PALEO

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An overview of the fossil record of cetaceans from the East Pisco Basin (Peru)

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ABSTRACT - The East Pisco Basin is one of the forearc basins that formed during the Cenozoic along the coast of Peru due to the subduction of the Farrallon-Nazca plate beneath the South American plate. The sedimentary fill of this basin is extensively exposed along the coastal Ica Desert, and includes a succession of Eocene to Pliocene marine sediments that account for a ~50-myr-long history of semi-continuous deposition. These rocks are characterized by an outstanding fossil content that remarkably contributed to our understanding of the evolutionary history of the main groups of Cenozoic marine vertebrates. In the Ica desert, the most common and significant vertebrate remains belong to cetaceans. Knowledge on the fossil cetaceans of the East Pisco Basin has grown dramatically in the last fifteen years thanks to several international research projects involving, among many others, the authors of the present article. These research efforts have led to the discovery of several hundred fossil skeletons, the most significant of which have been collected, prepared and partly published. Furthermore, interdisciplinary studies were also conducted in order to provide a high resolution chronostratigraphic framework for this fossil record. Remarkable cetacean specimens come from the Yumaque member of the Paracas Formation (middle to late Eocene), the Otuma Formation (late Eocene), the Lower Miocene (~19-18 Ma) portion of the Chilcatay Formation, and allomembers P0 (14.8-12.4 Ma), P1 (9.5-8.5 Ma) and P2 (8.4-6.7 Ma) of the Middle Miocene to Pliocene Pisco Formation. The Lutetian (42.6 Ma) Yumaque strata are home to the quadrupedal protocetid archaeocete Peregocetus pacificus, *which documents the first arrival of cetaceans in the Pacific Ocean. Geologically younger (36.4 Ma) Yumaque deposits have yielded the holotype skeleton of* Mystacodon selenensis, *the oldest mysticete ever found. This ancestor of the modern baleen whales had a skull provided with a complete dentition and retained hindlimbs, albeit reduced in size. In the Otuma Formation, a nine-m-long basilosaurid (*Cynthiacetus peruvianus*) has been discovered. The Chilcatay Formation records the first great radiation of the odontocetes, represented by Inticetidae (*Inticetus vertizi*), basal Platanidelphidi (*Ensidelphis riveroi*), Squalodelphinidae (*Furcacetus flexirostrum, Huaridelphis raimondii, Macrosqualodelphis ukupachai and* Notocetus vanbenedeni*), Platanistidae (aff.* Araeodelphis*), Physeteroidea (*Rhaphicetus valenciae *and cf.* Diaphorocetus*), Chilcacetus cavirhinus, indeterminate Eurinodelphinidae, and Kentriodontidae (*Kentriodon*). Overall, this roughly coeval assemblage displays a considerable disparity in terms of skull shape and body size that is possibly related to the development of different trophic strategies, ranging e.g., from suction to raptorial feeding. In the Pisco Formation, starting from P0, the baleen-bearing whales (Chaeomysticeti) represent the most frequent cetacean fossils (only a few mysticetes are known from the Chilcatay strata). Two chaeomysticete lineages are found in the Pisco Formation: Cetotheriidae (from* Tiucetus rosae *in P0 to* Piscobalaena nana *in P2) and Balaenopteroidea (from* Pelocetus *in P0 to several undescribed species of Balaenopteridae in P2, testifying to a progressive trend toward gigantism). Odontocetes are rare in P0, the "kentriodontid"* Incacetus broggii *being the only species described from these strata, but they become more abundant and diverse in P1 and P2. In P1, the commonest toothed whale is* Messapicetus gregarius, *a member of Ziphiidae featuring an extremely elongated rostrum and a complete set of functional teeth. Another ziphiid from P1 is* Chimuziphius coloradensis, *known only from the fragmentary holotype cranium. The P1 strata also record the appearance of the crown Delphinida, with the superfamily Inioidea being represented by two small pontoporiids (*Brachydelphis mazeasi *and* Samaydelphis chacaltanae*) and one iniid (*Brujadelphis ankylorostris*). Moreover, P1 is also home to the stem physeteroid* Livyatan melvillei*; featuring a three-m-long skull and teeth reaching 36 cm in length,* L. melvillei *was one of the largest raptorial predators and, possibly, the biggest tetrapod bite ever found.* Acrophyseter *is another macroraptorial sperm whale, distinctly smaller than* L. melvillei, *known from both P1 and P2. Even smaller in size are the kogiids* Platyscaphokogia landinii *and* Scaphokogia cochlearis, *both of which are known from the upper strata of P2. The same allomember is also home to the ziphiids* Chavinziphius maxillocristatus *and* Nazcacetus urbinai, *the "kentriodontids"* Atocetus iquensis *and* Belenodelphis peruanus, *and undescribed members of Phocoenidae.*

INTRODUCTION

What is a mammal? Many educated persons may answer that a mammal is an animal provided with mammary glands, ear ossicles and hair, and such a reply would be hard to rebut in general. Now however, one of the most charismatic groups of extant mammals has skins that are completely hair-free. Furthermore, the same idiosyncratic mammals have abdicated the terrestrial lifestyle that is proper of "ordinary" mammals and other tetrapods to turn back, in a sensational evolutionary turnaround, to the aquatic environments that the mammals' ancestors left some 350 million years ago. These are only some of the several characters that divide extant cetaceans - that is the name of the aforementioned, as yet enigmatic group! - from most other mammals, and in light of which whales, dolphins and porpoises were once recognised as "the most peculiar and aberrant of mammals" (Simpson, 1945, p. 213).

Truth to be told, the fossil record of cetaceans is now rich enough to allow for sketching a rather comprehensive picture of the mode and tempo of cetacean evolution. It is now universally accepted that the first cetaceans emerged from within artiodactyls in earliest Eocene times (Gingerich et al., 2001; Thewissen et al., 2001), the oldest "whales" being represented by four-legged, largely

terrestrial forms such as pakicetids, all of which have been found as fossils in the Indo-Pakistani region (Gingerich et al., 1983). These small predators inhabited the coasts of the eastern Tethys and likely fed in aquatic environments, mainly in fresh- or brackish-water basins (Clementz et al., 2006). The first signs of adaptation to aquatic life are to be found in the weighting of the skeleton (interpreted in terms of "ballasting" to the seafloor) and in some modifications of the auditory bones that connect the pakicetids to the more advanced cetacean lineages (Luo & Gingerich, 1999). Pakicetids were the first among the "archaeocetes" that made the transition from land to water; slightly more derived, amphibious forms like the ambulocetids and remingtonocetids display a trend of increasing body sizes and a marked morphological convergence with marine crocodiles (Thewissen et al., 1994, 1996; Thewissen & Bajpai, 2001, 2009). With the subsequent protocetids, cetaceans dispersed for the first time outside the Tethyan realm, and their evolutionary history thus became a truly global phenomenon that ultimately led to the origin and radiation of the modern cetacean clades - echolocating toothed whales (Odontoceti) and baleen-bearing whales (Mysticeti) (Uhen, 2010).

One of the most privileged locations for unraveling the evolutionary history of cetaceans is undoubtedly the East Pisco Basin of southern Peru. Here, fossil marine vertebrates (mammals, birds, reptiles, and bony and cartilaginous fishes) occur within a semi-continuous, Eocene to Pliocene stratigraphic succession (e.g., Muizon & DeVries, 1985; Muizon, 1988a; Brand et al., 2004; Esperante et al., 2008, 2015; Lambert et al., 2010b, 2015a; Parham & Pyenson, 2010; Collareta et al., 2015, 2017a, 2020b, 2021b; Bianucci et al., 2016b, c; Gioncada et al., 2016; Di Celma et al., 2017; Landini et al., 2017, 2019; Bosio et al., 2021; Boskovic et al., 2021). In the course of the last forty years, palaeontological investigations on the fossil record of the Pisco Basin have led to describing a plethora of new species of archaeocete, odontocete and mysticete taxa, as well as to identifying crucial fossils that illustrate the skeletal anatomy, morphofunctional adaptations and palaeoecological habits of cetaceans through most of the Cenozoic.

