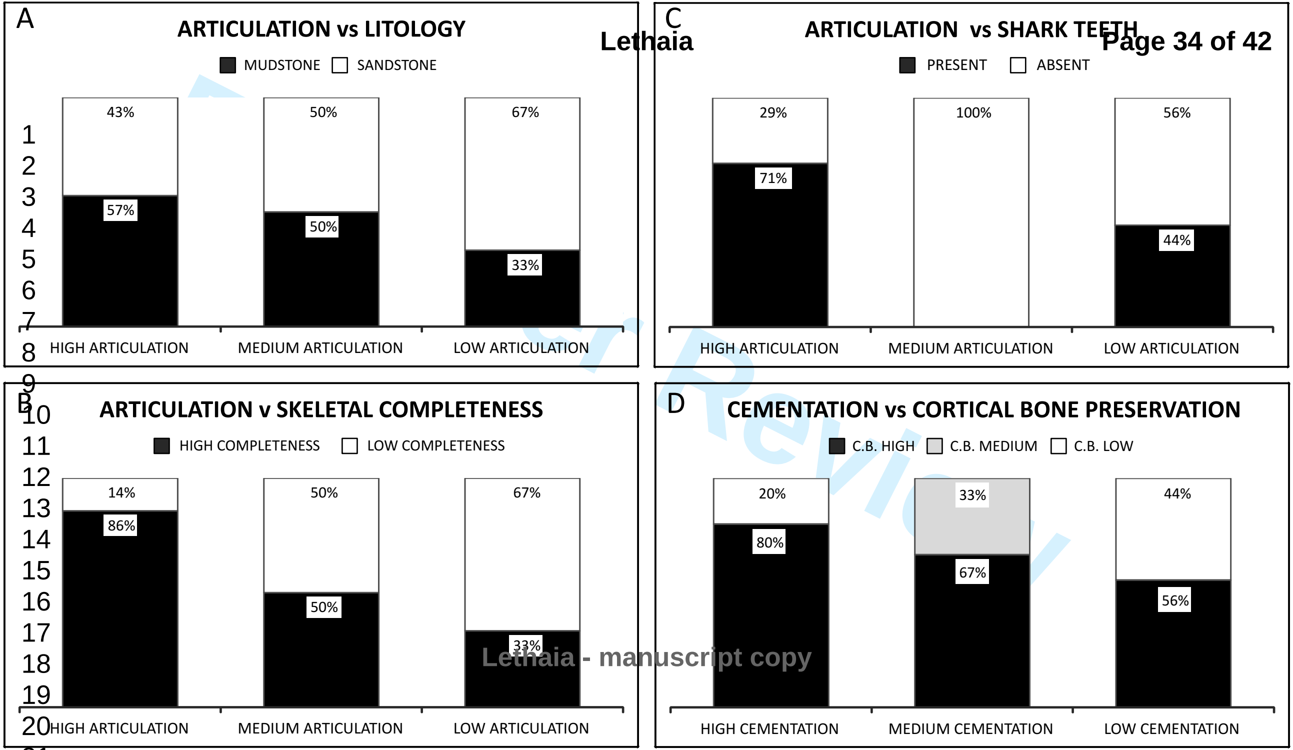


Lethaia - manuscript copy
For Peer Review

For Peer Review

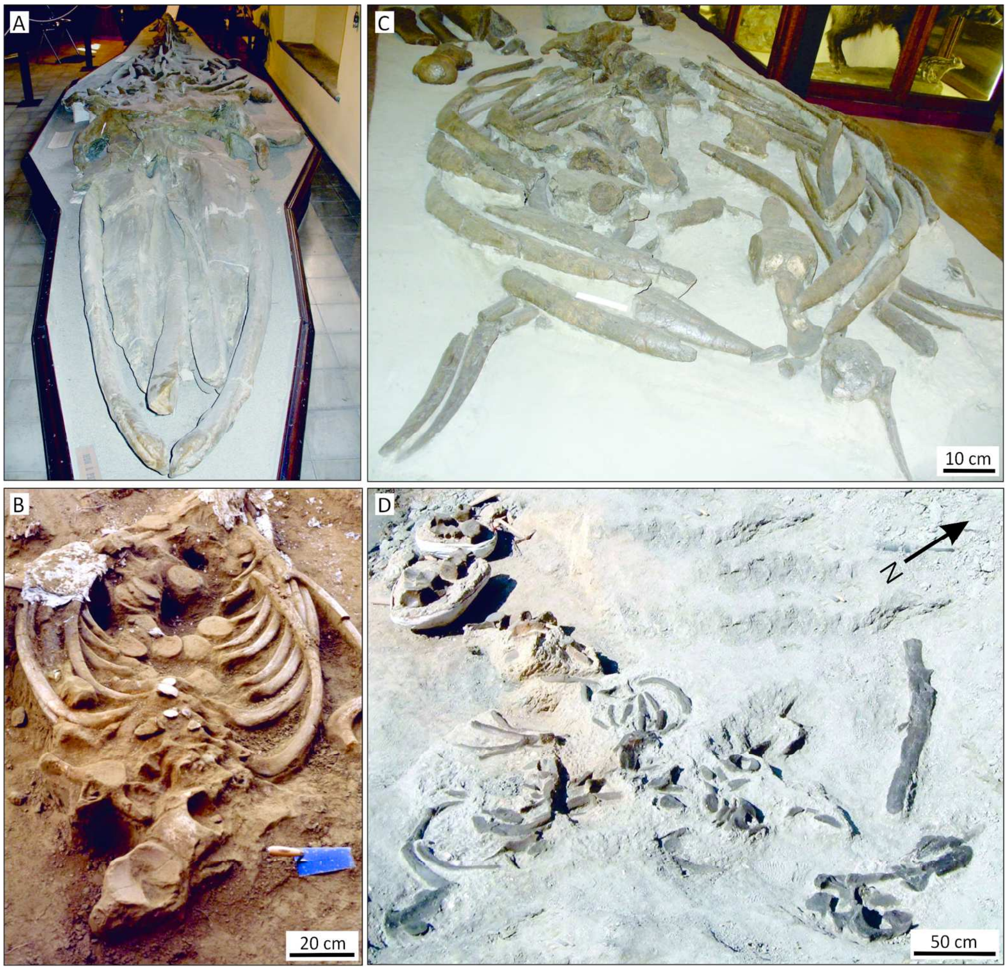


Lethaia - manuscript copy



For Review

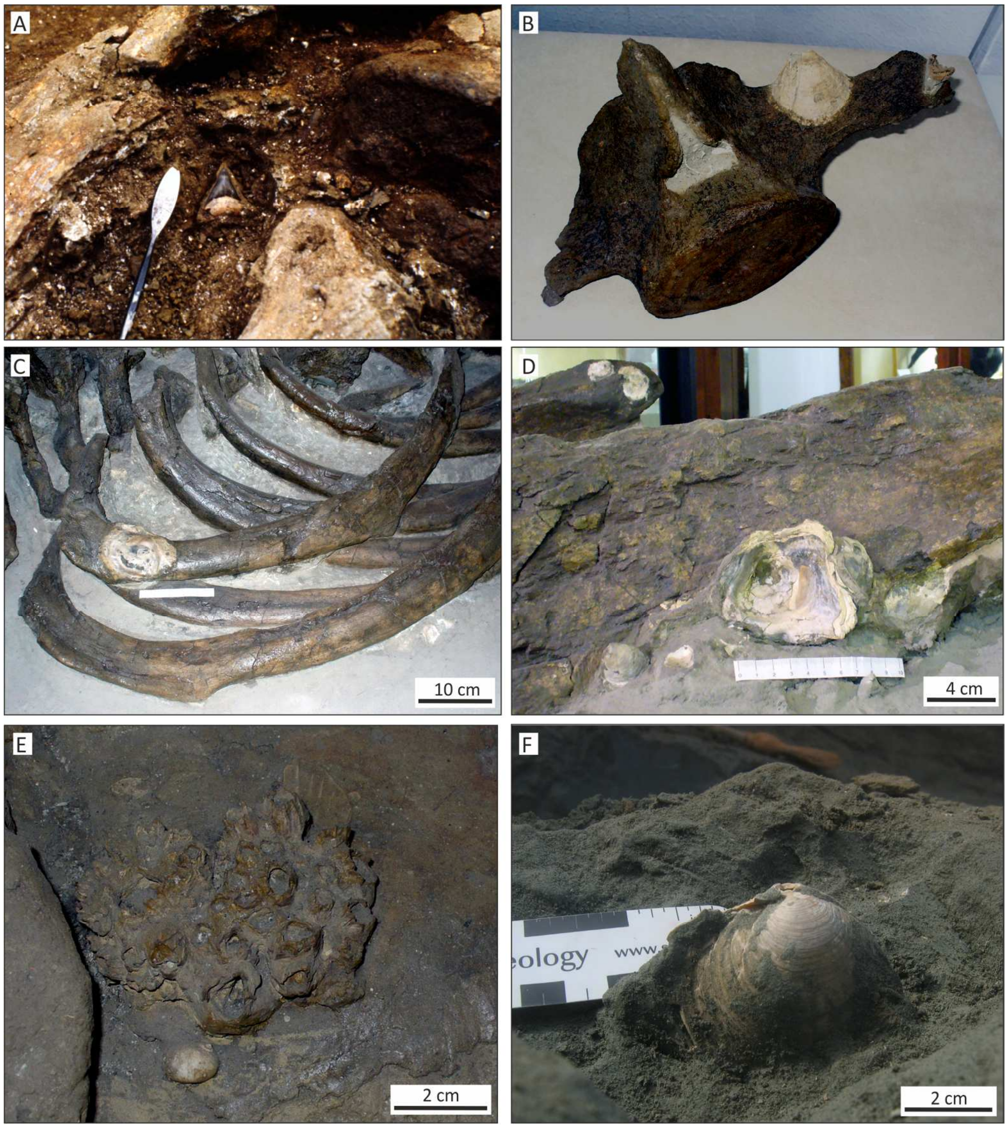
