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Taphonomy and paleoenvironmental conditions of deposition of fossil whales in the diatomaceous sediments of the Miocene/Pliocene Pisco Formation, southern Peru—A new fossil-lagerstätte

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ABSTRACT

The Pisco Formation in Peru contains abundant fossil cetaceans in middle Miocene to lower Pliocene sandstone, siltstone, and tuffaceous and diatomaceous mudstone. Fossil whales are especially abundant in the uppermost diatomaceous units. Most specimens are well articulated or partially disarticulated but associated. Degree of preservation is exceptionally high and uniform among articulated and disarticulated specimens and on the lower and upper surfaces of the bones. Some specimens have baleen preserved in anatomical position. Bones show no evidence of bioerosion by macro- or micro-invertebrates, except for a very limited amount of microbial borings. Diatomaceous layers seem to lack bioturbation. However, bioturbation did occur in a few tuffaceous silty and sandy layers of the lower part of the formation. Shark teeth are found associated with many of the specimens; however, despite abundance of whale skeletons, shark tooth marks are extremely rare. Several lines of evidence indicate that sediments and whales were deposited in a shallow-to-deep shelf environment (an embayment), and not in a beach environment. The thick diatomaceous successions record conditions of strong ocean upwelling indicated by the abundant occurrence of the diatom species *Thalassionema nitzschioides*. The exceptional preservation of diatom frustules suggests that they reached the seafloor very rapidly and were not successively reworked. The hundreds of whale specimens found, their excellent preservation, and their high degree of articulation make the Pisco Formation fossil whales the best representative assemblage of fossil Mysticeti known so far. The abundance of whale skeletons and other vertebrates in the diatomaceous beds, their excellent preservation, including evidence that soft tissue (baleen) was still present at burial, and the degree of articulation, point to frequent mortalities followed by rapid sedimentation that prevented decay of the skeletons and colonization by invertebrates. Sedimentation rates appear much higher than rates inferred from some other modern and ancient settings where whale skeletons have been found.

1. Introduction

The global record of Neogene fossil cetacean assemblages is typified by specimens of the suborder Mysticeti (baleen whales), of which families Balaenopteridae and Balaenidae are the most abundant, and few occurrences of family Cetotheriidae (extinct small baleen whales), and by toothed whales of the suborder Odontoceti, of which the family Delphinidae is widely represented by a great diversity of species. The cetacean assemblage of the Miocene/Pliocene has been documented in many places around the world and is well represented in sediments in six large areas: the east North Atlantic (e.g. Morgan, 1994; Godfrey, 2004; Beatty and Dooley, 2009), the west North Atlantic (e.g., Abel, 1905; Cabrera, 1926; Sendra and De Renzi, 1999; Agnolin and Lucero, 2004; Estevens and Ávila, 2007; Esperante et al., 2009), the Pacific rim (from Chile to Peru, from Baja California in Mexico to Washington State in the United States, from Japan to Australia and New Zealand) (e.g., Barnes, 1976; Orr and Miller, 1983; Romero et al., 1993; Oishi and Hasegawa, 1994; Esperante et al., 2002; Fitzgerald, 2007; Esperante et al., 2008; Esperante et al., 2011), around the Mediterranean Sea (e.g., Pilleri, 1987; Bianucci, 1997; Sendra and De Renzi, 1999; Dominici et al., 2009), the Caucasus region (Mchedlidze, 1988), and Antarctica (Selby, 1990). Most of these occurrences consist of isolated bones; however local concentrations (bone-rich beds) of mostly disarticulated bones, or single articulated or disarticulated specimens have also been reported. A remarkable example is the cetacean bone-rich bed in the Round Mountain Silt member at the top of the Temblor Formation in the Sharktooth Hill area near Bakersfield (California),

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extending over several square kilometers, with abundant disarticulated bones and a few articulated specimens of marine mammals (Pyenson et al., 2009). In other areas of California, several specimens of fossil marine mammals have been found, including some fully articulated, complete skeletons of Mysticeti (Minch, 1996; Deméré, 1998, 2000). Numerous well preserved, complete or semi-complete marine mammal skeletons have been reported from Italy (e.g., Caretto, 1970; Pilleri, 1985, 1986; Bianucci, 1995, 1997; Bianucci et al., 1998; Dominici et al., 2009), some of them fully articulated.

The middle Miocene–lower Pliocene Pisco Formation in Peru contains hundreds of fossil cetaceans (Esperante and Brand, 2002; Esperante et al., 2002; Esperante et al., 2008). In this formation, Mysticete whales are by far the most abundant and well-preserved specimens, many of them partially or fully articulated, some with their baleen structures preserved (Pilleri, 1989; Esperante et al., 2008). In addition to the rich cetacean assemblage, the Pisco Formation contains an abundant and diverse fossil assemblage of mollusks (gastropods and bivalves), crustaceans (cirripeds and decapods), corals, rhodoliths, selachians (sharks), teleosts, crocodiles, turtles, birds (cormorants, penguins, and others) (Cheneval, 1993; Urbina and Stucchi, 2005; Göhlich, 2007; Stucchi, 2007; Ehret et al., 2009a), and as well as other mammals (phocids, otariids, xenarthrans) (Alleman, 1978; Muizon, 1981; Muizon and McDonald, 1995).

To date, the preservational features of the abundant, well preserved marine fossils of the Pisco Formation have not been thoroughly studied. This paper describes the taphonomy of the cetacean fossils that occur in the upper diatomaceous units of the Pisco Formation in the southern part of the north Pisco–Ica sub-basin, and suggests a model for their deposition and preservation. A total of 571 marine mammal specimens were studied and 32 specimens excavated for detailed examination of state of preservation of the bones. Most of the specimens are fully or partially articulated, some with baleen preserved. All the specimens show excellent bone preservation with minimum microbioerosion, in contrast with the poor preservation shown by modern time whale carcasses on the seafloor, which are quickly destroyed by erosion and scavengers (Allison et al., 1991; Jones et al., 1998; Smith and Baco, 2003; Lundsten et al., 2010).

2. Geologic setting

The Pisco Formation is found along the southern coast of Peru and occurs in two sub-basins, the Sacaco sub-basin and the Pisco–Ica sub-basin. This study was carried out along exposures in the Pisco–Ica sub-basin where the Pisco Formation was deposited during the middle Miocene to the lower Pliocene in a shallow protected embayment with pre-Cenozoic igneous islands offshore (Muizon and DeVries, 1985) (Fig. 1). Several stratigraphic models have been proposed for the succession of deposition of sediments (Macharé, 1987; Dávila, 1989; Dunbar et al., 1990; León et al., 2008). This article follows DeVries (1998) and DeVries et al. (2006) who proposed that the sedimentary succession of the Pico Basin are, from oldest to youngest, the Paracas Formation, the Otuma Formation, the Chilcatay Formation, and the Pisco Formation.

The clastic sediments in the Pisco–Ica sub-basin consist of repeated fining-upward successions of fine sandstones and siltstones, with tuffaceous siltstones dominating the middle section and thick, massive layers of tuffaceous diatomaceous mudstone capping the succession. Minor deposits of bioclastic conglomerates, phosphates, dolomites, limestones, and ash-falls occur as well (Lisson, 1898; Carvajal, 2002). At the bottom of some of the fining-upward successions there is a bone layer rich in phosphate clasts, marine mammal bones, fish bones, articulated bivalve shells, articulated and disarticulated balanid shells, unsorted, rounded and angular igneous cobbles and boulders, and petrified wood. The phosphate layers represent the onset of successive regressions over erosive surfaces indicated by bored pebbles and lithoclasts with *Gastrochaenolites* and *Trypanites* borings, truncated burrows, and lithic conglomerates.

These finning-upward successions suggest that the sedimentation in the Pisco Basin occurred in a series of major transgressions that started

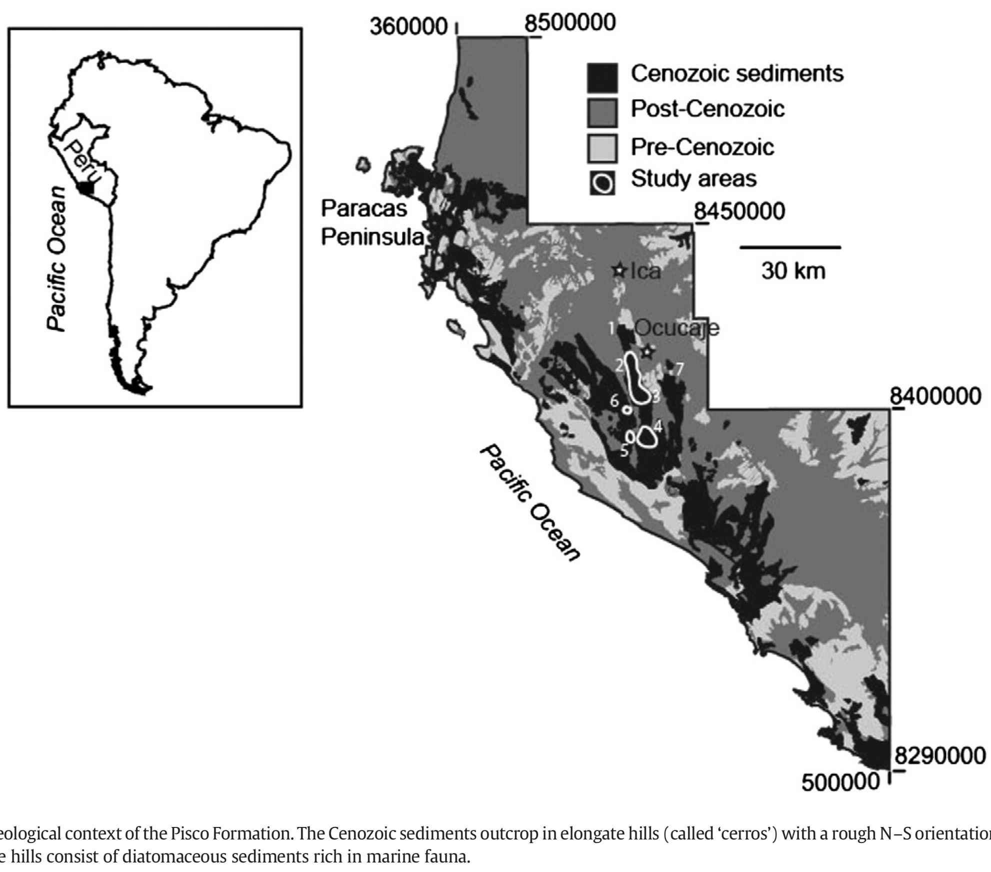


Fig. 1. Geographical and geological context of the Pisco Formation. The Cenozoic sediments outcrop in elongate hills (called 'cerros') with a rough N–S orientation. The top tens of meters of sequence in many of those hills consist of diatomaceous sediments rich in marine fauna.

in the middle Eocene. The last of these transgressions occurred during the middle Miocene resulting in the deposition of the sandstones, siltstones and diatomaceous mudstones of the Pisco Formation (Fig. 2). Sedimentologic evidence collected during our study suggests that this last transgression occurred in several pulses, most notably at upper Miocene and lower Pliocene, indicated by the deposition of several phosphate-rich horizons, flat-pebble and gravel conglomerates, and boulder-rich, bioturbated or bored layers. An upper thick diatomaceous succession represents the culminating phase of the marine transgression. Ar–Ar dates from biotite in tuffs within the diatomaceous succession range from 6.07 to 7.73 Ma (Kevin Nick, written communication, 2014).

A high resolution stratigraphic framework for the Pisco Formation by Brand et al. (2011) uses widespread layers within the area west and south of the town of Ocucaje and west of the town of Lomas to correlate the successions in the different hills (called Cerros). This stratigraphic framework is currently being geographically extended by study of tuff beds (Kevin Nick, personal communication, Loma Linda University, 2013).

There is a general consensus that the Pisco Formation was deposited in relatively shallow-to-deep platform water (depth < 200 m) based on diatom and radiolarian assemblages (Muizon and DeVries, 1985; Marty et al., 1987; Dunbar et al., 1990; Esperante, 2002), sedimentary structures, and lateral and vertical relationships of the tuffaceous and

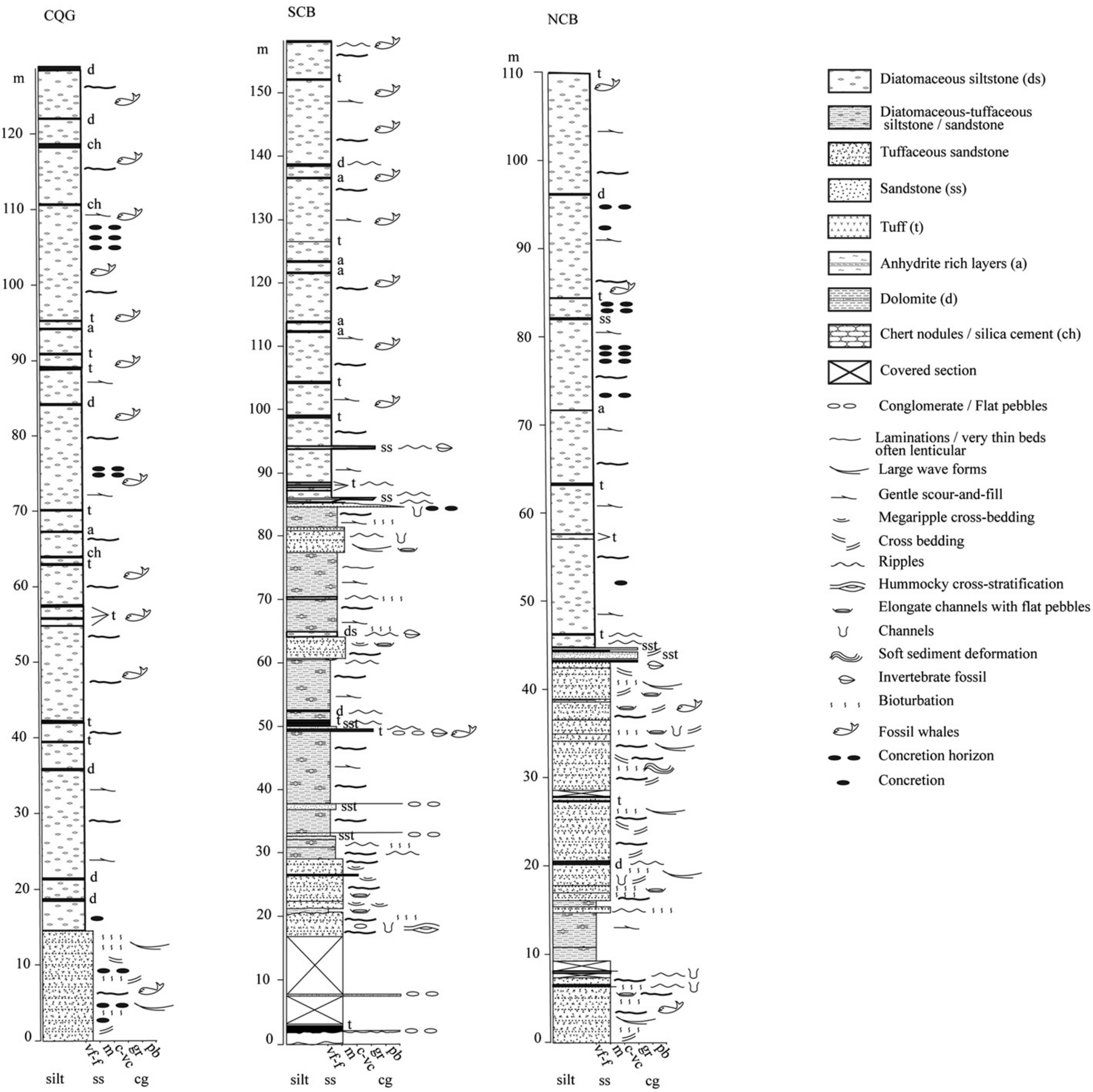


Fig. 2. Stratigraphic sections of three of the study areas east of the town of Ocucaje (modified from Carvajal, 2002). The Pisco Formation sequence in this area consists mostly of fine sandstones and siltstones in the lower half and diatomaceous and tuffaceous siltstones in the upper half, with interspersed pebbly phosphates, carbonates, and tuffs. Whale fossils occur throughout the sequence, but are more abundant in the upper siltstone and tuffaceous and diatomaceous layers. Whale specimens studied here occur in the diatomaceous siltstones of each area, indicated by abbreviations: SCB = South Cerro Blanco; CQG = Cerro Queso Grande; NCB = North Cerro Blanco.

diatomaceous deposits (Marty, 1989; Carvajal et al., 2000; Carvajal, 2002). The present study was conducted in the diatomaceous units of selected areas of the Pisco–Ica Basin in the Ocucaje area (Fig. 1).

3. Materials and methods

Field data on fossil specimens and associated sediments of the Pisco Formation were collected in areas west and south of Ocucaje, on Cerro Ballena, Cerro Blanco, Cerro Hueco La Zorra, Cerro Yesera de Amara, Cerro Los Quesos, and Cerro Queso Grande (Fig. 1). Large areas were surveyed focusing mainly on remains found on the surface, and specimens were mapped in relation to selected stratigraphic marker beds. Location and elevation of marker beds and fossils were determined with a high precision GPS (Javad GPS with Glonass L1 + L2, Survey Pro software) with centimeter-scale accuracy in relation to a base station. Numerous GPS waypoints were recorded along each marker bed and one location was recorded for each fossil specimen. A 200-m wide vertical transect was surveyed on north Cerro Blanco to estimate abundance of marine mammals per square kilometer. All the specimens on surface were counted and their relative position to the nearest marker bed was taken.

Data were collected from specimens already exposed at the sediment surface (and usually partially destroyed by modern erosion), and the associated sediment, including the following: GPS position, elevation, position relative to the marker beds, skull orientation, body orientation when differing significantly from skull orientation, skull length and width, length of post-cranial skeleton, dorsal-side up and ventral-side up position of the skull, degree of articulation of skull and body, degree of preservation of the bones (at the macroscopic level), occurrence and type of other fossils associated with the skeleton, type of lithology encasing the specimen, and variations in the sediment texture and in sedimentary structures. Because all specimens were parallel to the sedimentary beds, no measurement of the dip of the specimen was necessary.

Completeness was assessed for each individual based on the number of bones present. A complete specimen is one that has all or almost all the skeleton preserved regardless of degree of articulation. Specimens with a few missing bones (e.g., one or two dentaries, part of a limb, a few vertebrae, or a few ribs) were also counted as complete because most missing parts could be attributed to modern erosion. In many instances such missing bones were found lying a short distance as a consequence of rolling out from the rock mound containing the skeleton.

The following criteria were used in the field for determining whether a bone accumulation (a specimen) should be designated as a single individual: 1) one skull and other anatomical elements including vertebrae, ribs, and limbs; articulated or not, but all bones associated, of the appropriate size range for one individual, and clearly separate from any other specimens; and 2) a group of vertebrae (minimum of four, almost always many more), with ribs in approximately articulated position or associated but clearly distinguishable from another specimen; limb elements may also be present. The occurrence of isolated bones or associated bones not meeting any of the above criteria was recorded as “isolated bones”, and included single skulls, ribs, vertebrae and limb bones. They were not considered as individuals, since the encountered bones could have been transported from another recorded specimen.

Once it was determined that a group of bones belonged to a single individual, degree of articulation was noted for the following skeletal elements: 1) articulation of dentaries with skull; 2) articulation of skull with cervical vertebrae; 3) articulation of the vertebral column; 4) relative articulation of limbs with the vertebral column, and 5) articulation of bones within each limb.

The degree of articulation was assessed according to four categories proposed by Behrensmeyer (1991) for terrestrial vertebrate accumulations: 1) articulated: the bones retain their exact anatomical positions relative to one another; 2) disarticulated but associated: bones are separated from each other but are in close proximity, and can be determined to be part of one individual; 3) associated but dispersed: bones may be scattered over an area several times the size of the animal, but can be related to the same animal using anatomical characteristics, and 4) isolated and dispersed: bones are widely separated from others of the same skeleton; adjacent bones generally derive from different individuals.

Thirty-two skeletons were excavated at different locations, including 31 mysticetes and one odontocete. Criteria for selection were not based on completeness of the specimens, but on thickness of cover sediment, lithology, and accessibility. They were cleaned and photographed and then reburied. Degree of bone preservation was evaluated by the study of the upper and, when accessible, lower surfaces of excavated bones. Special attention was paid to features that could indicate pre-burial scavenging by other animals and/or deterioration due to long-term exposure on the seafloor, including the following: 1) macro-borings that could have been produced by invertebrates living or feeding on the skeleton; 2) bite marks or chewing marks due to other fauna living on the surface of the skeleton; 3) dissolution due to the chemical activity of the water; and 4) abrasion marks left by transport. Thin sections were made of bones from some specimens to evaluate degree of preservation at the microscopic level. Particular attention was paid to micro-fractures and micro-borings in the bone. Thin sections were made by National Petrographic Service, in Houston, Texas.

A careful search for associated non-cetacean fauna (i.e., bivalves, gastropods, echinoderms, etc.) or evidence of their activities on the bones before burial was carried out in order to determine possible ecological or trophic associations with the whale skeletons. Transverse trenches (cross sections) to expose the associated sediments perpendicular to and parallel to the vertebral column or to the skull were made during excavation, and lithologic samples were collected. The diatomaceous beds were also studied and samples collected at several sites in whale-bearing horizons, but not associated with specific marine mammals. X-ray diffraction (XRD) of several samples was done by The Mineral Lab Inc., Lakewood, Colorado. Sediment samples were prepared for diatom species identification, which was carried out by Winsborough Consulting labs, Austin, Texas. Samples were cleaned of organic material and carbonate in the preparation process for microscope analysis by boiling first in hydrogen peroxide and in nitric acid. Slides were scanned at 1500× and the first 500 diatoms were counted from each sample.