The history of scientific research on the fossil marine vertebrates of the coastal deserts of southern Peru dates back to the 19th century. Indeed, the Italian-born Peruvian geographer and naturalist Antonio Raimondi (†1890) was likely the first western scholar to report on fossil marine vertebrates from Neogene strata exposed in what has long been regarded as the southern termination of the East Pisco Basin (Bianucci, 2010). However, it was not before the pioneering studies by Christian de Muizon (e.g., Muizon & DeVries, 1985; Marocco & Muizon, 1988a; Muizon, 1988a) that the outstanding fossil record of vertebrates of the East Pisco Basin started to attract the attention of the global palaeontological community thanks to the description of several new taxa that greatly contributed to our knowledge of the evolutionary history of various groups of marine tetrapods (mostly cetaceans). These early results triggered a growing interest for the marine vertebrate-bearing Cenozoic deposits of Peru and led to new studies by various international research groups, including taphonomic investigations on the Neogene strata (Brand et al., 2004; Esperante et al.,

2008, 2015) and a growing attention to the systematics of the Palaeogene vertebrates (Clarke et al., 2007, 2010; Martínez-Cáceres & Muizon, 2011; Uhen et al., 2011). A key role in disclosing the fossil vertebrate content of the East Pisco Basin was played by Mario Urbina, the most prominent field palaeontologist of Peru, who discovered, collected and deposited at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima) tens of cetacean specimens, including several holotypes (Bianucci, 2010). In this framework of exciting finds, and starting in 2006, an international scientific team comprised of Belgian, Dutch, French, Italian and Peruvian researchers has focused on detailing the vertebrate palaeontology (with special attention to the marine mammals) of some selected localities of the Ica desert area where highly fossiliferous deposits are exposed (Figs 1, 2a-b). The most relevant results of such scientific expeditions include the discovery and description of the giant Miocene sperm whale *Livyatan melvillei* (Lambert et al., 2010b), a stem physeteroid representing one of the largest macroraptorial predators of all times, as well the biggest tetrapod teeth ever found (Lambert et al., 2010b) (Fig. 1c-d). This palaeontological team was later joined by experts in stratigraphy, sedimentology, tectonics, micropalaeontology, volcanology and mineral sciences in the context of a long-term research effort aimed at providing a comprehensive understanding of the sedimentary fill of the East Pisco Basin and its marine vertebrate fossil content (e.g., Gariboldi et al., 2015, 2017; Di Celma et al., 2016a, b, 2017, 2018a, b, 2019; Gioncada, 2016, 2018; Bianucci et al., 2018b, c, d; Bosio et al., 2020a, b, 2021; Collareta et al., 2021a, b; Malinverno et al., 2021) (Fig. 2c-f), with special attention to the cetacean component of these assemblages (Bianucci et al., 2015, 2016d, 2018a, 2020; Collareta et al., 2015, 2020a; Lambert et al., 2015a, b, 2017a, b, c, 2018b, 2020, 2021a, b; Martínez-Cáceres et al., 2017; Marx et al., 2017a, b; Muizon et al., 2019).

Several summaries of the evolutionary history of cetaceans have been published to date (e.g., Barnes, 1984; Fordyce & Barnes, 1994; Muizon & Fordyce, 2001; Bianucci & Landini, 2007; Uhen, 2007; Marx et al., 2016b; Fordyce, 2018). However valuable, due to the frantic pace of discoveries of significant fossil specimens, such efforts are in need of being updated constantly. Here, we aim at providing a synoptic overview of the cetacean fossil record of the East Pisco Basin. In doing so, we will see how this unique fossil record sheds light on some iconic macroevolutionary events, including the definitive acquisition of fully aquatic adaptations in the Palaeogene cetaceans, the origins of the odontocete and mysticete clades, and the rise of the extant cetacean lineages.

GEOLOGICAL SETTING

Since the Mesozoic, the tectonodynamics of Peru have been controlled by the convergence between the oceanic Nazca/Farallon Plate and the largely continental South American Plate. Such a convergence induced both the deformation of the leading edge of the South American Plate (thus ultimately producing the emerged portion of the Andean orogen) and the development of

Fig. 1 - Scientific field expeditions in the Ica Desert of Peru. a) Excavation of the holotype skull of *Messapicetus gregarius* at Cerro Colorado (2006). b) Measurement of a balaenopterid skeleton at Cerro la Bruja (2007). c-d) The discovery of the holotype skull of *Livyatan melvillei* at Cerro Colorado (2008).

a composite transform-convergent margin along the Peruvian forearc; here, the activity of normal and strike-slip faults (Rustichelli et al., 2016; Viveen & Schlunegger, 2018) led to the formation of several extensional/pull-apart longshore basins (e.g., Kulm et al., 1982; Dunbar et al., 1990; León et al., 2008). According to Thornburg & Kulm (1981), two trench-parallel structural highs formed on the continental shelf and upper slope during the Late Cretaceous and early Palaeogene, namely, the Outer Shelf Structural High and the Upper Slope Ridge. These two ridges segmented the Peruvian offshore realm into several sedimentary basins which could be divided

into a landward set of shelf basins and a seaward set of slope basins (Fig. 3a).

Representing one of the basins of the onshore sector, the East Pisco Basin (Fig. 3b) is a northwest-southeast elongated sedimentary basin that extends along the narrow coastal plain of southern Peru south of Pisco, being located just landward of where the Peru-Chile trench is impinged on by the aseismic Nazca Ridge, a region of topographically high and buoyant oceanic crust (Pilger, 1981; Hsu, 1992; Macharé & Ortlieb, 1992; Hampel et al., 2004) (Fig. 3a). The basin infill is about two-km-thick and comprises, from oldest to youngest,

Fig. 2 - Scientific field expeditions in the Ica Desert of Peru (continued). a) Excavation of the holotype skeleton of *Mystacodon selenensis* at Media Luna (2010). b) Excavation of the holotype skeleton of *Peregocetus pacificus* at Media Luna (2011). c) Stratigraphic survey near a cetotheriid skeleton at Cerro Colorado (2014). d) Discovery of a balaenopterid skeleton at Cerro los Quesos (2014). e) Examination of the phosphatised baleen of a balaenopteroid at Cerro Colorado (2015). f) Examination of a skeleton of *Piscobalaena nana* at Cerro Ballena (2016).

the Eocene Caballas and Paracas formations, the upper Eocene to lower Oligocene Otuma Formation, the upper Oligocene to Lower Miocene Chilcatay Formation, and the Middle Miocene-Pliocene Pisco Formation (Dunbar et al., 1990; DeVries, 1998) (Fig. 3c). These units are bounded by regionally extensive angular unconformities accounting for periods of subaerial exposure and erosion, and representing major breaks of the sedimentary record of the East Pisco Basin (DeVries, 1998). As such, these formations may rather be regarded as alloformations (North

American Commission on Stratigraphic Nomenclature [NACSN], 2005) or depositional sequences (Di Celma et al., 2017).

The East Pisco Basin is bounded to the east by the Coastal Batholith, a group of plutons that were mostly emplaced in Late Cretaceous-early Eocene times, when igneous arc activity took place close to the location of the present-day coastline (e.g., Cobbing, 1999; Mukasa, 1986; Romero et al., 2013) (Fig. 3a). Therefore, during deposition of its sedimentary infill, the East Pisco Basin

was a relatively shallow water, semi-enclosed embayment protected seawards by a chain of magmatic islands of the emerging Outer Shelf Structural High (Muizon & DeVries, 1985; Marocco & Muizon, 1988b) that restricted communications between this basin and the outer ocean (Fig. 3b). For most of its Cenozoic history, the East Pisco Basin was articulated in a series of communicating sub-embayments (Dunbar et al., 1990) that saw an alternation between periods of partially restricted circulation and periods of relatively open exposure to the Pacific Ocean (DeVries, 1988). Such a complex depositional scenario ultimately produced a complex horizontal and vertical distribution of facies, mostly referable to coastal and shallow-marine palaeoenvironments. Rapid uplift and inversion of the basin, thought to have started in Late Pliocene times, are likely related to the oblique subduction of the aseismic Nazca Ridge, which is presently being subducted beneath the South American Plate off the slope equivalent of the East Pisco Basin, i.e., the West Pisco Basin (Pilger, 1981; Hsu, 1992; Macharé & Ortlieb, 1992; Hampel, 2002).

No cetacean specimens are currently known from the continental and marginal-marine deposits of the Caballas Formation (Fig. 3c), which have been tentatively referred to the lower Eocene based on their molluscan content (DeVries, 2017, 2019).

The Paracas Formation consists of a coarse-grained lower portion (i.e., the Los Choros Member, including conglomerates and mixed siliciclastic-bioclastic sandstones featuring abundant tests of large benthic foraminifera) that passes upward into a division of finer sediments (i.e., the Yumaque Member, consisting of calcareous-terrigenous, silty sandstones and siltstones that preserve a rich planktic assemblage) (Rivera, 1957; Tsuchi et al., 1988; Dunbar et al., 1990; DeVries, 1998, 2017; León et al., 2008; Uhen et al., 2011; Coletti et al., 2019; Malinverno et al., 2021). Foraminiferal and calcareous nannoplankton biostratigraphy indicate that the Paracas Formation was deposited from the Lutetian through the Bartonian to the early Priabonian (Fig. 3c). In particular, in the broad Zamaca area, deposition of the Los Choros Member started around 43.6 Ma (Coletti et al., 2019), whereas the base of the Yumaque Member falls around 42.37 Ma, and its top occurs between 37.88/37.84 Ma and 37.46 Ma (Malinverno et al., 2021). Whereas the Los Choros strata testify to a tropical, shallow-marine setting close to a rocky shore, the Yumaque beds reflect overall warm-water conditions, with a cooling trend starting ~38 Ma in the framework of global climate change and/or the development of a weak upwelling system (Coletti et al., 2019; Collareta et al., 2020b; Malinverno et al., 2021).

