
Taphonomy of a Mysticeti whale in the Lower Pliocene Huelva Sands Formation (Southern Spain)

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| ABSTRACT |

This paper reports the occurrence of an incomplete fossil baleen whale skeleton in the Lower Pliocene Huelva Sands Formation (Guadalquivir basin) near the town of Bonares, southwestern Spain. The skeleton was found in the highly bioturbated glauconitic sandstone unit in association with *Neopycnodonte cochlear* shells. Several morphological features of the mandibles, scapula and vertebrae suggest that the specimen belongs in the suborder Mysticeti, family Balaenopteridae. Most bones show abrasion due to a long exposure on the seafloor, and some bones show shark tooth marks and both micro- and macro-bioerosion by scavengers. The position of the bones suggests that the carcass landed on the seafloor on its left side and then turned right side up. Sedimentological and paleontological features indicate that the whale was buried in shallow platform waters under low sedimentation rates.

KEYWORDS | Baleen whale. Mysticeti. Neogene. Guadalquivir basin.

INTRODUCTION

Fossil baleen whales are relatively common in Miocene-Pliocene marine siliciclastic deposits around the former Tethys Sea, with reports from Greece (Bartsiakas, 2000), Italy (Caretto, 1970), Slovenia (Pavsic and Mikuz, 1996), and the Caucasus region (Pilleri, 1986; Mchedlidze, 1988). Numerous marine mammal fossils (Odontoceti and Mysticeti) have also been reported in

Neogene sedimentary deposits of the Eastern North Atlantic Ocean region, including Belgium (Abel, 1905), and Portugal (Da Mata, 1962; Jonet, 1978). In southern Spain, cetacean fossils have been reported in siliciclastic sediments of three Neogene basins, namely the Guadalquivir (Huelva and Sevilla provinces principally; e.g., (Mayoral, 1986b), Bajo Segura (Alicante province; e.g., (Sendra, 1997), and Vera (Almería province; e.g., Sendra et al., 1998)) basins (Fig. 1). Most of the whale

skeletons reported from the southern Spanish Neogene basins consist of incomplete and partially or totally disarticulated specimens, and only a few show remarkable completeness and articulation (Sendra, 1997).

Cetacean fossils in the Huelva Province (SW Spain) were first reported in the late 19th century, when Gonzalo and Tarín (1878) mention whale fossils in the Neogene rocks of this southern region. Since then, brief reports from the area describe isolated skulls, vertebrae, ribs, and occasionally a few connected bones (Sendra et al., 1999). Frequent finding and reporting of fossil cetacean material by the public led the regional government of Andalucía to sponsor, from 2001 on, several excavations of specimens, which have been documented and described in unpublished official reports. A summary of these findings in the Guadalquivir Basin is provided in Table 1. Still, an in-depth study of the taphonomic characteristics and paleoenvironment of these marine mammal fossils is lacking.

This paper describes a partial fossil Mysticeti whale in the Lower Pliocene Huelva Sands Formation, near the town of Bonares, Huelva Province, its taphonomic characteristics, and supplements existing paleoenvironmental models for the deposition of the skeleton.

GEOLOGICAL SETTING

The Guadalquivir foreland basin is located between the Iberian passive Paleozoic basement of the Iberian Massif to the north and the External Zone of the Betic Cordilleras to the south (Fig 1). The basin shows an ENE-WSW trend with an elongate triangular shape and remarkable asymmetry. During the Neogene, collision of the African and Iberian plates caused asymmetrical uplift of the sediments filling the basin. As a result of differential uplift, the deposits of the easternmost side of the basin are now exposed at an elevation of more than 800 m

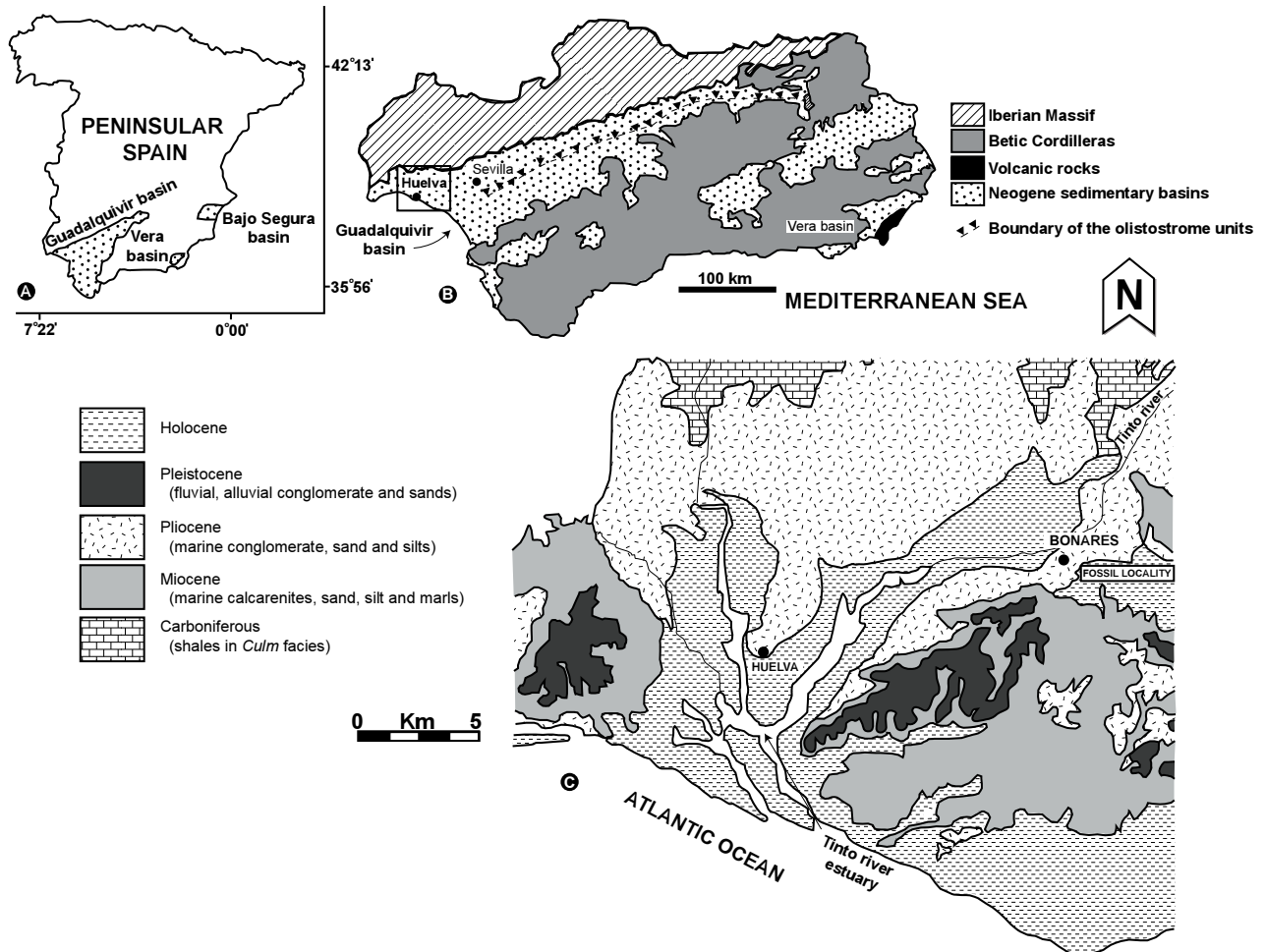


FIGURE 1 | Generalized geological map of the study area. A) Map of Peninsular Spain showing the extent of the Guadalquivir Basin. B) The Neogene Guadalquivir Basin, limited by two mountain ranges, the Sierra Morena to the north and west and the Betic Cordillera to the south and east. C) Detail map of the geologic formations near the fossil whale locality at Bonares. Study location indicated by the bold star symbol.