4. Sedimentology

4.1. Lithology

According to Dunbar et al. (1990), the Pisco Formation diatomaceous sediments have an opal content typically ranging from 25 to 50 wt.%. XRD analysis carried out for this research confirms this range, although some samples yielded an exceptionally high opal content of up to 90 wt.%. Clay minerals and unweathered volcanic glass are abundant in many diatomaceous samples (Fig. 3). Other minerals found in the diatom-rich sediments are gypsum, anhydrite, plagioclase feldspars, quartz, iron sulfates (jarosite), manganese oxides, calcite, and dolomite, minerals which are also common in variable quantities in most diatomaceous deposits of other formations (Bramlette, 1946). The quantitative data obtained from the XRD analysis and the observations of thin sections indicate that the whale-bearing beds consist of fine sandstone to silty tuffaceous mudstone with increasing diatom content toward the top of the succession.

Fresh, unweathered glass particles and biotite minerals from volcanic ash are relatively abundant in sediments associated with the whale skeletons. The low degree of weathering of diatom frustules and glass particles indicates that they were rapidly deposited and that they underwent little transport and dissolution before deposition. There are a few minor, thin layers of phosphate, dolomite, chert nodules, and lenticular coarse-grained sandstone, conglomerate and ooid silty sandstone. Conspicuous layers representing local ash-fall events

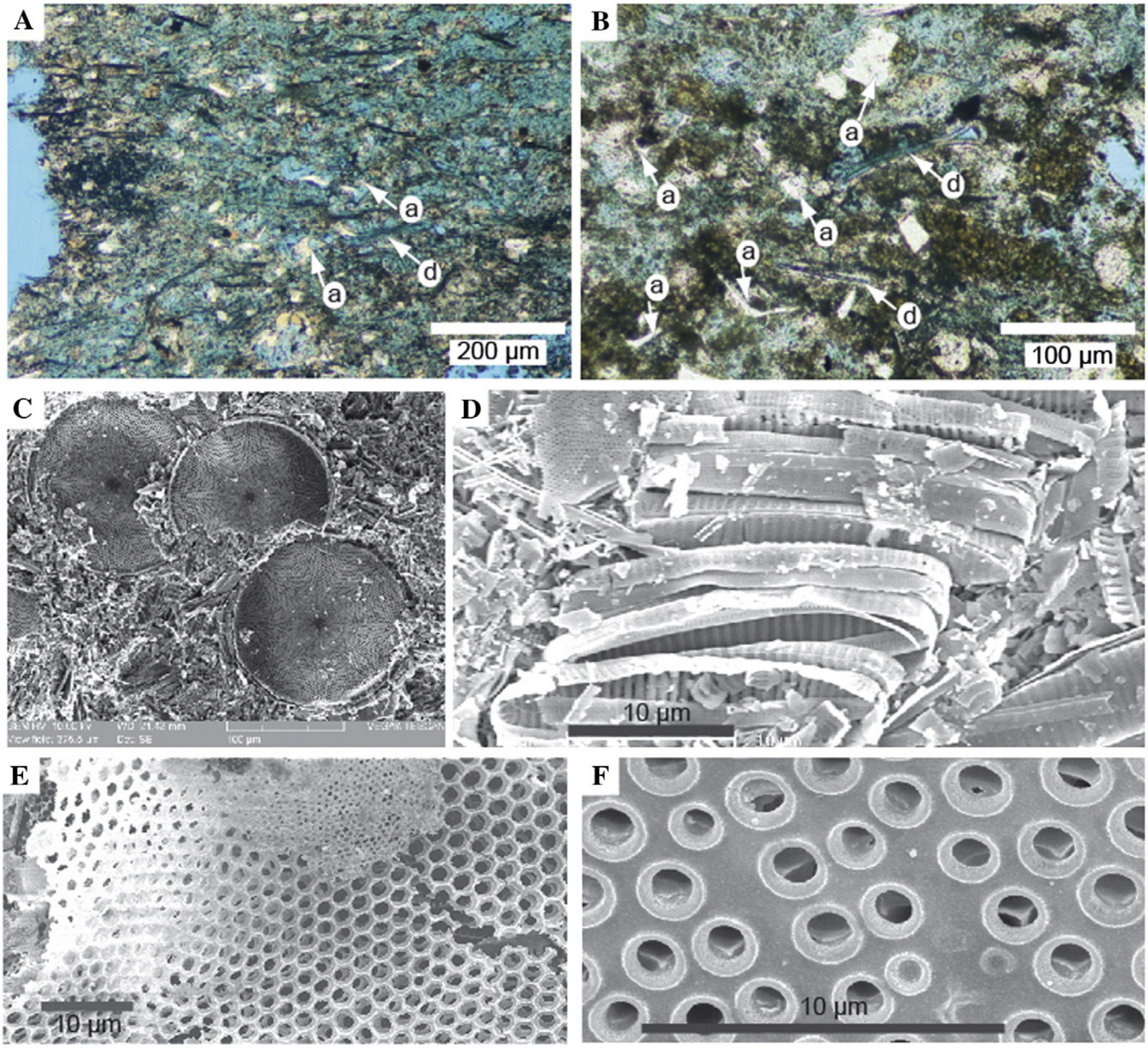


Fig. 3. Diatomaceous sediment associated with the fossil whales. A–B) Tuffaceous and diatomaceous mudstone associated with whale CB11-02. Note the abundance of diatoms (d) and sharp volcanic ash shards (a). C) SEM image of entire frustules of *Thalassiosira* diatoms in a matrix of broken diatoms, mud and ash particles. D–F) Detail of the excellent preservation of diatom frustules, showing no evidence of dissolution, suggesting that long residence on the water column or the sea floor did not occur. Scale bars D–F = 10 µm.

occur throughout the section with a thickness ranging from 1 cm to 30 cm. Volcanic ash is pervasive throughout the diatomaceous succession and abundant in the diatomaceous sediments associated with most of the whale assemblages (Fig. 2). Examples are shown in Fig. 3. Many of the ash particles consist of shards that have sharp edges.

Several thin layers rich in fish debris occur interspersed throughout the diatomaceous succession. Mostly the remains consist of fin rays and vertebrae, often articulated. These layers suggest mass accumulation and burial of fish within the basin. Moreover fish scales are pervasive throughout the sediment and sometimes concentrate around bones, sandstone channels and scours.

4.2. Diatom content

Thalassionema nitzschioides, *Delphineis* sp. 1 (formerly known as *Raphoneis ischaboensis*), and especially *Chaetoceros* resting spores, are the dominant diatoms in the samples associated with the whale skeletons. Eight other species are relatively abundant: *Nitzschia* (*Fragilaropsis*) *pliocena*, *Paralia sulcata*, *Rhizosolenia barboi*, *Stephanoyxis turris*, *Thalassiosira decipiens*, *Thalassiosira jacksonii*, *Thalassiosira oestrupii*, and *Thalassiosira tappanae*.

Some freshwater diatoms were found in the studied sediments, including *Luticola mutica*, *Pinnularia borealis*, *Aulacoseira italica* and *Epithemia turgida*, showing excellent preservation of the frustules. *L. mutica* and *P. borealis* are classified as aerophils although they are found in shallow water and temporary wet habitats.

Some diatomaceous samples are almost monospecific, e.g., dominated by a bloom of *T. decipiens* and many fragments of *Stephanopyxis turris*. Other samples are heavily dominated by *Chaetoceros* resting spores only.

The diatomaceous samples show a high degree of porosity. Observations under the SEM and the light microscope consistently show that most diatom frustules in all studied samples are fragmented, with pieces varying from tiny fragments to partially complete frustules (Fig. 3). Compaction may have played a role in fragmentation of the diatoms, although the original structure of the frustules is intact. The frustules do not show evidence of dissolution and/or abrasion due to prolonged residence in the water column after the cells died. Both

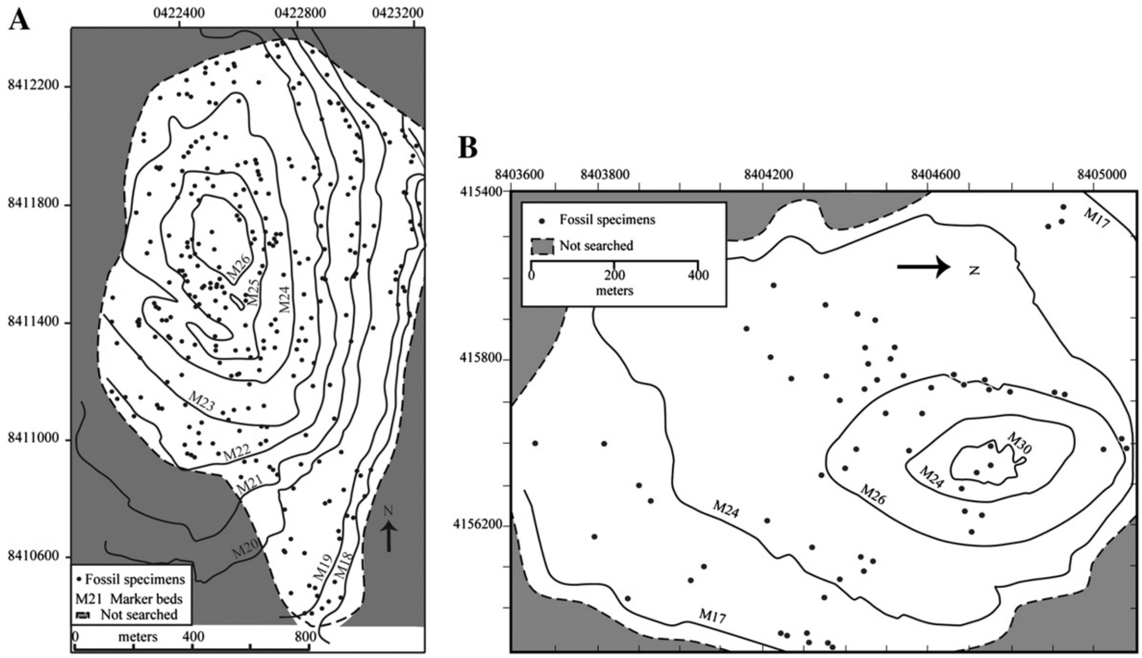


Fig. 4. Distribution of fossil marine mammals on North Cerro Blanco (A) and Cerro Queso Grande (B). Lines indicate selected marker beds in the diatomaceous units. Each dot represents a specimen, which in most cases is a complete or partially complete individual. Marine mammal fossils also occur outside these two areas in both diatomaceous and non-diatomaceous sediments but were not included in this study.

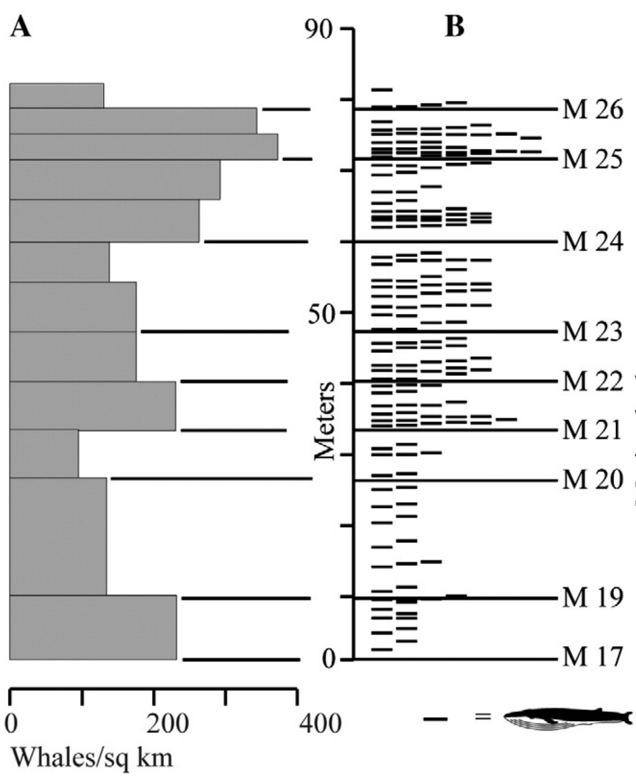


Fig. 5. Abundance and density of fossil marine mammals in the diatomaceous units on North Cerro Blanco. A. Marine mammals per square kilometer of exposed surface, at different levels. B. Each whale symbol represents one marine mammal specimen in its stratigraphic position relative to the marker beds. The fossil specimens are distributed throughout the diatomaceous sediments in this part of the Pisco Formation. This chart only provides a estimate of abundance and density because 1) some specimens may have been destroyed by recent erosion and 2) differences in the degree of slope in the studied section. Between marker beds M17 and M17 the slope is steep and exposure surface reduced compared to layers above M19, where the exposure surface is larger and the slope is not deep enough to make it difficult to find specimens.

XRD analysis and SEM images show that diatoms are preserved as opal-A silica, with almost no diagenetic alteration. They look like a detrital deposit, as observed by Macharé and Fourtanier (1987).

5. Whale taphonomy

5.1. Abbreviations used in figures

at = atlas; ba = baleen; ca = carpals; co = cochlea; cv = cervical vertebrae; dent = dentary; hu = humerus; max = maxillary; mc = metacarpals; oc = occipital condyles; ph = phalanges; pm = premaxillary; ra = radius; sc = scapula; st = shark tooth; tv = tail vertebrae; ul = ulna; vc = vertebral column; ve = vertebral epiphysis; vert = vertebrae; and za = zygomatic arch.

5.2. Whale distribution and abundance

Marine mammals are abundant and widely distributed in all the study areas and throughout most of the sedimentary succession of the Pisco Formation (Esperante et al., 2002, 2008). However, they are more abundant in the upper diatomaceous units, where a total of 571 specimens were located and studied belonging in the following taxonomic categories: 563 specimens in the suborder Mysticeti (baleen whales); four specimens in the suborder Odontoceti (toothed whales); four specimens in the suborder Pinnipedia. Location of most of the specimens found on Cerros Blanco North and Queso Grande is indicated in Fig. 4. Other studied whales were found outside these two areas. Fig. 5 shows density of marine mammal specimens in north Cerro Blanco, the largest of our study areas, where maximum density of specimens reaches approximately 350 specimens/km^2. There are two important factors revealed by this figure. First, the density of specimens is very high (left side of the figure), which increases toward the top of the slope (the differences in slope are not enough to significantly change the density/km^2 relationships, see Fig. 5 caption). Second, the right half of the figure shows that the whales are not in discrete mass mortality layers, with significant sediment thickness between the layers of whales. Rather, the whales are distributed more or less evenly, in their stratigraphic positions, so that the depositional environment that

Table 1
Taphonomic characteristics of 32 excavated specimens in diatomaceous sediments. Some specimens (LQ10-28, LQ10-36, LQ11-01, WQG-63) were incomplete and thus their taphonomic characteristics could not be fully assessed. Skull/body orientation refers to compass orientation. Skull dsv/vsu refers to the position of the skull: dorsal-side up vs. ventral-side up. The number of dentaries preserved and they articulation is recorded. The degree of original articulation or disarticulation of vertebrae and ribs refers to the inferred state of articulation before modern exposure or erosion. The number of limbs and their articulation to the body could not always be recorded. Incompleteness is indicated by "-" when the skeletal elements were missing, probably due to modern exposure, and "?" when the skeletal elements were not observed but might be buried. In other cases, their degree of articulation was not observed.

Specimen	Figure	Skull	Skull/body orientation	Skull dsu/vsu	Dentaries (articulation to skull)	Skull articulated to cervical vertebrae	Vertebral column	Originally articulated vertebrae	Ribs	Originally articulated ribs	Limbs (articulated)	Baleen
CB11-01	4	Yes	295	dsu	2 (yes)	Yes	Yes	Yes	Yes	Yes	2 (yes)	
CB11-02	4	Yes	134	vsu	2 (no)	No	Yes	Yes	Yes	Yes	1 + 1? (yes)	
CB11-03	4	Yes	44	dsu	2 (yes)	No	Yes	No	Yes	No	No	
CB11-04	5	Yes	230	vsu	2 (yes)	Yes	Yes	Yes	Yes	Yes	1 (yes)	
CBL-10	5	Yes	300	dsu	2 (yes)	Yes	Yes	Yes	Yes	Yes	2 (yes)	
CBL-11	5	Yes	25	dsu	2 (yes)	Yes	Yes	Yes	Yes	Yes	Yes	
FP08-12	6	Yes	300	vsu	2 (no)	No	Yes	Yes	Yes	Yes	Yes	
IC-1	6	Yes	135	vsu	2 (yes)	Yes	Yes	Yes	Yes	Yes	Yes	Yes
IC-41	6	Yes	250	Side	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
LQ10-28	6	Yes	125	vsu	2 (no)	No	No	–	No	–	–	
LQ10-34	7	Yes	70	dsu	1 (no)	Yes	Yes	8+	Yes	?	Yes (no)	
LQ10-35	7	Yes	60	dsu	2 (no)	No	Yes	No	Yes	No	1 (no)	
LQ10-36	7	Yes	325	vsu	2 (no)	No	Yes	?	?	?	?	No
LQ10-39	7	Yes	145	vsu	2 (no)	No	Yes	No	Yes	No	No	
LQ10-40	7	Yes	270	vsu	1 (no)	No	Yes	No	Yes	No	No	
LQ10-42	7	Yes	110	vsu	?	Yes	Yes	Yes	Yes	Yes	1	
LQ11-01	8	Yes	110	?	?	Yes	Yes	Yes	Yes	Yes	?	
LQ11-05	8	Yes	100	vsu	2 (yes)	?	Yes	Yes	Yes	Yes	?	
LQ11-10	8	No	135	vsu	Yes	Yes	Yes	Yes	Yes	Yes	Yes	
PIS09-26	8	Yes	190/250	dsu	2 (yes)	No	Yes	Yes	Yes	Yes	Yes	
WC-33	8	Yes	180	dsu	2 (yes)	Yes	Yes	Yes	Yes	Yes	?	Yes
WCBa-20	8	Yes	96	vsu	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
WCBa-32	9	Yes	100	vsu	2 (yes)	Yes	Yes	Yes	Yes	Yes	1 (yes)	
WCBa-112	9	Yes	200	vsu	2 (yes)	No	Yes	Yes	Yes	2	Yes	
WCBa-212	9	Yes	185	vsu	2 (no)	No	Yes	Yes	Yes	Yes	No	
WCBa-248	10	Yes	270	dsu	2 (yes, 1)	No	Yes	Yes	Yes	Yes	Yes	
WCBa-302	10	Yes	30	?	1 (no)	No	Partial	Yes	Yes	Yes	No	
WQG-60	10	Yes	330	vsu	1 (yes)	Yes	Yes	Yes	Yes	Yes	1 (yes)	
WQG-63	11	No	–	–	1 (no)	–	Yes	No	Yes	No	No	
WQG-67	11	Yes	120	dsu	No	No	No	No	No	No	No	
WQG-78		Yes	95	dsu	2 (no)	No	2 vert	No	No	No	No	
Z-51	11	Yes	135	Side	2 (yes)	Yes	Yes	Yes	Yes	Yes	Yes	–

resulted in the burial of the whales was quite uniform through the study section. Because some of the beds are only exposed along gently sloping hillsides, there are many more specimens buried in those layers extended into the hills. Also there are many specimens in diatomaceous layers outside our study areas.

Thirty-two whale specimens were excavated in different localities and detailed anatomical and sedimentologic observations were recorded. A summary of their anatomical content and taphonomy is presented in Table 1 and illustrated in Figs. 6–12, and details presented in Appendix 2. They range from fully articulated to fully disarticulated, and from complete to partially incomplete specimens. Most partially incomplete specimens can be explained as the result of modern weathering and gravity processes (skeletons lying on slopes).