The Otuma Formation is comprised of a basal sandstone division overlain by an alternation of calcareous and terrigenous siltstones and diatomites, the latter being particularly rich of pelagic microfossils and fish scales (DeVries, 1998; DeVries et al., 2017; Malinverno et al., 2021). At Zamaca, calcareous nannofossils, silicoflagellates and diatoms indicate that the Otuma Formation is Priabonian; its base is defined at ~37 Ma, whereas its top is older than 34.4 Ma (Malinverno et al., 2021). These data are consistent with previous biostratigraphic and radiochronological assessments of the Otuma strata (DeVries, 1998; DeVries et al., 2017);

however, the age of the uppermost Otuma beds is strongly controlled by a prominent angular unconformity occurring at the contact with the overlying Chilcatay Formation (Malinverno et al., 2021), hence the Oligocene age of some Otuma outcrops at other localities of the East Pisco Basin (DeVries et al., 2021, and references therein) (Fig. 3c). Palaeontological data indicate that the Otuma beds reflect a temperate palaeoclimate and moderate upwelling conditions, with a slight cooling trend and an increase in nutrient availability being observable up section (Malinverno et al., 2021).

In the Ocucaje area, the Chilcatay Formation is comprised of two genetic packages (depositional sequences, or allomembers), designated Ct1 and Ct2 in ascending stratigraphic order (note however that an older sequence, Ct0, has been reported from the remote Laberinto area by DeVries et al., 2021) (Fig. 3c-d). The Ct1 allomember consists of a threefold subdivision of sedimentary facies, including a basal division of sandstones and conglomerate beds (Ct1c facies association), a sub-horizontal package of interbedded sandstones, sandy siltstones and siltstones punctuated by conglomerate levels (Ct1a), and a stack of mixed siliciclastic-carbonate clinobeds (Ct1b), with Ct1a being particularly rich in cetacean fossils (Di Celma et al., 2017, 2018b, 2019). Ct1c represents a transgressive lag overlying a wave-ravinement surface, Ct1a an offshore setting, and Ct1b a prograding submerged delta; two coarse-grained beds from the Ct1a facies association have been interpreted as representing a tsunamite and a tempestite, respectively (Di Celma et al., 2019). The Ct2 allomember consists of a shoreface sandstone division (Ct2a facies association) followed upwards by offshore siltstones (Ct2b facies association). Extensive micropalaeontological investigations, including both silicoflagellates and diatoms, as well as geochronological studies on volcanic ashes, constrain the deposition of Ct1 and Ct2 between 19 and 18 Ma (Di Celma et al., 2018b) (Fig. 3c-d). The Chilcatay depositional setting was a marginal-marine, warm-temperate, sheltered embayment connected with riverine and open-ocean environments (Bianucci et al., 2018b; Coletti et al., 2018; Landini et al., 2019).

The Pisco Formation is extensively exposed in the Ica Desert, along both sides of the lower valley of the Ica River. This area is punctuated by a number of hills (locally known as "cerros") where remarkable concentrations of fossil vertebrates are commonly observed (Bianucci et al., 2016b, c). As observed by Di Celma et al. (2016a, b, 2018a), in the lower Ica valley the Pisco Formation is comprised of three allomembers or sequences, named P0, P1 and P2 from older to younger (Fig. 3d). Each allomember features a deepening-upward, transgressive trend in which downdip facies associations step up over updip facies associations; regressive facies successions are in turn lacking (Di Celma et al., 2017). At the allomember base, a transgressive lag is observed, consisting of a *Glossifungites* ichnofacies mantled by a relatively thin, boulder-rich interval; the latter is capped by sand-rich deposits, indicative of lower shoreface deposition above fair-weather wave base (Di Celma et al., 2018a). The upper part of each Pisco sequence is comprised of siltstones or diatomaceous mudstones reflective of deposition from
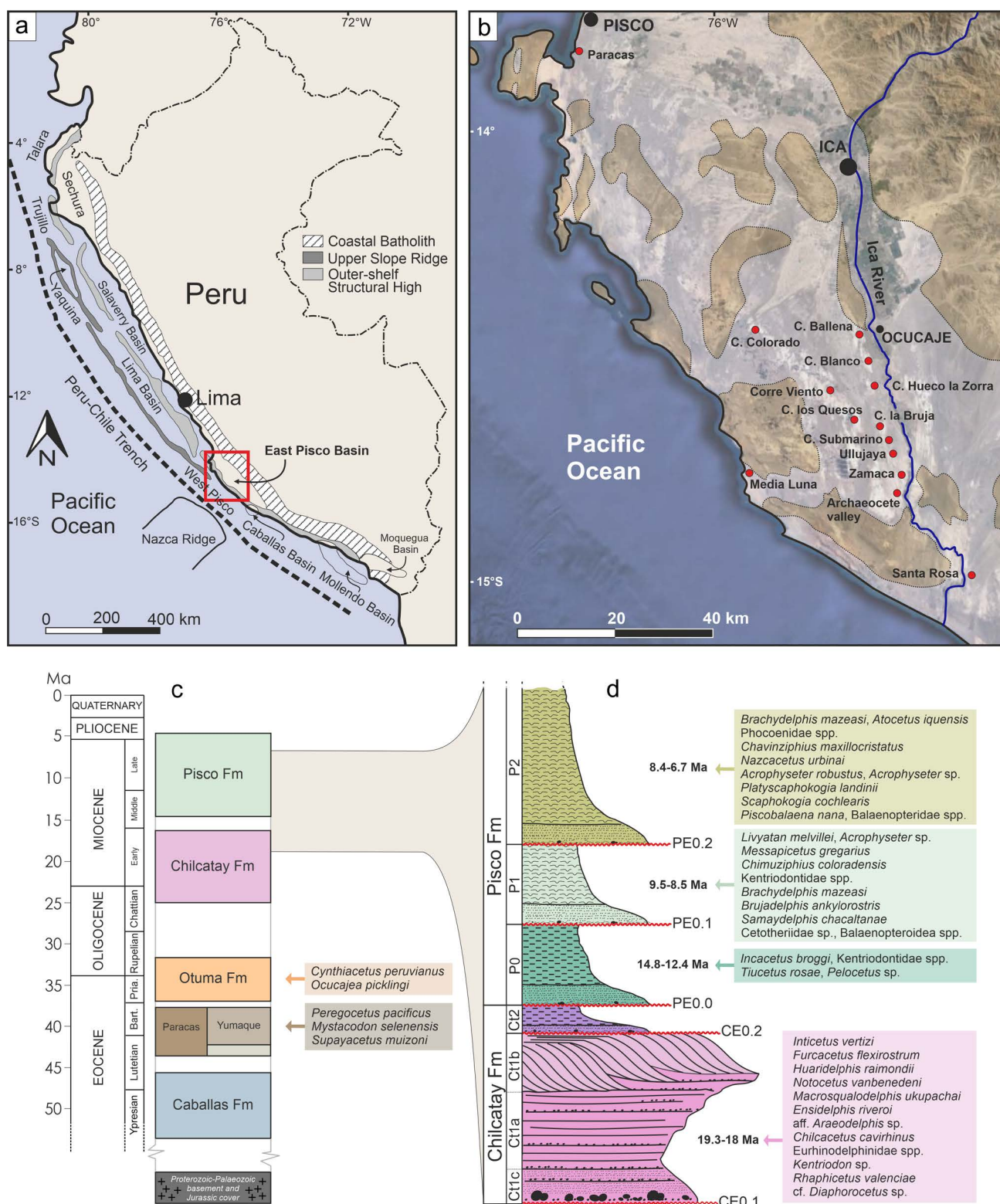
Fig. 3 - a) Map of the major Cenozoic sedimentary basins along the coast of Peru, showing the position of the Coastal Batholith and major trench-parallel structural highs (redrawn and modified after Travis et al., 1976 and Thornburg & Kulm, 1981). b) Schematic palaeogeographic map of the East Pisco Basin, showing the areas submerged during the Neogene (dark brown) and the investigated fossiliferous localities (red circles) (redrawn and modified after DeVries & Schrader, 1997). c-d) Stratigraphic distribution of the cetacean species found in the East Pisco Basin; c) stratigraphic column of the entire Cenozoic succession (redrawn and modified after Malinverno et al., 2021); d) close-up of the investigated portions of the Chilcatay and Pisco formations, showing the internal subdivision into allomembers with their respective interval in ages (modified after Di Celma et al., 2018a). The species included in each colored box are all from the same formation or allomember but are not listed in stratigraphic sequence.

suspension of organic-rich mud in a highly productive, low-energy, offshore shelf environment; volcanic ash layers, dolomitised mudstone horizons, and thin, fine- to medium-grained sandstone beds are also locally present (Di Celma et al., 2017). Whereas the P0 strata and their fossil content testify to warm, subtropical palaeoclimatic conditions, P1 and P2 reflect cooler, upwelling-influenced waters (Bosio et al., 2020a; Collareta et al., 2021a, b). The depositional age of P0 was, until recently, poorly constrained between 18.02 ± 0.07 Ma and 9.00 ± 0.02 Ma (Di Celma et al., 2017, 2018b). Age estimates obtained via strontium isotope (^{87}Sr/^{86}Sr) stratigraphy have recently allowed for placing the P0 deposits in the Middle Miocene (14.8-12.4 Ma, corresponding to the Langhian-Serravallian) (Bosio et al., 2020a) (Fig. 3d). The time of deposition of the P1 and P2 allomembers is in turn better constrained thanks to diatom biostratigraphy and calculated Ar-Ar ages (Di Celma et al., 2016a, b; Gariboldi et al., 2017; Bosio et al., 2019, 2020b). In light of these methods, the P1 allomember was deposited between 9.5 Ma and 8.5 Ma, whereas the P2 allomember is younger than 8.5 Ma and older than 6.71 ± 0.02 Ma (Di Celma et al., 2017, and references therein) (Fig. 3d). Elsewhere, strata assigned to the Pisco Formation are thought to extend into the Pliocene (Marty, 1989).