TABLE 1 | Fossil marine mammals from the Guadalquivir basin.

FORMATION AND PERIOD	LOCALITY (PROVINCE)	SUBORDER, FAMILY	MATERIAL	REFERENCES
Écija Formation, Lower Pliocene	Alcalá de Guadaira (Sevilla)	Mysticeti, Balaenopteridae?	Cranium, dentaries, vertebrae, ribs, scapulas, tympanic bullas	Sendra et al. 1996
Lower Pliocene	Lepe (Huelva)		Fragments of neurocranium and dentary, tympanic bulla	Sendra et al. 1999
Lower Pliocene	Lepe (Huelva)	Mysticeti, Cetotheridae	Fragment of skull	See caption
Lower Pliocene	Lepe (Huelva)	Mysticeti, Balaenopteridae?	Vertebrae, ribs	
Huelva Sands Formation Lower Pliocene	Huelva City		Vertebrae, ribs, limb bones, rostrum and neurocranium	
	Huelva City		Fragment of skull, dentaries, tympanic bulla, cervical vertebrae, phalanges	
	Huelva City		Lumbar vertebrae, tympanic, fragment of a dentary, phalange	
	San Juan del Puerto (Huelva)		Thoracic and lumbar vertebrae, vertebral epyphysis, fragments of dentaries	
	Bonares (Huelva)	Neurocranium, dentaries, vertebrae, ribs, limb bones	This paper	

This material was studied and excavated during several projects sponsored by the Consejería de Cultura of the Junta de Andalucía. Data collected are reported in the Anuario Arqueológico de la Junta de Andalucía, which has not yet been published to this date.

above sea level, whereas the western end of the basin (opening to the Atlantic Ocean) was much less affected by tectonism (Sanz de Galdeano, 1990; Braga et al., 2003). During the Miocene-Pliocene, the northern passive margin and the center of the basin were filled with autochthonous-parautochthonous terrigenous and biogenic deposits whereas the active south and southeastern margins were filled with allochthonous materials from the olistostrome structural unit (Valenzuela, 1982) (Fig. 1). In the Huelva Province, Neogene marine autochthonous sediments have been divided into four formations, which from bottom to top are the Niebla Formation, the Gibraleón Clays Formation, the Huelva Sands Formation, and the Bonares Sands Formation (Fig. 2). The fossil specimen described in this article was found in the northern autochthonous sedimentary layers from the Huelva Sands Formation.

The Niebla Formation (Baceta and Pendón, 1999), also called Basal Transgressive Complex (Pendón et al., 2004; Abad et al., 2005), consists of fluvial and deltaic sandstone and conglomerate materials, which vertically and laterally transition into calcarenites and bioclastic limestones that unconformably rest on the Paleozoic basement. In the westernmost area of the basin the siliciclastic materials predomi-

nate with sandstones, conglomerates and mudstones, interpreted as deltaic and shallow marine deposits (Baceta and Pendón, 1999). The occurrence of *Neogloboquadrina humerosa* in the lower part of the calcarenites suggests a late Tortonian age for the Niebla Formation (Sierro et al., 1990).

The top of the Niebla Formation is in sharp and irregular contact with the overlying Gibraleón Clays, which consist of glauconitic mudstone that grades into gray mudstone and marls, locally black in color, and capped by interbedded sandstones and mudstones. These deposits are interpreted as outer deep platform and slope turbiditic systems related to the drop of the sea level during the Messinian (Sierro et al., 1996). The lower sediments of this formation were deposited during the Upper Miocene (Upper Tortonian, *Turborotaria humerosa* biozone) and higher layers in the Lower Pliocene (*Globorotalia miotumida* and *G. margaritae* biozones (Sierro, 1985).

Overlying the Gibraleón Clays is the Huelva Sands Formation (Civis et al., 1987), which consists of a condensed basal level of glauconitic sandstone, with siltstone and fine sandstone above. The total thickness varies laterally between 10 and 30 m. These sedimentary rocks con-

