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The awkward record of fossil whales

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1.1 Introduction

Cetaceans are highly efficient aquatic mammals with different adaptations and behaviours, occupying apex positions in the marine trophic web. Their fossil record is rich with respect to that of sister clades, offering an unprecedented opportunity to study the macroecology and macroevolution of a key component of the largest among modern ecosystems. Stemming from terrestrial ancestors, the evolutionary history of cetaceans unrolled in about 55 million years and included a major turnover, when once successful primitive clades became extinct at the passage Eocene-Oligocene (Marx et al., 2015; Berta et al., 2016), outpaced by more advanced forms. These took advantage of global cooling and new oceanic configurations (Fordyce, 2003) and crown Cetacea radiated. Their Neogene and Quaternary fossil record is the means to understand the steps through which they came to be the most successful among modern large predators (Marx et al., 2015; Berta et al., 2016; Pyenson, 2017; Bisconti et al., 2019) and forms the focus of the present study. Within crown Cetacea, toothed whales (crown Odontoceti) are the most species-rich clade of modern seas, sharing the unique feature of echolocation, an adaptation used to track different live preys in a large variety of habitats, from freshwater to the open ocean. Originated in the Oligocene, about 25 million years ago, archaic toothed whales gradually gave way to modern forms during the Miocene, experiencing an evolutionary outburst during the Pliocene (Bianucci et al., 2011). Today the group includes three monophyletic clades, Physeteroidea, Ziphiidae and Delphinida, and the little resolved, probably polyphyletic Platanistoidea (Boersma et al., 2017; Lambert et al., 2017a, 2017b; Bianucci et al., 2018). Sperm whales (Physeteroidea) are open marine mammals that attained gigantic size early in the history of crown Cetacea, with adaptations to both raptorial and suction feeding (Lambert et al., 2010; Marx et al., 2015). They are the largest, but the less diversified among modern toothed whales, with only two genera and four living species. Radiating during the early Miocene, beaked whales of family Ziphiidae underwent a size increase and several morphological changes during the last 20 million

121
122 years, adapting to cold waters of the open ocean and to depths up to about 3000 m, where they
123 currently catch squids via suction (Lambert et al., 2013; Bianucci et al., 2016b). The highly-
124 diversified Delphinoidea, including families Delphinidae, Phocoenidae and Monodontidae, have a
125 size range starting at about 1m (Maoi's dolphin), pilot and killer whales attaining large and very large
126 size (commonly around 5 and 7 m, respectively). All delphinoid species feed by raptorial means on
127 different preys, from fish to seabirds to other marine mammals, and their diversity has steadily
128 increased during the last 12 million years, today including 27 genera and 80 species (Marx et al.,
129 2015). The second large and successful clade among crown Cetacea are the baleen whales (crown
130 Mysticeti), originated around 25 million years ago via toothed ancestors and sharing the unique
131 feature of filter feeding through a comb structure called baleen, allowing for a diverse array of feeding
132 strategies (Berta et al., 2016). With 15 living species, baleen whales are less species-rich than toothed
133 whales, but attain the largest size among marine animals, most adults being longer than 10 m, up to
134 30 m, weighting more than 20-30 tons. Baleen whales spend most of their time in the open sea where
135 they play a key role on the global marine ecosystem acting as top predators and moving huge
136 quantities of matter and energy across the oceans and across the water column (Roman et al., 2014).
137 Baleen whales experienced a number of diversity pulses and reached gigantic size apparently in
138 parallel with the Pliocene and Pleistocene climatic deterioration (Deméré et al., 2005; Berta et al.,
139 2016; Bisconti et al., 2019), details of this last evolutionary step being partly obscured by an
140 awkwardly poor Pleistocene documentation (Slater et al., 2017). The Paleobiology Database, the
141 largest available source to explore the steps of cetacean macroevolution, contains more than 1400
142 Neogene and Quaternary occurrences of crown Cetacea, subdivided in about 260 genera and 450
143 species-level units that have lived in the last 23 million years (PaleoDB, 2019). Only a few studies,
144 however, have explicitly tackled so far issues relating to the quality of the global (Uhen and Pyenson,
145 2007) and regional record (Villafaña and Rivadeneira, 2014). This paper aims at filling the voids.

175 **1.2 Matters of the record**

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184 Studies on fossil cetaceans have increased exponentially during the last decades (Marx et al., 2015),
185 mostly dedicated to taxonomy and phylogeny, some to local taphonomy. Available summaries
186 suggest that detecting dispersal events, measuring past diversity and testing hypotheses on the relative
187 role of climatic and biotic drivers on macroevolutionary patterns, may be hampered by sampling
188 artefacts and from the uneven geographic distribution of the record. Based on global studies, authors
189 admit that the record is too patchy to test species-level biogeographic distributions (Marx et al., 2015)
190 and that this is unbalanced towards the Northern hemisphere, whereas some of the richest grounds
191 for cetaceans, from the Oligocene to the Recent, were located in the Southern ocean (Pyenson et al.,
192 2010; Bianucci et al., 2016c). A drop in diversity of toothed and baleen whales registered during the
193 Messinian, when the Mediterranean underwent a salinity crisis and the regional record dropped to
194 zero, is recognised as an artefact (Marx and Uhen, 2010a), implying that the unusually abundant
195 European collections, relating to one of the most densely populated areas of the world and with the
196 longest tradition of paleontological studies (Uhen and Pyenson, 2007), might also be the factor behind
197 global diversity peaks (Marx et al., 2015). These occurred during the middle Miocene, where the
198 record largely stems from localities in Northwestern Europe, and the similarly well-sampled and
199 studied North American East Coast, and the Pliocene, with a large part of collections located in Italy.
200 One yet unresolved mystery is the advent of gigantism among whales (Deméré et al., 2005; Lambert
201 et al., 2010, 2013; Slater et al., 2017), given that the unexpectedly very limited Pleistocene global
202 record of the mysticetes fails to document critical evolutionary steps that lead to the modern fauna,
203 while single findings suddenly set the clock back with respect to previous generalisations (Bianucci
204 et al., 2019). The hypothesis that Pleistocene glacial cycles are responsible for an increased exposure
205 and erosion of shelf area, limiting the preservation potential of Pleistocene cetacean fossils (Deméré
206 et al., 2005; Slater et al., 2017), has not been tested, nor it is sustained by the Mediterranean geological
207 record, where a large volume of Pleistocene shelf and bathyal sediments has been available for
208 collecting (e.g., Benvenuti et al., 2006; Dominici et al., 2011; Zecchin et al., 2012; Regione Emilia-
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242 Romagna, 2019), with small results with respect to what is found in the Pliocene (Freschi et al., 2019).
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244 Think Pleistocene marine successions are also found in other regions (Van Couvering, 2004; Bianucci
245 et al. 2006). Local and regional studies are invoked as means to unravel relationships between
246 productivity and cetacean diversity (Pyenson et al., 2010; Marx and Uhen, 2010b), much insight on
247 ecosystem structure being gained by studying the taphonomy (e.g., Dominici et al., 2009; Gariboldi
248 et al., 2015; Gioncada et al., 2018) and the high-resolution stratigraphic framework of fossil cetaceans
249 (Peters et al., 2009; Pyenson et al., 2009, 2014; Danise et al., 2010; Boessenecker et al., 2014;
250 Bianucci et al., 2016b; Dominici et al., 2018; Freschi et al., 2019; Cutiño et al., 2019; Gee et al.,
251 2019). From two different perspectives, stratigraphic paleobiology (Holland and Pazkowski, 2012)
252 and cetacean actuopalaeontology (Schäfer 1972; Smith et al., 2015) help unveiling what taphonomic
253 factors lie behind the paleoenvironmental distribution of the carcasses of large marine vertebrates,
254 what regulates the quality of preservation and what information is transmitted by the rock record.
255 Available evidence suggests that the quality and quantity of fossil whales depends on position along
256 the bathymetric paleoprofile. Complete or partially articulated skeletons are particularly abundant in
257 offshore shelf marine sediments in the late transgressive and highstand systems tracts of depositional
258 sequences (basal Cetacea: Peters et al., 2009; crown Cetacea: Di Celma et al., 2018; Dominici et al.,
259 2018; Freschi et al., 2019). Isolated and reworked bones are often found in condensed deposits and
260 shell lags at maximum flooding intervals (Pyenson et al., 2009; Boessenecker et al., 2014; Dominici
261 et al., 2018), or in fluvial deposits above sequence boundaries (Peters et al., 2009). When comparisons
262 are made, slope deposits provide a small fraction of the total record of a given region (Dominici et
263 al., 2018; Freschi et al., 2019). Articulated whale skeletons in beach deposits are rare (Pyenson et al.,
264 2014; if present at all, the association with cross-bedded sandstones belonging to the category of delta
265 front paleoenvironments, where sudden sediment inputs eventually cover carcasses and allow for the
266 preservation of pristine skeletons: e.g., Dominici et al., 2018). Stratigraphic paleobiology requires
267 independent means to reconstruct marine depositional environments, ordered along a water depth
268 gradient and a carbonate-siliciclastic gradient (Dominici and Kowalke, 2007; Holland et al., 2007;
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302 Brett et al., 2016; Danise and Holland, 2017; Dominici et al., 2019). This knowledge includes a high-
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304 resolution sequence stratigraphic framework, data on the quality and quantity of skeletal preservation
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306 of individual specimens, and details on the associated fossils and sedimentary facies.
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309 In the light of the results of regional studies, still unsolved mysteries of the cetacean fossil record
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311 may be tackled by extracting an improved set of data from the global literature, fit to explore the
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313 facies distribution and taphonomy of Neogene and Quaternary whales, dolphins, porpoises and their
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315 kin, driven by knowledge of extant descendants.
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319 **2 The habitat of crown cetaceans**

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323 **2.1 Toothed whales**

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328 Modern odontocetes live in fluvial, estuarine and marine waters. River dolphins, a polyphyletic
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330 group, are of secondary importance to the present study and are not considered here. Marine and
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332 estuarine species of superfamily Delphinoidea, the most diverse family among toothed whales,
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334 occupy an array of ecological niches, both onshore and offshore (Fig. 1). Porpoises (family
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336 Phocaenidae) and onshore ecotypes of primitive, smaller dolphins, like *Delphinus*, *Tursiops* and
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338 *Stenella*, feed mostly on fishes and dwell in shallow marine and estuarine habitats. Offshore ecotypes
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340 of *Delphinus* and *Tursiops*, instead, dive deep over the slope (Tab. 1). All species of Monodontidae,
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342 ranging 2-6 m length, live in Arctic waters usually at 70-80 °N, in open marine settings or swimming
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344 upstream in estuaries of large rivers. Larger dolphins of genera *Globicephala* and *Grampus* are
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346 derived forms adapted to life at the shelf break or in the deep sea, where they feed on squids by
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348 suction. Killer whales are highly social mega-predators of uncertain phylogenetic affinities and live
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350 in variety of marine settings, from neritic to oceanic, with a diversified diet.
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354 Modern sperm whales (superfamily Physeteroidea), whether large (*Physeter*) or small (*Kogia*, Fig.
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356 Silhouettes), and beaked whales (superfamily Ziphiioidea) are dominant mesopelagic predators,
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361 typically diving deep along the continental slope (up to 3000 m), where cephalopods are most
362 abundant, and avoiding the shallow shelf. The Physeteroidea, with the longest geologic history among
363 crown Odontoceti, have included very large (Lambert et al., 2010) and small species (Collareta et al.,
364 2017) that fed by raptorial means, showing a wider range of adaptations. Stem ziphiids probably
365 foraged on fish at shallow depths (Lambert et al., 2015; Ramassamy et al., 2016).
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373 **2.2 Baleen whales**

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379 Living baleen whales (superfamilies Balaenoidea and Balaenopteroidea) are almost exclusively
380 offshore marine top predators (Berta et al., 2016; Goldbogen et al., 2016; Bisconti et al., 2019) and
381 their habitat varies, depending on their trophic and reproductive strategies (Sanderson and Wassersug,
382 1993). Bowhead and right whales of family Balaenidae are continuous, low-speed, unidirectional
383 skim-feeders of cold temperate and polar environments. They feed by swimming across swarms of
384 copepods and other small crustaceans at depths of 100-400 m. The pigmy right whale (*Caperea*
385 *marginata* of Neobalaenidae), a surface skimmer with a diet that includes copepods and krill, also
386 prefers environments near the shelf break. Rorquals (Balaenopteroidea) employ lunge-feeding, a
387 technique with a high energetic cost that decreases their diving capacity and forces them to target
388 extremely high dense krill masses (Goldbogen et al., 2011, 2012). They are ocean-going capital
389 breeders, reproduction and care of offsprings being decoupled from feeding, typically moving
390 between high-latitude, productive feeding areas in summer, and less productive, low-latitude breeding
391 areas in the winter. Fin whales (*Balaenoptera physalus*) and blue whales (*B. musculus*) are
392 stenophagic predators, preferring krill at the shelf break or seaward, off the continental shelf along
393 the 1000 m isobath. Smaller rorquals, like *Balaenoptera acutorostrata*, occur also in neritic
394 environments where they feed on krill and fish, depending on availability, but their populations are
395 densest near the shelf-break, on the continental slope at depth > 200 m and wherever abrupt
396 topography triggers upwelling of nutrients. The humpback whale *Megaptera noveanglae* feeds on
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422 krill and small fish using complex techniques (“bubble net” gulp-feeding), in productive waters at
423 high-latitudes. The grey whale (*Escherichtius robustus*, the only surviving species of family
424 Escherichtiidae) is the only baleen whale that inhabits shallow continental shelves at depths of <50
425 m, where it mostly feeds on on dense concentrations of benthic amphipods, migrating during the
426 reproductive season through the open ocean and reaching distant places, eventually dying offshore
427 during the trip.
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434 **3 Whale actuopalaeontology**