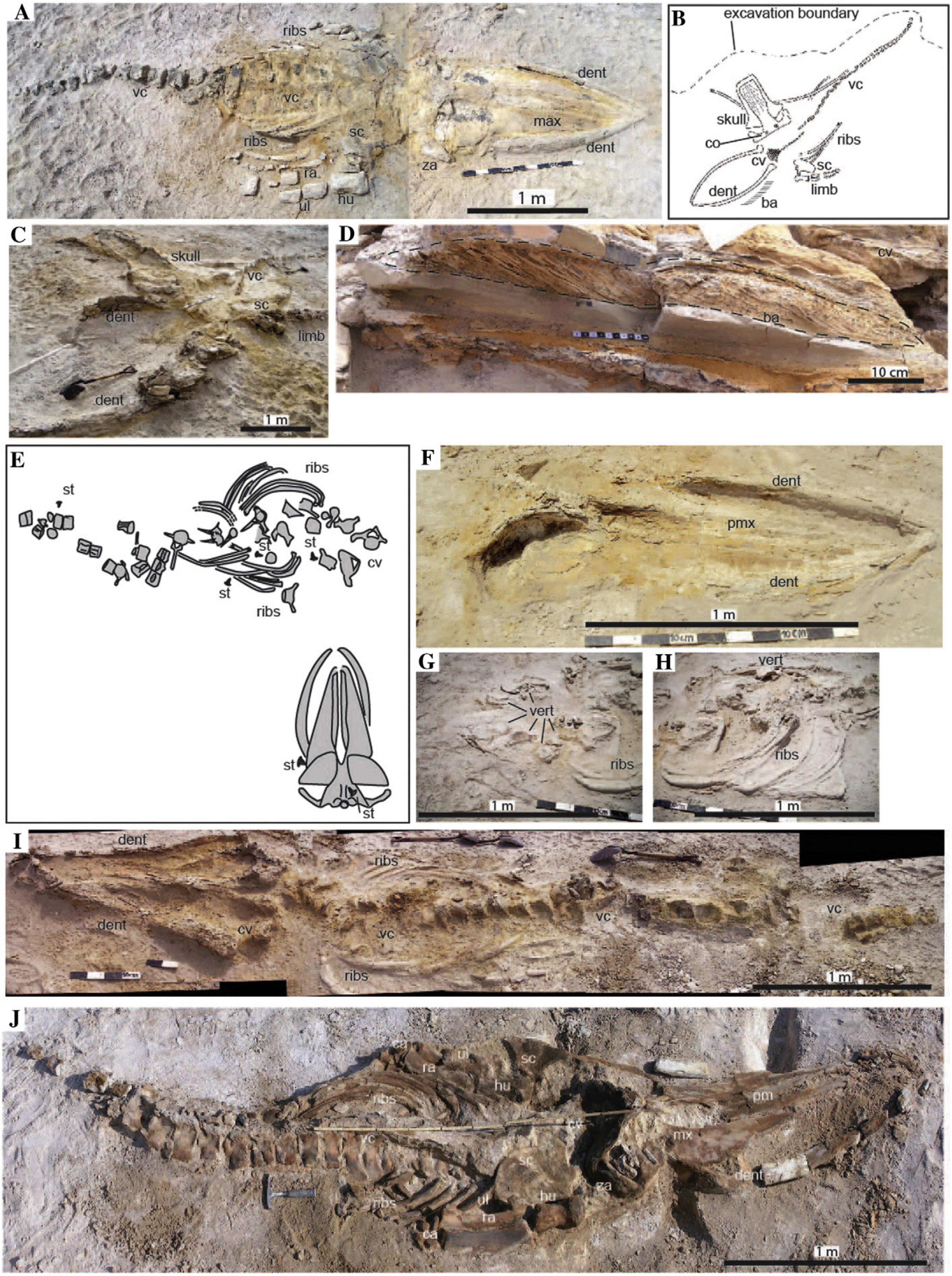
5.3. Completeness

Recent erosion has removed sediment from above and around most of the surveyed specimens, exposing and destroying some of the bones. Many specimens consist of clusters of partially exposed or loose bones, often remaining on top of a sediment mound, in some cases because the sediment associated with the skeletons is carbonate-cemented. Cementation of these mounds may be the result of microbial-mediated mineral precipitation during early diagenesis at the time of burial (Hendry, 1993; Castanier et al., 1999; Dupraz et al., 2009).

Due to weathering it is difficult to assess the original pre-exposure degree of skeletal completeness and articulation in some specimens. Two lines of evidence indicate that these assemblages may represent complete individuals. First, many rock fragments contain articulated bones and their degree of articulation clearly indicates that these clusters are the remains of more complete skeletons. Second, based on the high degree of completeness and preservation of excavated specimens that were partially or totally buried, it appears likely that most specimens found were more or less complete skeletons before modern exposure, except those that are clearly isolated bones (dentaries, skulls, ribs, limb bones, etc.). Fig. 6 and Appendix 1 summarize the main taphonomic features regarding completeness and articulation.

A total of 110 specimens are entirely complete without any destruction of bones due to weathering. Ninety-eight specimens consist of isolated bones (skulls, dentaries, humeri, ribs, vertebrae). Isolated vertebrae were not included because they occur on the surface and are likely to have rolled down from another weathered specimen, whereas the rest of the isolated specimens were buried, with no evidence for other associated bones and/or post-exhumation transport. These isolated bones must have been removed from the skeleton before burial, perhaps due to the scavenging action of sharks and other vertebrates, or the action of water currents. The remaining specimens ($n = 363$) show some degree of incompleteness, most commonly involving ribs, vertebrae, and limb bones. It is not possible to determine with certainty if the missing parts were removed prior to burial or during modern exposure (weathering), although the high degree of completeness of fully buried skeletons suggests that most specimens must have been complete or almost complete before modern exposure occurred. It is possible that some of the missing elements were not originally preserved, but were destroyed before burial.

Excavated specimens represent the full range of articulation or disarticulation, but not all of them are complete specimens because some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specimens had missing elements due to recent erosion. Regardless of their degree of deterioration by modern exposure, most specimens consist of both skull and some post-cranial bones, including vertebrae, ribs and limbs, and therefore should be considered as individuals (Table 1 and Appendix 1).

According to observations by Schäfer (1972), floating whale carcasses may follow a distinctive pattern of disarticulation before and during sinking. Dentaries detach first from the skull, and may sink rather quickly. Next, the skull detaches from the vertebral column and sinks to the seafloor, which would explain the occurrence of fifty isolated skulls, often without dentaries, in the Pisco Formation study areas (Appendix 1). In modern whale carcasses floating in the ocean surface detachment of the skull may be complete or partial, and the skull may be "hanging" from the rest of the floating body for some time, which may explain the occurrence of fossils with both skull and postcranial skeleton preserved but with the former detached and lying at an angle with the latter, or separately a short distance away. The high degree of completeness of the studied skeletons and the relatively low number of isolated or detached skulls and dentaries suggests that most individuals did not undergo detachment of skull and dentaries during flotation or reflotation.

Some fully articulated whales are especially remarkable because they have an entire portion of the skeleton missing. For instance, WCBa-32 shows excellent articulation and preservation, including the left side flipper, but lacks the right side flipper in its entirety (Fig. 10). Several shark teeth are associated with the skeleton, although no bite traces are found on the bones. It is possible that sharks removed the flipper and left the other flipper and rest of the skeleton intact, although this scenario seems unlikely. The possible role of scavengers is discussed below.

5.4. Position of the body and skull

During decay and flotation these large carcasses accumulate gases in their abdominal cavities, causing bloating and the rotation of their body resulting in carcasses lying ventral-side up or sideways on the seafloor. According to Barnes et al. (1987), most fossil baleen whales are in ventral-side up position. In the Pisco Formation, however, most fossil baleen whales are in dorsal-side up position. The position of the skull is the most clearly recognized indicator of the position. Out of the 218 skulls for which accurately observe position was observed, 130 specimens (~60%) have a dorsal-side up position, 86 specimens (39%) have a ventral-side up position, and two small specimens (1%) were found with their skull lying on their side. This suggests that the time span between death and sinking was relatively short, otherwise most of the carcasses would have rotated and lain in ventral-side up position.

5.5. Articulation

Forty-five percent of the specimens are fully articulated, 49% show both original articulation and disarticulation, and 6% show original complete disarticulation. Out of the 32 excavated specimens, 14 are fully articulated, 7 are fully disarticulated, and 11 have both disarticulated and articulated bones. Following Behrensmeyer's (1991) classification of terrestrial vertebrate accumulations, the majority of individuals (94%) in this study are articulated or mostly articulated and all others are disarticulated but associated. Other specimens show distinctive arrangement of the skeleton with partial disarticulation and reorientation of skeletal portions. For example, whales CBal-5 and WCBal-14 preserve the vertebral column broken into several major pieces, each with articulated vertebrae (Fig. 12). In each of these specimens, the skull is connected to the cervical vertebrae, and the thoracic vertebrae are articulated. In CBal-5 the lumbar vertebrae are grouped in one piece that is slightly displaced from the thoracic vertebrae, and the tail vertebrae form another group in which the orientation is inverted, i.e., the distal end points to the anterior end of the vertebral column and the skull. In WCBal-14, the articulated thoracic vertebrae are disconnected from the articulated cervical vertebrae, and the articulated lumbar vertebrae are preserved parallel to the thoracic vertebrae. Ribs are clustered into two groups, one of them beyond the group of lumbar vertebrae (Fig. 12). Some whale specimens have the skull resting at right angles to the post-cranial skeleton (for example, CB11-02, Fig. 6C, D), or resting on top of the cervical vertebrae and rib cage (for example, WCBa-248, Fig. 11A–C). These arrangements are unusual in the Pisco Formation and in the fossil record of whales in general.

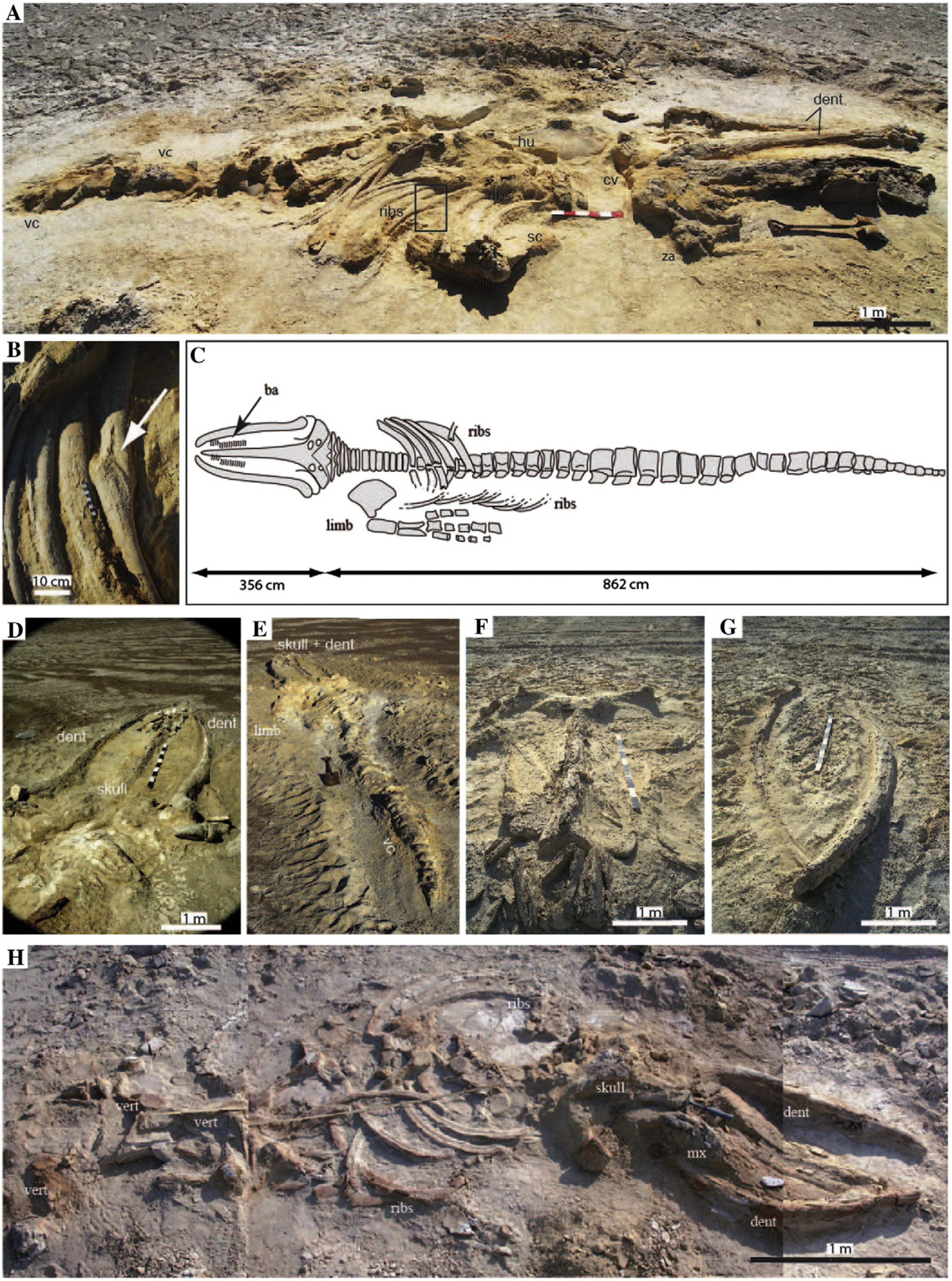
The breakage of the vertebral column could be attributed to 1) rapid decay of the connecting tissue during floating, 2) partial separation of body parts during floating and descent from the sea surface, 3) bloating and explosion of the carcass, 4) water currents, and 5) displacement by large size scavengers like sharks and large odontocete whales (Lambert et al., 2010). Rapid decay of connecting tissue could explain the selective breakage of the vertebral column, although it would seem unlikely to affect just one or two vertebral connections and not the rest of the vertebral column. Skeletal parts may separate from the body during flotation and descend (Schäfer, 1972), especially when aided by the feeding of large scavengers like sharks, which mainly affect the lower jaws and the flippers. Bloating may have played a significant role in the limited disruption in the order and disposition of bones in the skeleton. Observations of modern specimens show that the vertebral column may remain intact and articulated despite bloating and explosion due to the accumulation of gases (Michael Moore, Woods Hole Oceanographic Institution, personal observation 2012, and our own observations). The great number of fully articulated whales and the larger quantity of specimens that occur dorsal-side up versus ventral-side up indicates that most carcasses did not float and bloat for a long time, but sank shortly after death. Water currents may have played a role in displacing single skeletal elements but they are unlikely to move skulls or other large portions without also removing small ones (limbs). Displacement by large scavengers during feeding action is probable, although abundant tooth marks on the bones would be expected as a consequence. Moreover, it is difficult to envision how water currents or scavengers could move large portions of the vertebral column and leave the limbs intact in anatomical position (in CBal-5) or a group of four ribs perfectly parallel behind the lumbar vertebrae (in WCBal-14), or move a large skull onto the rib cage (in WCBa-248). It seems more likely that the position of these groups of bones resulted from disarticulation while sinking to the seafloor, although some arrangements remain intriguing.

6. Biostratinomy and fossilization

6.1. Cause of death

In modern environments, natural causes of mortality of marine mammals may include 1) stranding on the beach or in very shallow water, 2) senility, 3) injuries, 4) starvation, 5) climate conditions, 6) toxins and 7) disease and parasitism (Brongersma-Sanders, 1957; Kraus, 1990; Le Boeuf et al., 2000). Stranding on the beach or in very shallow water is not likely a cause for the carcasses buried in diatomaceous sediments, as

Fig. 6. Excavated fossil whales. A) Whale CB11-01. Fully articulated with almost the entire skeleton preserved; only a few distal limb bones are missing. Scale bar is 1 m long. Note that the whale skeleton is almost perfectly articulated in a symmetrical disposition with no displacement of the vertebrae and ribs, as would be expected if a long time residency on the seafloor occurred after decay. B–D) Whale CB11-02. Almost fully articulated specimen. C) Skull dislocated from the dentaries and cervical vertebrae. D) Baleen structure preserved in anatomical position and visible on the right side under the maxillary. Scale in cm. E–H) Whale CB11-03. Scale bar is 1 m. F) Skull displaced from the vertebral column, with the two dentaries in anatomical position. G–H) Part of the fully disarticulated but associated postcranial skeleton. I) Whale CB11-04. This whale is well articulated and mostly complete. Vertebrae are slightly displaced. Scale bar is 1 m. J) Whale CBL-10. Fully articulated and almost complete skeleton. Hammer for scale.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these deposits formed in the deeper water of the Pisco Basin, based on sedimentologic evidence. In the Pisco Formation there are several layers interpreted as foreshore and beach deposits (represented by lithic and bioclastic pebble conglomerates, with bored lithoclastics), and the sedimentologic and paleontological signature is rather different from what it is seen in the diatomaceous units. Because a number of specimens are juveniles and many are sub-adults, senility cannot be considered as the main cause of death of these specimens. Injuries are not likely to kill so many specimens throughout extended periods of time, and even if they did, they would have left evidence in the bones, at least to some degree. Besides whale FP08-12 (Fig. 7A–B), described in more detail by Belia and Esperante (2011), a few whale specimens have been found with evidence of bone injuries (fractures) (Esperante, personal observation, 2011), but they represent healed injuries that did not kill the whales. Climate conditions are unknown for the time of deposition and cannot be fully linked to the death of the whales. Starvation due to reduction in zooplankton availability triggered by climate change might have played a role in mass mortality (Alter et al., 2007), especially in a semi-confined embayment as hypothesized for the Pisco Basin. When a massive bloom begins to decay, the decomposing diatoms consume the available oxygen, suffocating other plants and animals, and depleting the resources needed by zooplankton, temporarily forcing animals to migrate (Anderson, 2004). Toxins from diatoms or dinoflagellates could account for mass mortality of marine mammals and fish during seasonal blooms (Hernández et al., 1998; Domingo et al., 2001). Toxins produced by algae or dinoflagellates have been linked with several mass die-offs of seals, manatees, dolphins and humpback whales in the Pacific and Atlantic oceans, and the Mediterranean Sea (Geraci et al., 1989; Domingo et al., 2001; Harwood, 2002). According to Van Dolah et al. (2003) compelling evidence points to the involvement of several algal toxins in marine mammal morbidity and mortality; however, confirmation of these toxins as the sole causative agent remains difficult. A few cases of cetacean die-offs have been attributed to disease, particularly to morbilliviruses (Lambertsen et al., 1986; Taubenberger et al., 1996; Domingo et al., 2001; Raga et al., 2008), although the link has not been strongly established (Harwood and Ailsa, 1990; Harwood, 2002). Analysis of the diatomaceous samples associated with the bones of the Pisco Formation whales did not provide any diatom species known to be toxic (although they could have been toxic in the past), and dinoflagellates were conspicuously absent.

The large number of fossil whales in the Pisco Formation could be attributed to several causes, including starvation, disease and toxicity of the food. In addition to these causes, the abundant volcanic ash that fell in the Pisco Basin may have adversely affected the whales as they surfaced to breathe causing asphyxiation of the cetaceans, and killing off their food source, such as krill. Volcanic ash is relatively abundant within the diatomaceous units, containing sharp glass shards (Fig. 3). The sharp ash shards could have seriously damaged the lungs of the animals coming to the water surface to breathe.

6.2. Mineralization and preservation

The bones of the Pisco Formation whales are fully mineralized. Cooper (2010) showed that diagenetic phases associated with the Pisco Formation whale bones include anhydrite, dolomite, gypsum and manganese oxides and no evidence of pyrite. This mineralogy suggests an oxidizing marine environment during diagenesis. Pores of all bones are filled with sediment and a combination of four cements, anhydrite, dolomite, gypsum and manganese oxide. SEM analysis suggests that halite was most likely present, but due to processing with water it was not identified in thin section. According to Cooper (2010), the mineralogy seems to follow one of three paths: The first path leads to infilling of the bone pores with sediment. The second path leads to infilling of the pores with manganese and ferroan oxides. In the third path the pores are filled with dolomite and/or evaporitic minerals. The localized variation in cementation of the bones and associated sediment may have been microbially induced (see Briggs, 2003; Daniel and Chin, 2010).

Smith and Baco (2003) indicate that bathyal carcasses pass through at least three successional stages in their decomposition: 1) a mobile-scavenger stage that lasts months to years, in which vertebrates and invertebrates remove soft tissue at high rates; 2) an enrichment opportunistic stage that lasts months to several years, in which bones are colonized by dense colonies of *Osedax* polychaetes and crustaceans; and 3) a sulphophilic stage that lasts several years, in which sulfur-oxidizing bacteria break down the bone lipids. Each stage implies a higher degree of bone degradation and destruction. Studies of modern whale carcasses on the seafloor of the Monterey Bay Canyon (Goffredi et al., 2004; Esperante, 2005; Lundsten et al., 2010), the Santa Cruz Basin and the Santa Catalina Basin off California (Smith et al., 1989; Feldman et al., 1998; Smith and Baco, 2003; Debenham et al., 2004), the Northeast Pacific (Bennet et al., 1994; Smith et al., 1998), the Northwest Pacific (Naganuma et al., 1996), and the North Atlantic (Jones et al., 1998; Dahlgren et al., 2006) indicate that whale carcasses are rapidly and thoroughly scavenged by both vertebrates (sharks and other fish) and macro-invertebrates (tanner crabs). Repeated monitoring of some of these carcasses reveals that the complete removal of soft tissue occurs within a few weeks to a few months, and bones began to be scavenged and bored before all the soft tissue is eliminated (Esperante, 2005). Observations of whale carcasses experimentally implanted in shallow-water depths indicate that they last a short time on the seafloor, ranging from a few weeks to a few years (Glover et al., 2005; Lundsten et al., 2010), and that heavy deterioration happens within a few weeks to a few months after the death of the whale, and even before all the soft tissue is removed from the carcass (Esperante, 2005; Lundsten et al., 2010). Thus whales in several different preservational stages should be found in the Pisco Formation if this was a record of attritional death in a normal marine setting. However, they are all in the same stage, showing excellent preservation without any deterioration due to scavengers or abrasion.

Except for deterioration due to weathering on exposed bones, all specimens examined in this study, including both excavated specimens and those buried and not weathered in recent times, show excellent preservation of both the upper and the lower surfaces. There is no evidence of erosion, abrasion, or dissolution due to long residence on the sea floor before burial. The bones are uniformly well preserved, and there is no difference in preservation between thick, large bones (vertebrae, skull, dentaries, humerus) and thin or small bones (ribs, distal limb bones) (Esperante and Brand, 2002; Brand et al., 2004). All these features are in stark contrast with modern whale skeletons on the seafloor, which commonly show significantly better preservation on the lower, buried side than on the upper surface that is exposed to the action of macro-scavengers and abrasion, and better preservation of distal limb bones (which are quickly buried) than larger bones (Allison et al., 1991; Esperante, 2005; Fujiwara et al., 2007; Higgs et al., 2011, 2012).