Lethaia - manuscript copy



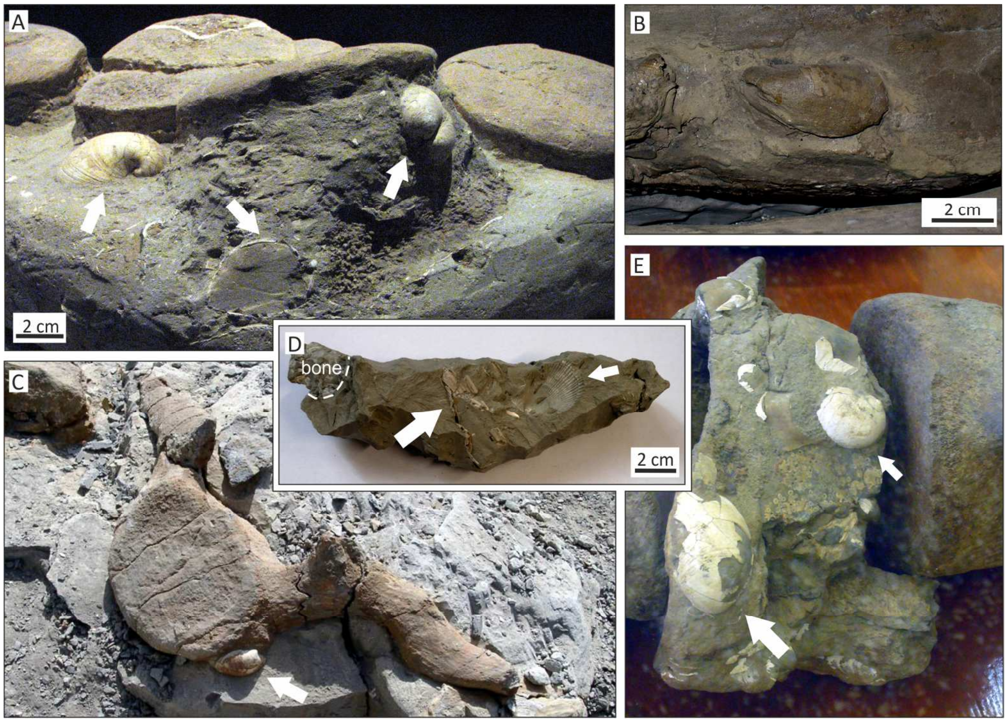
170x163mm (300 x 300 DPI)

170x153mm (300 x 300 DPI)

ew



170x190mm (300 x 300 DPI)



170x122mm (300 x 300 DPI)

Review

Table 1
Information on the studied Neogene fossil whales. Hosting institution abbreviation and taphonomic variable explained in the text. Among incomplete skeletons, * indicates acephalous specimens, " indicates specimens that conserve only the skull.