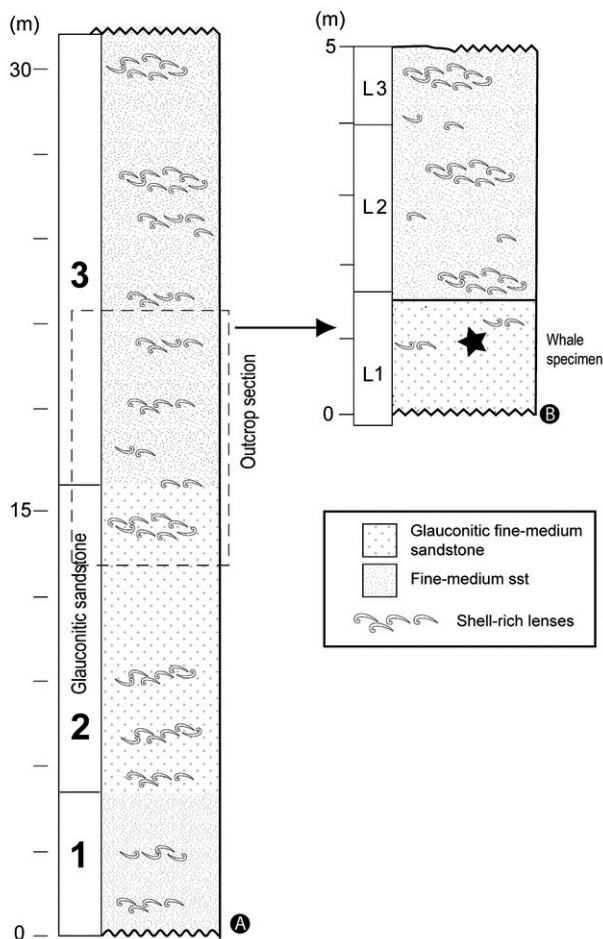


FIGURE 2 | A) Stratigraphic section of the Huelva Sands Formation. Sediment consists of fine-to-medium sandstone, with scattered shells and bioturbation throughout the sequence. Unit 2 is glauconite-rich and bioturbation has obliterated all primary sedimentary structures. **B) The outcrop at the Bonares locality shows three distinct levels based on differences in bioturbation and fauna content and abundance. The whale fossil was found in the upper half of the glauconite-rich L1 level.** Lithology and paleontological content of the three sedimentary levels observed at the Bonares fossil site: **Level L1:** 1.5-m thick fine glauconitic sandstone. Scarce, scattered and irregularly distributed fauna. Bivalves: *Acanthocardia*, *Amussium*, *Chlamys*, *Neopycnodonte*, *Ostrea*, *Pelecypora*. Gastropods: *Natica*, *Neverita*. Scaphopods: *Dentalium*. Chondrichthyes: *Isurus*, *Odontaspis*, *Carcharinus*, *Nothorynchus*, *Myliobatys*. Pisciformis. Bioturbation: abundant *Laminites*, *Palaeophycus*, *Taenidium*, *Teichichnus*, and *Thalassinoides*. Bioerosion: rare *Entobia* and *Gastrochaenolites*. Plant wood remains with *Teredolites* borings. **Level L2:** 2-m thick fine to medium sandstone. Poorly sorted, irregularly distributed shells. Bivalves: predominantly disarticulated and fragmented, and imbricated *Acanthocardia*, *Amussium*, *Azorinus*, *Callista*, *Chlamys*, *Corbula*, *Glycymeris*, *Lucinoma*, *Nuculana*, *Ostrea*, *Pecten*, *Pelecypora*, *Tellina*. Few articulated shells. Except for *Circumphalus*. Scaphopods: *Dentalium*. Gastropods: *Calyptrea*, *Gibberula*, *Lemintina*, *Turritella*, *Xenophora*. Scaphopods: *Dentalium*. Arthropods: *Balanus*. Vertebrates: Otoliths, fish teeth. Bioturbation: *Palaeophycus*, *Teichichnus*, *Thalassinoides*. Bioerosion: *Caulostrepsis*, *Entobia*, *Maeandropoydora*, *Oichnus*. **Level L3:** 1-m thick fine to medium sandstone. Medium to highly concentrated, irregularly distributed invertebrate fauna. Poorly sorted, locally imbricated valves, with medium to high degree of fragmentation. Bivalves: *Acanthocardia*, *Chlamys*, *Circumphalus*, *Corbula*, *Cuspidaria*, *Glycymeris*, *Diplodonta*, *Megaxinus*, *Nucula*, *Paphia*, *Pelecypora*, and *Tellina*. Gastropods: *Calyptrea*, *Nassarius*, *Naticarius*, *Neverita*, *Ringincola*, *Turritella*, and *Xenophora*. Scaphopods: *Dentalium*. Arthropods: *Balanus*. Bioturbation: similar to L2.

tain abundant and well-preserved invertebrate fossils at many levels throughout the section. The glauconitic facies are rich in bivalves (venerids, ostreids, pectinids, and cardids) and gastropods (mainly vermetids). Especially abundant are *Neopycnodonte* and *Ostrea*, which, according to Galán et al. (1989) indicate that the depth of this part of the basin reached 30-50 m. Galán et al. (1989) also evaluated the glaucony pellets and confirmed a glauconite mineralogy based on X-ray diffraction and chemical composition.

Marine mammals, fish, sharks, and ichnofossils are commonly associated with the glauconitic facies and have been interpreted as deposited in a low energy, open marine environment (Andrés, 1982; Mayoral, 1986b; Dabrio et al., 1988; Antunes et al., 1989; Galán et al., 1989; Sierro et al., 1990; González-Delgado et al., 1993). The studied section at the Bonares outcrop shows the highest degree of bioturbation in the area, characterized by *Cruziana* ichnofacies (Mayoral, 1986a; Galán et al., 1989). Sandstones show residual fossil associations that are likely the result of sediment by-pass and shell reworking during storm events on the siliciclastic marine platform (González-Delgado, 1983; Dabrio et al., 1988). These high-energy deposits are very conspicuous at the Bonares section, attested by the occurrence of communities of *Glycymeris*, *Corbula* and *Acanthocardia* (Mayoral, 1989b), that may have grown shielded by tide channels and scours. Based on the occurrence of *Globorotalia margaritae* and *G. puncticulata*, this formation is interpreted as Lower Pliocene (Sierro, 1985).

The Bonares Sands Formation occurs at the top of this Neogene sequence and it consists of medium- to very coarse-grained sandstones unconformably overlying the Huelva Sands Formation. These sandy deposits grade into pebble conglomerates and conglomerates, and are interpreted as very shallow marine and beach deposits with an increasing continental (fluvial) sediment input (Mayoral and Pendón, 1986-1987). Sierro et al. (1996) suggest an upper Lower Pliocene age for this unit materials, but at this time no well-established biostratigraphic data are available.

METHODS AND MATERIALS

The fossil Mysticeti whale was found in a trench along the road between the town of Bonares and the freeway A-49, in an outcrop of Lower Pliocene marine siliciclastic rocks of the Huelva Sands Formation, and assigned the name C1/BON06. When the specimen was found, only the top surfaces of the neurocranium and one vertebra were visible. The following excavation procedure was carried out so that the specimen could be removed to a facility for cleaning, preparing, and mounting.

1. The skeleton was excavated during June 2006 by careful digging with knives, small chisels, and other small

tools. A spade was used to remove the overburden on top of some bones. The original 1-m-wide trench was widened to two meters and deepened 50 cm more to expose the bones and the associated fossils. Widening of the trench was limited due to instability of the slope above.

2. Sediment was removed from the skeleton and the bones were stabilized with Paraloid B-72 (5-10% in acetone).

3. The position of all bones was mapped using a grid. Orientation of the skeleton was taken with a Brunton compass. Each bone received a catalog number to facilitate later reconstruction of the skeleton.

4. Smaller bones, including some of the limb bones, and vertebrae were completely removed from the host rock by excavating around them until they were left lying on two or three elevated, thin columns of the underlying sandstone. These sandstone columns were undercut using small chisels and the bones lifted and individually wrapped to protect them during manipulation and transport. Larger bones, including mandibles, skull fragments, and scapula were removed using the same technique, but with a thick portion of the underlying rock attached to the base of the bone to ensure preservation.

5. The bones and the underlying host rock were packed in polyurethane foam, removed from the outcrop, and stored in a facility for further study. In September 2006, the bones were unpacked for cleaning, detailed study, and description in the laboratory.

6. Bones were cleaned with small knives, trowels, and brushes. No water, detergents, or other liquids were used in this process. Sandstone adhering to the surface of the bones was poorly indurated so no mechanical chisel or hammer tools were needed for cleaning.

7. The sedimentary section associated with the skeleton was measured and studied. Samples of sediment adjacent to the bones were collected and labeled.

8. All bones were photographed both in the field and in the lab.

9. Thin sections of bones and associated sediment were prepared by National Petrographic Service, Inc., Houston, USA. Mineral compositions are visual estimates from the thin sections.

10. Thin sections were examined and photograph with a JenaPol 250 CF microscope and Nikon Coolpix 8700 camera.

Original fossil specimens collected in this study are housed in the Centro Provincial de Interpretación Paleontológica Ciudad de Lepe, Huelva, SW Spain, and the samples used for thin section and other analysis are housed in the Geoscience Research Institute, Loma Linda, California.

SEDIMENTOLOGY

The whale specimen was found buried in a single horizon of glauconitic sandstone and siltstone of the

Huelva Sands Formation. This glauconitic horizon is about 2 m thick at the study site, and the skeleton was preserved near the middle of the unit. The fossil was not encased in any kind of concretion and the sediment shows no obvious macroscopic difference as individual bones are approached. The glauconitic sandstone and siltstone show the highest degree of bioturbation within the entire section of the Huelva Sands Formation at the whale site. Microfossils in the sediment are very scarce, with sparse phosphatic spines, complete forams and fragments of forams.

Thin section analysis shows the clastic material encasing the bone is a mixture of about 50% medium sand-size glauconite pellets and 50% very fine sand- to silt-size quartz and feldspar grains with trace amounts of mica, fossil fragments, and coarse sand size polycrystalline quartz grains. Glauconite grains are ovoid and well rounded and have a homogenous internal texture with no core. Feldspar and quartz grains are angular to subangular. Grain contacts range from floating to long, leaving an estimated 25% intergranular porosity.

Small amounts of clay, fine-grained iron oxide, and very finely crystalline carbonate coats and loosely cements the framework grains. In most cases, there is no significant difference in the framework or authigenic components as you approach the bone margin. A few examples of cm-scale calcite cemented nodules were seen near the bones however.