About 60 kilometres south of Nazca, the Sacaco area is encountered. Sometimes referred to as the "southern Pisco basin" (e.g., Ehret et al., 2012), the Sacaco area extends along the southern Peruvian coastline from El Jahuay to Yauca. Currently, the Sacaco Desert is separated from the Ica Desert by a structural high of basement rocks that constitutes the reliefs of Cerro Huaricangana, southwest of Nazca. During most of the Cenozoic, the East Pisco and Sacaco areas may have been separated from each other, thus comprising different palaeoecological scenarios and depositional settings (Collareta et al., 2021b). Albeit the Upper Miocene and Pliocene marine deposits of the Sacaco area have been often regarded as belonging to the Pisco Formation (e.g., Muizon, 1984; Muizon & DeVries, 1985; Ehret et al., 2009, 2012; Ochoa et al., 2021), they are herein conservatively indicated as "Pisco-equivalent" strata, pending a better definition of the tectono-sedimentary relationships between the Ica and Sacaco palaeo-areas during the Late Miocene and Pliocene.

PEREGOCETUS, THE OLDEST CETACEAN FROM THE NEW WORLD

Similar to the earlier branching cetacean lineages, the family Protocetidae originated in the Indo-Pakistani region in early middle Eocene times (~48 Ma) (Gingerich et al., 2001, 2009). Protocetids display archaic skeletal characters such as the retention of the primitive mammalian dental formula (3.1.4.3/3.1.4.3) as well as fully developed fore- and hindlimbs (Uhen, 2010); the latter, however, contact a reduced sacrum, thus evoking limited subaerial locomotory abilities. In contrast, a rather uniform vertebral morphology suggests the emergence of an undulatory swimming mode that was unparalleled by more archaic cetaceans (Bianucci & Gingerich, 2011). Protocetid skeletons mostly come from coastal marine deposits,

which is suggestive of nearshore palaeoenvironmental habits. Protocetids have been interpreted as somewhat amphibious mammals that fed in the sea but returned to land to rest and give birth (Gingerich et al., 2009), though the latter find is somewhat disputed (Thewissen & McLellan, 2009; Geisler, 2019). Protocetids were the earliest branching cetaceans to spread worldwide, firstly along the coasts of Western Tethys (e.g., Fraas, 1904; Kassegne et al., 2021) and subsequently across the (Atlantic?) oceanic expanse to reach the Americas (e.g., Uhen, 1998b). Crucially, protocetids are also recognised as the group from which all the fully aquatic cetaceans (Pelagiceti, including both the basilosaurids and the modern cetacean lineages) originated (Uhen, 2008a, 2010).

Besides remains of the fully pelagic Basilosauridae (Uhen et al., 2011), the Paracas Formation hosts an exceptionally preserved skeleton of Protocetidae on which Lambert et al. (2019) based their description of *Peregocetus pacificus* Lambert et al., 2019. Discovered at the locality of Media Luna in Lutetian (~42.6 Ma) deposits assigned to the Yumaque Member, the holotype of *P. pacificus* consists of the mandibles and teeth, thoracic, lumbar, sacral and caudal vertebrae, ribs, sternal elements, and most of the forelimb (scapulae, humeri, radii, ulnae, carpals, metacarpals and manus phalanges) and hindlimb (innominates, femora, tibia, fibula, tarsals, metatarsals and pes phalanges) elements (Fig. 4). *Peregocetus pacificus* is thus the best-known quadrupedal cetacean from outside India or Pakistan, as well as one of the few for which most of the appendicular skeleton is known (Uhen, 2010). Both the astragalus and the calcaneus are known for *P. pacificus*; interestingly, the former displays the double pulley that is typical of terrestrial artiodactyls (see also Gingerich et al., 2001; Thewissen et al., 2001) (Fig. 4d). The fore- and hind-limb proportions (which are roughly comparable to those of geologically older four-legged cetaceans from the Indo-Pakistani region), the pelvis being firmly attached to the sacrum (which in turns includes two fused vertebrae plus an additional unfused sacral), the occurrence of a fossa for the insertion of the round ligament on the femur, and the retention of small hooves with a flat anteroventral tip at fingers and toes (Fig. 4b-c) show that *Peregocetus* was fully capable of standing and even walking on land (Lambert et al., 2019) (Fig. 4g2), likely more so than other protocetids such as the georgiacetines (Gingerich et al., 2019). At the same time, the dorsoplantar flattening of the phalanges with conspicuous lateral flanges indicates that the pes and manus were webbed, thus suggesting that hind limbs were actively used for swimming (Lambert et al., 2019). In addition, and similar to extant beavers and sea otters, the caudal vertebrae of *P. pacificus* bear bifurcated and anteroposteriorly expanded transverse processes (Fig. 4b) that evoke a significant contribution of the tail to underwater propulsion (Lambert et al., 2019) (Fig. 4g1). Unfortunately, the posteriormost caudal vertebrae are not preserved in the *P. pacificus* holotype, thus frustrating any speculation on whether a true tail fin was present.

The palaeobiogeographic meaning of the cetaceans remains from the Paracas Formation was firstly addressed by Uhen et al. (2011), well before the description of *Peregocetus pacificus* by Lambert et al. (2019). Three alternative routes were proposed by the former authors
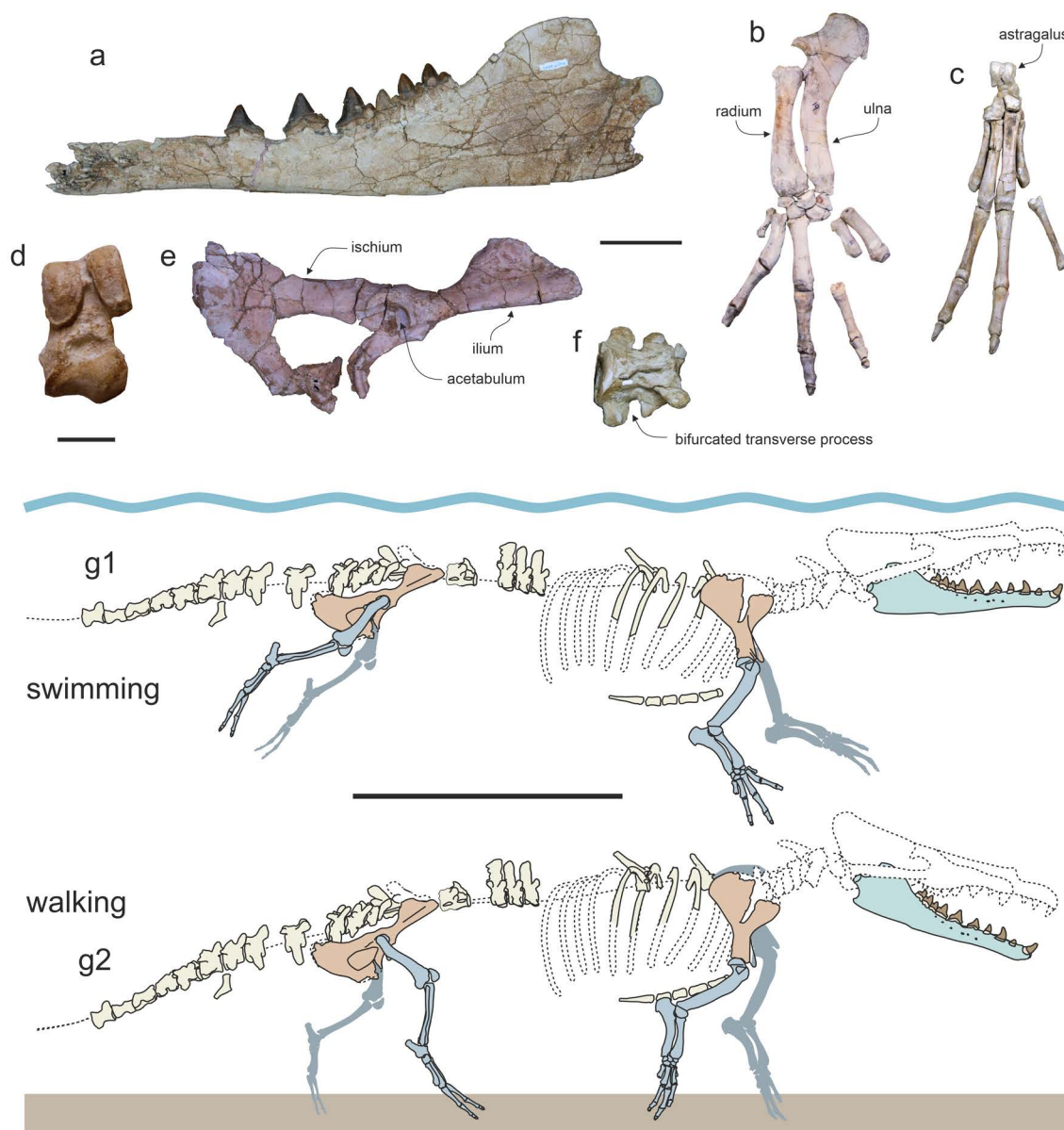
Fig. 4 - _Peregocetus pacificus_, MUSM 3580 (holotype), from the Yumaque beds of the Paracas Formation. a) Left mandible in lateral view. b) Left radius, ulna, and manus in lateral view. Metacarpals IV and V are from right manus. c) Right pes in anterior view. d) Left astragalus in anterior view. e) Right innominate in lateral view. f) Anterior caudal vertebra in dorsal view. g) Schematic drawings of the articulated skeleton showing the main preserved bones, in hypothetical swimming (g1) and terrestrial (g2) postures (redrawn and modified after Lambert et al., 2019). For paired bones, the best-preserved side was illustrated (sometimes reversed), or both sides were combined (e.g., mandible). Stippled lines indicate reconstructed parts. Scale bars are equal to 10 cm for panels a-c, e, and f; 2 cm for panel d; 100 cm for panels g1, g2.