Bone breakage is minimal and mostly attributable to the weight of overlying sediment. Most bone samples show microcracks and

Fig. 7. Excavated fossil whales. A–B) Articulated, complete skeleton of whale FP08-12. Scale bar is 60 cm. B) Detail of a rib with a healed fracture (arrow). Scale is 10 cm. C) Sketch of articulated whale IC-1. C–E) Whale IC-1, articulated with baleen present in anatomical position. D) View of skull and articulated cervical and thoracic vertebrae and ribs. Scale bar is 1 m. E) View of the entire specimen. F–G) Whale LQ10-28. Scale bar is 1 m. F) View of the skull from the distal end. G) View of the dentaries from the distal end. They lie parallel to the skull at a distance of 2.3 m. H) Whale CBL-11. Skull shows dentaries partially displaced. Postcranial skeleton is fully disarticulated but associated. Hammer for scale.

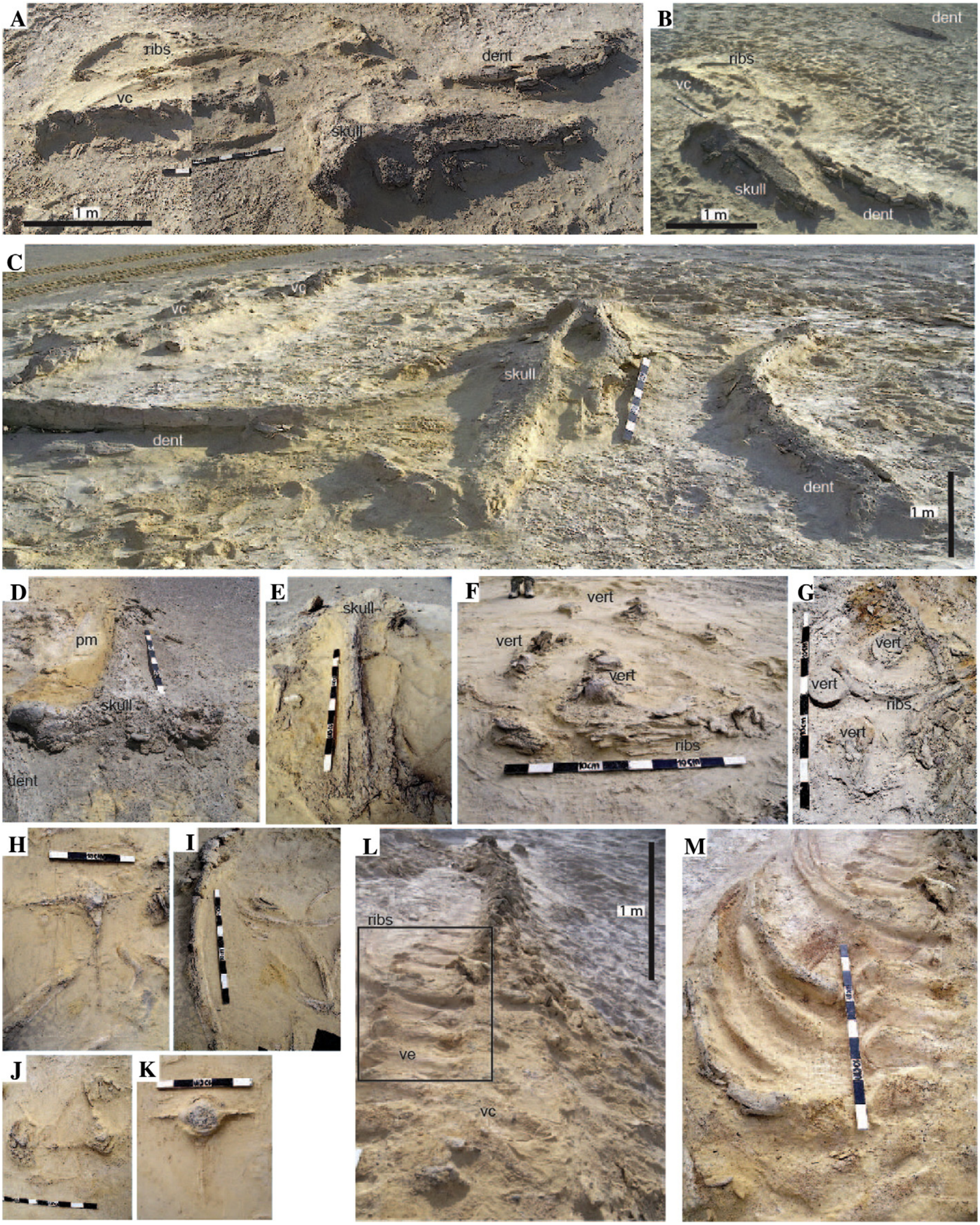


Fig. 8. Excavated fossil whales. A–B) Whale LQ10-34. A portion of the vertebral column is preserved and articulated. The two dentaries are disarticulated and displaced, one of them several meters from the skull (shown in B). C) Whale LQ10-35. Fully disarticulated skeleton with the bones associated (shown along the upper left part of the picture). The two disarticulated dentaries lie on either side of the skull. D) Skull of whale LQ10-36; the view is from the occipital side. E–G) Whale LQ10-39. E) View of the skull from the distal end. F–G) Part of the disarticulated but associated postcranial skeleton. Scale bar in A–G, and I–M is 1 m, and in H is 50 cm. H–K) Part of the disarticulated but associated skeleton of LQ10-40, showing well preserved vertebrae and ribs. L–M) Fully articulated postcranial skeleton of whale LQ10-42, showing well preserved vertebrae and ribs. Skull not in the pictures. Selected area in L) is shown in M).

microfractures in thin section. Principally these are located in a thin layer of trabecular bone below the superficial layer, which, nevertheless, have had little effect on the overall structure and preservation of the bone (Fig. 13A–C). The studied specimens do not show evidence of corrosion (i.e., destruction of bones by chemical reaction with water, which commonly results in the removal of the cortical bone and exposure of the underlying cancellous bone) or abrasion (i.e., erosion of bone by friction and impact of particles transported by water currents). Yet both corrosion and abrasion are common in shallow-water assemblages, both in ancient and modern settings (Liebig et al., 2007; Dominici et al., 2009; Esperante et al., 2009).

6.3. Lack of evidence for macro-scavenging

Shark attacks on humpback, gray and other whales have been reported in the media with numerous photographs and video recordings, but have not been documented in the scientific literature. Shark attacks on other marine mammals have been published (Ames and Morejohn, 1980). Several whale skeletons have associated shark teeth and shark teeth are relatively common in the sediments of the Pisco Formation. Also several shark skeletons have been found by members of this research team and others. Given the abundance of whale skeletons in the Pisco Formation, the relative abundance of shark teeth in the sediments and associated with the skeletons in the Pisco Formation, the evidence of shark attacks on fossil marine mammals found in other geologic settings (Demere and Cerutti, 1982; Cigala-Fulgosi, 1990; Spizuco et al., 1993; Bianucci et al., 2000, 2010; Boessenecker and Perry, 2011), and the ample actual evidence of white shark and other species attacking living and dead marine mammals in modern times (Arnold, 1972; Ames and Morejohn, 1980; Dudley et al., 2000), evidence of shark bites on the bones of these fossil specimens should be expected. During the survey of the Pisco Formation cetaceans only three whale specimens were found with evidence of shark bite activity; one consisting of a vertebral transversal apophysis with an embedded shark tooth, a skull containing an embedded shark tooth, and a rib with several shark tooth marks on the surface. Ehret et al. (2009b) reported a fourth case, consisting of a shark tooth embedded in the cortical bone of a dentary of a mysticete. However, out of the 571 specimens in the diatomaceous sediments studied for this paper (Appendix 1), none showed evidence of shark bite activity.

Moreover, modern whale carcasses are frequently extensively colonized by the siboglinid polychaete *Osedax*, which burrow into the bone and, in symbiosis with bacteria, digest whale fat and oils, contributing to the degradation of the bone (Rouse et al., 2004; Vrijenhoek et al., 2008). Bones retrieved from a whale carcass on the Monterey Bay seafloor show a density of 1–15 borings per square cm, each 1–3 mm in diameter. Sometimes, several borings coalesce and form open pits in the bone, and in time resulting in the destruction of entire portions of both compact and cancellous bone (Higgs et al., 2011, 2012). Also *Osedax* worms are known to rapidly colonize whale skeletons in shallow waters (Glover et al., 2005). Similar borings have been recently reported from Cretaceous avian bones (Kiel et al., 2011), and Oligocene and Neogene whale bones (Muñiz et al., 2010; Kiel et al., 2010, 2013). These borings are conspicuously absent in the Pisco Formation whale bones.

Evidence for other macro-vertebrates or macro-invertebrates scavenging in the Pisco Formation marine mammals is also virtually absent, with the possible exception of the few shark bites mentioned above. Many shark teeth have been recovered associated with the whale fossil carcasses; yet the evidence for shark tooth bites is scant. Scavenging and decay must have occurred within the basin because the soft tissue is not preserved, but it is possible that a high degree of turbidity slowed down the action of scavengers.

In the light of actualistic studies, the lack of evidence for scavenging in the Pisco Formation whales by both vertebrates and invertebrates is puzzling. Moreover, at least in some cases, trenches dug across whale skeletons indicate fine sediment structures and bedding extending to the surface of whale bones. This implies that the carcasses had to be free of soft tissue before burial and therefore the skeletons must have been exposed to both macro- and micro-scavengers at least for a short time on the sea bottom.

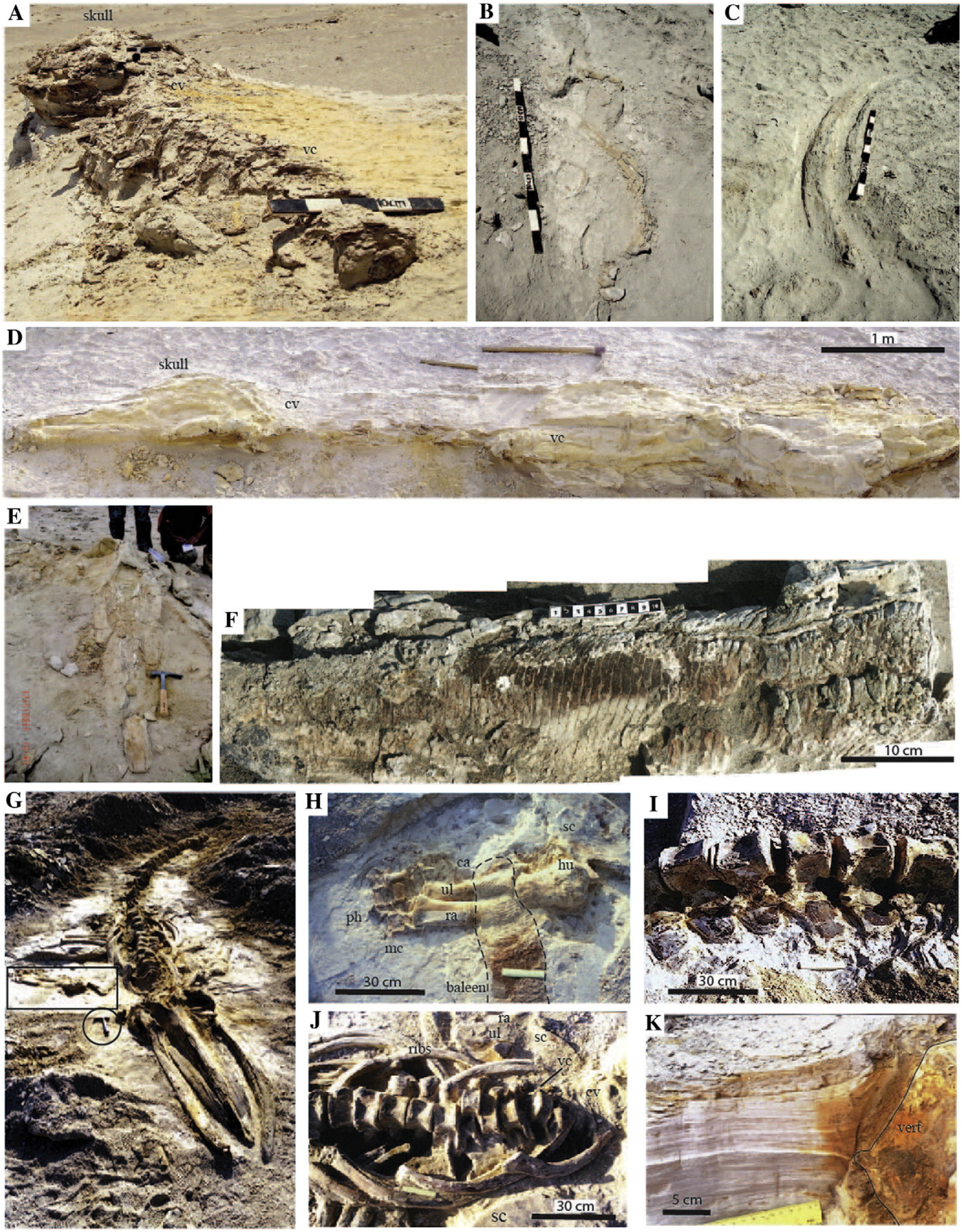
6.4. Bioturbation and microborings

In modern oceans, sediment associated with whale carcasses on the seafloor is rapidly and thoroughly colonized by invertebrates feeding on the substrate enriched in organic matter leached from the whale carcass (Smith et al., 1989; Allison et al., 1991; Bennet et al., 1994; Naganuma et al., 1996; Feldman et al., 1998; Smith et al., 1998; Smith and Baco, 2003). Experimentally implanted whale carcasses show that nematode assemblages are abundant in the sediment surrounding the carcasses out to a distance of at least 30 m (Debenham et al., 2004), which suggests that abundant traces of bioturbation should be found in the diatomaceous sediment associated with the Pisco Formation whales. However, burrows or other ichnofossils produced by invertebrate fauna living within the sediment were generally absent. The sediment layers and the white diatomaceous lenses are not disrupted by any burrowing activity. It is possible that the muddy diatomaceous bottom substrate was soupy and highly cohesive. Diatoms are known to produce extracellular polymeric secretions that stabilize muddy surfaces and prevent sediment resuspension (Decho, 2000; Stal and de Brouwer, 2003). The cohesive nature of the soft sediment may have hindered reflotation of the carcass, contribute to fast burial, the high degree of preservation, and the limited disarticulation and displacement of the bones. Also it may explain why the sediment is not bioturbated and the lack of bioerosion on the bones so common on modern whale carcasses. A similar scenario has been proposed by Reisdorf et al. (2012) to account for the excellent degree of preservation of ichthyosaurs in the Jurassic Posidonienschiefer Formation of Germany.

Several studies have shown the occurrence of microbial borings in modern whale falls (e.g. Allison et al., 1991; Deming et al., 1997; Higgs et al., 2011) and in ancient whale assemblages (e.g. Amano and Little, 2005; Esperante, 2005; Amano et al., 2007; Esperante et al., 2009; Shapiro and Spangler, 2009). The modern whale falls are thoroughly bored by both macro- and micro-borers, including bacteria, and perhaps fungi, which cause extensive destruction of the bone tissue. Microborings are also relatively common in most whale fossil skeletons, although not in all bones, but destruction of bone is limited to the outer 3 mm of trabecular or cortical bone (Shapiro and Spangler, 2009; Higgs et al., 2011).

In order to compare with those occurrences a search for microbial borings in the bones of the excavated whales was undertaken (Appendix 3). A thorough search for the occurrence of bacterial or fungal borings had already been carried out by Cooper (2010) using thin sections of bones of whale assemblages from the diatomaceous units of the Pisco Formation. She processed as thin sections a total of 77 individual bones from 17 assemblages. Only 15 samples, from a total of 6 whales, showed evidence of microbioerosion. In this study additional thin sections of many bones of other specimens were made. The results show few samples with microborings or other evidence of bioerosion of any type in the whale bones (Fig. 13, Appendix 3). Most bone samples lack any evidence of microborings, but when they do occur, they are limited to the outer surface of both cortical and trabecular bone (as in Shapiro and Spangler, 2009), and they do not affect the overall preservation of the bones (Fig. 13D–E).

Microborings consist of tunnels 5–10 μm wide and no more than 0.3 mm deep. They start at the periosteal surface and move inwards in a closely spaced, tortuous branching habit. They are similar to the Wedl type tunnels described by Davis (1997), who labeled cyanobacteria as the causal organism. The condition of the Pisco Formation bones is in direct contrast to the condition of bones from modern-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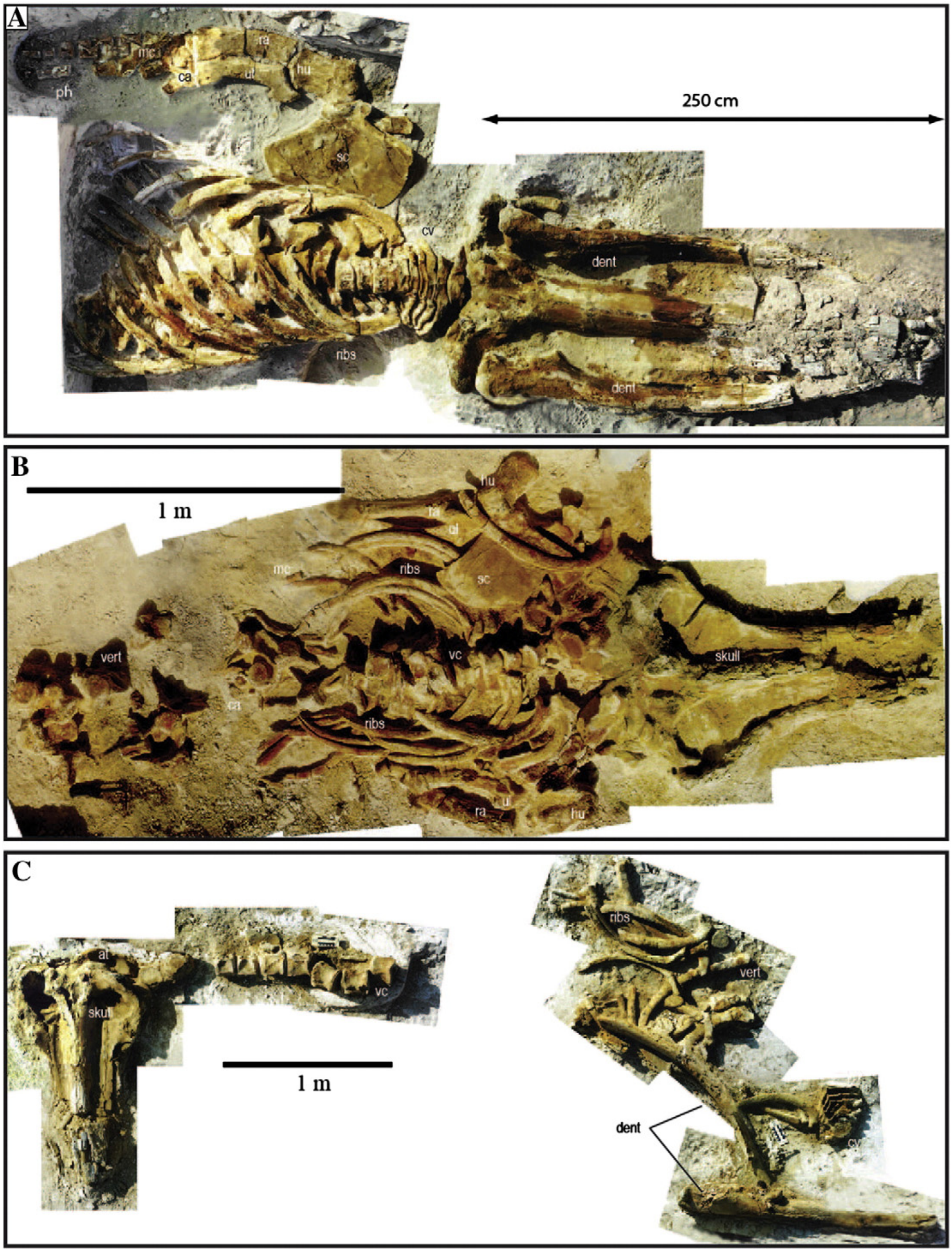


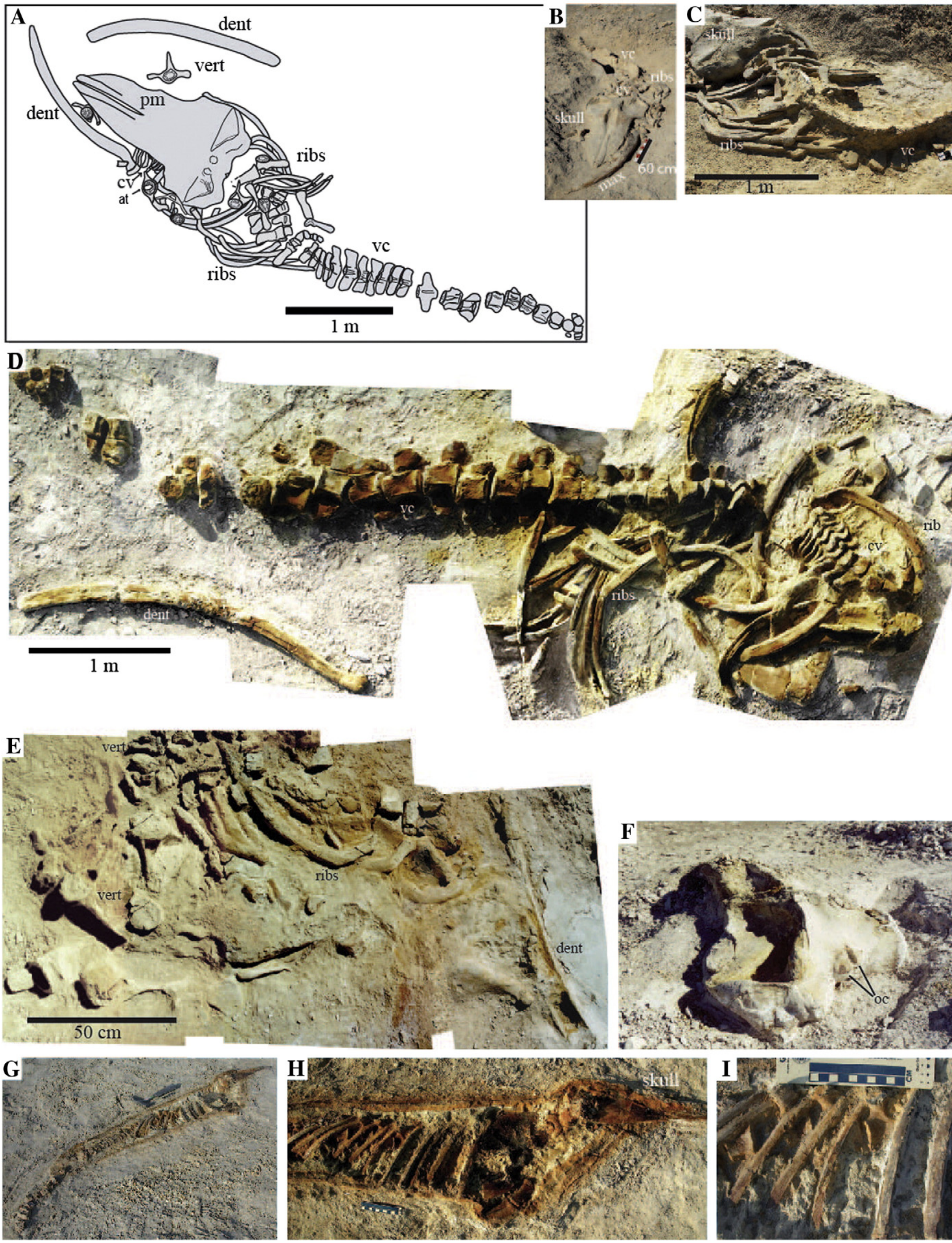
Fig. 10. Excavated fossil whales. A) Fully articulated and almost complete whale WCBa-32. Scale bar is 50 cm. B) Partially disarticulated whale WCBa-112. Lumbar and tail vertebrae, and carpals and metacarpals are disarticulated, although they are associated. Lower jaws are missing. C) Whale WCBa-212. Some vertebrae and ribs and all the limb bones are missing.

day whale falls and to those of other fossil whale skeletons, which show abundant microborings on the surface of most of the bones.