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441 Actuopalaeontological studies reveal that carcasses of whales, dolphins and porpoises either sink,
442 float or get stranded depending on biological and physical factors (Schäfer, 1972; Reisdorf et al.,
443 2012). Biological factors include the cause of death, which may be the stranding itself, or more likely
444 predation, illness or old age. The taphonomic path followed by the carcass of a stranded whale
445 depends on humidity and temperature, and eventually includes disarticulation of body parts (Schäfer,
446 1972). The density of whale bodies are higher than the density of seawater, a shared adaptation for
447 deep diving. Fat-rich right and sperm whales constitute a possible exception (Nowak, 1999; Residorf
448 et al., 2012), but death is expected to be associated with fat loss, making also some these carcasses
449 densest than sea water (Smith et al., 2015). Given the offshore habitat of most living cetaceans (Fig.
450 1; Tab. 1), the largest majority of carcasses sinks below the shelf break (> 200 m depth) and reaches
451 bathyal depths. All carcasses sunken onto offshore neritic and bathyal bottoms are expected not to
452 resurface, due to high water pressure inhibiting the formation of gas from decomposition (Allison et
453 al., 1991). Carcasses deposited on coastal settings at depths < 30 m (Smith et al., 2015), if not rapidly
454 covered by sediment, become inflated with putrefaction gases from bacterial activity and eventually
455 refloat (Schäfer, 1972; Reisdorf et al., 2012). Carcasses only seldom become stranded in intertidal
456 settings, even if belonging to coastal species such as grey whales (Smith, 2006). Whale biostratinomy
457 can therefore take two possible pathways, one typical of coastal settings, driven by either rapid burial
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482 or floating of smaller carcasses, the other of open shelf and bathyal bottoms, where sunken carcasses
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484 of both small and large whales (Fig. 1), remain on the seafloor, more or less far from sediment input
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486 and serving as food of the deep sea biota (Krogh, 1934). Known depths of final rest confirms that
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488 naturally sunken whale carcasses are distributed from outer shelf to bathyal depths (150-4000 m: Tab.
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490 2; depths of 3000-4300 m are reported by Krogh, 1934 and Schäfer, 1972). After reaching the final
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492 resting place, the degradation pathway of exposed carcasses depends on the interaction between body
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494 parts and the surrounding abiotic and biotic environment. Abiotic factors include water pressure,
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496 oxygen content, nature of the seafloor and sedimentation rate, while biotic factors that influence the
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498 course of carcass degradation go from microbes to numerous animal species that have adapted to
499
500 exploit the rich energy resource of cetacean tissues. Waters deeper than 200 m host in fact a
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502 diversified and specialised whale-fall community (Allison et al., 1991) that live and reproduce in
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504 proximity of these large organic particles, and develop along four recurring stages of an ecological
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506 succession recognised globally (Fig. 2; Smith et al., 2015). The mobile-scavenger stage occurs first
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508 and interests soft tissues, starting when the carcass reaches the seafloor and continuing for months,
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510 first by the sloppy action of large necrophages such as sharks and mixines, then by smaller fishes and
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512 amphipods (Smith and Baco, 2003). As the carcass and the surrounding sediment become enriched
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514 with organic matter that falls from the degradation of soft tissues, the enrichment-opportunist stage
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516 takes place, lasting for years or decades. During this lapse a microbial succession develops, from
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518 primarily heterotrophic (sulfate reducing and methanogenetic microbiota) to a mixed
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520 heterotrophic/chemosynthetic metabolism, with the addition of sulfide-oxidizing bacteria and
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522 anaerobic methanotrophic archaea (Smith et al., 2015). As soft tissue is removed, the cortex layer of
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524 exposed bones and the enriched sediments (Figs. 2 B-C, 3 A-B) become the food of specialised and
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526 highly diversified polychaetes of genus *Osedax*, possessing tissues that penetrate the bone up to
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528 several centimeters (Fig. 3 C, L; Vrijenhoek et al., 2009; Higgs et al., 2012, 2014; Taboada et al.,
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530 2017; Rouse et al., 2018). Bone-eating worms gradually feed on collagen until the cortex layer is
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532 eventually destroyed (Fig. 3 D-E, I; Higgs et al. 2012, 2014), while other organisms also contribute
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542 to bone destruction (Fig. 3 A). The peripheries of bones inhabited by *Osedax* worms become
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544 successively more porous, facilitating sulphate penetration and the subsequent action of sulphate-
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546 reducing bacteria (Higgs et al., 2011a). Due to the anaerobic degradation of bone lipids, and the leak
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548 of sulphide from the bones, the carcass and its surroundings (about 10 m for large whales) gradually
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550 become a chemosynthetic habitat (Treude et al., 2009). This sulphophilic stage, the third of the
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552 ecological succession, is so called because the characterising biota is adapted to withstand high
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554 quantity of sulphide. It may last for decades in the case of larger adult bones, providing a more
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556 persistent energy source (Smith, 2006). Bones exposed on the seafloor may host a suspension-feeding
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558 fauna that takes advantage of the organic particulate matter carried by water currents, constituting the
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560 reef stage of the ecological succession (Smith and Baco, 2003; Smith et al., 2015). The taphonomic
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562 pathway followed by a whale skeleton lying on the deep seafloor depends on the size of the carcass,
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564 the type of bones and their lipid content (Higgs et al., 2011b), and on the interaction between *Osedax*,
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566 with its heterotroph microbial symbionts, and the chemoautotroph microbiota that thrives on the
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568 sulphide produced during anaerobic decay of lipid-rich bones. *Osedax* modifies its habitat and acts
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570 as an ecosystem engineer (Higgs et al., 2011a; Tresguerres et al., 2013), forming a key component of
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572 a biotic chain that eventually leads to the complete destruction of smaller bones and cortical layer of
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574 larger bones (Smith et al., 2015). Other than the size and shape of individual bones (Fig. 4), another
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576 intrinsic variable is oil content, with larger and oil-rich bones, like skull, jaws and caudal vertebrae
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578 of great whales, lasting longer (Higgs et al., 2011b; Smith et al., 2015). Bone destruction is known to
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580 be directly correlated with depth, sometime leading to the complete disappearance of the skeleton
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582 (Braby et al., 2007; Lundsten et al., 2010b), densely mineralised ear bones being eventually the only
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584 skeletal element that remains (e.g., Krogh, 1934). Temperature, currents and sedimentary regime are
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586 other extrinsic variables that are known to impact on whale taphonomy.
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593 **4 Cetacean stratigraphic paleobiology**

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602 The entombment of cetacean bones in beach environments is a geologically ephemeral event, since
603 beach sediments get reworked by shoreface wave-ravinement during transgressions and by subaerial
604 erosion during regressions (Posamentier, 1992; Catuneanu, 2019). Whale bones, if preserved, would
605 ultimately scatter and become part of shoreface deposits. Delta front succession, built by high-density
606 hyperpycnal flows triggered by catastrophic river floods, are instead suggested as the only onshore
607 coastal environment where articulated and pristine fossilised skeletons can be possibly found
608 (Dominici et al., 2018). This is expected to occur during forced regressions, when high-density
609 turbidity currents become the main depositional mechanism seaward of river mouths (Catuneanu
610 2019). The best fossil record so far is associated with shelf and bathyal deposits, increasing in
611 thickness during transgressive pulses, at maximum flooding intervals, and during highstands of sea
612 level (Peters, 2009; Di Celma et al., 2018; Dominici et al., 2018; Freschi et al., 2019). Alongside a
613 recurring, sequence-stratigraphic control on the quality and abundance of fossil whales, bone-eating
614 worms could constitute a long-term unidirectional biotic driver in what has been called “*Osedax*
615 effect” (Kiel et al., 2010, see also Higgs et al., 2012). Regional studies confirm the existence of a
616 taphonomic-paleobathymetric gradient (Dominici et al., 2018). *Osedax* has no mineralised body parts
617 and its record is based on findings of the highly distinctive trace left in its preferred hard substratum
618 (Fig. 3 L; Higgs et al., 2012; 2014), starting from upper Cretaceous marine tetrapods from shallow
619 marine deposits, long before the evolution of whales (Danise and Higgs, 2015). Part of the wider
620 clade of siboglinid tubeworms, symbiotic metazoans adapted to a variety of deep sea extreme
621 environments (Hilário et al., 2011), *Osedax* and its heterotrophic symbionts diversified during the
622 Neogene, taking advantage of the radiation of crown Cetacea, which presently forms its main food
623 resource in the deep sea (Taboada et al., 2017). This record suggests that the “*Osedax* effect” may
624 have increased in efficiency during the Neogene and Quaternary and geographically expanded, as
625 whales extended their niches in an onshore and offshore direction, particularly when their bodies
626 became gigantic as an adaptation to colder climates of the ice age, and went global.
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5 Methods

5.1 Whale dataset

We analysed 719 records of Miocene, Pliocene and Pleistocene cetaceans, chosen in order to include a large number of taxonomic entities (162 genera and 220 species-level taxa), for which paleoenvironmental data (642 occurrences, 90%) and information on body parts (635 records, 88%) was available, and document their geographic and chronostratigraphic distribution (Supplemental Material, Tab. S1). For comparison we downloaded occurrence data from the Paleobiology Database (PaleoDB), obtaining a dataset of 1425 records (260 genera, 457 species: Supplemental Material, Tab. S2) and cross checked the two datasets. Our dataset excludes PaleoDB records that could not be connected to the stratigraphic unit in which the specimen was first entombed, like ice-rafted debris, bones collected by Neanderthals and most fossil specimens found lying on the seafloor. Reports relating to specimens that could not univocally be determined, those which did not allow to infer the associated paleoenvironment and, a small part of the total, reports which were not available to us were similarly excluded from our analysis. In our dataset, albeit smaller in size compared to the PaleoDB, metadata associated with each record includes: 1) links to the corresponding PBDB occurrence and collection number, if available, 2) geographic location, 3) geological data in terms of lithology, sedimentary structures and associated fossils, 4) paleodepth range (if stated in the literature) and inferred paleoenvironment, 5) chronostratigraphy, with best estimates available of minimum and maximum age, 6) time bin, 7) taxonomy, 8) taphonomy, 9) size, and 10) repository and accession number. All data are meticulously retrieved from the original report and subsequent literature, selecting papers that highlight stratigraphy, sedimentary facies, associated macro- and microfossils, vertebrate taphonomy and papers that comment on the associated paleoenvironment of deposition. Geographic location was coded depending on country or state (e.g., USA, Australia) and subdivided into nine geographic zones: 1) Western coast of Central and North America, 2) Western Coast of

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722 Southern America, 3) Eastern Coast of North America, 4) Eastern Coast of South America, 5)
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724 Western Coast of Europe and North Africa, 6) Mediterranean, Central and Eastern Europe, and Asian
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726 Near East, 7) Eastern Coast of Asia, 8) Oceania, 9) Indian Ocean and Austral Africa.
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731 *5.2 Lithology and paleoenvironment*

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735 Lithologies were subdivided into 14 categories of carbonate and siliciclastic rocks, in their turn
736 summarised into six lithology types (Tab. 3). These were one of the means to infer depositional
737 environments. Depositional environments were ranked depending on inferred paleobathymetry and
738 classified along an ideal bathymetric gradient into delta, upper shoreface, lower shoreface, inner shelf,
739 outer shelf and bathyal, from shallowest to deepest. Criteria used to define categories included
740 analysis of the associated fauna (usually mollusks or foraminifera), sedimentary structures and
741 lithology. Deltaic sediments are recognized by the occurrence of coarse-grained sandstones and
742 gravels in tabular massive or graded beds with reworked marine shells (e.g., Dominici et al., 2018).
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744 Upper shoreface is recognized by coarse-grained sandstones, with occasional fine gravels, in
745 bioturbated massive strata with a shallow marine, onshore shelly fauna. Lower shoreface is
746 represented by all bioturbated fine-grained sandstones and silty sandstones with an onshore marine
747 fauna and by all glauconitic sandstones, often associated with condensed deposits. All massive,
748 sometimes glauconitic and shelly sandy mudstones with a fully marine fauna are attributed to an inner
749 shelf paleoenvironment under conditions of low rates of sedimentary input. Massive and thick
750 successions of mudstones and claystones were interpreted a representing either outer shelf or bathyal
751 paleoenvironment, depending on the associated micro- or macrofauna. The boundaries between these
752 categories are sometimes blurry, as is expected when dealing with a gradient in paleodepths and with
753 a large variety of tectonic and dynamic settings, but are nevertheless interpreted as an efficient
754 independent means to rank fossil cetaceans with respect to the environment where they were finally
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784 *5.3 Chronostratigraphy and taxonomy*
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788 Minimum and maximum ages were taken from updated literature whenever possible, or in
789 coincidence of formal boundaries of stages associated with each occurrence. The average between
790 these two values offered a means to assign a point age to each fossil and to arrange occurrences in a
791 time continuum, segregating nine bins of 2.5 million years duration, overcoming problems that derive
792 from unequal lengths of formal stages. Taxonomy updates were taken from PaleoDB (Supplemental
793 Material, Tab. S2).
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803 *5.4 Taphonomy*
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807 Completeness of the skeleton considered a subdivision in four body parts: 1) skull, 2) dentaries, 3)
808 limbs and 4) rest of the post-cranial skeleton (Fig. 3). These are separated by weaker joints and
809 become more easily detached from each other during decay, independently from body size (Schäfer,
810 1972; Reisdorf et al., 2012). The skulls is further subdivided into 13 bones: one occipital, two
811 squamosals, two nasals, two maxillae, two praemaxillae, two tympanic bullae, two periotics. The
812 dentaries are two, and in odontocetes may include teeth, or fossilized baleen in mysticetes. Maxillary
813 and premaxillary teeth, if present, are grouped with mandibular teeth, since the two types cannot be
814 discriminated in many instances. Palatines, pterygoid, basioccipital, presphenoid and basisphenoid
815 are not counted, because rarely reported, possibly because preservation is hindered by their small
816 size. Limbs are two and include four large bones (scapula, humerus, ulna and radius) and several
817 smaller ones (carpal, metacarpal, phalanges). Post-cranial skeleton includes atlas, axis, five cervical
818 vertebrae, up to 17 toracic, 21 lumbar and 23 caudal vertebrae, sternum, manubrium, ribs and
819 chevrons. Specimen completeness was ranked into seven grades. Isolated bones (usually an ear bone
820 or a tooth, the most durable skeletal elements) were assigned grade 0; specimens that included more
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842 than one bone of an individual body part (usually the skull, comprising several tightly connected
843 bones) were assigned grade 1; specimens comprising several elements belonging to two body parts
844 (e.g., skull and mandibles) were given grade 2; specimen including three body parts (e.g., skull,
845 mandibles and at least one post-cranial starting from the third cervical vertebra) were given grade 3;
846 grade 4 if the body parts were four, but with less than 50 total bones (teeth excluded); grade 5 as the
847 previous case, but with more than 50 elements; grade 6 was assigned to the most complete specimens,
848 those that reached grade 5, but that included elements of both limbs or which preserved baleen in the
849 case of mysticetes (Tab. 4). To compare specimens size we collected data on three measures of skull
850 elements: length of tympanic bulla, byzygomatic width and condylobasal length. We collected at least
851 one measure each of 216 specimens. Repositories and accession numbers were useful to cross-check
852 that each individual was reported only once in the dataset.
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867 *5.5 Statistical treatment*