for explaining the presence of archaeocete remains in the middle Eocene of the East Pisco Basin: 1) dispersal from the southeastern United States, along the shores of GAARlandia (a long isthmus extending north of South America to include the Greater Antilles; Iturralde-Vinenet & MacPhee, 1999) and northwestern South America; 2) direct arrival from Northern or Western Africa, after crossing the Atlantic Ocean and 3) arrival from the Eastern Tethys, through the Pacific Ocean. The discovery of _P. pacificus_, which represents the first unambiguous record of a quadrupedal whale from both the coasts of the Pacific Ocean and the whole Southern Hemisphere, contributes to shedding light on these hypothetical scenarios. Sharing

features with other protocetids from the Bartonian of Morocco and Nigeria, _P. pacificus_ supports the hypothesis of an initial migration pathway across the South Atlantic, at least as far as the protocetid archaeocetes are concerned (Lambert et al., 2019) (Fig. 5). Such a dispersal route was likely favoured by the relatively limited distance between Africa and South America, which was much smaller during the Eocene than it is today, as well as by the presence of a westward sea-surface current running from central Africa to South America (Berggren & Hollister, 1978). During the Lutetian, the occurrence of a shallow-water passage likely suitable for amphibious vertebrates between the Caribbean and the central Eastern Pacific is also in agreement with
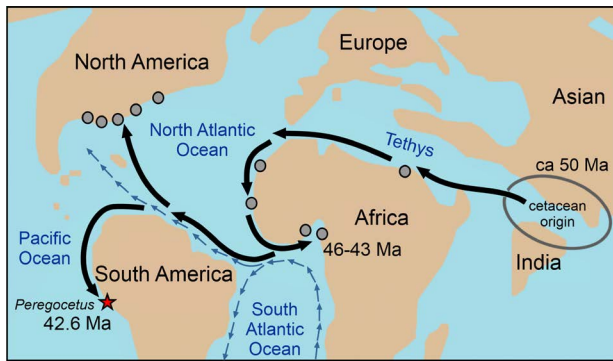
Fig. 5 - Dispersal of Protocetidae during the middle Eocene. The gray circles indicate the localities of fossil protocetid finds; the star indicates the type locality of *Peregocetus pacificus*. Thick arrows illustrate the hypothetical dispersal routes of the protocetids from the eastern Tethys to the southeastern Pacific Ocean. Thin arrows indicate surface palaeocurrents. Redrawn and modified after Lambert et al. (2019: fig. 4).

the distribution of large benthic foraminifera (Coletti et al., 2019). Regardless of these issues, the discovery of *P. pacificus* in the Yumaque beds exposed at Media Luna demonstrates that quadrupedal whales characterised by a combination of terrestrial and aquatic locomotion abilities attained a nearly circum-equatorial distribution less than 10 million years after their origin, and probably before a northward dispersal along the Atlantic coasts of North America (Lambert et al., 2019).

THE EARLIEST PELAGIC CETACEANS: *CYNTHIACETUS PERUVIANUS* MARTÍNEZ-CÁCERES & MUIZON, 2011 AND OTHER BASILOSAURIDS

The family Basilosauridae represents the oldest cosmopolitan group of cetaceans. Known from fossils as old as the Lutetian-early Bartonian (46-40 Ma; Buono et al., 2016), basilosaurids are found in deposits referred to the second half of the Eocene from all continents. Besides their broad geographic distribution, many anatomical features demonstrate that basilosaurids were fully aquatic animals, including the posteriorly displaced external bony nares, a well-developed pterygoid sinus (isolating the ear bones), a shortened neck, a flattened flipper-like forelimb, a relatively immobile wrist, and dorsoventrally flattened posterior caudal vertebrae (suggesting the presence of a soft-tissue tail fluke) (Uhen, 1998a, 2004). Furthermore, the basilosaurid hindlimbs are greatly reduced and completely detached from the vertebral column, so that a true sacrum is no longer identifiable in the latter; as a consequence of this, basilosaurids were unable of supporting their body weight on land (Uhen, 2018), thus foraging, mating and birth should have taken place in water. Other features that distinguish Basilosauridae from more archaic archaeocete families like the protocetids rely in their dentition: basilosaurids lack upper third molars and their cheek teeth display well-developed accessory denticles (Uhen, 2010). Some basilosaurids such as *Basilosaurus* developed a serpentiform trunk and titanic body size values (up to 16 m in total length); others, like *Saghacetus*, were in

the body size range of extant bottlenose dolphins (about four meters in total length) (Uhen, 2018). A few fossilised stomach contents indicate that both large- and small-sized basilosaurids were piscivorous, foraging on both bony and cartilaginous fishes (Swift & Barnes, 1996; Uhen, 2004), but *Basilosaurus* fed also on smaller cetaceans like *Dorudon* (Fahlke, 2012; Voss et al., 2019).

The geologically oldest basilosaurids of the East Pisco Basin come from the upper middle Eocene (Bartonian) beds of the Paracas Formation exposed in what is now known as the "Archaeocete valley"; they consist of the holotypes and only known specimens of *Supayacetus muizoni* Uhen et al., 2011 and *Ocucajea picklingi* Uhen et al., 2011. Both these species are among the smallest described basilosaurid taxa: they may have been even smaller than *Saghacetus* (Martínez-Cáceres & Muizon, 2011). *Supayacetus muizoni* is represented by a partial skeleton, including the teeth, fragmentary vertebral column, ribs, forelimb elements and manubrium; the latter, in particular, is curiously T-shaped, as observed in the protocetids *Rodhocetus* and *Georgiacetus* but unlike other basilosaurids (Uhen et al., 2011). The holotype of *Ocucajea picklingi* consists of a partial skull with mandibles and fragmentary teeth; it differs from other small basilosaurids based on a peculiar arrangement of the posterior termination of the maxilla relative to the nasals. *Supayacetus* and *Ocucajea* come from the same locality and stand among the earliest basilosaurids known to date (Uhen et al., 2011), but their evolutionary bearings may be different: whereas *Supayacetus* is regarded as one of the basalmost (and more protocetid-like) members of Basilosauridae, *Ocucajea* is a good candidate for representing the sister group of the modern cetacean clade, Neoceti (Uhen, 2018).