6.5. Baleen

Baleen is extremely rare in the fossil record, and only a handful of specimens were known until Esperante et al. (2008) reported 37 specimens with baleen in the Pisco Formation. To date, more than 70 whale specimens with baleen preserved have been found in the Pisco Formation, both in diatomaceous and non-diatomaceous layers, most of them showing baleen in anatomical position (between the maxilla and the dentaries) (Figs. 6B–C, 9F, H). Whale WCBa-20 shows baleen detached and preserved next to the right-side flipper (Fig. 9H). The pre-exposure degree of baleen articulation

Fig. 9. Excavated fossil whales. A) Whale LQ11-01. This specimen was partially eroded before excavation. View from the articulated thoracic vertebrae looking toward the skull. Scale bar is 50 cm. B–C) Disarticulated vertebrae and ribs of whale LQ11-05. Scale bar is 1 m. D) Articulated skeleton of whale LQ11-10. E) Skull and part of the lower jaws of whale PIS09-26. F) Baleen in anatomical position of whale WC-33. Scale bar is 10 cm. G–K) Fully articulated whale WCBa-20. Scale bar in H–K is 10 cm. Box in G) is shown in detail in H). H) Right side limb with a portion of baleen (dotted line) that detached from the mouth and was preserved on top of the ulna, radius and associated sediment. I) Detail of articulated lumbar vertebrae. J) Detail of articulated thoracic vertebrae, ribs and the two scapulae. K) Diatomaceous sediment associated with the vertebral column. Edge of vertebra outlined in black.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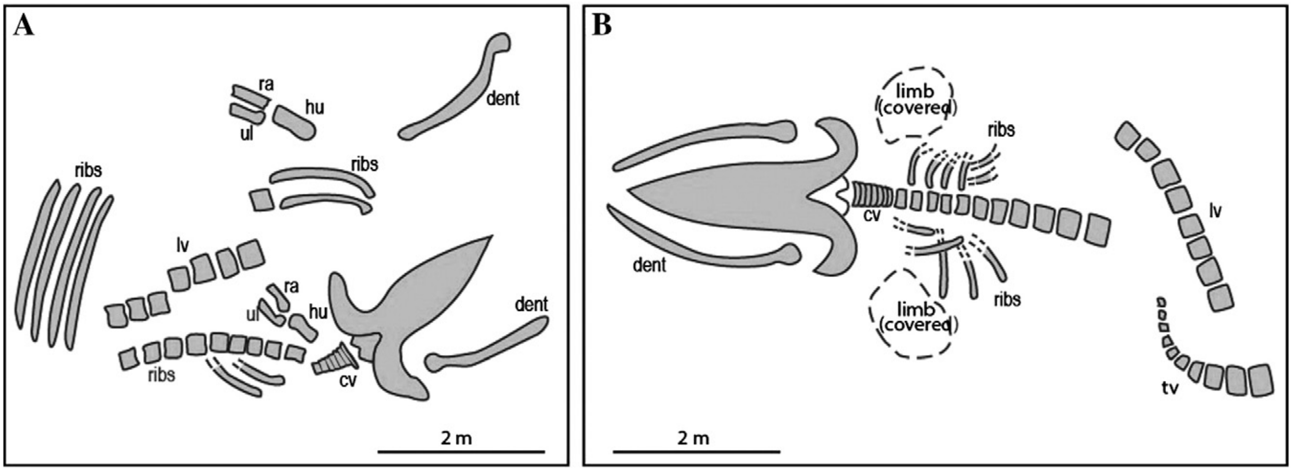

Fig. 12. Some unusual assemblages. A) Incomplete skeleton of whale WCBal-14. The incomplete vertebral column is broken in two pieces. Four ribs lie beyond the set of lumbar vertebrae. B) Whale CBal-5. The vertebral column is preserved into three pieces, with the set of caudal vertebrae pointing to the thoracic vertebrae. Limbs were not exposed during excavation.

of five other specimens is unknown because they were affected by modern weathering.

The occurrence of baleen is relevant for inferring paleoenvironmental conditions of deposition, as discussed by Esperante et al. (2008). Baleen consists of keratin, which decays relatively rapidly compared to bone. In addition, the baleen filtering apparatus is not rooted into bone as mammal teeth are, but only attached to the gum of the maxilla by means of connecting tissue, which decays rapidly after death, causing the structure to detach. Observations of stranded carcasses indicate that baleen detaches from the maxilla within one or two weeks after death. Therefore fossilization of baleen is very unlikely, and the quality and abundance of preservation of baleen in the specimens of the Pisco Formation qualifies them as both true conservation- and concentration-lagerstätten.

7. Depositional conditions

Geological evidence indicates that the Pisco Formation was deposited in a shallow protected embayment with pre-Cenozoic igneous islands offshore (Marty, 1989; Carvajal et al., 2000; Brand et al., 2011). There are no unconformities within the diatomaceous succession (Marty, 1989). At a large scale, the diatomaceous sediments of the upper Pisco Formation succession consist of thick to extremely thick beds, with scarce distinct sedimentary structures, including gentle scour-and-fill structures, and rare cross-lamination, soft sediment deformation, and hummocky and swaley cross-stratification. The strata are massive, without distinct, repetitive laminations, alternation of biogenic and detrital laminae, or varve-like layers characteristic of other diatomite deposits in the Monterey Formation, in the Gulf of California, in the eastern equatorial Pacific Ocean, and other places, in which seasonal variations in both plankton population and continental runoff are recorded in alternating biogenic and detrital laminae (Kemp, 1990; Kemp and Baldauf, 1993; Sancetta, 1995, 1996). The only layers in the Pisco Formation diatomaceous units that have some degree of lamination are rare very thin to thin laminae of white diatomite with a limited lateral extent from several centimeters to a few meters. Thin sections of these white laminations reveal that they have little or no clay content, but similar diatom content as the enclosing massive diatomaceous mudstone.

These features indicate that deposition of the diatomaceous sediments of the Pisco Formation appears to have been continuous without alternating seasonal cycles of terrigenous/diatom deposits. The Pisco Formation diatomaceous sediments could be the result of many persistent and massive diatom blooms accompanied by or interrupted by minor volcanic ash deposits, phosphate, and dolomite deposition.

Elongate, oval, and channel-shaped bodies of fine sandstone or siltstone, commonly with a thin layer of lag pebbles at the bottom, are widely scattered throughout the section, suggesting that water currents may have played a role in distributing the fine grained sediments on the bottom. Also there is evidence for frequent storm activity, both in the diatomaceous and the underlying siltstone and sandstone units (Carvajal, 2002). These storms may have played a role in bringing diatoms and whale carcasses from open ocean and concentrating them near shore in the bay (Brand et al., 2004). The absence of alternating detrital and biogenic laminations, the occurrence of massive diatomaceous beds, and the abundance of volcanic ash, indicate that the Pisco Formation diatomaceous deposits were deposited under different conditions from those suggested for the Monterey Formation, the Gulf of California, and the eastern equatorial Pacific Ocean.

Observations suggest that in the modern ocean the majority of silica dissolution occurs within the upper 200 m of the ocean (Passow et al., 2006). The excellent preservation of the diatom frustules of the Pisco Formation diatomaceous units (Fig. 3) (Brand et al., 2004) suggests that they were deposited in shallow water, which explains why they were not dissolved, as generally happens when diatoms sink slowly into deep water. They have not experienced dissolution, but they are fragmented. Fragmentation may be explained by both grazing by zooplankton and high-energy conditions within the environment.

Fig. 11. Excavated fossil whales. A–C) Whale WCBa-248. A) Diagram of the partially disarticulated skeleton, with the skull resting on top of the disarticulated cervical vertebrae and several ribs. Hammer for scale. B) View from the distal end of the skull. Scale bar is 60 cm. C) View of the articulated vertebral column and associated ribs and skull. D) Plan view of whale WCBa-302. The skull, located 3.5 m left of the dentary, is missing from the picture. E) Disarticulated skeleton of whale WQG-63. F) Isolated skull of whale WQG-67. Width = 160 cm, preserved length = 260 cm. G–I) Fully articulated skeleton of dolphin Z-51. I) Detail of articulated thoracic vertebrae and ribs.

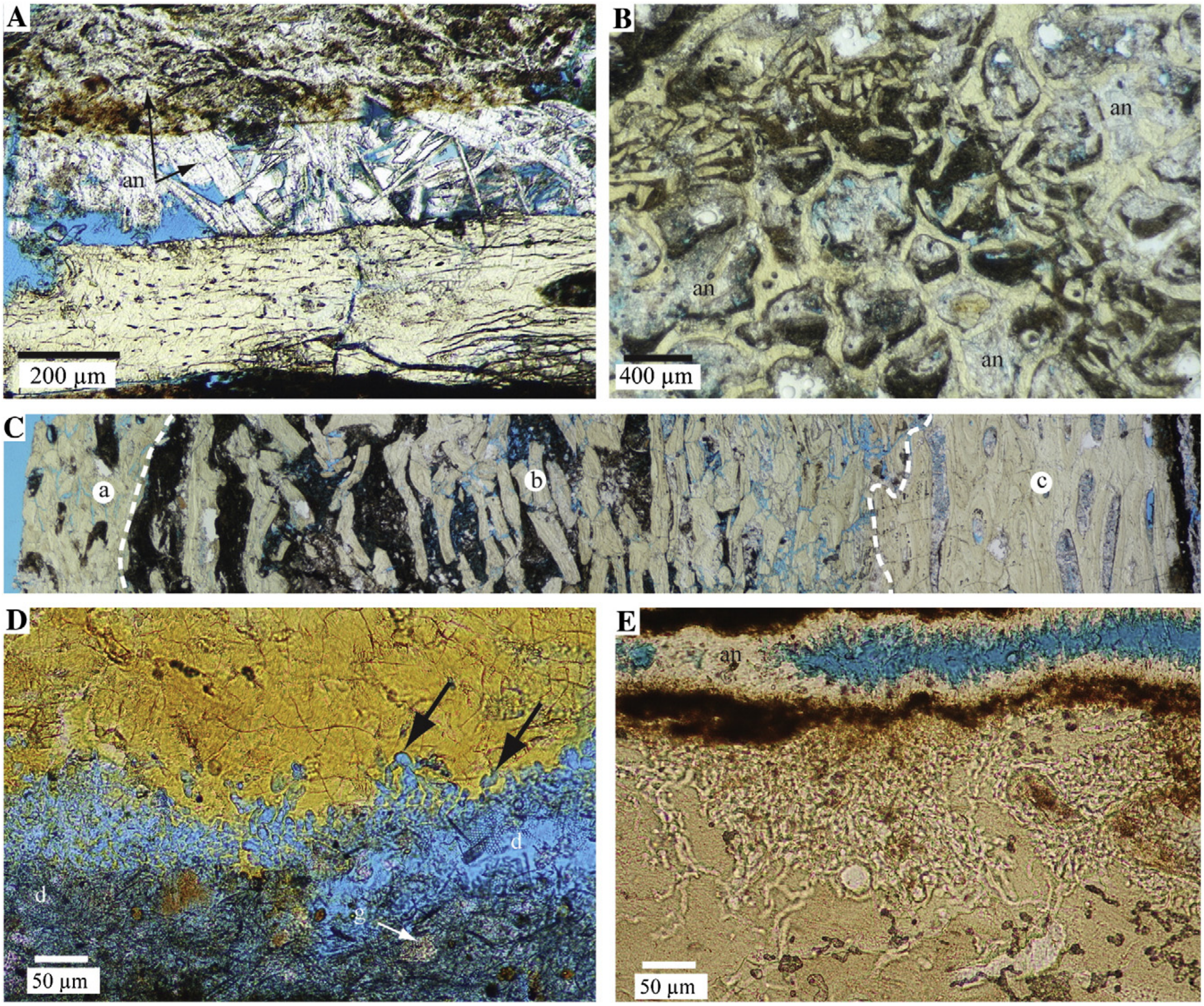

Fig. 13. Thin sections of bones. A) Surface of the vertebral neural spine of whale CB11-01. The photo shows the upper side of the bone, which was more exposed before burial. Note the excellent preservation of the bone. On top of the bones surface there is a precipitate of anhydrite (an) with some clay. B) Trabecular bone of a phalanx of whale LQ11-05, showing an area of crushed trabecular bone within intact bone. Cracking and crushing of the bone is a result of compaction of bone under sediment load. Bone pores are filled with anhydrite (an), and some clay minerals. C) Panorama of a sample of a vertebral transverse process of whale LQ11-05. The image covers a width of 12 mm across the bone showing both surfaces of the flat bone. The left side is the upper side that was more exposed before burial. Sediment underneath the bone is shown on the far right. This image reveals a frequent preservational pattern of three layers: a) trabecular bone, b) compacted and crushed bone in the middle showing microfractures, and c) compacted surficial bone (note the elongate pores to the right), and. D) Detail of microtubules on the surface of a rib from whale CB11-03. Associated sediment is diatomite (d) with some gypsum nodules (g). E) Surface of a vertebral transverse process of whale PIS09-34, showing long, thin microtubules. Anhydrite (an) precipitate covers the surface of the bone.

The *Thalassionema* species found in the samples are common in modern surface sediments (Campeau et al., 1999). *Delphineis* sp. 1 is a benthic, chain-forming species (Fourtanier and Macharé, 1986) which occurs only in coastal upwelling regions of the present oceans and in deposits interpreted as highly productive coastal environments of the past (Schuette and Schrader, 1979). *Delphineis* also indicates the occurrence of diatom mats within the water column and their deposition on the seafloor. *P. sulcata* is a non-motile, bottom-dwelling diatom, usually an epiphyte that attaches itself to the substrate by means of a mucus pad and forms long chains of many valves. It is a cosmopolitan marine species (Andrews and Abbott, 1985) that at present lives at depths between 0 and 175 m but is lifted into the plankton by storms. The abundance of *T. nitzschioides*, *Delphineis* sp. 1, *Chaetoceros* resting spores, and associated *Thalassiosira* species, and the absence of other taxa in many of the samples suggest that the diatomaceous sediment represented by these samples was deposited within the boundaries of specific coastal upwelling zones as opposed to nutrient-poor oceanic waters.

The dominance of *Chaetoceros* resting spores in all the diatomaceous samples is significant because the spores are heavily silicified stages in the life cycles of these coastal, neritic, centric diatoms. Spores are particularly common in boreal and temperate regions of both hemispheres, and are presumed to be a response to rapid nutrient depletion at the end of a phytoplankton bloom, which happens in the span of time of one or a few days. Spores appear specialized to persist in darkness or low light, and nitrogen deficiency is a common cause of spore formation (Hargraves and French, 1983). It is possible that ash falls from local volcanic activity contributed to diatom blooms and subsequently to the production of resting spores.

Short-term, strong but localized paleoenvironmental impacts influenced by volcanic ash deposits have been reported (Brant and Bahls, 1995). This same response could have affected the diatoms in the ancient coastal, restricted marine areas of Peru, by enhancing the quantity of locally available nutrients.

The abundance of clay, volcanic glass, quartz and other detrital minerals in the Pisco Formation diatomaceous rocks supports the claim that input of fine detrital material was high in the basin. Volcanic glass is pervasive in the section, indicating that ash was falling into the basin while deposition of diatoms occurred (Fig. 3A, B). This may have played a significant role in the enhanced production of diatoms in the basin because volcanic glass is highly reactive and readily provides solutes to the water, including phosphate, iron, silica, and manganese, favoring the bloom of diatoms (Frogner et al., 2001; Jones and Gislason, 2008). For example, Brant and Bahls (1995) suggest that volcanoes were responsible for the anomalous occurrence of the freshwater diatom *Navicula simplex* with volcanic glass in the Holocene Telegraph Creek marsh deposits from western Montana, USA. Several proxies suggest that the high concentration of this diatom species can be attributed to the leaching of minerals from the volcanic ash, which affected the chemistry of the water with increased values of silica and other minerals. Similarly, the frequent and abundant input of volcanic ash into the Pisco Basin could have contributed to increased planktonic production and higher rates of diatom sedimentation. Also the presence of volcanic ash and abundant clay particles may have affected the rate of flocculation and aggregation. Several other studies have linked high diatom productivity to ashfalls in other basins (Abella, 1988; Telford et al., 2004). It may be that volcanic ash and clay containing light metal sulfates of aluminum, potassium, and magnesium increased the nutrient load and favored flocculation and sedimentation of the diatoms with ash and clay. The positive role of clay and volcanic ash in the coagulation efficiency and aggregation of marine phytoplankton has been suggested in other studies (Avnimelech et al., 1982; Honjo, 1982).

The occurrence of near-monospecific assemblages in the sediments probably records the dominance of some diatom species in the phytoplankton blooms. The dominance of certain species in the rock samples might be the result of seasonal blooms in the seawater triggered by nutrient availability and also a consequence of selective preservation during and after deposition. Coastal planktonic diatoms such as *Chaetoceros* and their heavily silicified resting spores can periodically dominate assemblages in the water column, zooplankton pellets, and the underlying sediment (Stockwell, 1991), and sink to the bottom out of the euphotic zone as a survival strategy. Besides *Chaetoceros* other genera produce abundant spores in certain instances. Two of these species are *Skeletonema* and *Thalassiosira* (Chen et al., 2009). However, no spores of these species were found in the samples analyzed.

The diverse diatom content in the analyzed samples represent shallow marine to pelagic assemblages, where there were abundant nutrients, deep water or shallow water with high turbidity, favoring the bloom of certain filamentous, spore-forming species that respond to these conditions. The diatoms are typical of a neritic and nearshore assemblage but contain fragments of open ocean, planktonic taxa as well, which suggests that lateral advection occurred in the ancient eastern equatorial Pacific Ocean that brought water from the open ocean to the Peruvian coast. There is a conspicuous absence of benthic taxa, with the exception of *Delphineis*. Benthic diatoms can live only within the photic zone, usually with low levels of turbidity in the water. Therefore, the bulk of diatom composition represents an assemblage from shallow, nearshore waters, but from beyond the sublittoral zone.

The occurrence of intact freshwater diatoms *L. mutica* and *P. borealis* in the samples indicates continental input into the basin. The freshwater diatoms recorded in the samples of the massive diatomaceous units are robust species and could survive some transport from continental areas to marine shelves.

8. Rates of deposition and preservation

Brand et al. (2004) suggest three possible mechanisms for preserving the whales: (1) anoxia, (2) a covering of diatom mats, and (3) rapid burial. Anoxia could be invoked on the account of the high productivity of diatoms associated with high rates of decay on the seafloor leading to bottom-water anoxia. However, several lines of evidence indicate that the Pisco Formation sediments and whales were not deposited in anoxic water. In the diatomaceous units there is abundant evidence of shallow water, above storm wave base, and currents, including the occurrence of channel-like, scour-and-fill, swaley cross-stratification, and other sedimentary structures. There is also limited trace and invertebrate fossils (molluscs, balanids, etc.) typical of shallow or very shallow water subjected to tidal and storm current action (Carvajal, 2002, and our own data; Dunbar et al., 1990). It would also be unlikely that anoxic conditions would prevail in shallow water for all the time represented by the deposition of the thick diatomaceous sediments and the whale skeletons. But even if low-oxygen conditions occurred in the Pisco Basin during deposition of the whale-bearing diatomaceous layers, those conditions would not have prevented rapid decomposition of the whale. Numerous actualistic experiments show that anoxic conditions do not prevent decay and thus do not favor better preservation than oxygenated conditions. In actualistic experiments of decay and mineralization of proteinaceous macroorganisms in sediments, Allison (1988, p. 139) shows that “anoxia is ineffective as a long-term conservation medium in the preservation of soft-bodied fossils.” Experiments of disintegration of regular echinoids carried out by Kidwell and Baumiller (1990, p. 247) show that “the effects of aerobic versus anaerobic decay on disintegration were insignificant.” Studies show that putrefaction and cellular autolysis progresses rapidly independent of oxygen availability (Hood et al., 2003; Reisdorf et al., 2012), which is corroborated by the rapid decomposition of modern whale carcasses on the low-oxygen conditions of the deep-sea seafloor (Allison et al., 1991; Lundsten et al., 2010).