Pores in the bones locally contain silt size quartz and feldspar. A larger number of the pores contain pore lining and partial to complete pore fillings of siderite, green clay, and hematite. The hematite has textures that suggest it has replaced siderite or pyrite and may have filled porous clay cements. Some glauconite grains near some of the bones appear to be oxidized to an orange color. The combination of hematite cements and replacement and oxidized glauconite pellets give the bones an orange color.

TAPHONOMY

Bone assemblage and biostratigraphy

The excavated specimen consists of bones of a partial skeleton of a single Mysticeti whale (Fig. 3). Mysticeti identification is based on the shape and size of the vertebrae, limb bones, mandibles, and the lack of teeth. The shape of the scapula suggests that the specimen is *Balaenopterid*-like. Genus identification is not possible due to the lack of diagnostic skeletal elements (no ear or complete skull bones). The specimen is a juvenile baleen whale, indicated by the absence of the vertebral epiph-

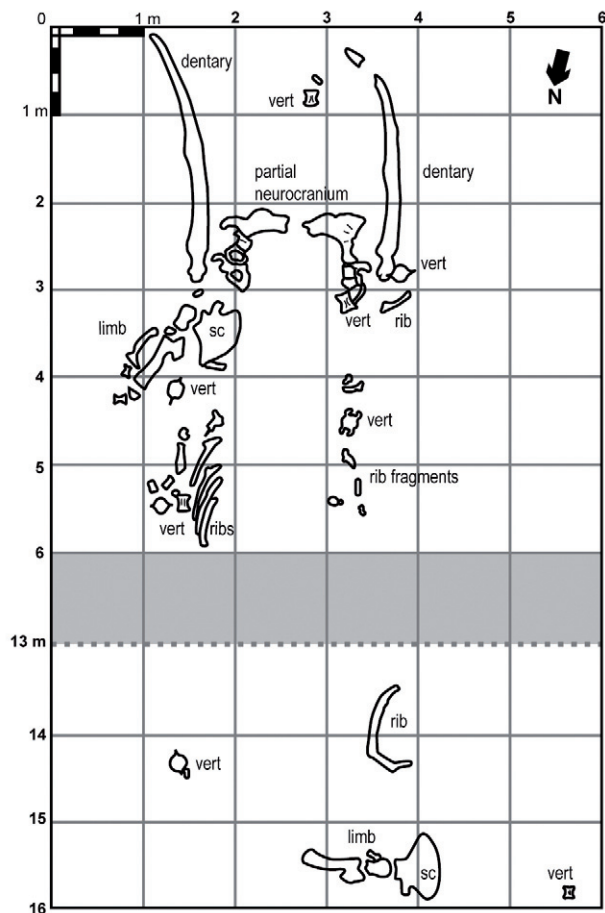


FIGURE 3 | Diagram of the specimen exposed during excavation. Elements preserved include the two dentaries, part of the neurocranium, ribs, vertebrae, phalanges, and limb bones. The bones are roughly oriented in life position, although the left dentary is rotated, some vertebrae are displaced and the right side limb is displaced about 12 m from its articulation position. The gray-shaded area indicates an area barren of any whale bone and a gap in the scale. sc: scapula, vert: vertebra.

ysis, which in juveniles are not fused to the centrum and tend to detach from the vertebra after death.

Preserved skeletal elements and their taphonomic conditions are described in Table 2. All the bones are preserved at the same level, except a fragmented rib that had one piece displaced a few cm above the level of the rest of the bones. The skeleton is disarticulated but associated (*sensu* Behrensmeyer (1991)) (Fig. 3). Most of the individual bones were not displaced from their original positions by more than a few centimeters; hence the overall shape of the whale skeleton has been retained. The two dentaries are disconnected from the skull and displaced a few centimeters, but nevertheless closely associated and aligned with the skull. The two limbs are partially articulated, although one of them is displaced 11 m from its original articulation place relative to the vertebral column. Vertebral processes and neural arches are missing from all

the preserved vertebrae. Removal or destruction of bones during recent exposure is unlikely because all the bones were either totally or partially buried in the host rock matrix, except for the top surfaces of some bones, including the neurocranium, the nasal, the rostrum and a vertebra that were partially exposed at the time of discovery, which caused severe damage by weathering and erosion. Other bones, including a phalange, a scapula, and cervical and thoracic vertebrae, show various degrees of damage by modern weathering due to water percolation through the porous sediment. One vertebra is known to have been excavated by an amateur collector and its whereabouts are unknown.

Fossildiagenesis

Bones are not heavily permineralized and remain relatively light, porous, and brittle. Destruction by diagenetic processes seems unlikely because we would expect to find intermediate stages in the preservation of some of the bones. During burial and compaction, many of the bones were cracked, some were crushed, but deformation is minimal. Thin sections reveal that surfaces of the bones are abraded and contain some microborings whereas the inner part of the bones is well preserved (Fig. 4). The diagenetic modifications of the bone and the occurrence of microborings are under study and will be published in forthcoming papers.

ASSOCIATED PALEOBIOTA AND ICHNOFOSSILS

During excavation of the skeleton, numerous specimens of both invertebrates and vertebrates were found in the glauconitic sediment and also associated with the bones (Table 3). Most associated fossils, including mollusks, teeth and ichnofossils, do not show any preferential orientation or concentration that can be related to whale bones. An exception is the occurrence of *Neopycnodonte* shells, which form several clusters cemented to the bones.

Invertebrate fauna

Invertebrate fauna associated with the bones is of low diversity and abundance, and consists mainly of bivalves, gastropods and scaphopods (Table 3). These molluscs are not preserved in a single bedding plane, but mainly concentrated at three different levels (see Fig. 2), although shells are also widely scattered throughout the entire section, including at the level of the whale bones.

The two most abundant genera are the Ostreoidea *Ostrea* and *Neopycnodonte cochlear*. Other less abundant genera include bivalves *Amussium*, *Panopea*, *Pelecypora*, *Chlamys*, and also gastropods in the family Naticidae.

TABLE 2 | Taphonomic characteristics of the excavated whale bones.

	Skeletal elements	Number	Bioerosion	Abrasion	Relative position	Articulation	Settlement	
Cranial	Rostrum	1	Shark bite. Borings	Most bones show abrasion on the upper surfaces	<i>In situ</i>	Disarticulated	Oysters	
	Neurocranium	1	Shark bite. Borings		Slightly displaced			
	Dentary	2			Left rotated			
Postcranial	Cervical vertebrae	2			Displaced	Disarticulated. Neural arches and processes missing		
	Thoracic vertebrae	6			Displaced			Oysters
	Lumbar vertebrae	1			Displaced			
	Caudal vertebrae	1			<i>In situ</i>			
	Ribs	7			Some in situ, others displaced			Oysters
Apendicular	Scapula	2	Borings and grooves		Left in situ, right displaced	Articulated		
	Humerus	2	Grooves		Left in situ, right displaced	Articulated	Oysters	
	Radius	1			<i>In situ</i>	Disarticulated		
	Ulna	2			Left in situ	Left articulated, right disarticulated		
	Carpal	1			<i>In situ</i>	Left articulated, right disarticulated		
	Metacarpal	2			Right in situ, left displaced	Disarticulated		
	Phalange	5	Grooves		Left slightly displaced	Disarticulated		
Undetermined bones	?	Multiple small fragments						

All body parts are represented, including skull, dentaries, limbs, vertebrae and ribs. Abrasion was probably the result of long exposure on the seafloor before burial.

