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A record of fossil shallow-water whale falls from Italy

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Shallow-water fossil whale falls from the Neogene of Italy

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1 **Shallow-water fossil whale falls from the Neogene of Italy**

2 Silvia Danise, Stefano Dominici

3 *short title: Fossil shallow-water whale falls*

4

5 Twenty-five Neogene whales hosted in Italian museum collections and their associated fauna
6 were analysed for evidence of whale fall community development in shallow water settings.
7 Degree of bone articulation, completeness of the skeleton, and lithology of the embedding
8 sediments were used to gather information on relative water depth, water energy,
9 sedimentation rate and overall environmental predictability around the bones. Shark teeth and
10 hard shelled invertebrates with a necrophagous diet in close association with the bones were
11 used as evidence of scavenging. Fossil bone bioerosion, microbially-mediated cementation
12 and other mollusc shells in the proximity of the remains informed on past biological activity
13 around the bones.
14 The results are consistent with the hypothesis that shallow-water whale falls differ from their
15 deep-water counterparts. Taphonomic pathways are more variable on the shelf and whale
16 carcasses may not go through all steps of the ecological succession as recognized in the deep
17 sea. Whilst the mobile-scavenger and the enrichment opportunistic stages are well
18 represented, chemosynthetic taxa typical of the sulphophilic stage were recovered only in one
19 instance. The presence of a generalist fauna among the suspension feeding bivalves and
20 carnivore gastropods suggests that competitions rules out whale-fall specialists from shallow
21 shelf settings.

22

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

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32 **Introduction**

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

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

only from few experiments on artificially-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; Wären 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 biostratigraphic 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

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

84 Fossil cetaceans are abundant in Neogene shallow marine sediments of Italy,
85 particularly in the central and northern regions of Piedmont, Emilia Romagna and Tuscany
86 (Bianucci & Landini 2005; Bisconti 2009). Museum collections host specimens excavated
87 from the 19th century, and for many of them information on the stratigraphic and taphonomic
88 settings at the excavation sites is available (Cortesi 1819; Capellini 1865; Strobel 1881; Portis
89 1885; Caretto 1970; Sarti & Gasparri 1996; Chicchi & Scacchetti 2001). Notwithstanding not
90 all the taphonomical data that can be gathered following a modern approach in the excavation
91 of large fossil vertebrates are available when studying museum specimens, some useful
92 information can be obtained. Different degrees of bone articulation, completeness of the
93 skeleton, and lithology of the embedding sediments can give information on water depth,
94 current intensity and rate of burial of the bones (Martill 1985; 1987; Lancaster 1986; Allison
95 *et al.* 1991). Shark teeth in close association with the bones, which past researchers seem to
96 have not missed (Bianucci *et al.* 2002), and hard shelled invertebrates with a necrophagous
97 diet, occasionally reported in past excavations, testify scavenging. Fossil bone bioerosion,
98 cementation, and hard shelled organisms in the proximity of the remains can inform on past
99 biological activity around the bones at the micro and mesoscale (Martill 1987; Allison *et al.*
100 1991).

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

106

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).

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, diachronous 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-

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

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

141 **Materials and methods**

142 During the excavation and the museum preparation of the Orciano Pisano fossil whale
143 (W1) information on the taphonomy of the bones and the position of the associated
144 macrofauna respect to the whale skeleton were recorded (Dominici *et al.* 2009; Danise *et al.*
145 2010). To evaluate the level of generality of the Orciano Pisano finding, Italian Neogene
146 collections were surveyed for large more or less complete whale skeletons that could have
147 hosted a whale fall community (n=25, including W1; Table 1). These include large skulls in
148 the absence of postcranial bones (n=2) and articulated vertebral columns in the absence of the
149 skull (n=3). We have not considered isolated bones, which were however abundant in some
150 collections. For each specimen information on the taphonomy of the fossil bones and on the
151 associated biota were collected (Table 2). Measured taphonomic data on the bones include (a)
152 articulation and (b) completeness of the skeleton; preservation of (c) cortical bones and (d)
153 vertebral processes; and (e) bone cementation. Information on the associated biota include the
154 presence/absence of (f) shark teeth, (g) chemosynthetic bivalves, (h) encrusting epibionts and

(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 completeness 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.

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).

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), *Odontaspis* sp. (W17), *Isurus oxyrinchus* (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 barbares, solitary (Fig. 6B) or in clusters (Fig. 6E). Bioencrustation was recovered both from specimens from sandy and muddy sediments.