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872 Absolute abundances of cetacean occurrences and richness through time, proportions of substrate and
873 environment in which cetaceans are found, and taphonomic grades, were calculated in R (R core team
874 2018). Cetacean geographic distribution was plotted using QGIS (QGIS Development Team 2018).
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878 Spearman correlation index was used to test similar patterns of the fossil record.
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882 *5.6 Relative thickness of Pleistocene marine strata*

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887 It has been suggested that a poor record of Pleistocene cetaceans with respect to other time intervals
888 of the same duration is due to a higher frequency and amplitude of Pleistocene global sea-level
889 changes, leading to a thinner record of marine rocks (Deméré et al., 2005; Slater et al., 2017). To test
890 this hypothesis we built a quantitative dataset for five regions worldwide and compared the relative
891 thickness of Pliocene and Pleistocene marine successions, the two consecutive epochs being of
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902 comparable duration. These regions are Italy, South-Eastern United States, North Atlantic and North
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904 Sea, Japan and New Zealand. We separated coarse-grained from fine-grained lithologies as a proxy
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906 of depth of deposition (Supplementary Material, Tab. S4).
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910 **6 Results**

911 912 913 914 *6.1 Geography*

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919 The geographic distribution of global occurrences is skewed towards the Northern hemisphere, with
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921 436 against 268 occurrences (Fig. 5). Particularly rich regions are 6 (Mediterranean, mainly Italy and
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923 Belgium, Eastern Europe and Russia) and 5 (Western North America, mainly Maryland and Virginia).
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925 The record from the Southern Hemisphere is improved with respect to PaleoDB (Supplemental
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927 Material, Fig. S1), thanks to the many recent discoveries dedicated to region 2 (Western South
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929 America, mainly Peru), many of which are yet taxonomically undetermined, but useful for studies in
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931 stratigraphic paleobiology and taphonomy. The Atlantic Ocean is much better represented than the
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933 Pacific Ocean, particularly the North Atlantic. The Indian Ocean and the Arctic Sea are almost absent
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935 from the dataset. Despite an improvement with respect to the highly skewed geographic distribution
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937 resulting from PaleoDB, large and important sectors of cetacean global distribution remain to be
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939 explored, particularly where upwelling leads to some of the largest feeding grounds of modern
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941 cetaceans, such as in Western Africa (Fig. 4; since the late Miocene: Diester-Haas et al., 2002) and
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943 around Antarctica (since the early Oligocene: Miller et al., 2009).
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949 *6.2 Stratigraphic distribution*

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953 The record shows a rough increase in number of occurrences, with some intervals represented by a
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955 poorer record. Starting from the early Miocene record (two oldest time bins, coinciding with most of
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961 the Aquitanian and the Burdigalian), it increases at the passage from early to middle Miocene (third
962 time bin, or upper Burdigalian-early Langhian). The middle Miocene (fourth and fifth time bins)
963 coincides with a gradual drop, with a minimum number of occurrences during the Serravallian-
964 earliest Tortonian. A peak is recorded during the Tortonian, with 182 records, followed by a second
965 drop in number during the Messinian. The second highest peak coincides with the Pliocene (eighth
966 time bin), whereas a third major fall in the number of records occurs in the Pleistocene (Fig. 6A). Not
967 all occurrences are however related to a sufficient taxonomic knowledge, and a genus-level
968 determination was available only in 65% of cases (Fig. 6; the Peruvian record contains many
969 taxonomic unresolved records: e.g., Gariboldi et al., 2015; Supplemental Material, Fig. S2). The time
970 distribution of cetacean genus richness reveals a pattern strikingly similar to the pattern of
971 occurrences (Fig. 6B) and a measure of the Spearman correlation index suggests that there appears to
972 be a strong positive correlation between the two data sets (r_s value = + 0.87398), with only a 5%
973 probability of no correlation ($p = 0.00206$, 95% statistical significance level) between number of
974 occurrences and genus diversity (raw data; the correlation remains strong when differencing the data
975 by using the difference between one time interval and the subsequent time interval: Supplemental
976 Material, Tab. S3). This implies that high diversity could simply depend on the high number of studies
977 dedicated to a better sampled time span. When Odontoceti and Mysticeti diversities are decoupled,
978 however, we find that Mysticeti contributed to the upper Tortonian diversity peak more than at any
979 other time. In fact, upper Tortonian genus richness of the odontocetes equates that of the Messinian
980 (Supplemental Material, Fig. S3).

1003 *6.3 Lithology and paleoenvironment*

1011 The categorisation of lithologies associated with each occurrence reveals that carbonates contribute
1012 a very small fraction to the total, and that most fossil whales are found in fine-grained siliciclastic
1013 deposits. Diatomites, siltstones, claystone and marls jointly amount to little less than 70% of
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1022 occurrences, sandstones being about 30% (glaucopitic and phosphatic deposits counting 10%: Fig.
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1024 7). The distribution according to lithologies in PaleoDB differs, because most fossils associated with
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1026 diatomites and siltstones, from Peru and taxonomically unresolved (Gariboldi et al., 2015), but
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1028 important to understand the global stratigraphic paleobiology, are not considered by PaleoDB. The
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1030 figure that is obtained shows a larger proportion of sandstone-associated fossils, but those associated
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1032 with fine-grained siliciclastics still prevail (57% of the total). Lithology is only roughly correlated
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1034 with paleodepth of deposition, and other proxies are needed to better define paleoenvironments.
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1036 These were derived from the interpretation of associated biota, mostly mollusks and foraminifera.
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1038 The frequency distribution of the seven paleoenvironmental categories recognised in each time bin
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1040 allows several considerations (Fig. 8). In the first place, upper shoreface and delta front deposits
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1042 account for a very limited fraction of the total, independently from time. The same can be said for
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1044 bathyal deposits. The largest part of the whale fossil record comes from the lower shoreface and from
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1046 inner and outer shelf deposits. Looking closely at the stratigraphic distribution of these three
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1048 categories, lower shoreface deposits appear to be particularly abundant during the Aquitanian, the
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1050 late Serravallian-early Tortonian and the Pliocene-Pleistocene. The importance of remains from inner
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1052 + outer shelf deposits steadily decreases from the Messinian to the Pleistocene (Fig. 8).
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1058 *6.4 Completeness*

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1062 The largest majority of findings are isolated remains or skulls (grades 0-1, 25-80% of the total,
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1064 depending on time bin), with a trend towards less complete specimens increasing in time. The percent
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1066 of isolated remains is highest in the late Burdigalian-early Langhian and in the Pleistocene. Complete
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1068 skeletons account for a small part of the total, independently of time (grades 5-6, ranging 10-15% in
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1070 each time bin: Fig. 9).
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1075 *6.5 Size*

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1084 Based on recent phylogenies crown Odontoceti were subdivided into 1) heterodont forms and
1085 Platanistoidea (primitive odontocetes), 2) Physeteroidea and Ziphiioidea and 3) Delphinoidea
1086 (Boersma et al. 2017, Lambert et al. 2017b). The three components of head morphology measured in
1087 the three groups of odontocetes, including bizygomatic width (the single proxy conventionally most
1088 used to measure cetacean body size: Lambert et al., 2010; Pyenson and Sponberg, 2011; Slater et al.,
1089 2017), are allometric and suggest phylogenetic heterochrony. The group merging heterodont and
1090 platanistoid cetaceans (N = 48), comprising several extinct clades and a clade with only one living
1091 descendant (the river dolphin *Platanista gangetica*), show an overall increase in skull size and a slight
1092 decrease in the size of the tympanic bulla. The Physeteroidea (N = 29), comprising families
1093 Physeteridae, Kogiidae and Ziphiidae, all with extant members, show that skull length and
1094 bizygomatic width remain on average constant, whereas the tympanic bulla increases in size. The
1095 same trend is measured in the Delphinoidea (N = 51), with a record starting from the upper Miocene,
1096 with a constant bizygomatic width and skull length, and an increase in the size of the tympanic bulla.
1097 Mysticeti (N = 75) show a more isometric evolutionary trend, with both skull length and width
1098 increasing in size at a rather steep rate, followed by the tympanic bulla, albeit at a slower rate (Fig.
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1120 **7 Discussion**

1121 *7.1 Tempo and mode*

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1129 Cetacean macroevolution can be investigated through molecular phylogeny (e.g., McGowen et al.,
1130 2009; Raboski, 2014), discordant pictures arising as population dynamics, i.e. microevolutionary
1131 processes, are taken into consideration (Pereira and Shrago, 2018). If this approach offers stimulating
1132 results when applied to the study of dolphins, a clade experiencing a relatively young radiation and
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1142 possibly with more extant species than at any given time in past oceans (Cunha et al., 2011; Raboski,
1143 2014; Pereira and Shrago, 2018), it cannot be comparably used in the study of clades that have
1144 undergone turnovers and have had past diversities higher than the modern. The latter case is
1145 exemplified by the baleen whales, and in particular by the Balaenopteridae, the most successful
1146 among modern filter-feeders, currently less species-rich than dolphins. Against at least 39 known
1147 Neogene and Quaternary mysticete genera (and more already appearing in morphological
1148 phylogenies, but yet to be formally described), and considering the two enigmatic balaenopterid
1149 turnovers measured at the passages Tortonian-Messinian and Zanclean-Piacenzian, the modern
1150 gigantic and ecologically unprecedented baleen whales appear an insufficient genetic sample on
1151 which alone to reconstruct evolutionary relationships (Bisconti et al., 2019; see also Marx et al.,
1152 2019). The recurrence to total evidence approaches, based on both molecular and morphological data
1153 from fossils, helps to overcome these problems (Steeman et al., 2009; Berta et al., 2016; Slater et al.,
1154 2017), but in the search for the best fitting methods and as more new morphological data are included
1155 (Marx, 2011), interpretations become more relevant, shifting the focus on the quality of the fossil
1156 record on which total evidence methods rely (see discussion in Bisconti et al., 2019). Among crown
1157 Odontoceti, another group whose macroevolution can be known only starting from fossils, are the
1158 beaked whales, which shows 20 extinct genera, well-diversified during the late Miocene. The only 6
1159 living ones possibly radiated during the Zanclean within crown Ziphiidae, in coincidence with the
1160 extinction of most stem clades (Bianucci et al., 2016c). A still more controversial and heterogeneous
1161 group among crown Cetacea, open to new hypotheses as new fossils are found, is constituted by the
1162 more basal platanistoid odontocetes, with only one extant species living in riverine habitats (Boersma
1163 et al., 2017; Lambert et al., 2017b; Bianucci et al., 2018). Stem platanistoids became in fact extinct
1164 before the middle Miocene, substituted among generalist predators by the more advanced delphinoids
1165 (Lambert et al., 2017a; Bianucci et al., 2018). These are cases in which fossil evidence becomes
1166 increasingly more important, marginalising the use of molecular data, particularly in more
1167 comprehensive phylogenies (e.g., McGowen et al., 2009; see also Marx, 2011) where lineages need
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1202 to be postulated, and where a good fossil record is needed to reliably check macroevolutionary
1203 hypotheses (Marx et al., 2015). Our overview on the global quality of fossil whales and their kin
1204 suggests that phylogenetic hypotheses should particularly consider an under-sampling of late
1205 Burdigalian-early Langhian and late Miocene cetaceans (Fig. 3), respectively important to shed light
1206 on the turnover among stem Platanistoidea (Allodelphinidae and Squalodelphinidae: Boersma et al.,
1207 2017) and Delphinoidea (Delphinidae, Monodontidae and Phocoenidae: Lambert et al., 2017a), and
1208 to reconstruct the steps in the emergence of modern dolphins and beaked whales.
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1219 *7.2 The place of whales*