Most *Neopycnodonte* have the two valves articulated and in life position and some others have just one valve preserved, commonly with the small valve missing. They appear isolated or forming clusters and are both in association (cemented) with bones (Fig. 5) or apart from them.

Vertebrate fauna

Besides the whale skeleton, other vertebrate fauna include isolated teeth of fish, rays and sharks, bones of fish (otoliths and vertebrae), and unidentified vertebrae and teeth (Table 3). They are well preserved, lacking evidence of abrasion, bioerosion or weathering. Fish vertebrae have both the haemal and neural arches detached, but are nevertheless well preserved.

Ichnofossils

The glauconitic sandstone in which the whale is encased is highly bioturbated (Fig. 6b), with an ichnofabric index of 6 as defined by Taylor and Goldring (1993). Sediments with

this degree of bioturbation lack any primary sedimentary structure. In the studied section, bioturbation also affects sediment adjacent to the bones (Fig. 6b). The trace fossil assemblage consists of ichnospecies *Thalassinoides* isp., *Taenidium* isp. (Fig. 6a, c), *Teichichnus rectus*, assigned to crustacean sediment feeding (Bromley and Frey, 1974; D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994), *Palaeophycus* isp., associated with annelid sediment feeding (Pemberton and Frey, 1982; Keighley and Pickerill, 1994), and *Laminites* isp., a trace fossil assigned to a spatangoid echinoid with sediment feeding behaviour (Smith and Crimes, 1983; Plaziat and Mahmoudi, 1988).

Several bones, including one scapula, one humerus and a dentary, show distinctive bioerosion traces by possible decapod crustaceans (Esperante and Muñiz, 2008). Especially remarkable are the marks in the left scapula (Fig. 7), which include borings that extend all the way through the bone, superficial grooves, regular indentations on the edge of the bone, and wide galleries that represented entire portions of scavenged bone.

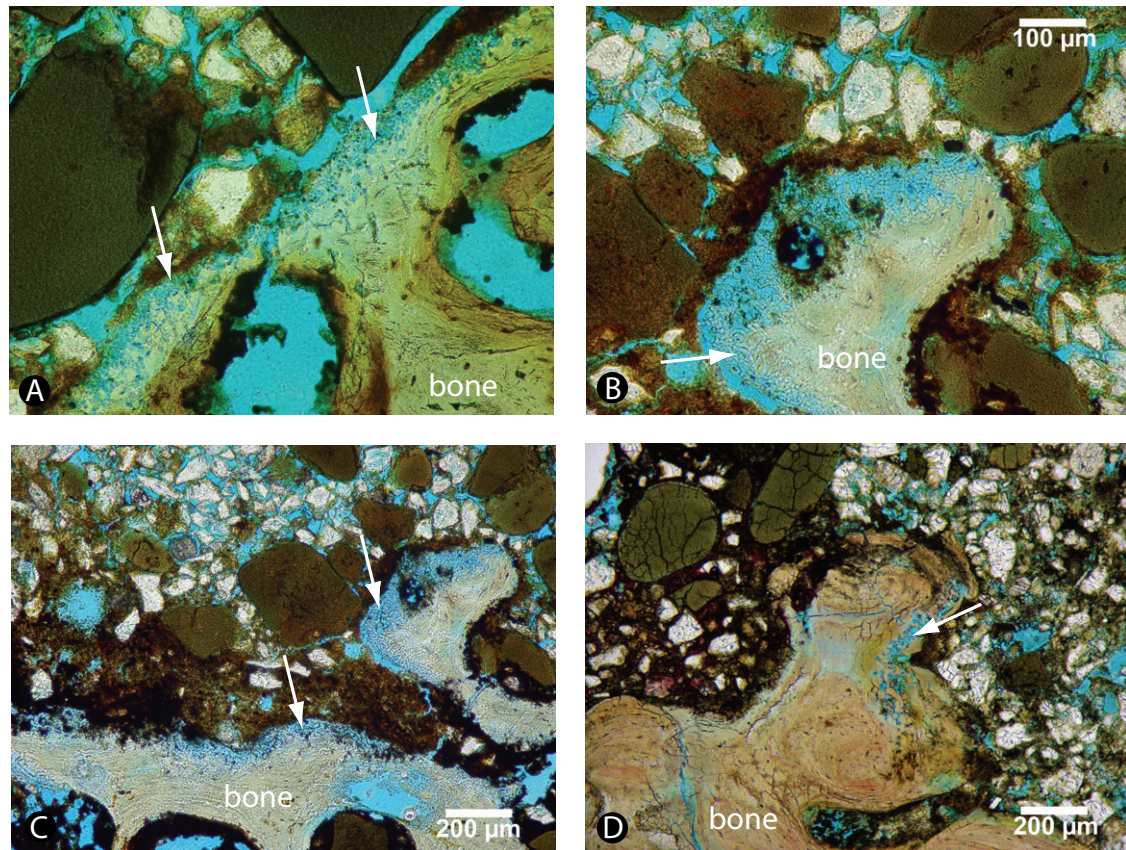


FIGURE 4 | Thin sections of bones and associated sediment. Large dark green particles are glauconite grains. Arrows indicate microborings on the surface of the bones, which may have been caused by algae, cyanobacteria and/or fungi. Blue-dyed epoxy shows primary intergranular and intraparticle porosity and secondary borings.

Bioerosion structures on bivalves in the glauconitic horizon are almost absent, and only two *Neopycnodonte cochlear* shells have been found with evidence of borings, represented by *Entobia* isp. (produced by boring sponges) and cf. *Gastrochaenolites* isp. (clavate borings produced by bivalves). *Oichnus simplex* borings (produced by predatory or parasitic gastropods) have been observed in a few gastropod and bivalve shells.

Numerous wood fragments showing bioerosion (*Teredolites clavatus*.) were found in the associated sediment. These structures were probably caused by the xylophagus activity of Teredinidae bivalves. The skull has a bite trace that could be attributable to a shark or other large vertebrate.

Possible cause of death

The cause of death of the whale cannot be satisfactorily determined. Possible causes include senility, poisoning of food, disease, predation, and stranding in very shallow water. Senility can be ruled out because the specimen was a juvenile whale (absence of vertebral

epiphysis). Poisoning of the food chain is difficult to ascertain and cannot be positively demonstrated using available sedimentological and paleontological techniques. None of the preserved bones shows any evidence of disease, although we cannot exclude the possibility of death by a disease that did not leave any mark on the bones. Therefore, it is likely that death was caused by disease, stranding, predation by sharks, or a combination of factors.

The occurrence of a bite mark on the skull could be attributable to a shark, and thus predation could be the cause of the whale's death. However, this bite mark could be the result of scavenging after death (Corral et al., 2004). Moreover, both predation and scavenging could account for some or all of the missing and displaced skeletal elements, but evidence is inconclusive.