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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 *Pelecypora 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

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 gases 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 pore fluid alkalinity (Coleman & Raiswell 1993). Carbonate cements

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

281 The abundance and diversity of shark teeth in close association with the bones indicates
282 an interaction between pelagic sharks and whales. In the modern Mediterranean, cetaceans
283 represent a significant component of the diet of large size white sharks, either through
284 scavenging or predation on living animals (Mojetta *et al.* 1997). Considering the body size of
285 Pliocene white sharks, Bianucci *et al.* (2002) hypothesized that active predation was possible
286 only on small Mysticeti, as some cetotheriids and baleanids (*eg.*, *Balaenula*), whereas in all
287 other instances concerning larger specimens, the association with shark teeth must have been
288 true scavenging. In the present dataset shark teeth are all associated with large specimens (7-
289 10 m long), which can be considered positive evidence for scavenging. The correlation
290 between high degree of articulation and occurrence of shark teeth (Fig. 3C) suggests that in
291 shallow waters the action of scavengers is not intense enough to disarticulate whale carcasses
292 and disperse their bones. This datum is in accordance with what observed from a modern
293 shallow water study of a North Atlantic minke whale carcass at 125 m depth, which was
294 consumed by sharks and hagfishes within 6 months without significant disarticulation
295 (Dahlgren *et al.* 2006). It is important to note that no data are available on the presence and
296 importance of hagfishes as taphonomic agents in the Mediterranean, modern or ancient.

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

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),

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

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

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

(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

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373 succession, and have been or are inhabited by large-sized shelled specialists, suggesting very
374 similar taphonomic pathways (Allison *et al.* 1991; Naganuma *et al.* 1996; Goffredi *et al.*
375 2004; Lundsten *et al.* 2010). The ample variety of taphonomic states encountered in the
376 Italian Neogene whale record, and in other sparse instances (*e.g.*, Esperante *et al.* 2009),
377 suggests instead that in shallow marine bottoms the destiny of whale carcasses can be more
378 variable than in the deep sea. Because of the wider ranges of variation of physical and
379 biological factors, the way carcasses are recycled on the shelf can vary to a large degree.

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

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

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.

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.

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- 421 (i) In shallow marine bottoms the destiny of whale carcasses can be more variable than in
- 422 the deep sea, and the ecological succession more irregular.
- 423 (ii) The mobile scavenger stage at shelf depths, testified by shark teeth and possibly by
- 424 shelled predatory invertebrates common around the bones of large specimens, is
- 425 similar to the mobile scavenger stage in deeper settings.
- 426 (iii) The enrichment opportunist stage is indirectly attested by the general downgrading of
- 427 the bones, exceptionally by traces of the bone-eating worm *Osedax*, and possibly
- 428 by predatory active carnivores that preyed on soft bodied biota living around the
- 429 whale carcasses.
- 430 (iv) The sulphophilic stage was recognized in only one instance; this was not probably just
- 431 overlooked during the majority of past excavations, but it might have been
- 432 altogether absent, especially at very shallow depths.
- 433 (v) The reef stage was testified by cemented epifauna resting on downgraded bones.
- 434 Bioincrustation on pristine bone suggests that successional stages can be
- 435 intermingled.
- 436 (vi) The presence of a generalist fauna among the suspension feeding bivalves and
- 437 carnivore gastropods suggests that competition is a possible factor ruling out
- 438 whale-fall specialists from shallow shelf whale falls.
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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

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

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

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

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

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

FINDING LOCALITY
OF THE STUDIED FOSSIL WHALES

- MID PLEISTOCENE TO HOLOCENE DEPOSITS
- LATE MIOCENE TO PLEISTOCENE BASINS
- OLIGO-MIOCENE BASINS
- LIGURIAN UNITS
- TUSCAN UNITS
- UMBRIA-ROMAGNA UNITS
- METAMORPHIC UNITS
- MAGMATIC ROCKS
- MAJOR TRUST

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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	LENGTH (m)	BONE ARTICULATION	COMPLETENESS	CORTICAL BONE PRESERVATION	VERTEBRAL PROCESS PRESERVATION	BONE CEMENTATION	SHARK TEETH	CHEMOSYMBIOTIC BIVALVES	ENCrustING EPIBIONTS	OTHER INVERTEBRATES	REFERENCES
Orciano Pisano (PI)	W1	MSNF	<i>Mysticete</i>	Silty -fine grained sandstone	10	high	high	low	low	medium	yes	Lucinidae, Bathymodiolineae	yes	see Danise et al. 2010	Dominici et al. 2009, Danise et al. 2010
Vigliano d'Asti (AT)	W2	MGPT	<i>Balaenoptera acutorostrata</i>	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	<i>Balaenoptera acutorostrata</i>	Mudstone	8	low	low	high	high	low	yes	n.d.	yes	Carnivores (<i>Nassarius italicus</i>), suspension feeders (<i>Amusium cristatum</i> , <i>Atrina pectinata</i> , <i>Anadara diluvii</i> , <i>Pelecypora broccchii</i> , <i>Neopicnodonte cochlear</i>), deposit feeders (<i>Aporrhais uttingeriana</i> , <i>Tellina compressa</i>) and browsing carnivores (<i>Epitonium turtoni</i>)	Damarco 1995, Dominici et al. 2009
Portacomaro d'Asti (AT)	W4	MSNT	<i>Balaenula astensis</i>	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	<i>Balaenoptera acutorostrata</i>	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	<i>Archaeobalaenoptera castriarquati</i>	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	<i>Balaenoptera acutorostrata</i>	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	<i>Mysticete</i>	Mudstone	n.d.	n.d.	low*	n.d.	n.d.	n.d.	no	n.d.	no	Suspension feeders (<i>Glossus humanus</i>)	Lo Russo and Miti pers. comm.
Monte Falcone - Castell'Arquato (PC)	W9	MGC	<i>Balaenoptera acutorostrata</i>	Mudstone	n.d.	low	high	high	low	medium	no	n.d.	no	n.d.	Francou 1994
Monte Falcone - Castell'Arquato (PC)	W10	MPP	<i>Cetotherium capellinii</i>	Sandstone	9	medium	low*	low	n.d.	medium	no	n.d.	no	n.d.	Scabelli 1843