The geologically younger *Cynthiacetus peruvianus* is known from an almost complete skeleton from upper Eocene (Priabonian) deposits of the Otuma Formation exposed at the Paracas Bay (Martínez-Cáceres & Muizon, 2011) (Fig. 6). *Cynthiacetus peruvianus* resembles the congeneric species *C. maxwelli* Uhen, 2005 (a coeval form from the Atlantic coast of the USA) in featuring strongly tapering nasals, but differs from the latter in having fewer accessory cusps on the cutting edges of the lower premolars (Fig. 6a1-2). The skull of *C. peruvianus* displays the (quite monotonous) general structure of the basilosaurid skull, but is much larger than observed in the otherwise similar *Dorudon* (Martínez-Cáceres & Muizon, 2011). *Cynthiacetus peruvianus* displays a slenderer rostrum compared to that of *Basilosaurus*; at the same time, with a total body length of about nine meters, it approaches the latter in total body length, being indeed one of the largest members of Basilosauridae (Martínez-Cáceres et al., 2017). The most characteristic features of *C. peruvianus* are found in its postcranial skeleton (Fig. 6a3); these include the presence of large vertebrarterial foramina on the cervical vertebrae, the lack of ventral expansions of the transverse processes of C3-C5, and the high number of thoracic vertebrae (i.e., 20, the greatest number observed in cetaceans) (Martínez-Cáceres et al., 2017). Like all other basilosaurids, *C. peruvianus* was a pelagic organism; its long rostrum, bearing sharp incisors and canines, evokes the grasping of individual prey items. Supporting this interpretation, the skull of a large-sized
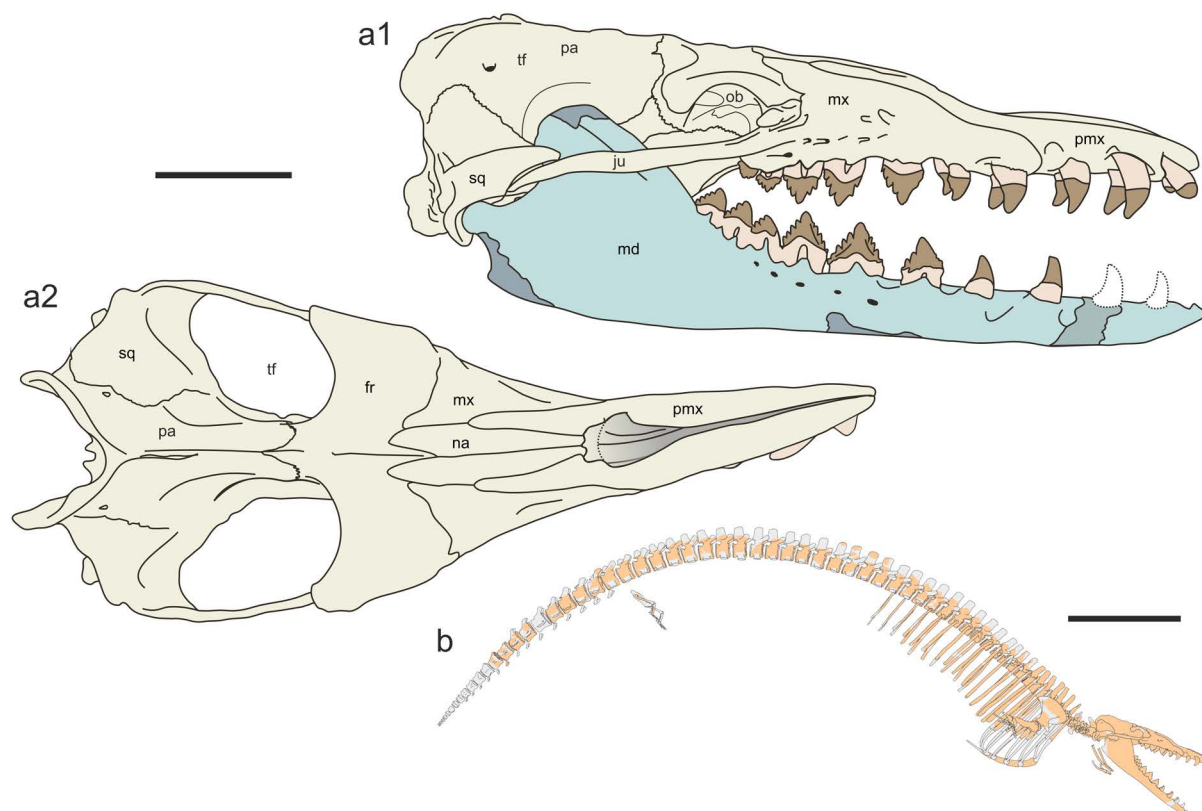
Fig. 6 - *Cynthiacetus peruvianus*, MNHN.F.PRU10 (holotype), from the Otuma Formation. a) Skull in right lateral (a1) and dorsal (a2) views. Stippled lines indicate reconstructed parts. b) Schematic drawing of the articulated skeleton, indicating the preserved parts (orange-shaded areas). Abbreviations: fr, frontal; ju, jugal; md, mandible; mx, maxilla; na, nasal; ob, orbit; pa, parietal; pmx, premaxilla; sq, squamosal; tf, temporal fossa. Redrawn and modified after Martínez-Cáceres et al. (2017: figs 5, 6, 8, 26). Scale bars are equal to 20 cm for panels a1, a2; 100 cm for panel b.

(~1.5 m long) scombrid fish was discovered in the anterior part of the thoracic region of the *C. peruvianus* holotype (Martínez-Cáceres et al., 2017). Besides teleosts, *C. peruvianus* may have foraged on tetrapods such as giant penguins (Martínez-Cáceres et al., 2017) and smaller basilosaurids (Uhen, 2018).

MYSTACODON SELENENSIS LAMBERT ET AL., 2017, THE OLDEST "MODERN" CETACEAN

The monophyly of extant cetaceans has long been supported by a number of morphological observations (e.g., Van Valen, 1968; Barnes, 1990; Fordyce & Barnes, 1994; Uhen, 1998a; Fordyce & Muizon, 2001; Geisler & Sanders, 2003) and, lately, by means of molecular phylogeny (e.g., McGowen et al., 2009, 2020; Gatesy et al., 2013), with most studies further indicating that odontocetes (echolocating toothed whales) and mysticetes (baleen-bearing whales) are each other's closest relatives. The geologically youngest common ancestor of all living cetaceans and all of its descendants are collectively referred to as Neoceti (Fordyce & Muizon, 2001). The most obvious characters distinguishing archaeocetes and neocetes rely in the development of an immobile elbow joint (linked to the transformation of forelimbs into true flippers) and posteriorly extended premaxillae

(strengthening the interlocking between the rostrum and neurocranium) in the latter (Geisler, 2018). Sometimes during the Bartonian or early Priabonian, the earliest neocetes diverged from the coeval cetaceans, thus initiating the modern cetacean clade. Most studies maintain that Neoceti evolved from within Basilosauridae; however, some analyses have proposed that both neocetes and basilosaurids originated from protocetids (Van Valen, 1968) or from an as yet unknown middle Eocene cetacean group (Fitzgerald, 2010).

A highly valuable source of information about the origin of neocetes comes from the holotype and only known specimen of *Mystacodon selenensis* (Fig. 7). The latter consists of a partial skeleton (including the cranium, mandibles, teeth, cervical, thoracic, lumbar and caudal vertebrae, ribs, partial forelimbs, and the left innominate) from lower Priabonian (~36.4 Ma) strata of the Yumaque Member of the Paracas Formation exposed at the coastal locality of Media Luna (Lambert et al., 2017c) (Fig. 2a). Overall, this specimen looks fairly archaeocete-like in displaying clearly plesiomorphic traits such as a strongly heterodont dentition (which bears the same dental formula as basilosaurids) (Fig. 7a2), a sutured mandibular symphysis and a well-defined acetabulum on the innominate (Fig. 7c), the latter character suggesting the retention of hindlimbs that protruded from the abdominal wall. At the same time, *M. selenensis* is reminiscent of

later mysticetes and odontocetes by displaying a partly open mesorostral groove (Fig. 7a1) and a distal epiphysis of the humerus that is divided in two angled radial and ulnar facets (thus hinting at an immobile elbow). Further recalling the baleen-bearing whales, *M. selenensis* exhibits a large palate with a dorsoventrally flattened rostrum, a thin lateral edge of the rostral portion of the maxilla, a clearly defined antorbital process of the maxilla and a triangular supraoccipital shield (Fig. 7a1). Thus, *M. selenensis* is currently regarded as both the geologically oldest member of the modern cetacean clade (Neoceti) and one of the earliest branching mysticetes, though one that like many other Palaeogene "baleen" whales bore teeth and not baleen. Different phylogenetic analyses have retrieved *M. selenensis* either as the sister group of all other mysticetes (Lambert et al., 2017c; Muizon et al., 2019) or just crownward of the Oligocene Carolinian species *Coronodon havensteini* Geisler et al., 2017, forming a clade with the somewhat gigantic (total body length up to 12 m; Marx et al., 2019a) Antarctic genus *Llanocetus* (Fordyce & Marx, 2018). As a consequence of this, the currently monotypic genus *Mystacodon* has alternatively been classified in its own family, Mystacodontidae (Lambert et al., 2017c; Muizon et al., 2019), or among the llanocetids (Fordyce & Marx, 2018; Buono et al., 2019; Marx et al., 2019a).