It is also possible that death of the whale was caused by stranding in very shallow waters or on the beach. The characteristics of the enclosing sediments, including lack of typical foreshore, low-angle planar lamination, lack of ripple lamination, and the high degree of biotur-

bation, indicate that the sediments are not beach sediments. Galán et al. (1989) suggest a water depth of 30–50 m based on the occurrence of *Neopycnodonte cochlear* shells and other ostreids, glauconite pellet shapes and homogeneous composition, and the ichno-

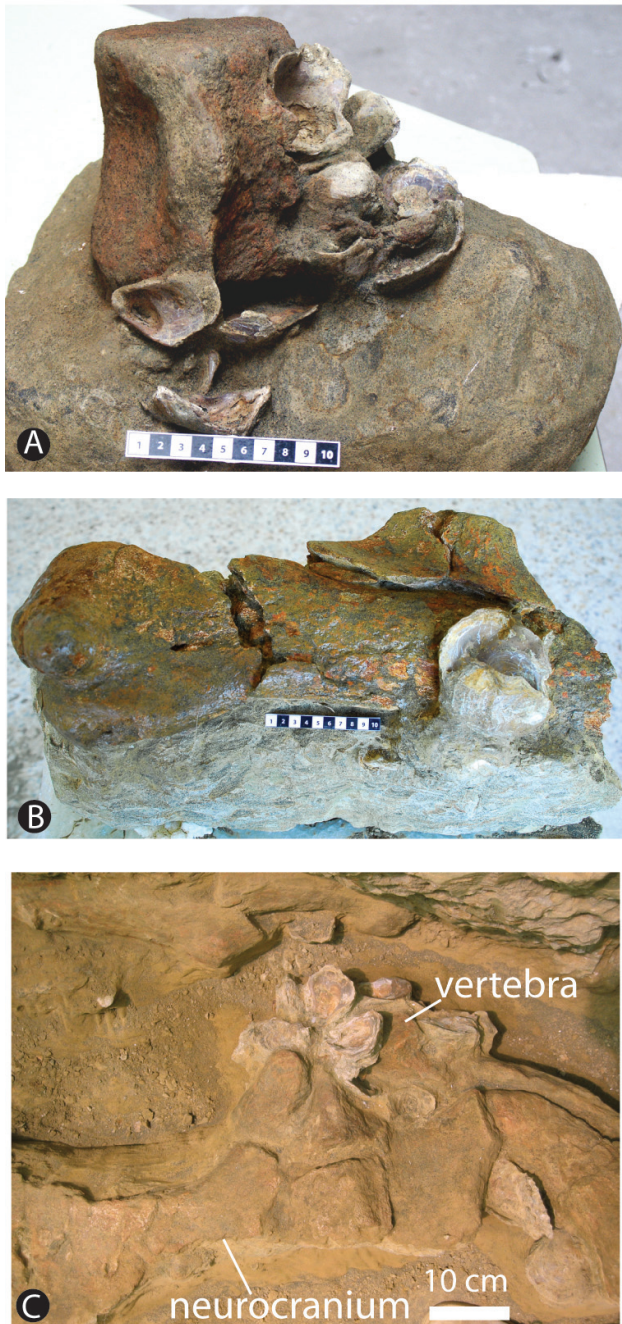


FIGURE 5 | Clusters of *Neopycnodonte* shells associated with the whale bones. A) Shells attached to a thoracic vertebra. B) Shells attached to a fragment of one of the dentaries. The bone shows three major cracks with little displacement of the fragments. C) Shells arranged in a rosette-like cluster in association with the neurocranium of the whale. All the shells in association with the bones are unarticulated. Scale in cm.

fabrics. However, stranding should not be ruled out because it is possible that the animal became stranded and died and then was later carried back into deeper water by tidal currents. Subsequently, sharks and scavengers could have detached or destroyed parts of the skeleton as they removed the soft tissue.

Biostratinomy

Schäfer (1972) shows that high-fat whale carcasses tend to float for a certain time due to the accumulation of gases in the decaying body cavity. As gases fill up the abdominal cavity, decaying whales tend to rotate placing the heavier dorsal side down and the lighter ventral side up above the water. In our studied specimen the overall alignment of the skull, limb bones and ribs on the left side of the figure, indicates that the carcass was partially articulated until burial. Other bones are disarticulated and displaced from their life position, including all the vertebrae, several ribs, and the other limb, which still has the scapula, humerus, and ulna articulated (see Fig. 3). Some skeletal elements were removed or destroyed before burial.

Several lines of evidence suggest that the whale carcass landed on the sea bottom on its left side and decayed in that position. Five ribs on the left side are well preserved, aligned and near life position, whereas the ones on the other side of the body are heavily damaged, displaced or absent. This is what we would expect if the whale was resting on its left side. The body side in contact with the seafloor would be more protected from scavengers and water currents than the top side. The exposed body side parts would be the first removed. The limb on the left side is in its normal anatomical position, which is what we would expect if the whale landed on that side, hiding the limb under the thorax and protecting it from scavengers until the soft tissue decayed. The other limb was fully exposed to scavengers, which may explain why it was found removed and displaced 11 m from its normal articulated position.

The orientation of the two dentaries (see Fig. 3) in this skeleton suggests that the whale's initial landing position on its left side was temporary and that the whale skull rotated from resting on its left side to a dorsal-side up position after initial decay of the skull-cervical vertebrae articulation. During the rotation of the skull the left dentary disengaged from the skull and remained in the position in which it had landed on the seafloor, with the anterior end pointing outward. This explains why the two dentaries lay parallel and show the same orientation with respect to the skull.

The study of skeleton positions of one hundred thirty six fossil whales by Esperante et al. (2002) in the Pisco Formation, Peru, found approximately equal numbers of

TABLE 3 | Associated fossils found in the studied glauconitic sands and silts.

	CLASS	TAXA		
INVERTEBRATES	BIVALVIA	<i>Acanthocardia</i> aff. <i>paucicostata</i>		
		<i>Amussium cristatum</i>		
		<i>Chlamys</i> sp.		
		<i>Neopycnodonte cochlear</i>		
		<i>Ostrea edulis</i>		
		<i>Pelecypora gigas</i>		
	GASTROPODA	<i>Natica</i> sp.		
		<i>Neverita</i> sp.		
	SCAPHOPODA	<i>Dentallium</i> sp.		
VERTEBRATES	CHONDRICHTHYES	<i>Carcharinus</i> sp.		
		<i>Carcharinus</i> cf. <i>egertoni</i>		
		<i>Carcharinus</i> cf. <i>priscus</i>		
		<i>Isurus hastali</i>		
		<i>Notorhynchus primigenius</i>		
		<i>Myliobatys</i> sp.		
		<i>Odontaspis</i> aff. <i>acutissima</i>		
	OSTEICHTHYES	<i>Sparus</i> sp.		
		Otolith, genus indet.		
		Jaw bone, genus indet.		
		Radius, genus indet.		
		Vertebra, genus indet.		
		STRUCTURES		ICHNOTAXA
		BIOTURBATION	<i>Laminites</i> isp.	
<i>Palaeophycus</i> isp.				
<i>Taenidium</i> isp.				
<i>Teichichnus rectus</i>				
<i>Thalassinoides</i> isp.				
BIOEROSION	<i>Entobia</i> isp.			
	<i>Gastrochaenolites</i> isp.			
	<i>Oichnus simplex</i>			
	<i>Teredolites clavatus</i>			
	Ichnogenus indet. Decapod crustacean bioerosion			

Bivalves are the most abundant associated fossils, followed by gastropods and scaphopods. Many shells show evidence of bioerosion by sponges and other organisms. Vertebrate fauna is represented by bones and teeth of fish. As explained in the main text, bioturbation is thorough and extensive.

dorsal-side up and ventral-side up specimens. Further study of more than five hundred whale specimens in the same formation yielded only two small skeletons of cetotheriids lying on their sides, with all the others either dorsal-side up or ventral-side up. Therefore, the side orientation is not common in the fossil record because of its instability on the seafloor.