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1223 Our analysis reveals geographic blurry, or blank, spots of the record. Despite recent improvements,
1224 some regions have not been studied long enough to fully exploit their potential, while others are
1225 underrepresented (Fig. 5), notwithstanding they host a diverse and abundant cetacean fauna since the
1226 onset of the Antarctic Circumpolar Current (Fordyce, 2003; Marx et al., 2015). The South-Western
1227 Pacific record, with the incredibly rich and well-preserved finds in Peru (Muizon and DeVries, 1985;
1228 Gariboldi et al., 2015; Bianucci et al., 2016b) and Chile (Pyenson et al., 2014), and a younger history
1229 of research with respect to Europe and North America, reveals a still unexplored potential, where new
1230 studies based on single specimens have quickly changed our view of cetacean macroecology and
1231 macroevolution (Lambert et al., 2010, 2013, 2017a, 2017b; Collareta et al., 2017; Bianucci et al.,
1232 2019a, 2019b), and where much of the record needs to be taxonomically identified (e.g., Esperante
1233 et al., 2014; Gariboldi et al., 2017). A well-constrained chronostratigraphic framework has been only
1234 recently available for the highly fossiliferous Pisco Formation in the Pisco Basin, in Peru (localities
1235 Cerro Colorado and Cerro Los Quesos, Ica Desert: Gariboldi et al., 2017), and the age of the main
1236 bone beds of the Sacaco Basin, the first to be described and studied (Muizon and DeVries, 1985;
1237 Villafaña and Rivadeneira, 2014), has been lately revised (Collareta et al., 2017), so that available
1238 timings of clade divergence (e.g., McGowen et al., 2009; Marx et al., 2015) need to be revised.
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1262 Current studies in Chile and Argentina frame fossil whales and their taphonomy in context within a
1263 high-resolution stratigraphic paleobiological setting. However, similarly to Peru, taxonomies remain
1264 poorly resolved (Pyenson et al., 2014; Cuitiño et al., 2019). The Neogene and Quaternary record of
1265 Antarctica and the southern half of Africa is virtually unknown, with the Southern Atlantic and Indian
1266 Oceans underrepresented in the global picture (Pyenson et al., 2010). The Arctic record, the fertile
1267 grounds where modern monodontid whales dwell, are totally absent from available datasets (Fig. 5;
1268 Supplemental Material, Fig. S1). To make biogeographic patterns more complicated than formerly
1269 assumed, even in the Mediterranean the recent studies of the largest fossil whale ever (Bianucci et
1270 al., 2019b) and of the enigmatic pigmy right whale (Tsai et al., 2017) open new scenarios for the
1271 Pleistocene and Recent history of the cradle of cetacean paleobiology (Collareta et al., 2019). In the
1272 Mediterranean, the situation does not get better as we shift focus back in time, considering that the
1273 Zanclean is underrepresented with respect to the Piacenzian (Dominici et al., 2018; Freschi et al.,
1274 2019; Bigazzi et al., 2019), there is a lack of a Messinian record, casting doubts on the value of global
1275 diversity trends (Marx and Uhen, 2010), and there is a relatively rich, but little studied, Tortonian
1276 record (Bianucci et al., 2011, 2016a) that offers new insights on global biogeographic patterns as
1277 taxonomies are refined (Bianucci et al., 2019a). These evidences suggest that to prove a global
1278 correlation between cetacean evolution and its possible drivers, whether biotic or abiotic (Marx and
1279 Uhen, 2011; Pyenson and Lindberg, 2011; Marx et al., 2015), an evenly distributed global record is
1280 needed so as to meaningfully compare diversities (Marx and Uhen, 2010; Pyenson et al., 2010; Marx
1281 et al., 2015; Pimiento et al., 2017). Our review shows the presence of pitfalls suggesting that more
1282 data are needed for under-represented time spans and regions.

1300 7.3 A geological “Osedax effect”?

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1313 A second perspective is yet offered as we compare the habitat of crown Cetacea with the facies
1314 distribution of their fossils. Whales and dolphins largely exploit waters deeper than 200 m (Fig. 1),
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1322 but their fossils are mainly distributed in inner and outer shelf deposits, only rarely recovered in
1323 bathyal paleoenvironments. This evidence is largely independent from time (Fig. 8). One way to
1324 explain this phenomenon is calling again into play the “*Osedax* effect” as an underpinning factor of
1325 the global record (Kiel et al. 2010). Within whale-fall communities, *Osedax* is often recognised as
1326 the main responsible of the complete destruction of whale carcasses in a matter a few years, based on
1327 time series analyses along the continental slope of the California offshore (Braby et al., 2006;
1328 Lundsten et al., 2010b). This is by no means the only species rapidly degrading whale bones
1329 (Lundsten et al., 2010b; Johnson et al., 2010; Sumida et al., 2016), an “*Osedax* effect” being
1330 understood in a wider sense, that is, relating to all the organisms that feed on tissues of the skeleton
1331 or otherwise destroy bones (Figs. 2 C, 3 A). Whale fall communities, and bone-eaters in particular,
1332 radiated in parallel with the diversification of crown Cetacea (Vrijenhoek et al., 2009), exploiting
1333 carcasses large and small (Kiel and Goedert, 2006; Pyenson and Haasl, 2007), preferring habitat
1334 below the shelf break, and gaining a global distribution (Taboada et al. 2015). They were positively
1335 affected by the evolutionary increase to gigantic size of baleen whales (Vrijenhoek et al., 2009;
1336 Tresguerres et al., 2013; Taboada et al., 2015), a phenomenon documented by several previous studies
1337 (Lambert et al., 2010; Pyenson and Sponberg, 2011; Slater et al., 2017; Bianucci et al., 2019b) and
1338 consistently confirmed by our analysis. This contrasts with the trend shown by other crown cetaceans,
1339 overall constant in size during the Neogene and Quaternary (Fig. 10). Any hypothesis on the
1340 taphonomic role played by the Mysticeti-*Osedax* coevolution should also include a discussion of the
1341 awkward drop in the number of findings at the passage Pliocene-Pleistocene. Recognised at different
1342 levels (Marx and Uhen, 2010b), the relatively poor Pleistocene record has long puzzled authors, who
1343 advanced the hypothesis of a connection with a fall in the volume of Pleistocene shelf sediments
1344 available for study (Morgan, 1994; Deméré et al., 2005; Slater et al., 2017; a similar relationship
1345 between low diversity with prolonged sea-level lowstand is mentioned for the Rupelian record
1346 (Fordyce, 2003; Uhen and Pyenson, 2007), examples of the common-cause hypothesis (see Peters,
1347 2005; Peters and Heim, 2011). Pleistocene shelf and bathyal sediments abound however in intensely
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1382 studied regions of the world (Supplemental Tab. S4), particularly in the Mediterranean, where thick
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1384 sedimentary successions of both Pliocene and Pleistocene age represent all types of
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1386 paleoenvironments (e.g., Benvenuti et al., 2006; Ciaranfi et al., 2009; Maiorano et al., 2010; Zecchin
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1388 et al, 2012; Dominici et al., 2018; Freschi et al., 2019), but where the cetacean fossil record is strongly
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1390 skewed towards the Pliocene (Fig. 11 A). Thick Pleistocene successions outcrop also in other
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1392 collisional margins, such as those of Japan and New Zealand, suggesting that the relatively thin
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1394 Pliocene and Pleistocene successions of coastal regions of the Atlantic and the North Sea (passive
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1396 margins; Fig. 11 B) cannot account alone for the Pleistocene drop in the raw number of fossil whales
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1398 recorded, ruling out the hypothesis of an artefact of the variable quantity of the rock record. Thick
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1400 successions from open shelf and bathyal paleosettings gigantic whales should have a better record,
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1402 but on the contrary they are only exceptionally unearthed (Bianucci et al., 2019b; Fig. 11 A).
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1404 Considering the sudden expansion of the habitat of whale fall communities connected with the advent
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1406 of gigantism, increasingly efficient bone-eaters are likely candidates to explain lower records also at
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1408 shelf depths, where *Osedax* currently extends its influence (Vrijenhoek et al., 2009; Smith et al.,
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1410 2015). The presence of large baleen whales is in fact, and nonetheless, indirectly recorded by the
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1412 thick shells of their coronulid commensals, increasingly abundant in Pleistocene sediments, widely
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1414 used as proxies to document the presence of their obligate hosts (Bianucci et al., 2006; Dominici et
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1416 al., 2011; Collareta et al., 2016; Taylor et al., 2019). Not all studies, however, agree on the impact of
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1418 *Osedax* on whale bone preservation. A recent review based on more than twenty years of deep sea
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1420 research on modern whale fall communities has downplayed the role of siboglinid worms (Smith et
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1422 al., 2015). So, while *Osedax* has colonized most of 16 study sites off California, Oregon Washington,
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1424 Antarctica and Sweden (no *Osedax* was found in the Hawaii), where whale carcasses or deployed
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1426 whale bones were studied for more than one year, they have never formed really dense colonies nor
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1428 destroyed the larger bones adult whales, even for carcasses of adult whales at the seafloor for 45-60
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1430 years (based on a radiometric dating technique in Schuller et al., 2004: Craig Smith, personal
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1432 communication, October 2019). As an additional element to consider, the spotty record that results
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1442 from a review of ecological studies should be framed against the background of anthropogenic factors
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1444 in the biogeography of whales, hindering the straightforward application of available results to
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1446 macroecological analysis. For example, several sources reveal that grey whales, today restricted to
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1448 the Northern Pacific, existed in the Northern Atlantic until the 18th century (Bryant, 1995; Rodrigues
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1450 et al., 2018). The North Atlantic population of right whales has also come to near-extinction from
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1452 centuries of man hunting, as revealed by different historical sources (Aguilar, 1986; Reeves et al.,
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1454 2004; Rodrigues et al., 2018). New techniques based on archeological data suggest that the
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1456 disappearance of right and grey whales from the Mediterranean region, the two species possibly
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1458 forming the basis of a forgotten whaling industry, is likely to have had a broad ecosystem impact
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1460 (Rodrigues et al., 2018). The major role was played by commercial whaling in the nineteenth and
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1462 twentieth centuries, drastically reducing the occurrence of detrital whales in all marine ecosystems,
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1464 and leading to the loss of 65-90% of the whale-fall habitat (Smith, 2006). This huge decrease has
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1466 been only partly mitigated by protocols by the International Whaling Commission, designed since
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1468 more than 70 years to increase the standing stocks of impoverished populations (International
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1470 Convention for the Regulation of Whaling, 1946). Extant blue whales, for instance, presently
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1472 correspond to only 3-11% of the 1911 population size (Cooke & Reeve, 2018). These factors are
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1474 known to have cascading effects on the open ocean ecosystem (Higgs et al., 2011b; Roman et al.,
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1476 2014), presumably leading to substantial species extinction in deep-sea whale-fall assemblages
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1478 (Smith, 2006).
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1482 Independent tests of the timings of radiation of bone-eaters are needed to test the hypothesis of a
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1484 correlation with the rise of whale gigantism, including improved molecular phylogenies of bone-
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1486 eating worms, experiencing a modern diversity peak (Taboada et al., 2015). Available studies of the
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1488 fossil record of *Osedax* trace fossils, together with modern evidences, offer at present only a
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1490 fragmentary picture (Supplemental Tab. 5). Research efforts have in fact so far tackled the record
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1492 only partially, aiming at finding the oldest evidence of *Osedax* traces (Kiel et al., 2010), also by
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1494 focusing on other large marine vertebrates such as Mesozoic reptiles (Danise and Higgs, 2016), or
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1502 trying to prove the generalist diet of bone-eaters (Jones et al., 2007; Rouse et al., 2011). Focused
1503 efforts have proved fruitful (Higgs et al., 2012) when applied on a predictive basis at instances where
1504 fossil whale fall communities were already known, in Pliocene open shelf sediments (Dominici et al.,
1505 2009). At other times data are contradictory: *Osedax* ‘craters’ are common on bones and teeth in
1506 Oligocene marine vertebrate assemblages from shelf deposits, apparently on a global basis (New
1507 Zealand and Southeastern USA: Boessenecker and Fordyce, 2015), but not evident in Neogene
1508 specimens from comparable paleosettings (e.g., Purisima Formation and Sharkooth Hill bonebed, in
1509 California; Yorktown Formation and Pungo River Limestone in North Carolina; Calvert Formation,
1510 in Maryland, after visually analysing hundreds of specimens of whale bones: Robert W.
1511 Boessenecker, personal communication, October 2019; with very rare exceptions: Boessenecker et
1512 al., 2014, p. 39 and Fig. 29 D). This may signify that *Osedax*, once living at shelf depths during the
1513 Oligocene, was excluded from the same habitat during part of the Neogene.
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1530 7.4 Whale size

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1534 Proverbially, “whale” is synonym with “large marine mammal”. Killer whales, beaked whales and
1535 sperm whales are indeed large, but, among all cetaceans, today’s all-time giants are the baleen whales
1536 (Alexander, 1998; Clauset, 2013; Goldbogen et al., 2012, 2017; Vermeij, 2014). The evolution of
1537 gigantism among mysticetes has been the subject of several studies, all evidence suggesting that this
1538 took place around the passage Pliocene-Pleistocene (Steeman et al., 2009; Slater et al., 2017; Bianucci
1539 et al., 2019b), in coincidence with an extinction event of the global megafauna (Pimienta et al., 2017).
1540 Our review of the fossil record confirms the overall size increase of baleen whales during the Neogene
1541 and Quaternary, in parallel with the development of extremely productive feeding grounds at high
1542 latitudes. This is not matched by an analogous trend in toothed whales, which have maintained a
1543 wider variety of ecological niches, avoiding direct competition with filter-feeding giants (Fig. 1).
1544 Sperm and beaked whales, together with the delphinoids, show in fact an overall stability in average
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1562 size (Fig. 10), suggesting that evolutionary rates in the two clades, experiencing the equally important
1563 innovations of filter feeding and echolocation (Marx and Uhen, 2010; Pyenson, 2017), are decoupled.
1564 We conclude that, in deep time, the relative role of sperm whales as ecosystem engineers, despite
1565 similarities (Roman et al., 2014), has been inferior to that of baleen whales. Cascading effects must
1566 have triggered a rise of evolutionary rates and a global spread of whale-bone eaters such as *Osedax*
1567 (Taboada et al., 2015), pre-adapted well before the advent of large marine mammals (Danise and
1568 Higgs, 2015). This effect started to be particularly severe, as it is today, at the passage Pliocene-
1569 Pleistocene.
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1581 *7.5 Completeness in the record*