The robust postcanine teeth and large palate of *Mystacodon* support a raptorial feeding strategy that likely incorporated some degree of suction. Apical wear facets are developed all along the tooth rows (Fig. 7b), being subhorizontal on the anterior teeth, whereas they moderately slope on the cheek teeth; in addition, differing from the condition observed in several basilosaurid skulls, no subvertical occlusal facets occur in *Mystacodon* (Lambert et al., 2017c; Muizon et al., 2019). Such a tooth wear pattern is suggestive of high rates of dental abrasion due to foraging upon abrasive food items or to the intake of water laden with prey and sediment, which in turn may reflect feeding close to the seafloor. Several characters of the highly peculiar forelimb bones indicate powerful shoulder movements, thus evoking an active use of the flipper during bottom feeding (Lambert et al., 2017c; Muizon et al., 2019). In light of this, the transition from raptorial to baleen-assisted filter feeding that accompanied the early evolutionary history of the ancestors of modern baleen whales was likely mediated by suction (Lambert et al., 2017c; Muizon et al., 2019), an interpretation that is also supported by the fossil record of aetiocetids,
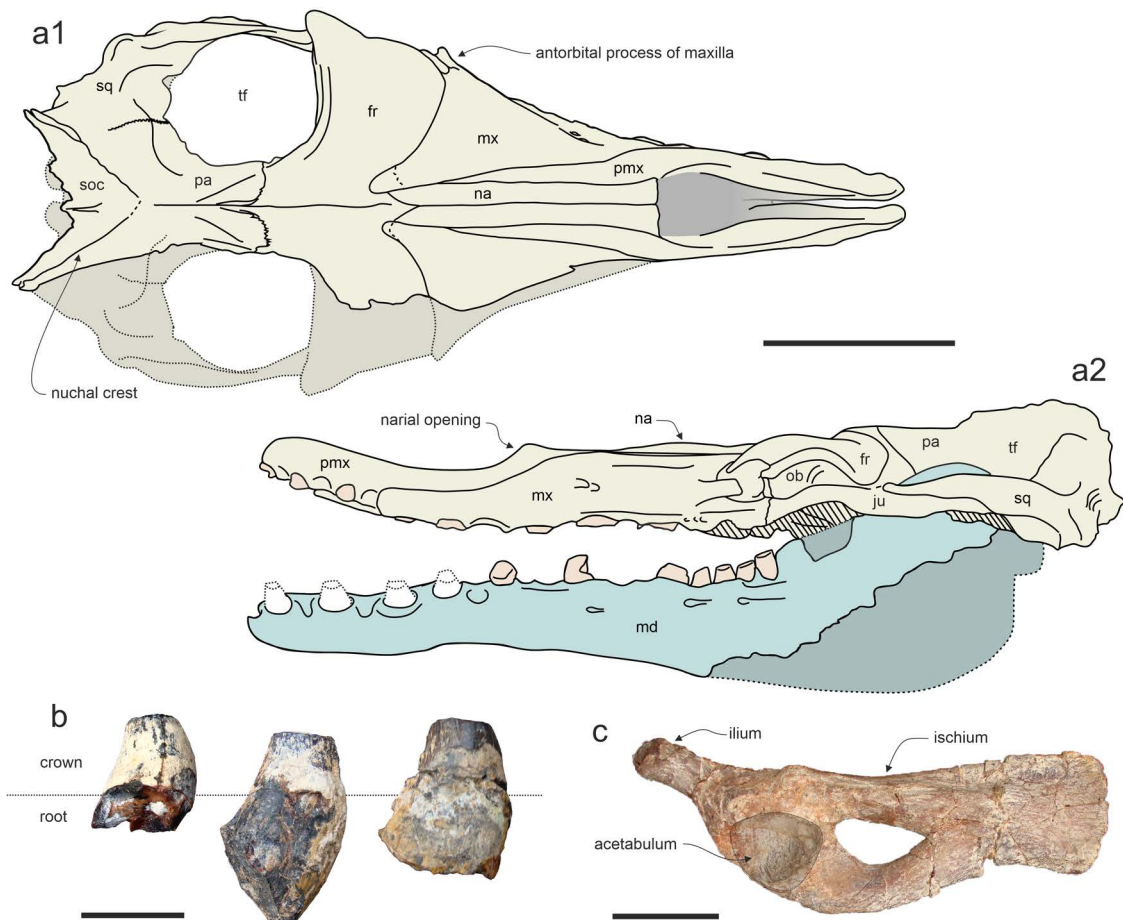

Fig. 7 - *Mystacodon selenensis*, MUSM 1917 (holotype), from the Yumaque beds of the Paracas Formation. a) Skull in dorsal (a1) and left lateral (a2) views. Stippled lines indicate reconstructed parts (redrawn and modified from Muizon et al., 2019: figs 4, 6, 18). b) Three detached anterior lower teeth (from left to right: incisor, incisor/canine, and ?first premolar) in lingual/labial view. c) Left innominate in lateral view. Abbreviations: ex, exoccipital; fr, frontal; la, lacrimal; md, mandible; mx, maxilla; na, nasal; ob, orbit; pa, parietal; pmx, premaxilla; sq, squamosal; tf, temporal fossa. Scale bars are equal to 20 cm for panels a1, a2; 2 cm for panel b; 4 cm for panel c.

llanocetids and mammalodontids (Fitzgerald, 2012; Marx et al., 2015, 2016a; Fordyce & Marx, 2018).

CHAEOMYSTICETI, THE BALEEN-BEARING MYSTICETES

Instead of teeth, the modern baleen whales bear comb-like, keratinous, bristle-fringed baleen plates that allow for bulk-filter feeding on vast amounts of small prey. Fossils of baleen-bearing mysticetes (Chaeomysticeti) occur in both the Chilcatay and Pisco formations, although with starkly contrasting patterns of diversity and abundance. Only two chaeomysticete specimens are currently known from the Chilcatay Formation. Discovered at the highly fossiliferous locality of Zamaca, these fossils consist of a skull (from Ct1a) and a mandible (from Ct2b), both of which are poorly preserved and remain indeterminate so far (Di Celma et al., 2019). At other well-investigated localities like Ullujaya (Di Celma et al., 2018b), mysticetes have not been detected (Bianucci et al., 2018b). The overall rarity of baleen whale fossils in the Chilcatay strata is reminiscent of many Aquitanian and lower Burdigalian (~18 Ma or earlier) marine mammal-bearing assemblages worldwide (Bianucci et al., 2018b), and appears to reflect a real decline in mysticete diversity and abundance rather than taphonomic or collecting biases (Marx et al., 2019b). This interval, sometimes referred to as a "dark age" in the fossil history of baleen whales, was likely driven by environmental change (possibly an abrupt and significant drop in sea level at the Chattian-Aquitanian transition) that led to the disappearance of the Oligocene coastal mysticete assemblages (dominated by small, ecologically disparate forms of toothed mysticetes like aetiocetids and mammalodontids), leaving the nearshore environments virtually devoid of mysticetes (Marx et al., 2019b). Large forms of toothless (chaeomysticete) filter-feeders, which formed the core of the Oligocene offshore mysticete assemblages, are believed to have persisted in open-ocean environments through a five-myr-long time span, and eventually reinvaded the coastal habitats at the onset of the Middle Miocene Climatic Optimum (Marx et al., 2019b). In addition, the high-latitude, circum-Antarctic waters may also have served as refugia for baleen whales during the Early Miocene dark age of mysticetes (Bianucci et al., 2018b).

The marine vertebrate content of the Middle Miocene P0 sequence of the Pisco Formation is dominated by chaeomysticetes, which at Cerro Submarino and nearby localities account for more than two thirds of the vertebrate specimens preserved as bony elements (Collareta et al., 2021a). Albeit most of these chaeomysticete fossils remain indeterminate, ten of them have been assigned to either *Pelocetus* or *Tiucetus* (Marx et al., 2017b; Bosio et al., 2020; Collareta et al., 2021a). The former are congeneric with the stem balaenopteroid *Pelocetus calvertensis* Kellogg, 1965 from the lower Middle Miocene of the Eastern USA and otherwise indeterminate remains from Japan (Kimura et al., 2007) based on the observation of characters like a narrowly triangular supraoccipital shield, a narrow nasal, a wide squamosal fossa, a proportionately small tympanic bulla, and a well developed subcondylar furrow on the posterior face of

the mandibular ramus (Bianucci et al., 2019b) (Fig. 8). While hinting at the onset of mysticete cosmopolitanism during the Middle Miocene Climatic Optimum (Marx et al., 2019b), the P0 specimens of *Pelocetus* are remarkable in being conspicuously large-sized (estimated body length about 11.8-13.7 m), which in turn suggests an early and gradual origin for the signature gigantism of modern baleen whales (Bianucci et al., 2019b; but see also Tsai & Kohno, 2019 for an alternative point of view on the emergence of giant body sizes in the mysticete clade).