Preservation of the bones

Judging by the degree of disarticulation, loss of caudal vertebrae and vertebral processes, destruction, abrasion

and bioerosion of bone, and moderate growth of epibionts such as oysters on the bones, burial of the carcass was not rapid. Our own observations of modern whale carcasses on the seafloor indicate that most of the scavenging is carried out by macrofauna, including grenadier fish, hagfish, sharks, and crustaceans (Jones et al., 1998; Curtis et al., 2000). Shark scavenging does not always leave an abundance of shark tooth marks on the bones. The study of several hundred fossil whales in the Pisco Formation by one of the authors revealed that shark teeth were common in association with some skeletons, but no tooth marks were found on the well-preserved bones of the whales (Esperante, 2002; Esperante and Brand, 2002). This is probably due to the feeding preferences of some sharks, which take advantage of the blubber but seem to avoid the whale muscle, although this has not been established for all shark species. It is also possible that the occurrence of shark teeth in the sediment adjacent to the bones might be the result of shark predation activity elsewhere above the location of the whale carcass, and subsequent teeth falling to the seafloor.

We can divide the bones into three preservation groups: 1) well-preserved, 2) partly deteriorated due to pre-burial biostratinomic processes, and 3) deteriorated by recent weathering and erosion. Group 3 bones could have been affected by pre-burial deterioration as well, but this is not possible to determine. All the bones show some degree of abrasion due to pre-burial exposure. Microborings observed in the thin sections (see Fig. 4) may have been the result of pre-burial fungal or algal activity.

The pattern of bone damage differs considerably from that found on a modern whale skeleton studied by Allison et al. (1991) on the deep seafloor, and on two whale skeletons on the deep seafloor and one on continental platform studied by Esperante (2005). In all these modern cases, the bones were heavily damaged by the loss of compact bone. The bone surfaces exposed above the sediment and subjected to corrosion showed the highest degree of compact bone loss, while buried surfaces were less damaged because they were protected by the sediment. In contrast, both the upper and lower surfaces of individual bones of the Bonares whale show similar degrees of damage and bone loss, except for osteophagous activity by scavengers on the upper surfaces of some bones.

Recent deterioration of the bones was caused by running water and water percolation from the surface through the porous, loose sediment into the bones. Most bones are also affected by biogenic deterioration caused by the fine roots of modern plants. The combined action of weathering and root-growth has caused so much damage that some bones could not be unearthed as a whole,

but only in multiple pieces and splinters. Bones damaged by modern weathering include one entire scapula and humerus, and the nasal and premaxillary bones.

Associated fauna of this Bonares specimen is different than associations reported from modern and other ancient examples. Fauna of cnidarians, polychaetid annelids, sipunculids, anemones, bivalves, gastropods and scaphopoda mollusks, ophiuroid and echinoid echinoderms, lysianassid amphipods, and crustaceans, all reported in association with modern whale carcasses on the seafloor are absent on this skeleton and in the associated sediment. This fauna has been reported in association with modern whale carcasses in the Monterey Bay and Santa Catalina Basin, offshore California (Allison et al., 1991; Bennet et al., 1994; Smith et al., 1998; Goffredi et al., 2004), the Torishima Seamount in the Western Pacific Ocean (Bennet et al., 1994; Naganuma et al., 1996; Smith et al., 1998; Goffredi et al., 2004; Nesbitt, 2005), and the shallow north Atlantic, offshore Sweden (Glover et al., 2005; Dahlgreen et al., 2006). Invertebrate fauna has also been found in association with fossil marine mammals in the Eocene of Louisiana (Lancaster, 1986), the Oligocene of the Washington State, United States (Goedert et al., 1995; Nesbitt, 2005), the Miocene of Hokkaido, northern Japan (Amano and Little, 2005), the Miocene of Austria (Pervesler et al., 1996), and the Plio-Pleistocene of Ecuador (Bianucci et al., 2006). However, it is possible that the ichnofossils associated with the Bonares whale specimen might be the result of the activity of some of those invertebrates, which nevertheless left no body fossils in the associated sediment. Encrusting organisms (e.g., serpulid worms) are absent on the studied whale.

Approximately one-third of the oil content of a whale occurs within its skeleton (Slijper, 1962), which can provide a long-term supply of food for other organisms after the soft tissue of the carcass has been removed. Smith and Baco (2003) have suggested that the decomposition of large whale falls provides a surge of nutrients on the seafloor that follows a three-stage path, consisting of 1) a mobile-scavenger stage, during which soft tissue is removed from the carcass by mobile scavengers; 2) an enrichment-opportunist stage, during which an assemblage of sessile and mobile heterotrophic macrofauna colonizes the bones and associated sediments; and 3) a sulphophilic stage, during which a chemoautotrophic assemblage colonizes the bones to feed on the sulphide emitted from the bacterial decomposition of bone lipids. Significant destruction of the bones occurs especially during the enrichment-opportunistic stage when most of the bone mass is scavenged by polychaete *Osedax* worms and crustaceans preferentially attacking the upper, uncovered surfaces of the bones (personal observation 2005, 2007). This kind of bioerosion by *Osedax* worms has been

reported from whale carcasses in both deep-water (Bennet et al., 1994; Rouse et al., 2004; Fujikura et al., 2006) and shallow water (Glover et al., 2005). These worms drill characteristic holes into the bones and grow fine branch-

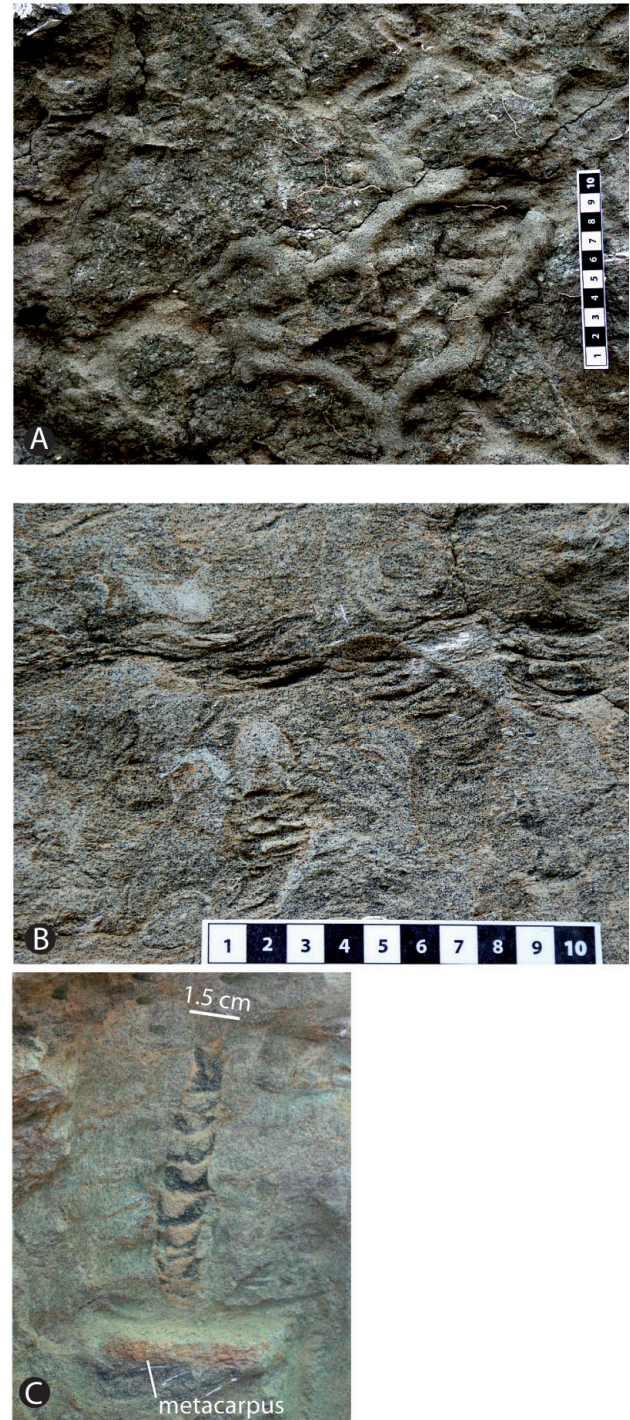


FIGURE 6 | Trace fossils occurring in the glauconitic sandstone. A) Specimen of *Taenidium* isp. preserved in full relief. B) General view of the ichnofabric. C) Longitudinal section unusual zigzag-packed menisci of *Taenidium* isp. above the whale bone. Scale in cm.