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1585 The chronostratigraphic even distribution of taphonomic grades (Fig. 96) suggests that skeleton
1586 completeness is not controlled by the same factors that control abundance of specimens (Fig. 6) and
1587 facies (Fig. 58), because peaks are offset. The average completeness decreases in time (i.e., the sum
1588 of grades 0-2 augments in frequency, peaking in the Pleistocene), consistently with an hypothesis of
1589 increasing efficiency of bone-eaters. The probability to preserve a complete skeleton with bones in
1590 anatomical connection (grades 5+6), however, depends on factors that have not changed with time.
1591 One such factor could be sedimentation rate, being time-independent to a large degree, mainly
1592 relating to water depth and sediment availability. This is consistent with the association of some
1593 complete and pristine skeletons with delta paleosettings (e.g., Dominici et al., 2018; possibly also
1594 Pyenson et al., 2014) and with the shelfal record being larger than the bathyal (Fig. 8).
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1609 **8 Conclusions**

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1613 The review of 719 reports of Neogene and Quaternary marine toothed and baleen whales (crown
1614 Odontoceti and crown Mysticeti) highlighted a record unevenly distributed both in space and time.
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1622 Fewer fossils are associated with the early Miocene, late Serravallian-Early Tortonian, Messinian and
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1624 Pleistocene, the richest records being associated with the middle and upper Tortonian and the
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1626 Pliocene. The chronostratigraphic distribution of occurrences closely matches the distribution of
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1628 genus-richness, suggesting that Neogene global diversity trends could be, at least in part, artifacts of
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1630 the variable quantity and quality of the rock record so far studied. The Southern hemisphere is less
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1632 represented than the Northern hemisphere, although differences are less with respect to previous
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1634 global studies. In the Northern hemisphere, collections from Europe and Northern America far
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1636 surpass all others in number, while the record for the Northernmost Atlantic and the Arctic Sea are
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1638 extremely poor, notwithstanding they have been important feeding grounds during the evolutionary
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1640 history of cetaceans. In the Southern hemisphere, the African record is particularly poor and the
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1642 taxonomy of the extremely rich South American record has been tackled only in small part. The
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1644 paleoenvironmental distribution of 642 whale fossils reveals that the record is preferentially
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1646 distributed in lower shoreface and shelf sediments, and is poor in very shallow marine settings. What
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1648 is odd, given the the fact that living cetaceans are most abundant above waters deeper than the shelf
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1650 break, is the extremely poor record associated with bathyal sediments. The chronostratigraphic
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1652 distribution of size of skull parts confirms the steady increase in size of mysticetes and their rise to
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1654 gigantism at the passage Pliocene-Pleistocene. This size increase is not matched by other long-
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1656 standing clades of large whales, such as beaked and sperm whales, suggesting that only baleen whales
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1658 have been true ecosystem engineers in deep time, possibly starting from their rise to gigantism. To
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1660 explain some of the odd distributions of fossil whales, we suggest that the record is obscured by an
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1662 “*Osedax*” effect as the collective effect of whale-fall communities, typified by bone-eating
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1664 polychaetes of genus *Osedax*. This world-wide fauna is particularly effective in deep-sea whale-fall
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1666 communities, where even large carcasses are totally destroyed in a matter of a few years, never
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1668 becoming part of the fossil record. We hypothesise that the rise to gigantism of baleen whales has
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1670 triggered a radiation of bone-eaters, presently living also at shelf depths. This effect would at least in
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1672 part explain the awkward poverty of the overall Pleistocene record. A comparison of thickness of
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1682 marine strata deposited during the Pliocene and the Pleistocene, two time spans of approximate
1683 duration, measured in five regions worldwide suggests that the Pleistocene is well-represented in
1684 collisional basins (e.g., Mediterranean and Japan), ruling out the common-cause hypothesis to explain
1685 the poor Pleistocene fossil record. The taphonomic review of 635 fossils shows that on average
1686 Neogene and Quaternary specimens are less complete. The frequency of complete carcasses is
1687 constant in time, so that completeness is controlled by time-independent factors, such as
1688 sedimentation rates in different marine environments. Industrial whaling and other human influences
1689 on the taphonomy of whale carcasses should be also considered to explain differences between
1690 modern distributions and the fossil record. The uneven sampling of some geographic regions and
1691 some time intervals, whether caused by differential study efforts or by objective differences in the
1692 quality of fossil record, suggests that future studies and new findings can still change our
1693 understanding of macroevolution, macroecology and paleobiogeography of crown Cetacea.
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1710 **Acknowledgments**

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3062 **Table captions**
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3066 Table 1: Size, habitat, geographic range, food and feeding-techniques of representative species of
3067 toothed and baleen whales.
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3071
3072 Table 2: Underwater whale actuopaleontology. Data refer to available evidence on the depth of
3073 deposition of naturally sunken whale carcasses. Note that all cases relate to baleen whales.
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3076
3077 Table 3: Characters of the 14 categories of carbonate and siliclastic rocks, grouped into six types
3078 based on composition and grain size.
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3082 Table 4: Taphonomic grades (completeness).
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3089 **Figure captions**
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3093 Figure 1: Relationship between size, trophism and habitat of living cetaceans, with emphasis on depth
3094 of seafloor. Toothed whales, of oldest origins, can be of all sizes, occupy a wide range of habitats,
3095 from estuarine to 3000 m depth, feed on a variety of preys and employ different techniques, either
3096 using their teeth (light grey silhouettes) or deep-sea diving and feeding by suction (dark grey
3097 silhouettes). Baleen whales are all from large to gigantic, most species living at the shelf break or on
3098 the upper slope, filter-feeding on copepods and dense concentrations of krill. The feeding grounds of
3099 baleen whales are mostly located at high latitudes, where populations of krill, copepods and
3100 amphipods are densest (Tab. 1). Whereas large size is highly correlated with filter-feeding in baleen
3101 whales, suction-feeding of toothed whales is a size-independent adaptation. Both clades particularly
3102 exploit productive waters at the shelf break or on the continental slope.
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Figure 2: Stages of ecological succession at whale falls on two implanted carcasses (A, D-E: ~30-ton gray-whale carcass at 1675 m, Santa Cruz Basin; F-G: adult fin-blue whale carcass at 960 m, San Nicolas Basin) and two natural occurrences (B: whale fall at 3238 m, Davidson seamount; C: whale fall at about 300 m, Monterey Canyon), all from the continental slope and ocean floor in the California offshore. A: The mobile-scavenger stage, with hagfishes and shark bite-marks, after 1.5 months of exposure on the seafloor. B: Transition between the mobile-scavenger stage (flesh is still present on the carrion; octopuses, eelpouts and grenadiers are scavenging, or feeding on smaller live prey), and the enrichment-opportunist stage, represented by the thick carpet of bone-eating worms of genus *Osedax*, covering the a large surface of the bones, and by a thick carpet of tube worms on the seafloor. C: Photomontage showing the enrichment-opportunist stage of a whale-fall community at about 3000 meters below the ocean surface in Monterey Canyon, as it appeared in February 2002, soon after its discovery by researchers at the Monterey Bay Aquarium Research Institute. Large numbers of red *Osedax* worms carpet the bones, which are already highly degraded. The small pink animals in the foreground are scavenging sea cucumbers. D: The enrichment-opportunist stage after 1.5 years at the seafloor (same carcass as in A), when the soft tissue has been removed from the skeleton and an opportunist fauna thrives on the enriched sediment (white spots on the sediment are bivalves, gastropods, dorvilleid polychaetes, and cumacean crustaceans). E: The sulfophilic stage after 6.8 years at the seafloor (same carcass as in A). Thick white and yellow mats of sulfur-oxidizing bacteria, along with anemones, are visible on the bones. Vesicomid clams, a shrimp, and ampharetid polychaete tubes can be seen in the surrounding sediments. E: Sulphophilic stage after 66 years at the seafloor. White bacterial mats still partly cover the bones. Adult vesicomid clams hosting chemosymbiotic bacteria that thrive on sulfide; an holothurian and a galatheid crab are also visible on the carcass. F: State of larger bones after 66 years at the seafloor. Skull bones and caudal vertebrae persist longer than all other skeletal elements. Underlying sediments probably still host an assemblage of chemolithoautotrophs that live on the sulfide emitted from the anaerobic bacterial decomposition

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3182 of bone lipids. Images A, D-G courtesy of C.R. Smith; image B courtesy of Ocean Exploration Trust
3183 and NOAA ONMS; image C courtesy of the Monterey Aquarium.
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3188 Figure 3: Actuopaleontological and paleontological evidences of whale bone bioerosion. A: Tiering
3189 of whale bone eaters on a whale fall at 3238 m, Davidson seamount (see Fig. 2 B): the tip of the right
3190 mandible has been deeply bioeroded, particularly its inner parts, possibly from galatheid crabs (one
3191 can be seen on the left), while *Osedax* is still feeding on bone cortex at a higher level with respect to
3192 the seafloor, where oxygen levels are higher; B: Tiering of bone-eating worms on transverse vertebral
3193 processes of a baleen whale (ventral side up): processes on the left of the image, where *Osedax* is
3194 densest, have been partly bioeroded, while those on the right are still pristine; C: Micro computed
3195 tomography scan of a boring made by *Osedax rubiplumus* in a cetacean carpal bone showing how
3196 *Osedax* borings expand below the external bone surface; D-E: Bioeroded mandible tip of a Pliocene
3197 baleen whale (D: outer surface, E: inner surface; Museum of Natural History - MSN, University of
3198 Florence, specimen IGF 102292 from Orciano Pisano, Tuscany,) showing general bioerosion; F-H:
3199 Ventral view of a bioeroded Pliocene cetacean vertebra (MSN, IGF 104276 from unknown locality,
3200 Tuscany); individual boreholes are recognizable in G, while the transverse processes have been
3201 completely destroyed (detail in H); I-L: Bioeroded radius of a Pliocene ?Ziphid (MSN, IGF IGF
3202 9361V from Orciano Pisano, Tuscany): the margins are heavily bioeroded, while individual *Osedax*
3203 boreholes are recognisable in cross section in the middle part of the bone (L: CT scan across the
3204 middle part of the bone).
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3227 Figure 4: Skeletons of modern toothed and baleen whales (scuba diver for scale). A: Bones of
3228 common bottlenose dolphin (*Tursiops truncatus*). B: Bones of blue whale (*Balaenoptera musculus*).

3231 The adult blue whale is about ten times longer than the adult bottlenose dolphin and, while the overall
3232 number and shape of bones is approximately the same, each bone of a blue whale is up to a thousand
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3242 times bigger than the corresponding bone of a bottlenose dolphin (the volume increases with the cube
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3244 of the distance).
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3248 Figure 5: Geographic distribution of 719 whale fossil records analysed. Regions are: 1) Western coast
3249 of Central and North America, 2) Western Coast of Southern America, 3) Eastern Coast of North
3250 America, 4) Eastern Coast of South America, 5) Western Coast of Europe and North Africa, 6)
3251 Mediterranean, Central and Eastern Europe, and Asian Near East, 7) Eastern Coast of Asia, 8)
3252 Oceania, 9) Indian Ocean and Austral Africa. Geographic localities are framed against the distribution
3253 of chlorophyll concentrations as measured by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS)
3254 satellite and the Moderate Resolution Imaging Spectroradiometer (MODIS) on NASA's Aqua
3255 satellite between March 21 and June 20, 2006. These concentrations, ranging 0.01-20 mg/m³, are a
3256 proxy of water productivity: low concentrations (i.e., black and dark blue) indicate oligotrophic
3257 waters; high concentrations (yellow to red) indicate thriving marine ecosystems, where cetacean
3258 populations currently abound. NASA image in the background is created by Jesse Allen, courtesy of
3259 NASA's Earth Observatory (downloaded from <https://earthobservatory.nasa.gov>, on June 19, 2019).
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3276 Figure 6: Chronostratigraphic distribution of 719 whale fossil records analysed, subdivided into nine
3277 time bins of equal duration (a). Number of occurrences are confronted with genus-level richness
3278 measured for each time bin (b).
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3284 Figure 7: Distribution of the whale fossil record based on the associated lithology, with a comparison
3285 between our dataset (N = 610) and PaleoDB (N = 841).
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3290 Figure 8: Paleoenvironmental distribution of 642 whale fossil records, an interpretation based on
3291 sedimentary facies or paleoecology of the associated fauna. Facies are distributed along a
3292 paleobathymetric gradient, from shallower to deeper going from left to right.
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3304 Figure 9: Distribution of taphonomic grades based on completeness of the skeleton subdivided per
3305 time bin (N = 635), in ascending order, grade 0 corresponding to isolated bones and grade 6 to highly
3306 complete skeletons (see text for explanation). Bones of complete skeletons are also usually in
3307 anatomical connection.
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3315 Figure 10: Size of fossil whales plotted according to their age as inferred from the literature. Size is
3316 measured as length of tympanic bulla (linear trends in yellow), bizygomatic width (linear trend in
3317 blue) and condylobasal length (linear trends in green), subdivided into four systematic groups:
3318 primitive Odontoceti (platanistoid and heterodont toothed whales), Physeteroidea (sperm and beaked
3319 whales), Delphinida (dolphins and porpoises) and Mysticeti (baleen whales). Note that scales are
3320 different.
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3330 Figure 11: Thickness of Pliocene and Pleistocene sedimentary successions, in meters. A: Pliocene
3331 and Pleistocene of Italy, subdivided by sedimentary facies and based on an extended database
3332 (Supplemental Tab. S4). In white, number of total per-epoch fossil whale occurrences. B: Comparison
3333 between the thickness of Italian formations and that of formations in four other regions, from different
3334 tectonic settings, together yielding the largest part of the fossil whale record reviewed (see
3335 Supplemental Tab. S1). Lithologies were subdivided in two broad groups (sandstone and mudstone,
3336 compare with facies in Fig. 10A).
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3347 **Supplemental Material**