LOCALITY	N°	HOSTING INSTITUTION	TAXON	LITOLOGY	LENGTH (m)	BONE ARTICULATION	COMPLETENESS	CORTICAL BONE PRESERVATION	VERTEBRAL PROCESS PRESERVATION	BONE CEMENTATION	SHARK TEETH	CHEMOSYMBIOTIC BIVALVES	ENCrustING EPIBIONTS	OTHER INVERTEBRATES	REFERENCES
Monte La Ciocca - Castell'Arquato (PC)	W11	MGC	<i>Balaenoptera sp.</i>	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	<i>Megaptera sp.</i>	Sandstone	12	low	low*	medium	low	low	no	n.d.	no	n.d.	Cortesi 1819
Montezago, Luganano Val D'Arda (PC)	W13	MPP	<i>Balaenoptera acutorostrata</i>	Mudstone	4	medium	high	high	high	high	no	n.d.	no	n.d.	Cortesi 1819
Gorgognano (BO)	W14	MGCB	<i>Balaenoptera acutorostrata</i>	Mudstone	9	medium	high	low	medium	medium	no	n.d.	yes	Suspension feeders (<i>Mytilus sp.</i>); deposit feeders (<i>Antalis sp.</i> , <i>Aporrhais uttingeriana uttingeriana</i>), carnivores (<i>Ficus sp.</i>)	Sarti and Gasparri 1996, Dominici et al. 2009
San Lorenzo in Collina (BO)	W15	MGCB	<i>Balaenoptera acutorostrata</i>	Silty -fine grained sandstone	8	low	low	high	low	medium	yes	n.d.	yes	Suspension feeders (<i>Pelecypoda brocchi?</i> , <i>Venus multilamella?</i>), carnivores (Naticidae)	Capellini 1865, Dominici et al. 2009
Castellarano (RE)	W16	MCRE	<i>Balaena sp.</i>	Silty fine grained sandstone	10	low	low	high	high	medium	yes	n.d.	yes	Suspension feeders (<i>Glycymeris inflata</i> , <i>Modiolus sp.</i> , <i>Ostrea sp.</i>), scavengers (decapods)	Chicchi and Scacchetti 2001, Dominici et al. 2009
Ponte a Elsa (PI)	W17	MSNF	<i>Balaena sp.</i>	Mudstone	10	high	high	high	n.d.	high	yes	n.d.	no	Suspension feeders (<i>Chlamys opercularis</i>), deposit feeders (<i>Aporrhais uttingeriana</i> , <i>Dentalium fossile</i>), scavengers (decapods)	Borselli and Cozzini 1992, Dominici et al. 2009
Castel San Gimignano (PI)	W18	MSNF	<i>Balaenoptera sp.</i>	Sandstone	8	medium	low*	high	high	low	no	n.d.	no	n.d.	Dominici et al. 2009
Montopoli (PI)	W19	MCPG	<i>Eubalena sp.</i>	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	<i>Idiocetus guicciardinii</i>	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	<i>Balaenoptera sp.</i>	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	<i>Balaenoptera sp.</i>	Silty -fine grained sandstones	10	low	high	high	high	low	yes	n.d.	no	n.d.	Dominici et al. 2009
Allerona (TR)	W23	MCGA	<i>Balaenula sp. (juvenile)</i>	Mudstone	2.5	low	high	medium	low	low	no	n.d.	no	n.d.	This study
Allerona (TR)	W24	MCGA	<i>Mysticete</i>	Mudstone	12	medium	high	high	medium	medium	no	n.d.	yes	Suspension feeders (<i>Pelecypoda brocchi?</i>)	This study
Cà del Monte (PV)	W25	CMSNV	<i>Mysticete</i>	Fine grained sandstone	n.d.	low	low	high	medium	high	no	n.d.	no	n.d.	Danise et al. 2013

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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.