FIGURE 7 | Scapula of the left side limb of the specimen. The scapula was articulated with the humerus and in near life position with respect to the vertebral column. The bone shows bioerosion traces as a result of osteophagous activity by possible decapod crustaceans. A) General view of the scapula. B) Detail of bioerosion traces. Scale in cm.

ing roots into the bone matrix, exploiting their organic content in association with endosymbiotic bacteria (Goffredi et al., 2005). The destruction of bone occurs so fast and is so extensive that these whale carcasses last only a few months to a few years on the seafloor (Slijper, 1962). Thus the possibility of one of these whale carcasses becoming fossilized under slow sedimentation rates is almost impossible (Esperante, 2005). In contrast with these modern examples, the Bonares whale bones show no evidence of bioerosion by *Osedax* worms.

However, the bioerosion marks in one of the humerus, a dentary and the left side scapula show evidence that some scavenging activity occurred. These features suggest that the scavenger, possibly a crustacean, fed intensively on the whale bone, exploiting its organic content. These bioerosion structures are the subject of current research by the authors and the results will be documented and published in an upcoming paper.

Paleoenvironment

The whale skeleton was buried in glauconitic sandstone of the lower section of the Huelva Sands Formation. The sediment is completely disturbed by bioturbation and lacks primary structures that could indicate water depth, current direction, and energy level. Interpretation of the paleoenvironment must be based mainly on lithology, ichnology and associated fossils.

The presence, within some bones, of pore lining siderite and pyrite indicates early mineral growth in reducing conditions. The complete replacement of pyrite and complete to partial replacement of siderite and clays by hematite suggests an Eh change during the formation of authigenic minerals associated with the bone.

Bioturbation activity in the glauconitic facies was dominated by sediment feeders (*Fodinichnia*), which settle in soft, organic-rich sediments (Buatois, 1998; Gibert and Martinell, 1998). According to Mayoral (1986a), this glauconitic facies belongs in the *Cruziana* ichnofacies, with *Taenidium* as the predominant ichnocoenosis in the Bonares outcrop (see Fig. 6). *Cruziana* ichnofacies commonly occurs in highly bioturbated muddy and sandy sediments, with high ichnodiversity, deposited in a sublittoral-circalittoral zone, under low to moderate sedimentation rates and low to moderate hydrodynamic energy. Galán et al. (1989) assert that the high degree of bioturbation indicates that the glauconitic facies was deposited in a semi-confined, open sea environment under low sedimentation rates. It has been suggested that these sediments were deposited during a transgressive pulse of sedimentation (Martínez del Olmo et al., 1984; Mayoral, 1989a), which caused the deepening of this area of the Guadalquivir Basin to an estimate of 50-60 m depth.

The fossil assemblage dominating the studied glauconitic sandstone and siltstone consists principally of

Neopycnodonte cochlear shells, with *Ostrea* and *Amussium* occurring less often. These organisms are adapted to low-energy, deep platform environment (Yesares-Garcia and Aguirre, 2004). The occurrence of the gryphaeid *Neopycnodonte cochlear* in association with the whale bones is consistent with a relatively shallow depth for the deposition of both the bones and the glauconitic sandstone and siltstone. According to Stenzel (1971) *Neopycnodonte* is the current representative of the oyster *Pycnodonte*, which is exclusively fossil. Stenzel asserts that *Neopycnodonte cochlear* has a worldwide distribution, and is found in euhaline deep waters, far removed from land. In the Mediterranean Sea, *Neopycnodonte cochlear* is an epifaunal bivalve present in shallow to deep waters (between 45 and 250 m).

In the studied outcrop *Neopycnodonte cochlear* bivalve shells occur in different sizes and ontogenic stages and they are both disarticulated and in life position, which suggests reduced transport for the shells. There is no evidence of sudden influxes of storm or flood generated sediment in the glauconitic sandstone that could have buried the whale skeleton and the shells. Colonization of the bones by *Neopycnodonte cochlear* is not extensive, but nevertheless taphonomically important. The nestling habit of *Neopycnodonte cochlear* shells leads to preferential attachment to hard substrates (rocks, bones) or the firm, stable sea floor. This is shown in the studied glauconitic level of the Bonares section, where *Neopycnodonte cochlear* is found in dense associations, forming small massive buildups or rosette clusters both in the sediment and cemented to the whale bones, although isolated specimens occur also. The attached shells occur on the west side of the bones (see orientation of the skeleton, Fig. 3). This feature is most likely related to the preferential orientation to the prevailing currents for optimal feeding.

Two conspicuous levels of disarticulated and imbricated shells representing storm events are preserved approximately 3.5 m above the skeleton, indicating a more energetic environment during a marine regression (Mayoral, 1989a), which occurred sometime after the burial of the skeleton.

CONCLUSIONS

The Bonares fossil whale represents a single juvenile individual that died and sank to the seafloor where it was subjected to intense scavenging by both invertebrate and vertebrate fauna. The post-burial position of the left limb and dentary suggests that the carcass landed on its left side and later rotated to a dorsal side up position. The degree of superficial damage of the whale bones, the low number of bones preserved and the occurrence of epibiotic *Neopycnodonte cochlear* shells suggest that

biostratinomic processes were relatively prolonged before burial. The occurrence of *Neopycnodonte cochlear* shells, glauconitic pellet facies and the *Cruziana* ichnofacies indicate that the whale was buried in a sublittoral-circalittoral zone, at water depth of approximately 30-50 m, under low to moderate hydrodynamic energy and sedimentation rates. A low degree of hydrodynamic energy is supported by the fact that the skeleton shows bones associated in anatomical position.

There is evidence for scavenging by both vertebrates and invertebrates, consisting of shark tooth marks, borings and galleries. The bones were not colonized by epifaunal species that characterize most modern and some fossil specimens. *Neopycnodonte cochlear* shells are relatively abundant, but they do not indicate a feeding association. The bones lack the characteristic holes left by the polychaete *Osedax* worms common in both shallow and deep water whale carcasses. Since the skeleton shows a high degree of disarticulation and damage, it appears that the missing invertebrate taxa had adequate time to colonize the whale if they had been present.

Both the sediment below and on top of the skeleton is highly bioturbated, nevertheless the bones do not show evidence of bioerosion caused by organisms buried in the sediment. Some bones, including the scapula, a humerus and the neurocranium, exhibit wide borings, galleries and grooves most likely caused by an unknown macro-scavenger.

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