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3351 **Supplemental Material, Table S1.** Dataset of 719 cetacean occurrences, with information on 1)
3352 corresponding PBDB occurrence and collection number, if available, 2) geographic location, 3)
3353 geological data in terms of lithology, sedimentary structures and associated fossils, 4) paleodepth
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3362 range (if stated in the literature) and inferred paleoenvironment, 5) chronostratigraphy, with best
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3364 estimates available of minimum and maximum age, 6) time bin, 7) taxonomy, 8) taphonomy, 9) size,
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3366 and 10) hosting institution and catalogue number.
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3371 **Supplemental Material, Table S2.** PaleoDB dataset of Neogene cetaceans, as downloaded on March
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3377 **Supplemental Material, Table S3.** Spearman rank correlation between cetacean occurrences and
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3379 genus richness.
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3383 **Supplemental Material, Table S4.** Thickness of Pliocene and Pleistocene coarse-grained and fine-
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3385 grained siliciclastic formations of Italy, Japan, New Zealand, US Atlantic Coast, Atlantic and North
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3387 Sea European coasts. Total values suggest that the Pleistocene record of both shallow and deep marine
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3389 paleosettings is comparable to that of the Pliocene.
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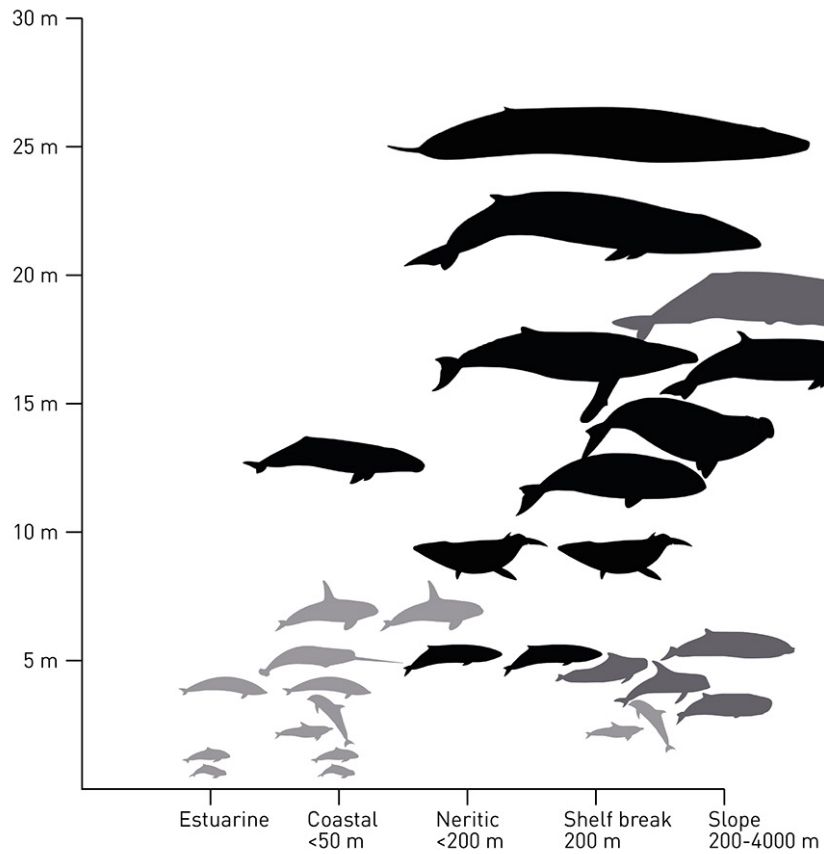
3394 **Supplemental Material, Table S5.** Fossil and modern records of *Osedax* traces.
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3398 **Supplemental Material, Fig. S1.** Geographic distribution of Neogene fossil cetaceans from the
3399
3400 PaleoDB dataset. The Northern hemisphere is represented by 1257 records, the Southern hemisphere
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3402 by 113 records. Many of the PaleoDB records from the Northern hemisphere were not considered
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3404 because they included ice-rafted material, bones from pre-Holocene human settlements and remains
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3406 found scattered on the seafloor that could be assigned to a rock unit.
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3411 **Supplemental Material, Fig. S2.** Chronostratigraphic distribution of genus-level richness of fossil
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3413 cetaceans, excluding the record from Peru. Peruvian records are particularly important for the study
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3415 of the upper Tortonian and Messinian. The difference in the number of occurrences (A), however, is
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3422 much more relevant than the difference in genus richness (B). This is possibly related because many
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3424 peruvian fossils, already introduced in the literature, need to be identified.
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3428 **Supplemental Material, Fig. S3.** Chronostratigraphic distribution of genus richness of Odontoceti
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3430 (A) and Mysticeti (B). Late Miocene trends are decoupled.
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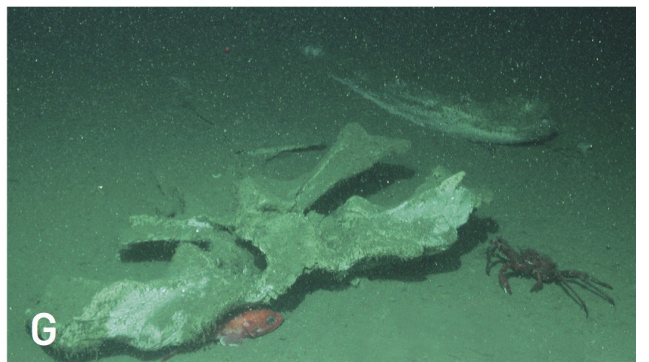
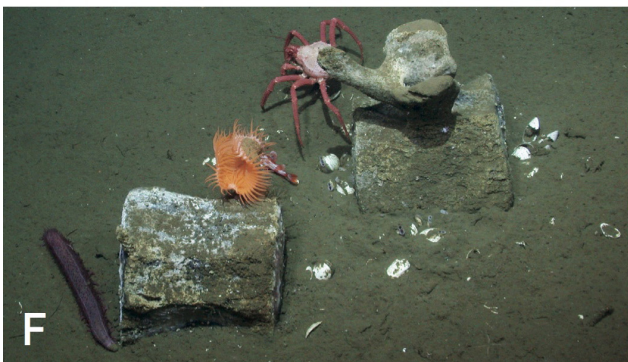
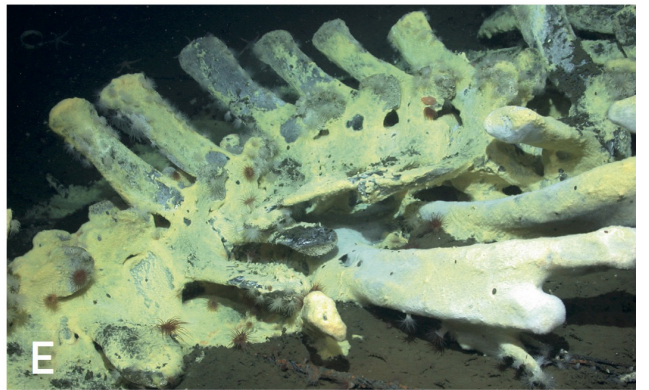
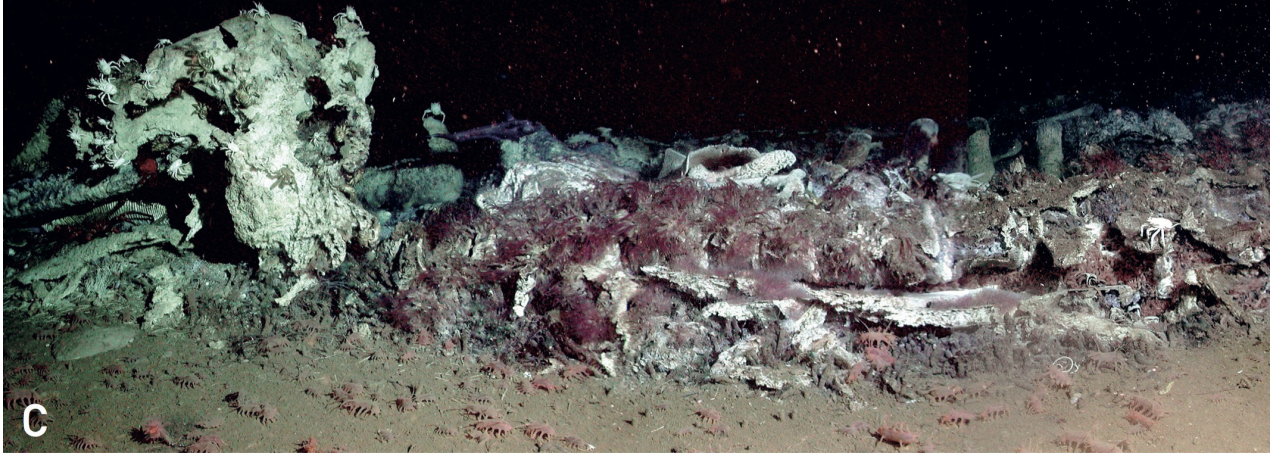
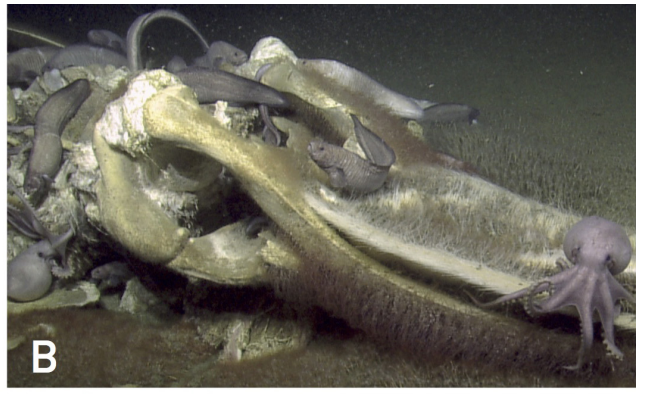
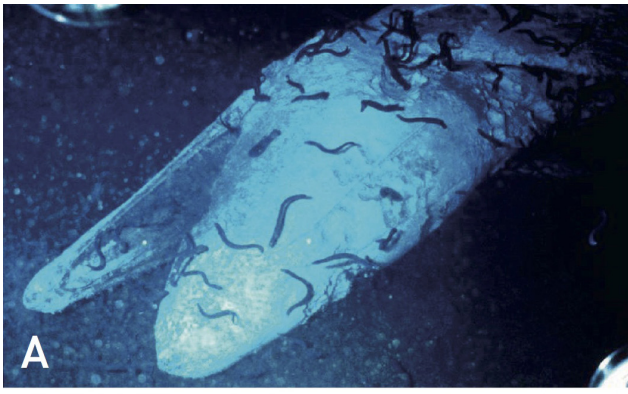


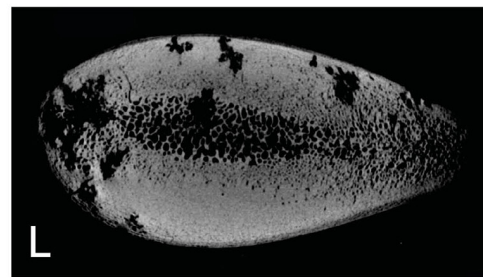
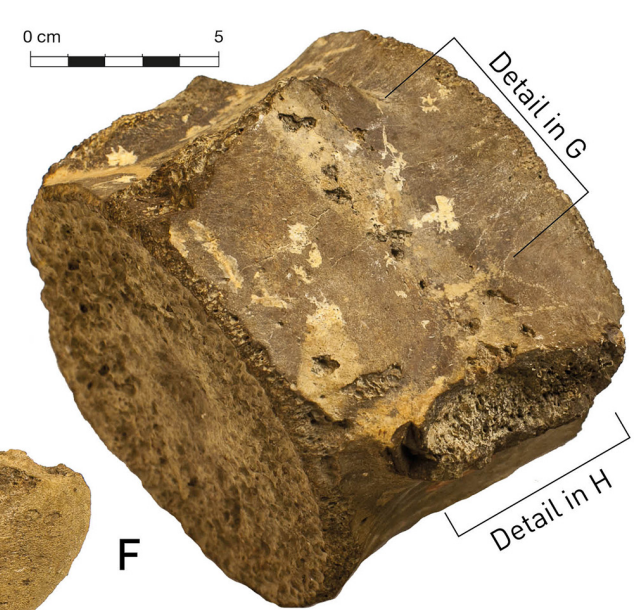
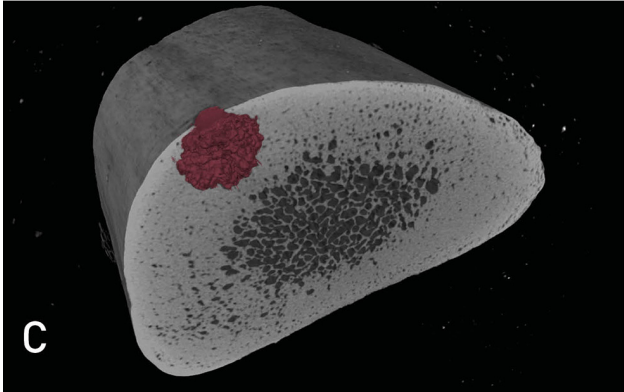
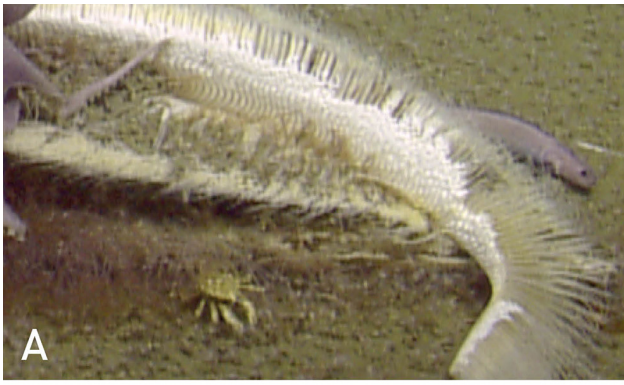
Toothed whales

-  *Physeter macrocephalus*
-  *Ziphius cavirostris*
-  *Kogia breviceps*
-  *Grampus griseus*
-  *Globicephalus macrorhynchus*
-  *Monodon monodon*
-  *Orcinus orca*
-  *Delphinapterus leucas*
-  *Tursiops truncatus*
-  *Stenella attenuata*
-  *Phocoena phocoena*
-  *Orcaella brevirostris*