Although diatom mats occur in the diatomaceous beds of the Pisco Formation, they are not extensive, continuous mats as those postulated in equatorial eastern Pacific Neogene deposits, which inhibit bioturbation and scavenger activity (Kemp and Baldauf, 1993; Kemp et al., 1995). Rather, the Pisco Formation diatom mats are speckles and fragments of mats that did not cover the large whale skeletons and therefore could not preclude scavenger activity.

Evidence for high rates of sedimentation within a shallow environment comes from the preservation of diatoms. The lack of evidence for dissolution and/or abrasion of the diatom frustules due to prolonged residence in the water column after the cells died indicates that they must have been buried very quickly to avoid deterioration, and that they sank within shallow water. Diatom fragmentation can be attributed to grazing by zooplankton or to mechanical processes, which also are more likely to occur in shallow, high-energy environments than in deep-water. Resistance to dissolution might have been enhanced by high concentrations of silica in water due to high amounts of clay, quartz, and volcanic ash from local volcanic eruptions on the continent.

Several lines of evidence suggest that the whales must have been buried very quickly after death, but after the soft tissue was removed from the carcass. Brand et al. (2004) suggest that the whales must have been covered by rapid diatom accumulation in the basin, caused by large-scale diatom blooms and lateral advection of diatoms from open ocean that accumulated the frustules at a rate of one to two orders of magnitude higher than in comparable modern diatomite-accumulating environments. This is supported by the excellent degree of preservation of the whale skeletons, the lack of scavenging, the preservation of baleen in anatomical position, and the absence of laminated sediments that imply seasonal alternation of diatom versus terrigenous or carbonate deposits. Moreover, the volcanic glass particles are sharp and angular, suggesting that they did not undergo a long process of winnowing, reworking or dissolution within the water column, but rather sank quickly to the sea bottom.

Unpublished (Kevin Nick, written communication, 2014) Ar–Ar dates from biotite in tuff have yielded the following age ranges from diatomaceous siltstone and silty diatomite dominated successions in the studied areas: Cerro Ballena 6.94 to 6.43 Ma; Cerro Blanco 6.82 to 6.07 Ma; Cerro Los Quesos 7.73 to 7.11 Ma, and Cerro Hueco La Zorra 6.78 to 6.16 Ma (Fig. 1). There are no major erosional levels apparent in the sedimentary sections between the dated tuff layers. Based on dates and GPS elevations, the calculated accumulation rate values are 11–30 cm/1000 yr. Observations of decaying modern whale carcasses on both shallow and deep marine seafloors suggest that these calculated sedimentations rates are too low to account for the excellent degree of preservation observed in the Pisco Formation whales. Clearly the diatomaceous units containing whales must have been deposited several orders of magnitude faster than what is observed in modern marine environments and what is estimated by sedimentation rates after Ar–Ar dates, otherwise the whale skeletons would have been destroyed before burial. Higher rates of sedimentation were also suggested by Brand et al. (2004) based on preservation of diatoms. In addition to a higher rate of diatom production and accumulation, hyperpycnal flows may have played a significant role in deposition of large volumes of fine-grained sediment within the Pisco Basin. Hyperpycnal flows originate when a river in flood discharges a sustained and relatively dense turbulent mixture of fresh water and sediments into a marine basin (Mulder and Chapron, 2011; Zavala et al., 2011). The flow of sediment-laden water from rivers into the basin would explain the small amount of freshwater diatoms, which would mix in with the relatively abundant neritic, pelagic and open-ocean diatoms brought in by upwelling and wind-driven currents.

It is possible that the muddy diatomaceous bottom substrate was partly soupy. The cohesive nature of that soft sediment may have hindered reflotation of the carcass, and contributed to the fast burial, the high degree of preservation, and the limited disarticulation and displacement of the bones. If skeletons sank into soupy, soft sediment sedimentary structures would result from the deformation of the layers. However, excavation of the thirty-two specimens did not show evidence of the skeletons sinking into soupy sediment.

9. Summary

The Pisco Formation sedimentary succession consists of fine sandstones and siltstones, thin carbonates, shell beds, phosphate nodules and diatomaceous and tuffaceous siltstones and mudstones. This study focused on the abundant cetacean skeletons found in the thick, massive diatomaceous, tuffaceous mudstones in the top tens of meters of the sedimentary section in numerous locations. Several lines of evidence suggest that the basin was not anoxic, and that sedimentation rates, including diatoms, siliciclastics, and volcanic ash, were very high. The diatoms in the analyzed samples represent shallow marine to pelagic assemblages, typical of a neritic and nearshore assemblage but containing fragments of open ocean, planktonic taxa, which suggests that lateral advection occurred in the ancient eastern equatorial Pacific Ocean that brought water from the open ocean to the Peruvian coast. The minor appearance of occasional freshwater diatoms indicates continental influx into the basin.

The large number of skeletons indicates that the basin was an environment for large populations of different species of cetaceans and other marine mammals. Perhaps some carcasses were brought into the embayment by offshore currents. Most specimens are either adult or sub-adult, indicating that the area was not a breeding ground. Most of the fossil whales show a high degree of articulation and all of them show excellent preservation. Baleen is found in anatomical position in many specimens. Thin sections of the bones reveal that the bones are well mineralized, and that microbial bioerosion is rare or minimal on the bone surface.

The skeletons do not resemble modern whale carcasses on the seafloor, which are rapidly scavenged, bioeroded and destroyed within a few months to a few years after death. The large numbers of whale skeletons in multiple strata (bone beds) in the Pisco Formation diatomaceous layers and their excellent, uniform preservation indicate that they are not an attritional assemblage, but the result of recurrent mass mortalities followed by rapid burial before scavenging and abrasion could damage the bones. Disease, starvation, and toxicity of the food may have been the main causes of mass mortality of the marine mammals. Also volcanic ash may have played a role in the massive die-offs because these marine mammals come up to the surface to breathe, and the sharp shards may have caused damage to the lungs and asphyxiation.

The high degree of articulation and completeness suggests that most of the individuals did not float or refloat for a long time and loss of skeletal parts (mostly skull, dentaries, limbs) did not occur before reaching the sea bottom. High rates of sedimentation of diatoms, mud and volcanic ash quickly covered the carcasses, but not before the soft tissue was eliminated. The very fine, soupy diatomaceous mudstone sediment may have retained the carcasses attached to the bottom of the ocean, hindering reflotation of most assemblages, and thus preventing disarticulation. Incomplete and disarticulated or partially disarticulated specimens may be explained by explosion due to bloating, water currents, or the feeding activity of large scavengers, which nevertheless did not leave tooth marks on the bones.

The diatomaceous units containing whales must have been deposited several orders of magnitude faster than what is observed in modern marine environments and what is estimated by sedimentation rates after Ar–Ar dates, otherwise the whale skeletons would have been destroyed before burial. The large number (thousands) of fossil cetaceans and their excellent degree of preservation, including the soft tissue of baleen, makes the Pisco Formation assemblage a true fossil lagerstätten (Seilacher et al., 1985).

Acknowledgments

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Appendix 1

Summary of completeness and articulation of the fossil marine mammals. Excavated assemblages of Fig. 1 are included here. Completeness and the degree of original articulation and disarticulation are based on visual assessment of the specimen on the surface of the sediment and partial excavation. Some specimens are currently preserved in several pieces of cemented rock containing several bones, showing sufficient evidence of their original degree of articulation. Sometimes the occurrence of certain skeletal elements (skull, vertebrae, dentaries, ribs, limbs) and their degree of articulation were difficult to determine due to burial conditions or weathering of the bones, or because it was not observed by the authors, and that is reflected in the table as blank cells and question marks. The shark teeth were found associated with several specimens, and sometimes the number of them was recorded. Abbreviations: artic. = articulated; cerv. vert. = cervical vertebrae; disart. = disarticulated; dsu/vsu = dorsal-side up/ventral-side up orientation of the skull; orient. = compass orientation of skull (only one figure is given when the orientation of skull and body is the same or slightly similar). FP08-20 is a phocid. CB11-05 is a seal.

Table A1
Fossils in diatomaceous sediments of the Pisco Formation.

Area: Cerro Blanco North												
	Articulation degree											
Specimen	Originally articulated vertebrae	Originally disarticulated vertebrae	Currently complete?	Skull	Skull dsu/vsu	Dentaries	Skull artic. to cerv. vert.	Ribs	Limbs	Skull & body orient	Shark teeth	Baleen
BALEENBIV	Yes	?	No	Yes	dsu	Yes	Yes	?	?	155		Yes, in situ
CB11-01	Yes	No	Yes	Yes	dsu	Yes	Yes	Yes	Yes	295		
CB11-02	Yes	No	Si	Yes	vsu	Yes	Yes	Yes	Yes	225/134		
CB11-03	Yes	No	No	Yes		Yes	No	Yes	No	44	Yes (4)	
CB11-04	Yes	Yes	No	Yes	vsu	Yes	Yes	Yes	Yes	148	No	
CB11-05 (seal)	Yes	Yes	No	Yes	?	Yes	Yes	Yes	Yes	?		
CBL-10	Yes	No	No	Yes	dsu	Yes	Yes	Yes	Yes	300	No	
CBL-11	Yes	Yes	No	Yes	dsu	Yes	Yes	Yes	Yes	25		
CBL-14	Yes	No	Yes	Yes	dsu	Yes	Yes	Yes	Yes	350		
CBL-16												
CBL-18	Yes	?	No	Yes	dsu	Yes	Yes	Yes	Yes	260		Yes
CBAL-2	?	?	No	Yes	dsu	Yes	No	Yes	?	180		
CBAL-3												
CBAL-4	Yes		No	Yes		Yes	?	Yes	Yes	106		
CBAL-5	Yes	Yes	Yes	Yes	vsu	Yes	Yes	Yes	Yes	30		
CBAL-6												
CBAL-7	Yes	?	No	Yes	vsu	Yes	Yes	Yes	Yes	40		
CBAL-8												
CBAL-9	Yes		Yes	Yes	vsu	Yes	Yes	Yes	Yes	140		
CBAL-10		?	No	Yes		Yes	Yes	?	?	80		
CBAL-11	?	?	No	Yes		Yes		?	?	70		
WCBa-12	No	No	No	No		No		Yes				
WCBa-13	Yes	?	No	Yes	vsu	?	Yes	?	?	242		
WCBa-14												
WCBa-15	Yes	?	No	Yes	?	?		?	?	/242		
WCBa-16	?	?	No	Yes		?		Yes	?	28		
WCBa-17	?	?	No	Yes				Yes		0		
WCBa-18	Yes	No	Yes	Yes	vsu	Yes	Yes	Yes	Yes	138	No	Yes in situ
WCBa-19	?	?	No	Yes	dsu	?	?	Yes	?	350		
WCBa-20	Yes	No	Yes	Yes	vsu	Yes	Yes	Yes	Yes	96	Yes (4)	Yes, disartic
WCBa-21			No	Yes				No		80		
WCBA-22		Yes	No					Yes		Not possible		
WCBa-23			No	Yes		No				334		
WCBA-24	Yes		Yes	Yes	dsu					42		
WCBA-25	Yes		?	Yes		?	Yes	Yes	?	262		
WCBA-26			No	Yes								
WCBA-27			Yes		dsu			Yes		202	Yes	
WCBa-28	Yes		No									
WCBa-29	Yes	Yes	No	Yes						106		
WCBa-30	Yes	Yes	No	Yes	dsu			Yes	Yes	18		
WCBa-31			No	Yes		?	No			38		
WCBa-32	Yes	No	Yes	Yes	vsu	Yes	Yes	Yes	1	100	Yes (4)	
WCBa-33	Yes		No	Yes	dsu		Yes	?	?	76/62		
WCBa-34	?	?	No	Yes		Yes	?	?	?	202		
WCBa-35	Yes	Yes		Yes	dsu	Yes	Yes	Yes	?	316		
WCBa-36												
WCBa-37	?	?		Yes		?	?	Yes	?	186		
WCBa-38	?	?	No	Yes	vsu					258		
WCBa-39			No									
WCBa-40			No		vsu					291		
WCBa-41	Yes	?	No	Yes			?	Yes	?	330		
WCBa-42	?	?	No	Yes	?	?	?	?	?	156		
WCBa-43	Yes	?	Yes	Yes	dsu	Yes	Yes	Yes	?	318		

(continued on next page)

Table A1 *(continued)*

Area: Cerro Blanco North

Specimen	Articulation degree		Currently complete?	Skull	Skull dsu/vsu	Dentaries	Skull artic. to cerv. vert.	Ribs	Limbs	Skull & body orient	Shark teeth	Baleen
	Originally articulated vertebrae	Originally disarticulated vertebrae										
WCBa-45	Yes	Yes	No	Yes	dsu					130		
WCBa-46			No	Yes	dsu			Yes		250		
WCBa-47	Yes		No	Yes	vsu	?	Yes	Yes	?	134		
WCBa-48	Yes		Yes	Yes		?		Yes	?	26		
WCBa-50			No	Yes						134		
WCBa-51			No	No		No		No	No		Yes	
WCBa-52	Yes	Yes	No	Yes		?		?	?	/176		
WCBa-53	Yes	?	No	Yes		?		Yes	Yes	132		
WCBa-54	Yes	?	No	Yes	dsu	Yes	?	Yes	Yes	260		
WCBa-55	Yes	?	No	Yes		Yes	Yes	Yes	Yes	194		
WCBa-56	?	?										
WCBa-57	Yes	?	No	Yes	dsu	?	Yes	Yes	?	122		
WCBa-58	?	?	No	Yes	dsu	?	No	Yes	?	348		
WCBa-59	?	?	No	Yes				Yes	Yes	276		
WCBa-60	Yes	?	No	Yes		?	Yes	Yes	?	296		
WCBa-61	Yes	No	Yes	Yes	?	Yes	Yes	Yes	Yes	300		
WCBa-62	Yes	Yes	?	Yes	?	Yes	?	Yes	?	242		
WCBa-63	Yes	?	No	Yes						115		
WCBa-64	?	?	No	Yes	dsu	No		Yes	?	335	Yes	
WCBa-65	?	?	No	Yes	dsu	?		?	?	12		
WCBa-66	Yes	Yes	No	No				?				
WCBa-67	Yes	Yes	Yes	Yes	dsu	Yes	Yes	Yes	?	0/294		
WCBa-68	Yes	Yes	No	Yes	vsu	Yes	?	Yes	?	142		
WCBa-69	Yes	Yes	No	No		No		Yes		/270		
WCBa-70	Yes	No	?	Yes	dsu	Yes	Yes	Yes	?	242		
WCBa-71	Yes	?	No	Yes	dsu	?	Yes	Yes	No	26		
WCBa-72	?	?	No	Yes	vsu	Yes		Yes		172		
WCBa-73	Yes	Yes	No	No		Yes				80		
WCBa-74	Yes		No	No						324		
WCBa-75		Yes	No	No	dsu	?		Yes		278		
WCBa-76				Yes	dsu					294		
WCBa-87	Yes	No	No	Yes	vsu	Yes	Yes	Yes	?	5		
WCBa-88	Yes	Yes	No	Yes	vsu	?	Yes	Yes	?	47		
WCBa-89		Yes	No	Yes	dsu	Yes		Yes	?	45		
WCBa-90		Yes	No	Yes	vsu	Yes	No	?	?	355		
WCBa-91			No	Yes	vsu	?				300		
WCBA-92	?	?	No	Yes						300		
WCBa-93	?	?	No	Yes		Yes		Yes	?	292		
WCBa-94	?	?	No	Yes	dsu	Yes		Yes	?	292		
WCBa-95	No	No	No	Yes		No		No				
WCBa-96	Yes		No	Yes	dsu	Yes	Yes	Yes	?	260		
WCBa-97	No	No	No	Yes		No	No	No	No	6		
WCBa-99	Yes	No	No	Yes	?	?	?	Yes	?	32		
WCBa-100	?	?	No	Yes			?	?	?			
WCBa-101	?	?	No	Yes	dsu	No	Yes	No	Yes	230		
WCBa-102	?	?	No	No			No					
WCBa-103			No	No		Yes						
WCBa-104	Yes	No	No	Yes	dsu	Yes	Yes	Yes	?	326		
WCBa-105		Yes	No									
WCBa-107	Yes	Yes	No	Yes	?	Yes	?	Yes	Yes	28		
WCBa-108			No									
WCBa-110	Yes		No	Yes	?	?	?	Yes				
WCBa-111			No									
WCBa-112	Yes	Yes	Yes	Yes	vsu	Yes	Yes	Yes	Yes	186	Yes (4)	
WCBa-113			No									
WCBa-114	?	?	No					Yes				
WCBa-115	?	?	No					Yes				
WCBa-117	Yes	Yes	No	Yes	?	?	Yes	Yes	?	38		
WCBa-118			No									
WCBa-119			No									
WCBa-120	Yes	?	No	Yes	?	?	?	Yes	?	0		
WCBa-121	Yes		No	Yes		Yes	Yes	Yes	?	230		
WCBa-122	Yes		No	Yes	vsu	Yes	Yes	Yes	?	285		
WCBa-126												
WCBa-127	?	?	No	Yes	dsu	?	Yes	Yes	Yes	220		
WCBa-128												
WCBa-129												
WCBa-130	?	?	No	Yes	dsu	?	?	?	?	180		
WCBa-132	Just 2 vertebrae											
WCBa-134			No	Yes								
WCBa-135	Yes		No	Yes	?	?	Yes	Yes		34		

Table A1 *(continued)*

Area: Cerro Blanco North												
	Articulation degree											
Specimen	Originally articulated vertebrae	Originally disarticulated vertebrae	Currently complete?	Skull	Skull dsu/vsu	Dentaries	Skull artic. to cerv. vert.	Ribs	Limbs	Skull & body orient	Shark teeth	Baleen
WCBa-136												
WCBa-137	?	?	No	Yes	dsu			Yes		305		
WCBa-138											Yes (1)	
WCBa-139	Yes	Yes	No	Yes	dsu	Yes	Yes	Yes	Yes	217		
WCBa-140			No	Yes	dsu					215		
WCBa-141	Yes	?	No	Yes	?	Yes	No	Yes	?	274		
WCBa-142	Yes	Yes	No	Yes	vsu	No	Yes	Yes	?	263		
WCBa-143	Yes	Yes	No	Yes	dsu	Yes	No	Yes	?	285		
WCBa-144										275		
WCBa-200	Yes	?	No	Yes	?	?	Yes	Yes	Yes	220		
WCBa-201	Yes		No	Yes	?	Yes	Yes	Yes	?	85		
WCBa-202	Only skull and dentaries preserved			Yes	vsu	Yes	No	No	No	25		
WCBa-203			No									
WCBa-204			No	Yes								
WCBa-205	Yes	No	No	Yes	dsu	Yes	No	Yes	?	320		
WCBa-206	Yes		No	Yes	dsu	Yes	No	Yes	?	200		
WCBa-207												
WCBa-208												
WCBa-209												
WCBa-210			No	Yes	?	Yes		Yes	?	105		
WCBa-212	Yes	Yes	No	Yes	vsu	Yes, dis	No	Yes				
WCBa-214	Bone fragments		No									
WCBa-215			No			Yes		Yes	Yes			
WCBa-219	7 disartic vertebrae		No									
WCBa-220		Yes	No	Yes	dsu	Yes, dis	No	Yes	Yes	65		
WCBa-223	Yes	Yes	No	Yes	vsu	Yes	Yes	Yes	Yes	155		
WCBa-224	?	?	No	Yes	?	Yes, dis	?	?	Yes	190		
WCBa-225												
WCBa-228	Yes	Yes	No	Yes	vsu	Yes, dis	?	Yes	?	350		
WCBa-229	Yes	Yes	No	Yes	?	Yes, dis	?	Yes	Yes	135		
WCBa-231	Yes	Yes	Yes	Yes		Yes	Yes	Yes	Yes			
WCBa-232			No									
WCBa-234	?	?	No	Yes	?	?	?	?	?	160		
WCBa-235	?	?	No	Yes	?	Yes	?	?	?	230		
WCBa-237	?	?	?	Yes	dsu	?	?	?	?	40		
WCBa-238												
WCBa-240			No									
WCBa-241	Yes	Yes	Yes	Yes	dsu	Yes	No	Yes	Yes	255		
WCBa-242	Yes	No	No	Yes	vsu	Yes	Yes	Yes	Yes	115		
WCBa-243	Yes	?	No	Yes		?		Yes	?			
WCBa-244	?	?	?	?	?	?	?					
WCBa-245	Yes	No	Yes	Yes	vsu	Yes	Yes	Yes	Yes	185		
WCBa-246	?	?	Yes	Yes	dsu	?	?	?	?	115		
WCBa-247	?	?	No	Yes	dsu	?	?	?	?	50		
WCBa-248	Yes	Yes	Yes	Yes	dsu	Yes	Yes	Yes	Yes	272		
WCBa-249	Yes		No	Yes	vsu	Yes	Yes	Yes	?	320		
WCBa-250	?	?	No	Yes	dsu	Yes	?	Yes	?	250		
WCBa-251	Yes		Yes	Yes	dsu	Yes	Yes	Yes	Yes	65		
WCBa-252												
WCBa-254	?	Yes	No	Yes	dsu	Yes, dis	?	?	?	314		
WCBa-255	Yes	No	No	Yes	dsu	Yes	Yes	Yes	?	297		
WCBa-256	Yes	No	No	Yes	vsu	Yes	Yes	Yes	Yes	303		
WCBa-257	Yes	?	No	No		No	No	No	No			
WCBa-258	?	?	No	Yes	?	?	?	?	?			
WCBa-259	Yes	No	No	Yes	vsu	Yes	Yes	Yes	?	116		
WCBa-260	?	?	No	Yes	?	?	?	Yes	?			
WCBa-261	?	?	No	Yes								
WCBa-262	?	?	No									
WCBa-264	?	?	No	Yes	dsu	No	No	No	No	234		
WCBa-265			No	Yes								
WCBa-266	?	?	Yes	Yes	?	?	Yes	Yes	?	55		
WCBA-267	?	?	No									
WCBA-272			No									
WCBa-273	?	?	?	Yes	vsu	Yes	?	?	?	130		
WCBa-274			No									
WCBa-275			No									
WCBa-277		Yes	No	Yes	vsu	Yes	No	Yes	?	185		
WCBa-278	?	?	No	Yes	dsu	?	?	?	?	165		
WCBa-279	Yes	?	No	No		No		Yes	?			
WCBa-280			No	Yes	?	No	No					