LOCALITY	N°	HOSTING INSTITUTION	TAXON	LITOLOGY	LENGHT (m)	BONE ARTICULATION	COMPLETENESS	CORTICAL BONE PRESERVARTION	VERTEBRAL PROCESS PRESERVATION	BONE CEMENTATION	SHARK TEETH	CHEMOSYMBIOTIC BIVALVES	ENCRUSTING EPIBIONTS	OTHER INVERTEBRATES	REFERENCES
Orciano Pisano (PI)	W1	MSNF	*Mysticete*	Silty -fine grained sandstone	10	high	high	low	low	medium	yes	Lucinidae, Bathymodiolinae	yes	see Danise et al. 2010	Dominici et al. 2009, Danise et al. 2010
Vigliano d'Asti (AT)	W2	MGPT	*Balaenoptera acutorostrata*	Silty fine-grained sandstone	8	high	high	high	high	medium	no	n.d.	yes	n.d.	Caretto 1970, Dominici et al. 2009
San Marzanotto (AT)	W3	MPSC	*Balaenoptera acutorostrata*	Mudstone	8	low	low	high	high	low	yes	n.d.	yes	Carnivores (*Nassarius italicus*), suspension feeders (*Amusium cristatum, Atrina pectinata, Anadara diluvii, Pelecyora brocchii, Neopicnodonte cochlear*), deposit feeders (*Aporrhais uttingeriana, Tellina compressa*) and browsing carnivores (*Epitonium turtoni*)	Damarco 1995, Dominici et al. 2009
Portacomaro d'Asti (AT)	W4	MSNT	*Balaenula astensis*	Silty fine-grained sandstone	6	medium	low"	high	n.d.	medium	no	n.d.	no	n.d.	Trevisan 1941, Dominici et al. 2009
Castell'Arquato (PC)	W5	MPP	*Balaenoptera acutorostrata*	Mudstone	8	high	high	high	medium	high	no	n.d.	yes	Carnivores (Naticidae), suspension feeders (Mytilidae, Pectinidae)	Strobel 1881, Dominici et al. 2009
Rio dei Carbonari -Castell'Arquato (PC)	W6	MGC	*Archaebalaenoptera castriarquati*	Silty fine-grained sandstone	7	high	low"	high	n.d.	low	yes	n.d.	yes	n.d.	Bisconti 2007, Dominici et al. 2009, Lo Russo and Miti pers. comm.
Rio Stramonte - Castell'Arquato (PC)	W7	No longer available	*Balaenoptera acutorostrata*	Mudstone	7	high	high	medium	high	low	yes	n.d.	yes	n.d.	Cortesi 1819, Dominici et al. 2009
Rio Stramonte - Castell'Arquato (PC)	W8	MGC	*Mysticete*	Mudstone	n.d.	n.d.	low*	n.d.	n.d.	n.d.	no	n.d.	no	Suspension feeders (*Glossus humanus*)	Lo Russo and Miti pers. comm.
Monte Falcone - Castell'Arquato (PC)	W9	MGC	*Balaenoptera acutorostrata*	Mudstone	n.d.	low	high	high	low	medium	no	n.d.	no	n.d.	Francou 1994
Monte Falcone - Castell'Arquato (PC)	W10	MPP	*Cettotherium capellinii*	Sandstone	9	medium	low*	low	n.d.	medium	no	n.d.	no	n.d.	Scabelli 1843