Baleen whales

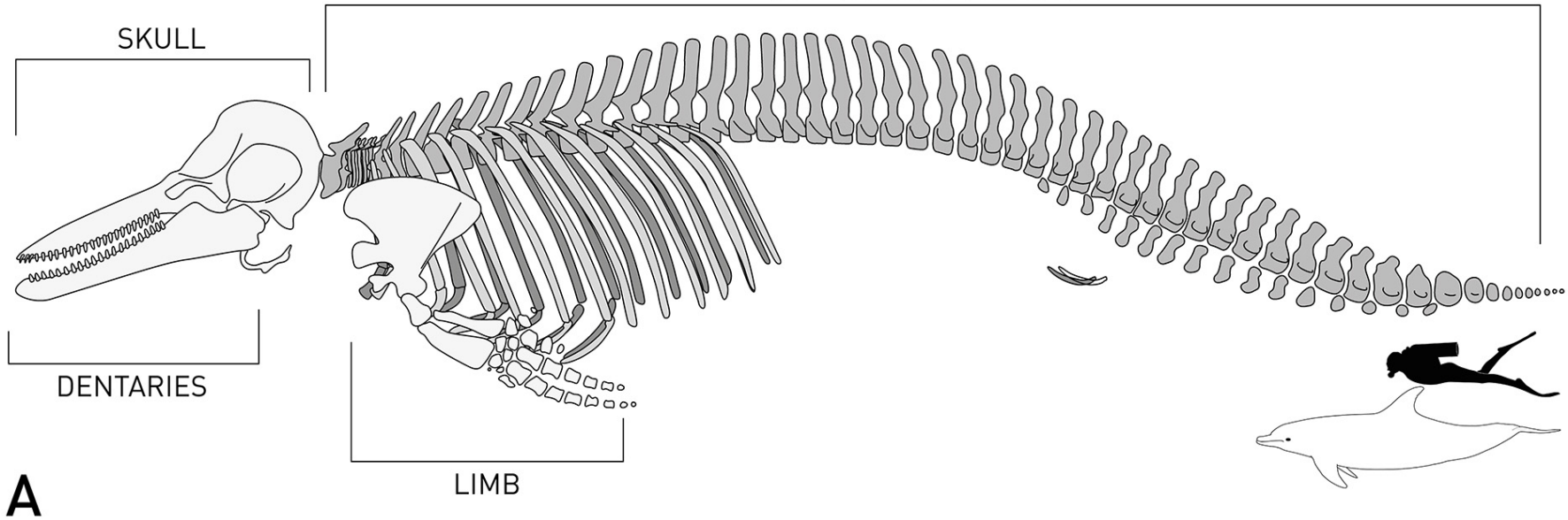
-  *Balaenoptera musculus*
-  *Balaenoptera physalus*
-  *Megaptera novaeangliae*
-  *Balaenoptera borealis*
-  *Eubalaena glacialis*
-  *Balaena mysticetus*
-  *Eschrichtius robustus*
-  *Balaenoptera acutorostrata*
-  *Caperea marginata*