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Table A1 *(continued)*

Area: Cerro Blanco North

Specimen	Articulation degree		Currently complete?	Skull	Skull dsu/vsu	Dentaries	Skull artic. to cerv. vert.	Ribs	Limbs	Skull & body orient	Shark teeth	Baleen
	Originally articulated vertebrae	Originally disarticulated vertebrae										
WCBa-281	Yes	?	Yes	Yes	dsu	Yes	Yes	Yes	?	105		
WCBa-284	Yes		No	Yes	vsu	?	Yes	Yes	?	260		
WCBa-285	8 articulated vert small animal, other bones											
WCBa-286	No	Yes	No	?	?	Yes	No	Yes	Yes			
WCBa-289	?	Yes	No									
WCBa-290	?	?	No	Yes	vsu	No	No	No	No	340		
WCBa-291	Yes	No	No	Yes	vsu	Yes	Yes	Yes	?	50		
WCBa-293	?	?	No	No		No		No	Yes			
WCBa-295			No									
WCBa-296			No									
WCBa-297			No									
WCBa-298			No					Yes				
WCBa-299			No									
WCBa-300	?	?	No	Yes	?	Yes		?	?	270		
WCBa-301	Yes	?	No	Yes	dsu	?	Yes	Yes	Yes	190		
WCBa-302	Yes	Yes	No	Yes	dsu	Yes	No	Yes	Yes	30/	Yes	
WCBa-303	Yes	No	No	Yes	?	Yes	Yes	Yes	Yes	320		
WCBa-304	?	?	Yes	Yes	?	?	?	?	?	135		
WCBa-305	?	?	No	Yes	?	?	?	Yes	?	?		
WCBa-306	Yes		No	Yes	dsu	Yes	Yes	Yes	Yes	346		
WCBa-307	?	?	No	Yes								
WCBa-309			No									
WCBa-310	No	Yes	No	Yes	dsu	Yes	No	Yes	?	200		
WCBa-311	Yes	Yes	No	?	?	?	?	Yes	?			
WCBa-312	Yes	Yes	Yes	Yes	dsu	Yes	Yes	Yes	Yes	76		
WCBa-313	Yes	?	No	Yes	?	Yes	?	Yes	?	115		
WCBa-314			No									
WCBa-315	?	?	No	Yes	?	Yes	?	Yes	?			
WCBa-322			No	?		Yes						
WCBa-317	Yes	No	No	Yes	dsu	Yes	Yes	Yes	Yes	290		
WCBa-318	Yes	No	Yes	Yes	vsu	Yes	Yes	Yes	Yes	105		
WCBa-319	?	?	?	?	?	?	?	Yes	?			
WCBa-321	?	?	No	Yes	?	?	?	Yes	?			
WCBa-323		Yes	No	?		Yes		?	?			
WCBa-325	Yes	No	No	Yes	vsu	Yes	Yes	Yes	Yes	270		
WCBa-326	One single vertebra											
WCBa-327	?		No	Yes	dsu	Yes	No	No	No			
WCBa-328	Yes	No	No	Yes	dsu	Yes, dis	Yes	Yes	?	234		
WCBa-329	Yes	No	No	Yes	dsu	Yes	Yes	Yes	Yes	295		
WCBa-330	?	?	No	Yes	dsu	?	?	?	?	272		
WCBa-332						Yes						
WCBa-333	Yes	Yes	?	Yes	vsu	Yes	No	Yes	Yes	105		
WCBa-334	Yes	?	No	Yes	?	?	?	Yes	?	275		
WCBa-335	Unidentified bones											
WCBa-336	Yes	Yes	No	Yes	dsu	Yes	Yes	Yes	Yes	22		
WCBa-337	Yes	Yes	No	Yes	dsu	?	No	Yes	?	197/20		
WCBa-338	Yes	No	No	Yes	vsu	Yes	Yes	Yes	?	195		
WCBa-339	Yes	?	No	Yes	?	?	Yes	Yes	?	160		
WCBa-340	?	?	No	Yes	?	Yes	?	?	Yes	220		
WCBa-341			No	Yes	dsu	?	No	No	?	302		
WCBa-342	Weathered disartic vert											
WCBa-343	Yes		No	Yes	dsu	No	Yes	Yes	Yes	170		Yes, in situ
WCBa-345	1 isolated dentary					1						
WCBa-346	Yes	No	Yes	Yes	?	Yes	Yes	Yes	Yes	/292		
WCBa-347	No	Yes	No	Yes	dsu	Yes	No	Yes	?	115		
WCBa-348		Yes	Yes	Yes	dsu	Yes	Yes	Yes	?	0		
WCBa-349			No	Yes	?	Yes	No	No	No	240		
WCBa-350			No	Yes	vsu	Yes	No	No	No	232		
WCBa-351			No	Yes	vsu	Yes	No	No	No	268		
WCBa-352	A pile of disartic bones		No									
WCBa-353			No	No		No		Yes	Yes		Yes (3)	
WCBa-354		Yes	No	Yes	dsu	Yes	No	?	?	154		
WCBa-355	6 large, disartic vert		No									
WCBa-356												
WCBa-357	Pieces of a skull		No	Yes								
WCBa-358			No	Yes	dsu	Yes	No	No	No	244		
WCBa-359	?	?	No	Yes		?	?	Yes	?			
WCBa-360	?	?	No	No		No		Yes	Yes			
WCBa-361												

(continued on next page)

Table A1 *(continued)*

Area: Cerro Blanco North												
	Articulation degree											
Specimen	Originally articulated vertebrae	Originally disarticulated vertebrae	Currently complete?	Skull	Skull dsu/vsu	Dentaries	Skull artic. to cerv. vert.	Ribs	Limbs	Skull & body orient	Shark teeth	Baleen
WCBa-362				Yes		No					Yes	
WCBa-363	?	Yes	No	Yes		?		Yes	?			
WCBa-364	?	Yes	?	Yes	dsu	Yes	?	Yes	?	268		
WCBa-365												
WCBa-366	Yes	Yes	No	Yes	vsu	Yes	No	Yes	?			
WCBa-367	Yes	Yes	No	No		No		Yes	?			
WCBa-370				Yes								
WCBa-371	Yes	Yes	Yes	Yes	vsu	?	Yes	Yes	?	232		
WCBa-372	Yes	?	Yes	Yes	dsu	Yes	No	Yes	?			
WCBa-373	Yes	No	Yes	Yes	vsu	Yes	Yes	Yes	?	130		
WCBa-374	Yes	Yes	?	?	?	?	?	Yes	?			
WCBa-375	No	No		Yes		?	No	No	No			
WCBa-376	?	Yes	No	No		No		Yes				
WCBa-377	Yes	No	No	Yes	vsu	Yes	Yes	Yes	?	353		
WCBa-378	Yes	Yes	No	Yes	?	Yes	?	Yes	?	56		
WCBa-380	Yes	No	No	Yes	dsu	Yes	No	Yes	?	298		
WCBa-381	No	No		Yes	vsu	Yes	No	No	No	348		
WCBa-382												
WCBa-383			No	Yes	vsu	?						
WCBa-384												
WCBa-385	?	?	No	Yes	dsu	?	Yes	?	?	243		
WCBa-386												
WCBa-387	?	?	No	Yes		Yes	?	?	Yes			
WCBa-388												
WCBa-389	Yes	Yes	No	Yes	dsu	Yes	No	Yes	?	70/55		
WCBa-392	?	?	Yes	Yes	?	?	?	?	?	15		
WCBa-393			No	Yes	dsu	?						
WCBa-394	Yes	?	No	Yes	vsu	?	Yes	Yes	Yes	260		
WCBa-396				Yes								
WCBa-395	Yes	No	No	Yes	vsu	Yes	Yes	Yes		317		
WCBa-397												
WCBa-398	Yes	?	No	Yes	?	Yes	Yes	Yes	?	320		
WCBa-400	Yes									180		
WCBa-401	?	?						Yes				
WCBa-402	Yes	?	No	?		?		Yes	Yes			
WCBa-403	Yes	?	No	Yes	?	Yes	?	Yes	?	200		Yes
WCBa-404	Yes	?	No	Yes	dsu	Yes	Yes	Yes	Yes	150		Yes, in situ
WCBa-405	Yes	?	No	Yes	vsu	?	Yes	Yes	?	80		
WCBa-407	Yes	?	No	?		?		?	?			
WCBa-408	?	?	No					Yes				
WCBa-410	?	Yes	Yes	Yes	?	?	?	Yes	?	222		
WCBa-430	?	?	No	Yes	?	?	?	Yes	?	?		
WCBa-431	?	?	No	Yes	dsu	?	?	Yes	?	?		
WCBa-433			No									
WCBa-434	Yes		No	?		?	Yes					
WCBa-435	?	?	No	Yes		Yes		Yes				
WCBa-463	Yes	Yes	No	Yes	vsu	Yes	No	Yes	Yes	188/30		
WCBa-464	Only disarticulated vertebrae											
WCBa-501	Disarticulated bones											
WCBa-502	Yes		No	No		No		No	No			
WCBa-516	Yes	Yes	No	No		No		?	?			
WCBa-517	Yes	Yes	No	No				Yes				
WCBal-14	Yes	Yes	No	Yes	dsu	Yes	Yes	Yes	Yes	280/330		
WCBal-15												
WCBal-16												
WCBal-17	Yes		No	Yes	dsu	Yes	Yes	Yes	Yes	250		Yes
WCBal-18												
WCBal-19	Yes	Yes	No	Yes	dsu	Yes	?	Yes	?	5		
WCBal-20												
WCBal-21	Yes		Yes	Yes	dsu	Yes	Yes	Yes	?	10		
WCBal-22										75		
WCBal-23		?	No	?		?		Yes				
WCBal-24												
WCBal-25												
WCBal-26												
WCBal-27												Yes
WCBal-28	Yes		Yes	Yes	dsu	Yes	Yes	Yes	Yes	340		
WCBal-29	Yes		Yes	Yes	dsu	Yes	No	Yes	Yes	340		
WCBal-30												
W1												

(continued on next page)

Table A1 *(continued)*

Area: Cerro Blanco North												
	Articulation degree											
Specimen	Originally articulated vertebrae	Originally disarticulated vertebrae	Currently complete?	Skull	Skull dsu/vsu	Dentaries	Skull artic. to cerv. vert.	Ribs	Limbs	Skull & body orient	Shark teeth	Baleen
W8				Yes		Yes			Yes			
W13	Yes	No	Yes	Yes	dsu	Yes	Yes	Yes	Yes	238		
W14	Yes	No	No	Yes	dsu	Yes	No	Yes	?	80		
W15	Yes	?	No	?	?	?	?	Yes	?	?		
W500			No									
W503	Yes	?	No	Yes	dsu	Yes	Yes	Yes	?	355		
W-504												
W-505								Yes				
W-506								Yes				
W-507	?	?	?	Yes	dsu	?	?	?	?	212		
W-508												
W-509	?	Yes	No	?	?	?	?	Yes	?			
W-510												
W-511												
W-512												
W-513	Yes	?	No	Yes	vsu	?	Yes	Yes	?	35		
W-514	?	?	No	?	?	?	?	Yes	?	?		
W-515	?	?	No	Yes	vsu	Yes	No	No	No	317		
W-518	No	Yes	No	No		No	No	Yes	?			
W-519	No	Yes	No	?	?	?	?	Yes	?			
W-520			No			Yes						
W-521			No									
W-522			No									
W-523			No									
W-524												
W-525	Yes		No	Yes	dsu	Yes	Yes	Yes	?	130		Yes, in situ
W-526												
WCB1			No									
WCB2	Yes	No	No	Yes	vsu	Yes	Yes	Yes	?	93		Yes
WCB3	Yes	Yes	Yes	Yes	vsu	Yes	?	Yes	Yes	95/305		
WCB4	Yes		No	Yes	vsu	Yes	Yes	Yes	Yes	255		
WCB5			No					Yes (2)				
WCB6	Yes		No	Yes	dsu	Yes	Yes	Yes	Yes	178		
WCB7	Yes	?	No					Yes	?			
WCB8			No	Yes						18		
WCB9												
WCB10								Yes				
WCB11												
WCB12				Yes								
WCB16												
Area: Cerro Blanco North												
WC-1	Yes		No	Yes		?	Yes	Yes	?	150		
WC-2	Yes	?	No	?		?		?	?			
WC3			No									
WC4			No									
WC5	Yes	?	No	Yes			Yes	?	?	290		
WC6	Yes		Yes	Yes	dsu	Yes	Yes	Yes	?	182		
WC7	Yes		No	Yes	vsu	Yes	Yes	Yes	No	120		
WC8	?	?	No	Yes		?	?	?	?			
WC9		Yes										
WC10	Yes	Yes										
WC11	Yes	Yes	?	Yes	vsu	?	?	Yes	?	35		
WC12				Yes	dsu					175		
WC13												
WC14				Yes	dsu					40		
WC15									Humerus			
WC16	Yes	?										
WC17				Yes						73		
WC18	Yes	?	No	Yes		?	Yes	Yes	?	110		
WC19	Yes	?	Possible	Yes	vsu	Yes	Yes	Yes	?	203		
WC20	Yes	?	No	No								
WC21	Yes		No	Yes	vsu	Yes	?	Yes	Yes	295		
WC22			No			Yes						
WC23	Yes	Yes	?	Yes	dsu	Yes	Yes	Yes	?	182		
WC24												
WC25			No									
WC26	Yes	?	No							145		
WC27	?	?	No	Yes		Yes	?	Yes	?			
WC28	Yes	Yes	No	Yes		?	?	Yes	?			

Table A1 *(continued)*

Area: Cerro Blanco North												
	Articulation degree											
Specimen	Originally articulated vertebrae	Originally disarticulated vertebrae	Currently complete?	Skull	Skull dsu/vsu	Dentaries	Skull artic. to cerv. vert.	Ribs	Limbs	Skull & body orient	Shark teeth	Baleen
WC29			No			Yes						
WC30	Yes		No	Yes		?	?	Yes	?	150		
WC31						Yes						
WC32			No	Yes	dsu	?				195		
WC33	Yes	?	No	Yes	dsu	Yes	Yes	Yes	?	180		Yes in situ
WC34	?	?										
WC35												
WC36												
WC37												
WC38	Yes		?	Yes		?	Yes	Yes	?	323		
WC39												
WC40												
WC41						Yes						
WC42												
WC43				Yes	dsu	Yes				108		
WC44						Yes						
Area: Cerro Hueco La Zorra												
IC-41	Yes	No	Yes	Yes	Side	Yes	Yes	Yes	Yes	250		Yes, in situ
Z51 (dolphin)	Yes	No	Yes	Yes	Side	Yes	Yes	Yes	Yes	135		
PIS09-26	Yes	Yes	No	Yes	dsu	Yes	No	Yes	Yes	190/250		
Area: Cerro Queso Grande												
WQG-10	?	?	No	Yes	?	?	Yes	Yes	?	186		
WQG-11			No									
WQG-12			No									
WQG-13	Yes	No	?	Yes	vsu	Yes	Yes	Yes	Yes	163		
WQG-31	?	?	No	Yes	vsu	Yes	No	No	No	151		
WQG-32	?	?	No	Yes	?	?	?	?	?	63		Yes, in situ
WQG-33	?	?	No	Yes	dsu	No	No	No	No	12		
WQG-34	?	?	No	Yes	vsu	Yes	No	?	?	335		
WQG-35	Yes	No	No	Yes	dsu	?	Yes	Yes	Yes	242		
WQG-36	Yes	?	No	Yes	dsu	Yes	Yes	Yes	?	335		
WQG-37	?	?	No	?	?	?	?	Yes	?			
WQG-38	Yes	?	No	Yes	dsu	?	Yes	Yes	?	204		
WQG-39				?								
WQG-40				No				Yes				
WQG-41	Yes	?	?	Yes	dsu	Yes	?	Yes	?	136		
WQG-42	Yes	No	No	Yes	?	Yes	Yes	Yes	?	291		
WQG-43			No									
WQG-44			No					Yes				
WQG-45			No			Yes						
WQG-46			No									
WQG-47	?	?	No	Yes	dsu	?	?	?	?	46		
WQG-48	?	?	No	Yes	dsu	Yes	No	?	?	341		
WQG-49	Yes	No	Yes	Yes	vsu	Yes	Yes	Yes	Yes	331		
WQG-50			No									
WQG-51			No									
WQG-52			No	Yes	dsu	?				321		
WQG-53			No									
WQG-54			No	Yes								
WQG-55			No	Yes	dsu	Yes	No	No	No	21		
WQG-56			No			Yes						
WQG-57	No	Yes	No	Yes	vsu	Yes	No	Yes	Yes	26		
WQG-58			No									
WQG-59			No									
WQG-60	Yes	?	?	Yes	vsu	No	Yes	Yes	Yes	316		
WQG-61	Yes	?	No	Yes	?	Yes	?	Yes	?	146		
WQG-63	No	Yes	No	No		Yes		Yes	Yes			
WQG-64			No			Yes						
WQG-65			No			Yes						
WQG-66			No	Yes								
WQG-67	No	No	No	Yes	dsu	No	No	No	No	120		
WQG-68			No			Yes						
WQG-69			No					Yes				
WQG-70			No									
WQG-73	Yes		No	Yes	vsu	Yes	Yes	Yes	?	125/111	?	?
WQG-74			No	Yes	?	No	No	No	No	132		
WQG-75			No	No		No		1	No			
WQG-76			No									
WQG-77			No									

(continued on next page)

Table A1 *(continued)*

Specimen	Articulation degree		Currently complete?	Skull	Skull dsu/vsu	Dentaries	Skull artic. to cerv. vert.	Ribs	Limbs	Skull & body orient	Shark teeth	Baleen
	Originally articulated vertebrae	Originally disarticulated vertebrae										
Area: Cerro Blanco North												
WQG-78	No	Yes (2)	No	Yes	vsu	Yes	No	No	No	316		
WQG-78a	?	?	?	Yes	dsu	Yes	?	Yes	Yes	236		
WQG-79			No									
WQG-80			No	No		Yes						
WQG-81	?	?	No	Yes	dsu	Yes	?	Yes	?	236		
WQG-82			No									
WQG-83	?	?	No	Yes	dsu	?	?	Yes	?	237		
WQG-84			No									
WQG-85	?	?	No	Yes	dsu	Yes	?	Yes	Yes	171		
WQG-86	?	?	No	Yes	vsu	?				229		
WQG-87	?	?	No	Yes	vsu	?	?	?	?	286		
WQG-88			No	Yes						281		
WQG-89				Yes								
WQG-90												
WQG-91												
WQG-92				Yes								
Area: Cerros La Bruja and Amara												
WIR-74	Yes	No	No	Yes	dsu	Yes	Yes	Yes	?			Yes in situ
PIS09-31	?	?	No	?	?	?	?	Yes	?	?		
PIS09-32	?	?	No	Yes	?	?	?	Yes	?	?		
PIS09-33	?	?	No	Yes	vsu	?	?	Yes	?	?		
PIS09-34	?	?	No	?	?	?	?	Yes	?			
PIS09-35	Yes		No	Yes	?	Yes	Yes	Yes	Yes			
Area: Cerro Los Quesos												
FP08-12	Yes	Yes	Yes	Yes	vsu	Yes	No	Yes	Yes	300	Yes	
FP08-13	?	?	No	Destroyed	?	?	?	Yes	Yes	?		Yes, in situ
FP08-14			No	Destroyed								Yes, in situ
FP08-15	Yes		Yes	Yes	?	?	?	Yes	Yes			?
FP08-16	?	?	No	Yes	?	?	?	Possibly	Possibly			Yes, in situ
FP08-17	Yes		Yes	Yes		?	?	Yes	?	/70		Yes, in situ
FP08-18	Yes		No	Yes	dsu	Yes	Yes	Yes	Yes			
FP08-19	Yes		Yes	Yes	dsu	Yes	Yes	Yes	Yes	102		Yes, in situ
FP08-20 (Phocid)	?	?	No	Yes	–	Yes	?	Yes	Yes			–
FP08-21	Yes		No	Yes	dsu	Yes	Yes	Yes	?	340		
IC-1	Yes	No	Yes	Yes	vsu	Yes	Yes	Yes	Yes	135		Yes, in situ
LQ10-01	?	?	No	No		No	?	Yes	Yes			
LQ10-02	Yes	?	No	Yes	dsu	Yes	Yes	Yes	?	15		
LQ10-03	Yes	?	No	No		No		Yes				
LQ10-04	?	?	No	No		No		No	No			
LQ10-05			No									
LQ10-06	Yes		No	Yes	vsu	Yes	No	Yes	?	255		
LQ10-07			No					Yes (1)				
LQ10-08			No									
LQ10-09			No									
LQ10-10	?	?	No			Yes		Yes				
LQ10-11	Yes	?	No									
LQ10-12	?	Yes	No									
LQ10-13			No	Yes	yes							
LQ10-14	?	?	No	Yes	?	Yes		Yes	Yes			
LQ10-15	Yes	?	No	?		?		Yes				
LQ10-16	?	?	No	Yes	dsu	Yes		?	?	20		
LQ10-17	No	No	No	Yes	dsu	No		No	No	40		
LQ10-18												
LQ10-19	A seal, missing skull											
LQ10-20	?	?	No	Yes	dsu					230		
LQ10-21												
LQ10-22	?	?	No	Yes	dsu	Yes	?	?	?	30		
LQ10-23	?	Yes	?	?	?	?	?	Yes	?	?		
LQ10-24	No	Yes	No	Yes	?	Yes	?	Yes	Yes			
LQ10-25	?	?	No	Yes	dsu	?	?	?	?	160		
LQ10-26	?	?	No	Yes	dsu	?		?	?	320		
LQ10-27	?	?	No	No		Yes		Yes	?			
LQ10-28	?	?	?	Yes	vsu	Yes, disart	No	?	?	125		
LQ10-29			No									
LQ10-30	?	?	?	Yes	?	Yes	?	?	?	100		
LQ10-31			?	Yes						75		
LQ10-32												Yes, in situ
LQ10-33	?	?	?	?	?	?	?	Yes	?			