For Peer Review

For Peer Review

LOCALITY	N°	HOSTING I NSTITUTION	TAXON	LITOLOGY	LENGHT (m)	BONE ARTICULATION	COMPLETENESS	CORTICAL BONE PRESERVARTION	VERTEBRAL PROCESS PRESERVATION	BONE CEMENTATION	SHARK TEETH	CHEMOSYMBIOTIC BIVALVES	ENCRUSTING EPIBIONTS	OTHER INVERTEBRATES	REFERENCES
Monte La Ciocca - Castell'Arquato (PC)	W11	MGC	*Balaenoptera sp.*	Muddy sandstone	n.d.	low	low	medium	medium	low	no	n.d.	no	n.d.	Lo Russo and Miti pers. comm.
Montezago, Luganano Val D'Arda (PC)	W12	MPP	*Megaptera sp.*	Sandstone	12	low	low*	medium	low	low	no	n.d.	no	n.d.	Cortesi 1819
Montezago, Luganano Val D'Arda (PC)	W13	MPP	*Balaenoptera acutorostrata*	Mudstone	4	medium	high	high	high	high	no	n.d.	no	n.d.	Cortesi 1819
Gorgognano (BO)	W14	MGCB	*Balaenoptera acutorostrata*	Mudstone	9	medium	high	low	medium	medium	no	n.d.	yes	Suspension feeders (*Mytilus sp.*); deposit feeders (*Antalis* sp., *Aporrhais uttingeriana uttingeriana*), carnivores (*Ficus* sp.)	Sarti and Gasparri 1996, Domínci et al. 2009
San Lorenzo in Collina (BO)	W15	MGCB	*Balaenoptera acutorostrata*	Silty -fine grained sandstone	8	low	low	high	low	medium	yes	n.d.	yes	Suspension feeders (*Pelecyora brocchi*?, *Venus multilamella*?), carnivores (Naticidae)	Capellini 1865, Dominici et al. 2009
Castellarano (RE)	W16	MCRE	*Balaena sp.*	Silty fine grained sandstone	10	low	low	high	high	medium	yes	n.d.	yes	Suspension feeders (*Glycymeris inflata, Modiolus* sp., *Ostrea sp.*), scavengers (decapods)	Chicchi and Scacchetti 2001, Dominici et al. 2009
Ponte a Elsa (PI)	W17	MSNF	*Balaena sp.*	Mudstone	10	high	high	high	n.d.	high	yes	n.d.	no	Suspension feeders (*Chlamys opercularis*), deposit feeders *(Aporrhais uttingeriana, Dentalium fossile*), scavengers (decapods)	Borselli and Cozzini 1992, Dominici et al. 2009
Castel San Gimignano (PI)	W18	MSNF	*Balaenoptera sp.*	Sandstone	8	medium	low*	high	high	low	no	n.d.	no	n.d.	Dominici et al. 2009
Montopoli (PI)	W19	MCPG	*Eubalena sp.*	Very fine-silty sandstone	n.d.	n.d.	low	medium	n.d.	n.d.	yes	n.d.	no	n.d.	Bisconti 2002
Montopoli (PI)	W20	MSNF	*Idiocetus guicciardinii*	Sandy mudstone	n.d.	n.d.	high	high	high	low	no	n.d.	no	Carnivores (Naticidae, Nassaridae), suspension feeders (Pectinidae)	Capellini 1905
Castelfiorentino (FI)	W21	MSNF	*Balaenoptera sp.*	Mudstone	8	high	high	medium	medium	high	yes	n.d.	yes	Suspension feeders (Mytilidae, Pectinidae)	Dominici et al. 2009, this study
Montalcino (SI)	W22	CVB	*Balaenoptera sp.*	Silty -fine grained sandstones	10	low	high	high	high	low	yes	n.d.	no	n.d.	Dominici et al. 2009
Allerona (TR)	W23	MCGA	*Balaenula sp. (juvenile)*	Mudstone	2.5	low	high	medium	low	low	no	n.d.	no	n.d.	This study
Allerona (TR)	W24	MCGA	*Mysticete*	Mudstone	12	medium	high	high	medium	medium	no	n.d.	yes	Suspension feeders (*Pelecyora brocchi*?)	This study
Cà del Monte (PV)	W25	CMSNV	*Mysticete*	Fine grained sandstone	n.d.	low	low	high	medium	high	no	n.d.	no	n.d.	Danise et al. 2013

For Peer Review

TAPHONOMY OF THE BONES		
a	Bone articulation	high, medium, low
b	Completeness of the skeleton	high, low
c	Cortical bone preservation	high, medium, low
d	Vertebral process preservation	high, medium, low
e	Bone cementation	high, medium, absent
BIOTA ASSOCIATED WITH THE BONES		
f	Shark teeth	present, absent
g	Chemosymbiotic bivalves	present, absent , n.d.
h	Encrusting epibionts	present, absent
i	Other invertebrates	present, absent , n.d.

Table 2. List of the main taphonomic and paleoecologic variables considered in this study.

For Peer Review