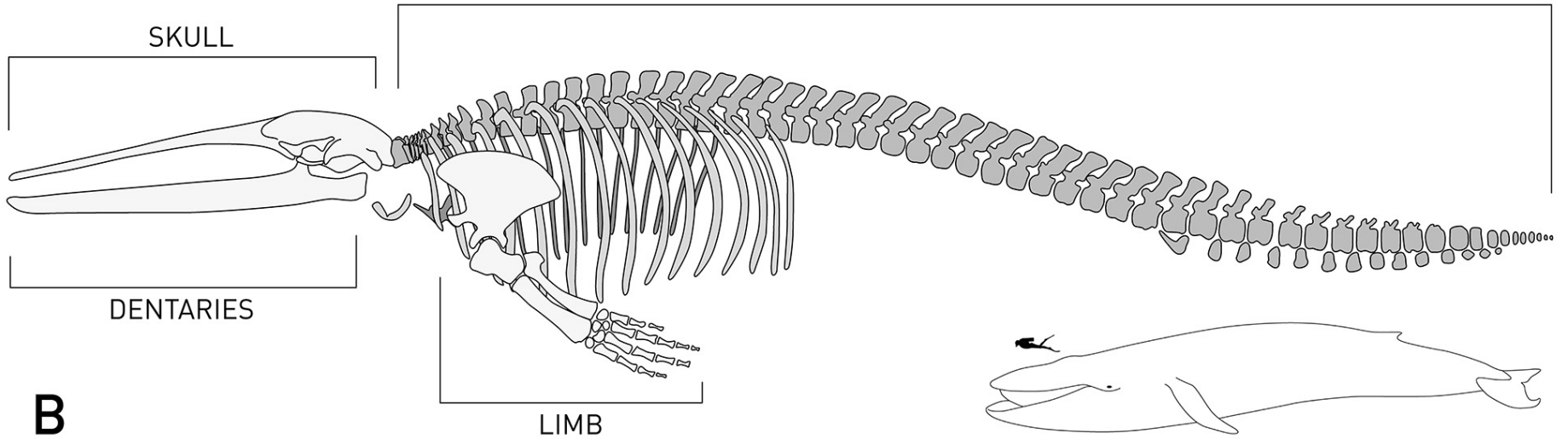
Cross section in L

POST-CRANIAL SKELETON

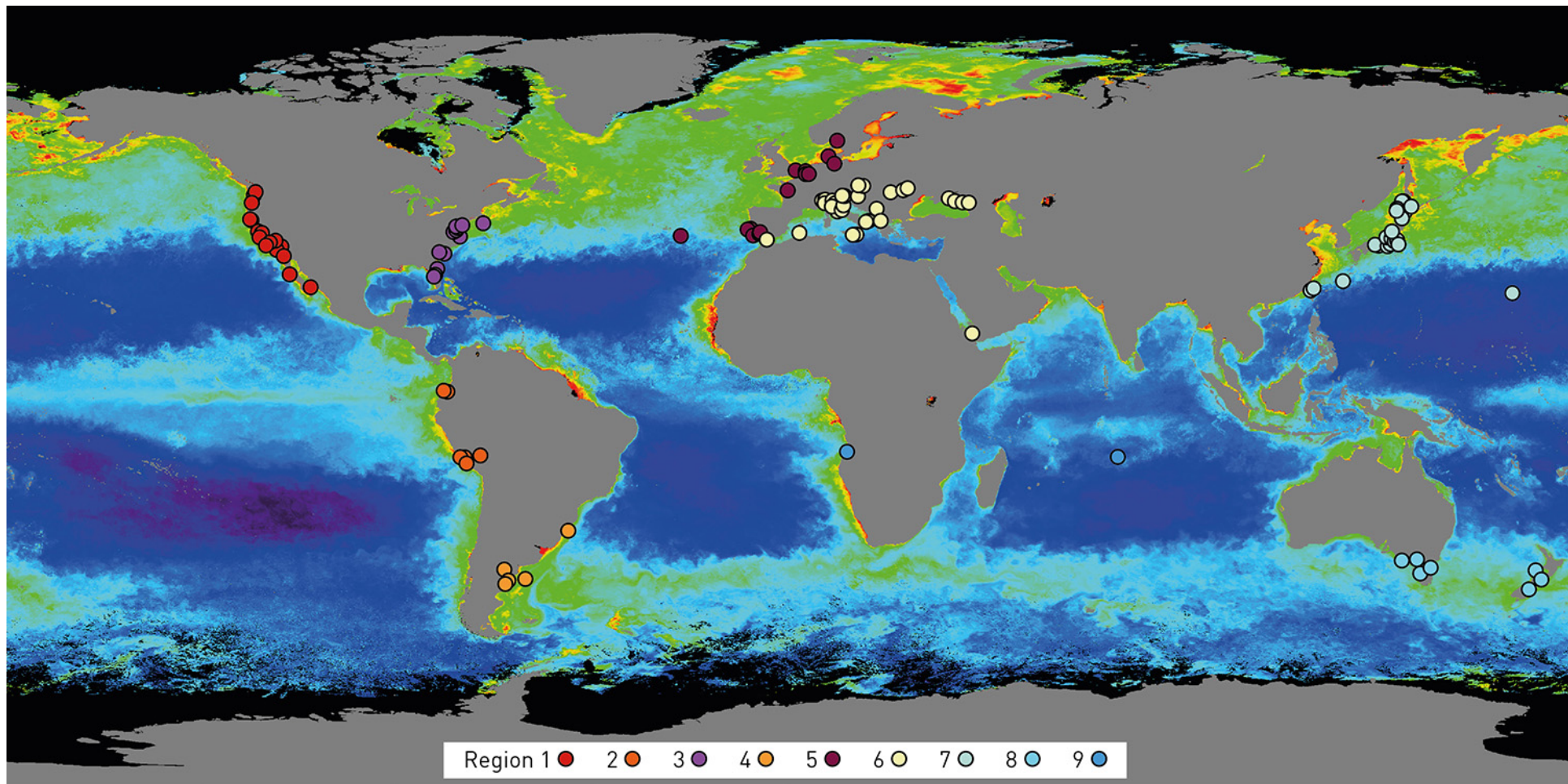


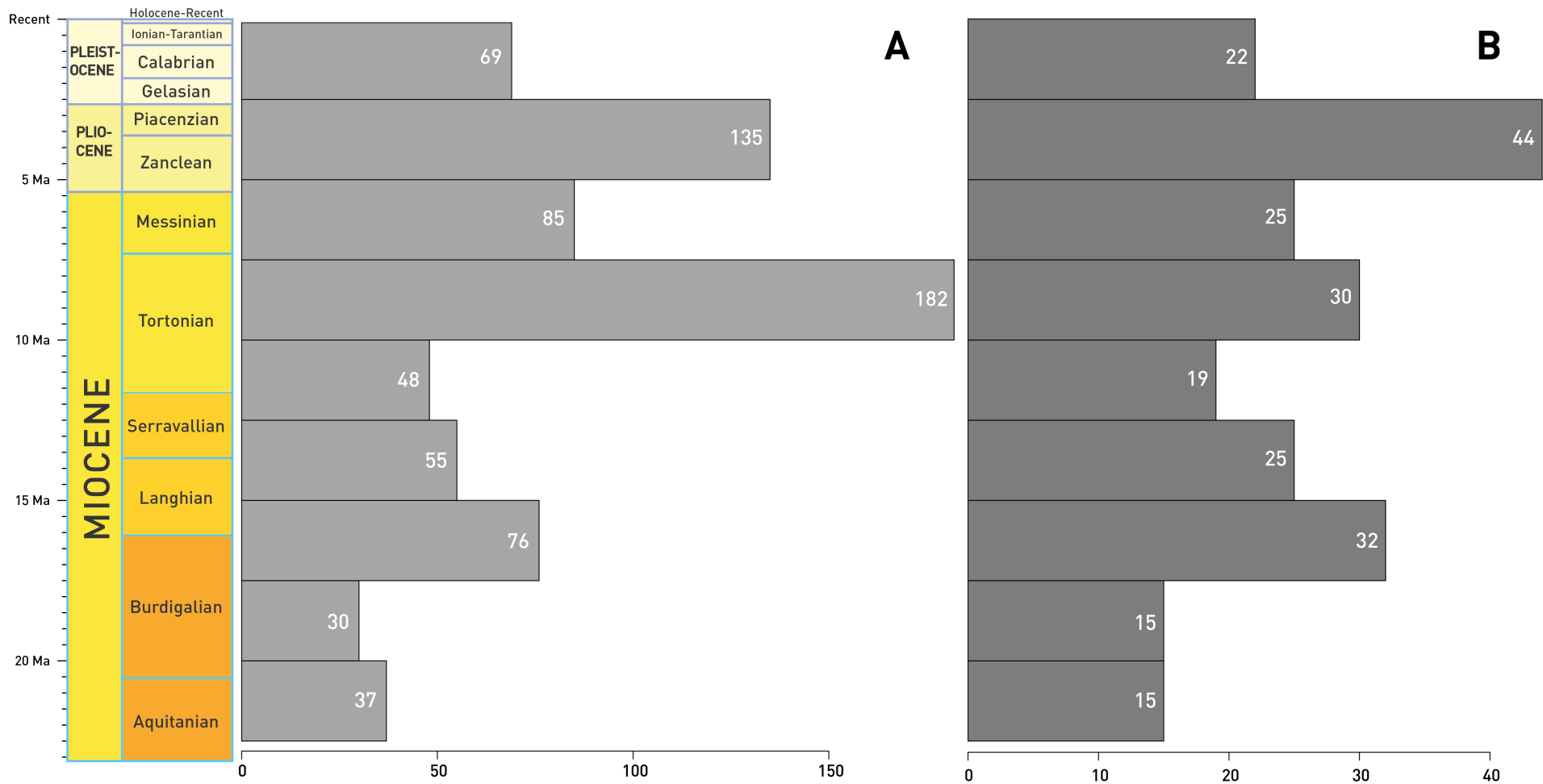
A

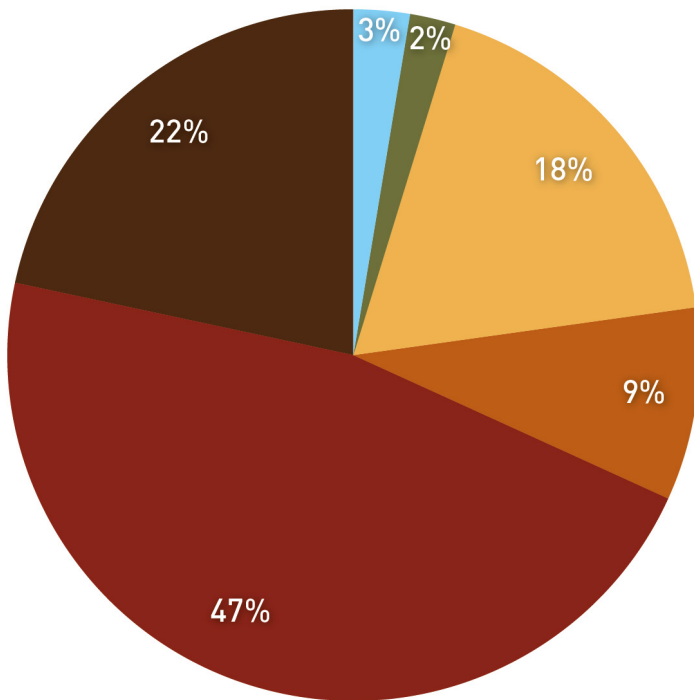
POST-CRANIAL SKELETON



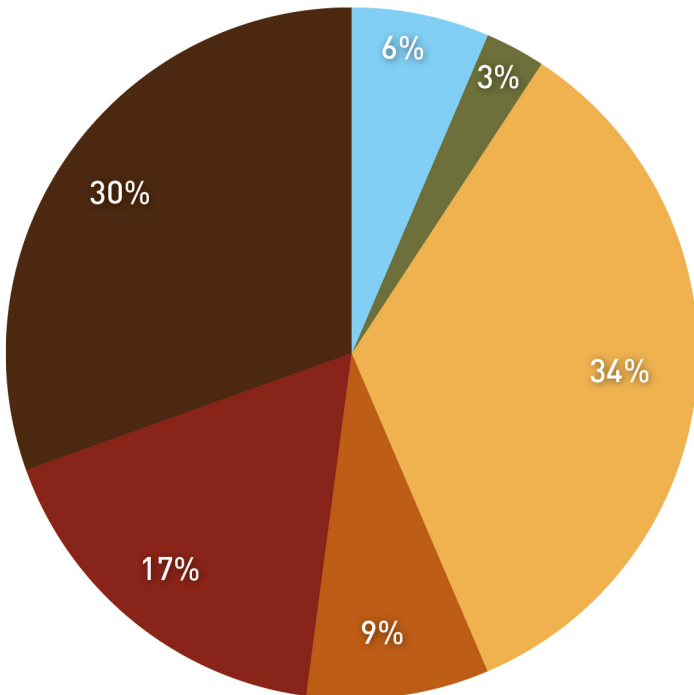
B





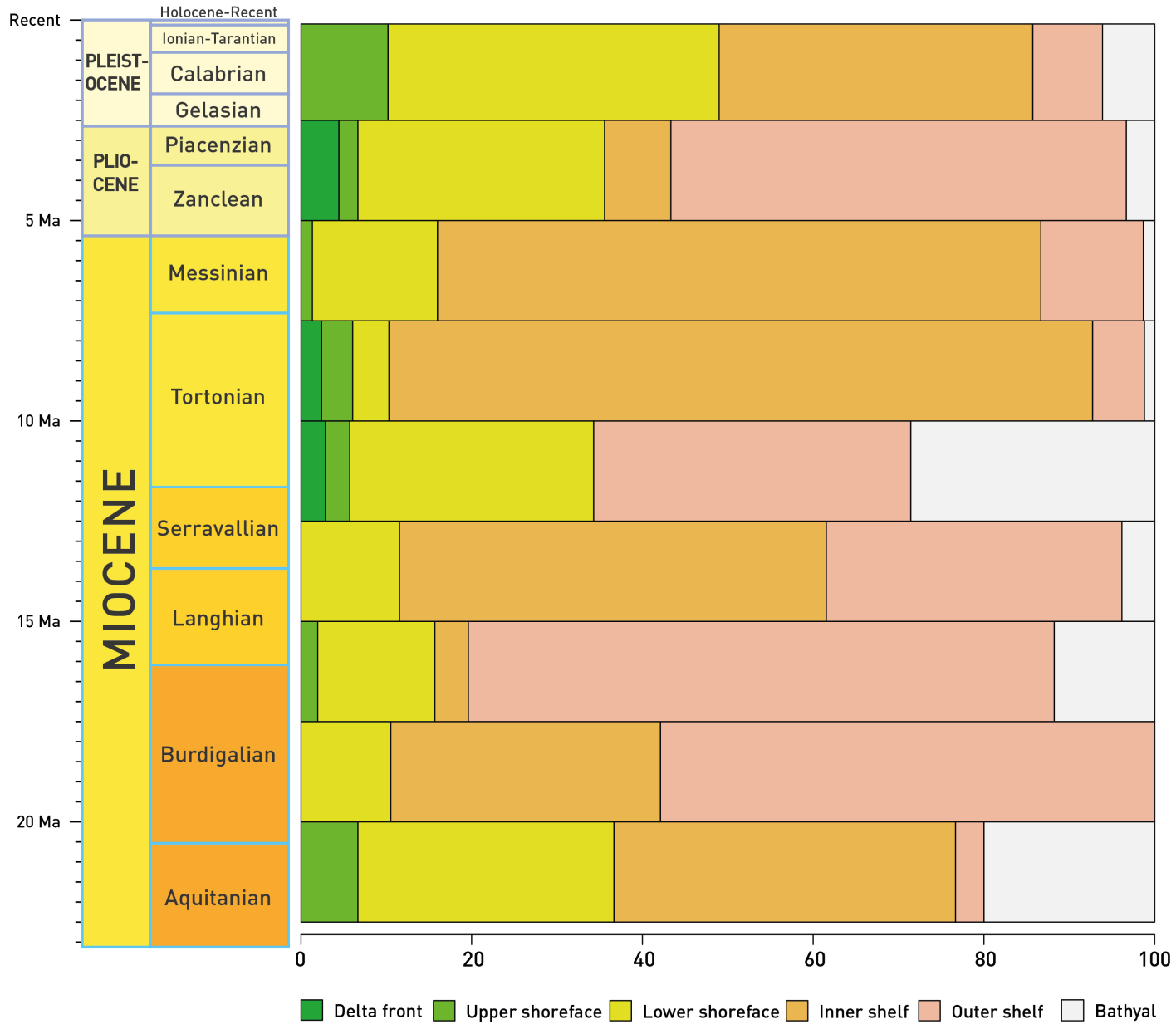


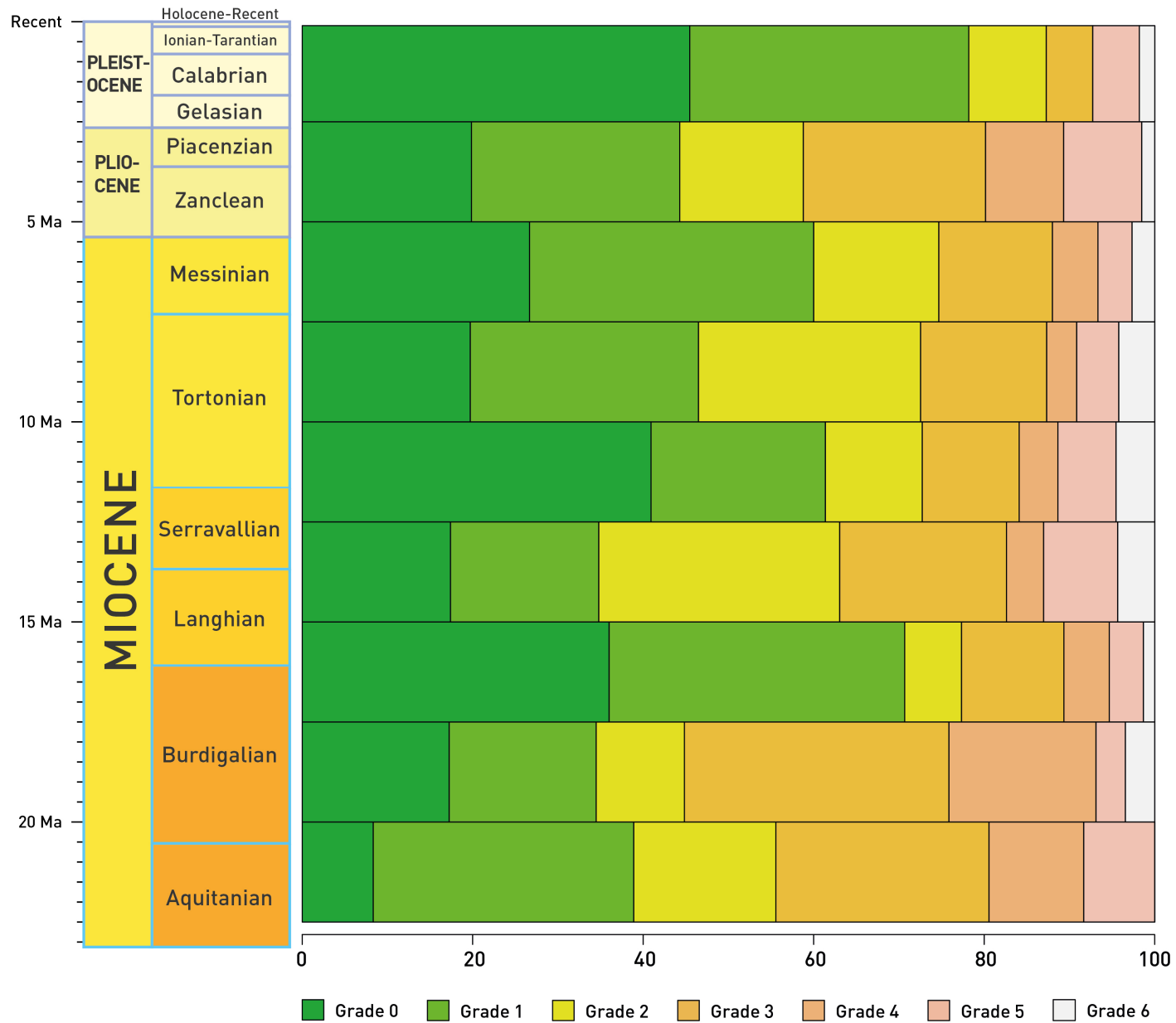
Present dataset

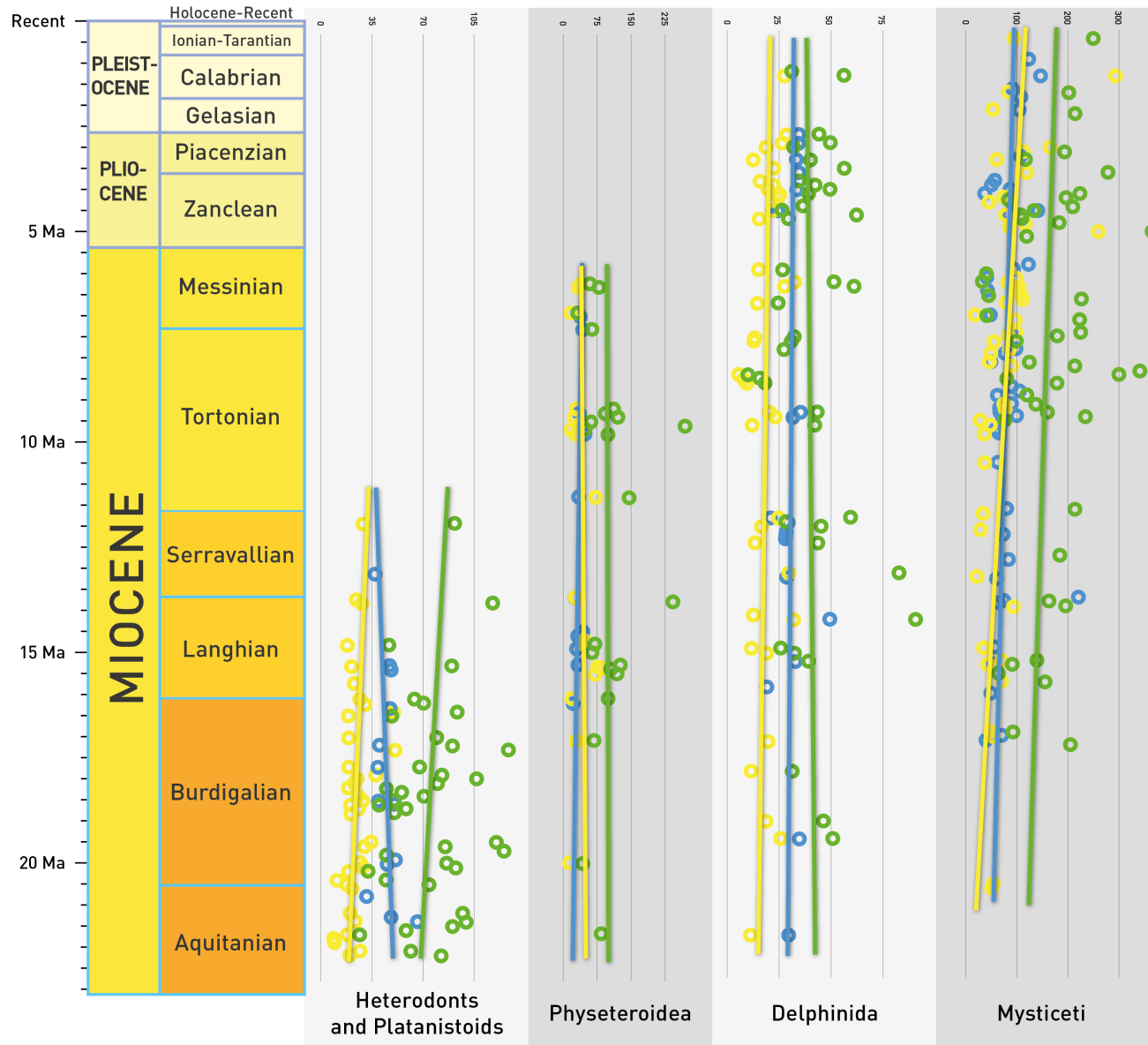


PaleoDB

- Carbonates
- Gravels/Gravelly sandstone/Coarse sandstone
- Sandstone
- Shelly/Glauconitic/Phosphatic sandstone
- Diatomite/Silty sandstone/Siltstone
- Mudstone/Claystone/Marl







● Tympanic bulla length (in mm)
 ● Bizygomatic width (in cm)
 ● Condylbasal length (in cm)