Table A1 *(continued)*

Area: Cerro Blanco North												
	Articulation degree											
Specimen	Originally articulated vertebrae	Originally disarticulated vertebrae	Currently complete?	Skull	Skull dsu/vsu	Dentaries	Skull artic. to cerv. vert.	Ribs	Limbs	Skull & body orient	Shark teeth	Baleen
LQ10-34	Yes	?	?	Yes	dsu	Yes	Yes	Yes	?	70		
LQ10-35	Yes	Yes	No	Yes	dsu	Yes	?	Yes	?	60		
LQ10-36	?	?	No	Yes	vsu	Yes	?	Yes	?	325		
LQ10-37	?	?	No	?	?	?	?	?	?	?		
LQ10-38	?	?	No	?	?	?	?	Yes	?			
LQ10-39		Yes	No	Yes	vsu	Yes	Yes	Yes	?	145		
LQ10-40		Yes	No	Yes	vsu	Yes	?	Yes	?	270		
LQ10-41		Yes	No	Yes	vsu	No	No	Yes	Yes	0		
LQ10-42	Yes	?	No	Yes	vsu	Yes, disart	Yes	Yes	Yes	110		
LQ11-01	Yes	No	No	Yes	?	?	Yes	Yes	?	110		
LQ11-02						1						
LQ11-03												
LQ11-04												
LQ11-05		Yes	No	Yes	vsu	Yes, disart	No	Yes	Yes	100		
LQ11-06			No	Yes	vsu							
LQ11-07												
LQ11-08												
LQ11-09	?	?	?	Yes	dsu	1		Yes	Yes	60		
LQ11-10	Yes	Yes	No	Yes	?	Yes	Yes	Yes	Yes	135		
LQ11-11				Yes	dsu	No						
LQ11-12	Yes	?	No	?	?	?	?	Yes	?			
LQ11-13	Yes	No	No	Yes	vsu	?	?	?	?	?		
LQ11-14												
LQ11-15												
LQ11-16	Yes	?	No	?	?	?	?	?	?			
Area: Cerro Ballena												
PIS09-13	Yes	Yes	No	No	?	No	No	Yes	Yes	220		
PIS09-14	Yes	Yes	No	Yes	dsu	Yes	No	Yes	Yes	295		
PIS09-15	Yes		No	Yes	vsu	Yes	Yes	Yes	Yes	60		
PIS09-16	?	?	No	Yes	dsu	?	?	Yes	Yes			
PIS09-17	Yes	No	No	?		?		Yes	?	260		
PIS09-18	Yes	Yes	Yes	Yes	dsu	Yes	Yes	Yes	Yes	180		
PIS09-19												
PIS09-20	Yes	No	No	Yes	vsu	Yes	No	Yes	Yes	230		
PIS09-21	?	?	No	Yes	?	?		Yes	?	310		
PIS09-22	Yes	?	No	?	?	?	?	Yes	?	?		
PIS09-23												
PIS09-24	Yes	No	No	Yes	vsu	Yes	Yes	Yes	Yes	88	Yes (1)	

Appendix 2. Descriptions of excavated whales

Abbreviations in figures

at = atlas; ba = baleen; ca = carpals; co = cochlea; cv = cervical vertebrae; dent = dentary; hu = humerus; max = maxillary; mc = metacarpals; oc = occipital condyles; ph = phalanges; pm = premaxillary; ra = radius; sc = scapula; st = shark tooth; tv = tail vertebrae; ul = ulna; vc = vertebral column; ve = vertebral epiphysis; vert = vertebrae; and za = zygomatic arch.

CB11-01 (Fig. 6)

Fully articulated specimen, including the two dentaries with closed symphysis gap, vertebral column and limbs. Cervical vertebrae are aligned and atlas bone is attached to the occipital condyles. Ribs and both limbs lie in symmetrical position on both sides of the vertebral column.

CB11-02 (Fig. 6)

Probably a complete specimen; some bones, including several ribs and an entire limb could be buried under the vertebral column and skull. Some phalanges of the preserved limb are missing due to recent weathering. Most of the vertebral column is articulated; some of the vertebrae are slightly dislocated or twisted, especially in the tail. Both cochleas occur in anatomical position. Both the two dentaries and cervical vertebrae are in anatomical position; however the skull is dislocated and lying ventral-side next to the cervical and thoracic vertebrae at a 90-degree angle. This whale fossil was reported in Esperante et al. (2011).

CB11-03 (Fig. 6)

Almost complete specimen, with missing bones probably due to recent weathering. Vertebral column is entirely disarticulated, but vertebrae and ribs remain roughly aligned along the original articulation sequence, with two clusters of two and three bones, respectively, still articulated. Skull is complete with one dentary in anatomical position and the other with its articulation end under the maxillary. Skull is preserved at a distance of 2.5 m away from the atlas bone, which is the nearest bone. Five shark teeth were found associated with the skeleton, one on top of the skull frontal bone another next to the right-side mandibular condyle, and three others in close proximity of vertebrae. No shark tooth marks were observed on any bone.

CB11-04 (Fig. 7)

Almost complete specimen except for one limb and some bones of the other limb. Skull articulated to the atlas. The two dentaries lie near anatomical position. The vertebral column is mostly aligned and articulated, although some vertebrae are slightly dislocated. A few lumbar and tail ventral are slightly displaced and lying on their centrum. Ribs are roughly aligned on both sides of the thoracic vertebrae.

CBL-10 (Fig. 7)

Fully articulated and almost complete skeleton. Specimen was found partially encased below a thin, cemented dolomite crust that covered all the thoracic area. The edges were eroded, which could account for the missing bones of the limbs and ribs. Also missing due to modern erosion are some lumbar and tail vertebrae. Dentaries were fragmented due to recent weathering, although the pieces remained aligned in close proximity to the skull. Skull articulated to vertebral column, which is fully articulated and slightly bent. Ribs occur in anatomical position and articulated on the thoracic vertebrae. Right-side limb is in anatomical articulation; left-side scapula is dislocated but lying next to thoracic vertebrae and ribs. Both limbs have scapula, humerus, ulna, radius, and carpals, but are missing metacarpals and phalanges due to modern weathering.

CBL-11

This skeleton is fully disarticulated but all the bones are closely associated and lying near their anatomical position. Left dentary is articulated; right dentary is disarticulated but near anatomical position. Almost all vertebrae are lying on their centra and show their transverse processes and neural spines fully attached to the body of the vertebrae. Most limb bones are missing, only one scapula, ulna and radius and 3 phalanges are preserved. Ribs clustered on both sides of the line of disarticulated vertebrae. Missing ribs, vertebrae and limb bones most likely due to erosion of the associated sediment.

FP08-12 (Fig. 7)

This skeleton was found on a gently sloping hillside. The distal part of the lumbar and caudal vertebral column extended into the slope, and was not excavated. Also, erosion of the slope caused destruction and/or weathering of some ribs, limb bones, skull and dentaries. The skull is partially detached from the atlas. Both dentaries lie on the same side of the skull. The right-side dentary lies next to the skull in near anatomical position, and is flat due to the weight of sediment. The left-side dentary was displaced from its original anatomical position, and lies with its proximal end on the supraorbital process of the frontal. Most vertebrae are either articulated or slightly dislocated, with some resting on their centra. Their transverse processes are attached to the body of the vertebrae. Both limbs occur in near anatomical position. Left-side humerus dislocated from scapula, and phalanges buried under the ribs. Right-side humerus and scapula visible, but the rest of the limb probably preserved under the ribs. This specimen was reported in Belia and Esperante (2011)

IC-1 (Fig. 7)

This is a large skeleton (12.6 m long) of a complete, entirely articulated fully adult whale. The two dentaries are in anatomical position with the symphysis gap closed. Skull articulated to atlas and the seven cervical vertebrae are fused, a sign of adulthood. Ribs are articulated on the thoracic vertebrae, although not all are exposed; some are inferred to be buried in the thoracic area. The entire vertebral column (54 vertebrae) is preserved and articulated, except for the slight displacement between vertebrae 28 and 29. The left-side limb is entirely preserved and articulated, whereas the right-side one only shows the scapula exposed with the rest of the elements likely buried under the ribs. This specimen shows exceptional occurrence of baleen in anatomical position (see Esperante et al., 2008).

IC-41 (Fig. 7)

This is a small juvenile specimen of a fully articulated baleen whale. Skull is lying on its left side, and shows the right-side dentary articulated and baleen preserved in anatomical position. The ribs are wrapped around the articulated vertebral column, and partially covered by the articulated bones of the right-side limb. Only the cervical, thoracic and proximal lumbar vertebrae were exposed; the lumbar and caudal vertebrae were not exposed but remained covered. Baleen is preserved in anatomical position (see Esperante et al., 2008).

LQ10-28 (Fig. 7)

This specimen consists of a large skull and its two dentaries; the postcranial skeleton is missing, although it could be buried in the vicinity. The two dentaries lie parallel to the skull at a 2.3 m distance. The arrangement of the two dentaries in anatomical position suggests that the skull rested dorsal-side up on the seafloor, then detached from the dentaries subsequently lying ventral-side up at a close distance, without disturbing the position of the dentaries.

LQ10-34 (Fig. 8)

The skull of this specimen was exposed above ground, thus showing significant deterioration and fractures from weathering. The left-side dentary is preserved disarticulated slightly from the skull; the right-side dentary lies 6 m away to the north of the skull. Vertebral column is detached from the skull, although it remains articulated and with ribs in close association. The distal part of the lumbar vertebral column and the tail are missing, although they might be buried under the slope. No limb bones were found, which might have been destroyed by modern erosion of the slope.

LQ10-35 (Fig. 8)

Large skull with its occipital area resting on top of one of the scapulae, and the two dentaries disarticulated and twisted from their original anatomical disposition. The distal end of both premaxillaries broke up after death and lies at an angle to the axis of the skull, partly attached to it. Thoracic vertebrae are articulated but the rest of the vertebral column is disarticulated, with some vertebrae resting on their centrum. This specimen was found partially exposed on the ground, which may account for the missing bones, including many ribs, some vertebrae, and limb bones.

LQ10-36 (Fig. 8)

This specimen consists of the skull, two dentaries and disarticulated postcranial bones. Both dentaries disarticulated before burial and occur behind the skull, one of them 6 m away. Disarticulation of postcranial bones most likely happened before burial, although this cannot be assessed.

LQ10-39 (Fig. 8)

Fully disarticulated partial specimen, although all the bones are associated. Disarticulation happened before burial. Dentaries occur detached and separate from skull. Some vertebrae, ribs and carpals preserved, but other postcranial bones missing due to modern weathering (skeleton is on the slope). Most preserved vertebrae occur lying on their centrum and show their transversal and neural apophyses attached to the body of the vertebrae.

LQ10-40 (Fig. 8)

Fully disarticulated partial specimen, although all the bones are associated. Disarticulation happened before burial. Preserved bones include skull, one dentary, some vertebrae and ribs. Many missing bones most likely destroyed or removed by modern weathering (skeleton is on the slope). Most preserved vertebrae occur lying on their centrum and show their transversal and neural apophyses attached to the body of the vertebrae.

LQ10-42 (Fig. 8)

Almost fully articulated specimen, including skull, one dentary, vertebral column and ribs. One dentary is in anatomical position and the other lies underneath the ribs and scapula. Some ribs are articulated to the respective thoracic vertebrae, others are slightly dislocated but closely associated around the vertebral column. Right-side limb preserved near life position, although partially disarticulated.

LQ11-01 (Fig. 9)

Articulated specimen lying on the edge of a bed on the slope, which probably accounts for removal of skull, ribs and dentaries. Preserved vertebral (cervical, thoracic and proximal lumbar) column is fully articulated, with transversal apophyses attached to the vertebral centra.

LQ11-05 (Fig. 9)

Fully disarticulated partial specimen, with all bones closely associated, lying partially exposed on the faulted slope, which could account for the missing bones. Skull with tympanic bullae preserved. The two dentaries are detached from the skull. Preserved vertebrae lie on their centra with the transversal and neural apophyses attached to the body of the vertebrae. A radius occurs on top of the left-side maxillary.

LQ11-10 (Fig. 9)

This specimen is fully articulated although the vertebral column is broken into two pieces. Skull rests on its right side, articulated to the atlas. Twenty-three vertebrae are articulated, including cervical, thoracic and the proximal half of lumbar. A second group of seven articulated vertebrae lies parallel to the thoracic vertebrae area and include the distal half of lumbar and the proximal half of the tail. All vertebrae have their transversal and neural apophyses attached to the body of the centra. Ribs are preserved in anatomical position. Specimen is on the slope, which caused one side to be heavily eroded resulting in missing bones, including an entire limb and ribs. The other side is buried and ribs and the other limb may be preserved.

PIS09-26 (Fig. 9)

Preserved specimen consists of skull, dentaries and part of the post-cranial skeleton. Left dentary in anatomical position; right dentary displaced and moved over the left side of the rostrum with its articulation end lying on the premaxillary. Cervical vertebrae disarticulated but clustered behind the occipital condyles. Thoracic vertebrae are articulated. Other vertebrae were not exposed during excavation. Both limbs were preserved, although incomplete due to modern erosion.

WC-33 (Fig. 9)

Fully articulated whale skeleton resting on a mound. Heavily deteriorated by modern erosion. Baleen was preserved in anatomical position (see Esperante et al., 2008).

WCBa-20 (Fig. 9)

Fully articulated and almost complete whale skeleton. The left dentary in anatomical position; the right dentary is disarticulated but its anterior end lies next to the articulation point on top of the squamosal. Ribs clustered in almost symmetrical arrangement on both sides of the articulated vertebral column. Several shark teeth found associated with the skeleton and sediment. A shark tooth found embedded in the skull. Baleen detached from its anatomical position in the mouth and lying on top of the right side limb and associated sediment (see Esperante et al., 2008).

WCBa-32 (Fig. 10)

Only the skull, and the proximal post-cranial skeleton were excavated, the rest remained under thick diatomaceous mudstone. The exposed skeleton is fully articulated with excellent preservation. Both dentaries in articulation position. Cervical vertebrae, and thoracic vertebrae articulated and ribs symmetrically wrapped around the vertebral column. Only one limb is preserved, the other one is missing and was not present when the whale was buried. Several shark teeth found but no shark tooth marks on bones.

WCBa-112 (Fig. 10)

Partially disarticulated, almost complete whale skeleton. Both dentaries near anatomical position and slightly rotated. Skull disarticulated and slightly displaced from cervical vertebrae. Thoracic vertebrae roughly articulated, with some vertebrae rotated. Lumbar and caudal vertebrae disarticulated and clustered in two groups; most of them lying on their centra. Ribs in symmetrical arrangement on both sides of the vertebral column. Both limbs preserved on either side of the vertebral column, although most of the small distal bones are missing.

WCBa-212 (Fig. 10)

Disarticulated whale skeleton preserved in two clusters of bones: one group consisting of skull, atlas bone, seven articulated and two disarticulated vertebrae, and a second group consisting of a few disarticulated vertebrae, fourteen ribs, the two dentaries and six articulated cervical vertebrae. The latter group is distanced about 6 m from the skull. Atlas bone disarticulated from the occipital condyles but lying flat next to them. Several shark teeth found but no shark tooth marks on bones.

WCBa-248 (Fig. 11)

Partially disarticulated, almost complete whale skeleton. The skull rests on top of the disarticulated cervical vertebrae and anterior portion of the thoracic vertebrae. The rest of the vertebral column is well articulated and bent 45° at the beginning of the lumbar section. Ribs clustered on both sides of the vertebral column. Dentaries disarticulated and lying on both sides of the skull. Both limbs missing, possibly buried under the skull.

WCBa-302 (Fig. 11)

Partially disarticulated whale skeleton lying under a flat cover of dolomitic mudstone that only covered the specimen. Skull lies 3 m to the south of the lumbar vertebrae. The first two cervical vertebrae disarticulated, the other five and three thoracic vertebrae articulated forming a cluster. The rest of the thoracic and lumbar vertebrae are articulated and aligned, with some vertebrae slightly rotated. Tail vertebrae disarticulated and clustered in three groups. Twenty-one one ribs preserved, nineteen of them on the right side of the vertebral column. One scapula and ulna preserved under the ribs. One dentary preserved between the skull and the vertebral column.

WQG-60

Only the skull, cervical and proximal thoracic vertebrae and limbs were partially excavated because of the burden of the slope sediment. Skull detached from the cervical vertebrae. Dentaries missing, probably due to modern erosion of the hillside. Articulated thoracic vertebrae, with ribs on both sides. Right side limb in anatomical position, including scapula, humerus, ulna, radius, and carpal bones.

WQG-63 (Fig. 11)

Fully disarticulated whale skeleton on the slope, consisting of vertebrae, ribs, one dentary and several limbs bones. Skull missing, although it could be buried under the slope. Vertebrae with neural and lateral processes intact.

WQG-67 (Fig. 11)

Isolated skull of a baleen whale on the slope. No dentaries. Post-cranial skeleton could be buried separately a few meters away.

WQG-78

This specimen consists of a large skull, two dentaries and two vertebrae buried on the slope. Dentaries detached from the skull and lying parallel on the east side of it. Two disarticulated vertebrae occur between the skull and one dentary.

Z-51 (Fig. 11)

A specimen of a fully articulated, almost complete small infant whale. Only partially excavated. Baleen preserved in anatomical position (see Esperante et al., 2008).

Appendix 3. Bioerosion features observed in thin sections of bones. Most bones show little or no bioerosion

Table A3
Bioerosion in bones.

Specimen	Quantity of thin sections	Skeletal parts examined	
CB11-01	5	Left dentary, neural spine, phalange, rib, ulna	No bioerosion
CB11-02	26	Baleen, centrum, dentary, maxilla, neural spine, rib, squamosal, transverse processes of thoracic and tail vertebrae, zygomatic arch	No bioerosion. Microfractures due to compaction
CB11-03	19	Rib, vertebral process, skull	Minor bioerosion
CB11-04	6	Maxilla, rib, vertebral process	Minor bioerosion. Microfractures due to compaction
CBL-10	6	Dentary, phalange, rib, transverse process	No bioerosion
CBL-11	1	Baleen	No bioerosion
FP08-12	3	Rib, vertebral process	Bioerosion in some bones
IC-1	8	Baleen, neural spine, rib, transverse processes of thoracic and tail vertebrae	No bioerosion
IC-41	–		
LQ10-28	–		
LQ10-34	–		
LQ10-35	2	Rib, transverse process	No bioerosion. Microfractures due to compaction
LQ10-36	1	Maxilla	
LQ10-39	6	Dentary, pelvis, rib	Minor bioerosion. Microfractures due to compaction
LQ10-40	6	Centrum, rib	Bioerosion in some bones
LQ10-42	8	Neural spine, phalange, rib, transverse process	No bioerosion. Microfractures due to compaction
LQ11-01	–		
LQ11-05	5	Neural spine, phalange, rib, transverse process	Bioerosion. Microfractures due to compaction
LQ11-10	4	Rib, neural spine, transverse process	No bioerosion. Microfractures due to compaction
PIS09-26	5	Rib, neural spine, transverse process	Minor bioerosion
WC-33	2	Baleen	
WCBa-20	–		
WCBa-32	5	Dentary, rib, transverse process	No bioerosion
WCBa-112	8	Dentary, phalange, rib, transverse process	Bioerosion
WCBa-212	5	Dentary, rib, transverse process	No bioerosion
WCBa-248	7	Dentary, rib, transverse process	No bioerosion
WCBa-302	1	Transverse process	No bioerosion
WQG-60	6	Phalange, rib, transverse process,	Bioerosion in one rib. Lacking in the rest
WQG-63	5	Ribs, transverse process	Bioerosion in two ribs and one vertebra. Lacking in the rest
WQG-67	–		
WQG-78	–		
Z-51	–		
Total	150		

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