Similarly, remarkable are the P0 specimens of *Tiucetus* (Fig. 9). The holotype of the only known species of *Tiucetus* (namely, *Tiucetus rosae* Marx et al., 2017b) comes from the lowest (likely P0) strata of the Pisco Formation exposed at the largely unexplored locality of Santa Rosa, in the southern part of the East Pisco Basin. Based on the observation of a distally expanded compound posterior process of the tympanoperiotic, an enlarged paroccipital concavity, and a well-developed posteroventral sulcus, *T. rosae* has been recognised as belonging to the family Cetotheriidae (Marx et al., 2017b). As redefined by Bouetel & Muizon (2006) and Steeman (2007), this once wastebasket family forms a clade of mostly small-sized, Neogene and Quaternary mysticetes that characteristically display a slender rostrum, a V-shaped posterior margin of the rostral bones, an X-shaped skull vertex, and a somewhat enlarged (either dorsoventrally thickened or posteriorly elongated) angular process of the mandible (Boessenecker, 2013; El Adli et al., 2014; Bisconti, 2015; Gol'din & Startsev, 2017; Marx et al., 2019c; Collareta et al., 2021c). Cetotheriids have long been regarded as extinct, but the extant pygmy right whale *Caperea marginata* Gray, 1846 (once regarded as the sole living member of the "balaenoid" family Neobalaenidae) has been recently revealed to be a highly autapomorphic relic cetotheriid (Fordyce & Marx, 2013; Marx & Fordyce, 2015), although not without controversies (e.g., Bisconti, 2015; Tsai & Fordyce, 2015; Marx & Fordyce, 2016). In light of its geological age and phylogenetic relationships, *T. rosae* has been recognised as one of the oldest and earliest branching members of Cetotheriidae, thus shedding light on the very roots of this successful mysticete clade (Marx et al., 2017b, 2019c).

Given their speciosity and prominence in many Neogene (mostly Late Miocene) marine vertebrate assemblages, the palaeoecology and palaeobiology of Cetotheriidae (most of which conform to extinct morphotypes that have no analogues among extant mysticetes) has been the subject of several researches, including some that hinted at possible autecological affinities between the cetotheriids and the living eschrichtiine grey whales (e.g., El Adli et al., 2014; Gol'din et al., 2014; Tarasenko, 2014). In this respect, the fossil content of the Tortonian P1 sequence significantly contributes to understanding the cetotheriid radiation. Here, mysticetes are still more common than odontocetes, and together they comprise the greatest part of the identified vertebrate skeletons; furthermore, the most common cetacean taxon is an as yet unnamed cetotheriid species, ranging between five and eight meters in total length (Collareta et al., 2015; Bianucci et al., 2016c). This cetotheriid form is phenetically very close to the geologically younger species *Piscobalaena nana* Pilleri &
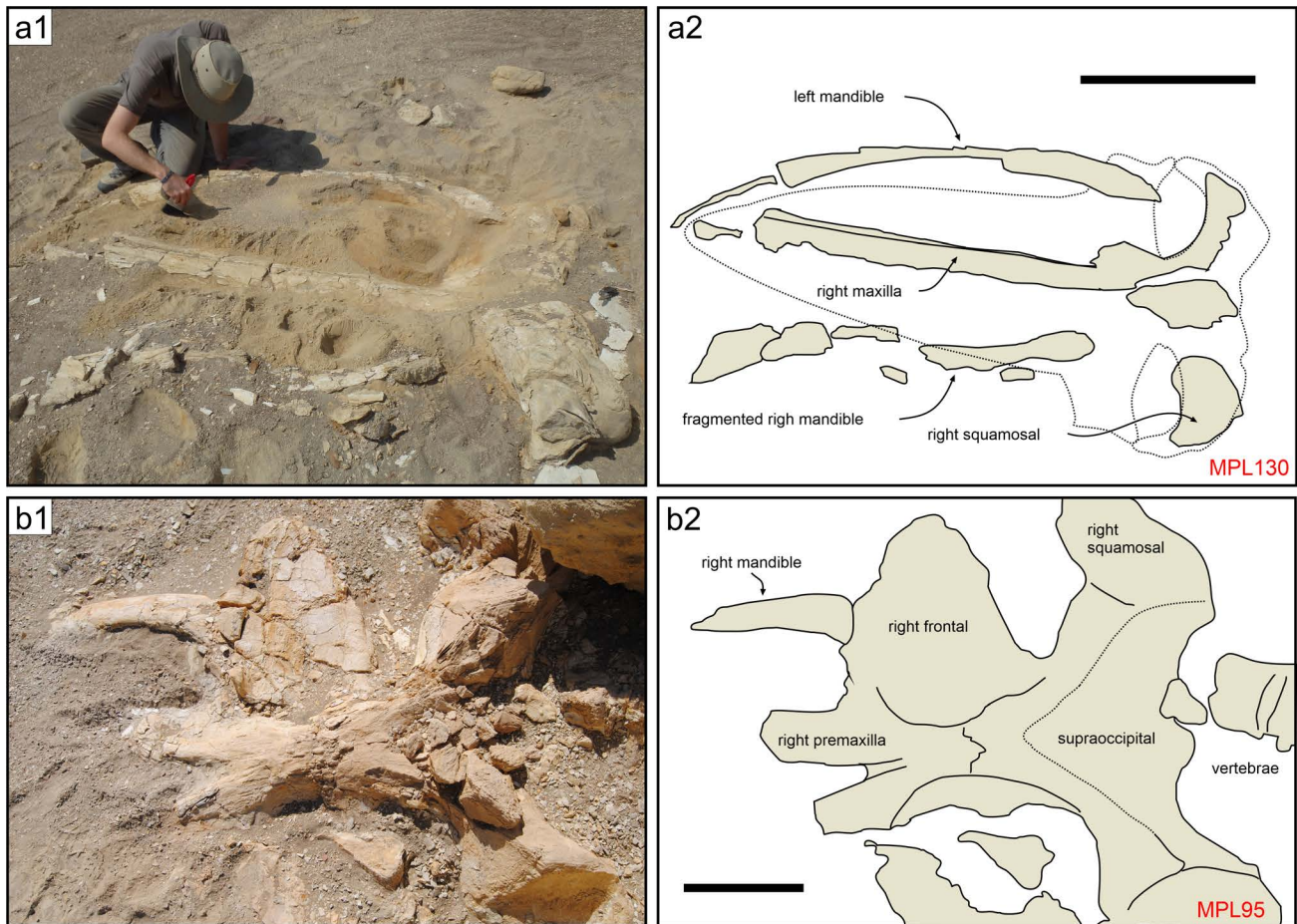
Fig. 8 - Stem balaenopteroids from the P0 beds of the Pisco Formation. a) Skull of cf. *Pelocetus* sp.: field photograph (a1) and corresponding schematic drawing (a2). Stippled lines indicate reconstructed parts. b) Skull and cervicals of cf. *Pelocetus* sp.: field photograph (b1) and corresponding schematic drawing (b2). The field numbers are reported at the bottom right of panels a2 and b2. Scale bars are equal to 50 cm.

Siber, 1989 (see below), from which it mainly differs by displaying longer nasals, a slightly different morphology of the mandibular ramus, and a larger body size (Figs 2c, 10). At Cerro Colorado, two skeletons of the P1 cetotheriid have been found in close associations with tightly packed fish remains (Collareta et al., 2015, 2021b; Bosio et al., 2021). One of these aggregates, taking its place in-between the posterior ribs of the host cetacean, was revealed to be comprised of bony and dermal elements that indicate the Pacific pilchard *Sardinops*; furthermore, the structure of this accumulation, coupled with its preservation state and overall architecture, shows that it represents the fossilised (fore)stomach content of the host whale (Collareta et al., 2015). This find, the first stomach content ever reported from a crown cetacean, indicates that at least some cetotheriids were ichthyophagous and fed upon schooling epipelagic fishes, and this may explain why they were particularly abundant in upwelling-related, highly productive shelfal ecosystems (Gol'din et al., 2014; Collareta et al., 2015). The high predator-prey body size ratio inferred from the Cerro Colorado digestive tract contents suggests that, similar to the modern mysticete families (Berta & Lanzetti, 2020; Werth, 2000), the P1 cetotheriid used some kind of bulk feeding strategy, either lunge- or suction-based (Collareta et al., 2015; Marx et al., 2017a). Some support to the latter hypothesis may derive

from observing the distribution of the palatal nutrient foramina and sulci, which is often regarded as a proxy of the anteroposterior extent of the baleen racks: much as in *Piscobalaena*, in the P1 cetotheriid they extend just slightly beyond the rostrum mid-length (see discussion on *P. nana* below).

Besides cetotheriids, balaenopteroids are also present in the P1 strata with skeletons that belong to at least two different species (Collareta et al., 2021b) (Fig. 2d-e). One of these balaenopteroid specimens (Fig. 2e) features well-preserved, densely spaced fossilised baleen plates as well as fine baleen bristles whose size and arrangement is reminiscent of the extant sei whale (*Balaenoptera borealis* Lesson, 1828), thus suggesting predation upon very small-sized prey items like planktonic copepods (Gioncada et al., 2016).

Whereas cetotheriids are more abundant than balaenopteroids in the P1 sequence, the opposite is true for the overlying, Tortonian-Messinian P2 allomember (Collareta et al., 2021b). Here, balaenopteroid skeletons (Figs 1b, 11) mostly conform to the extant family Balaenopteridae (rorquals and humpback whales) by displaying a recurved mandibular neck (Bianucci et al., 2019b); they comprise at least three different species, including one that resembles the living humpback *Megaptera novaeangliae* Gray, 1846 (Collareta et
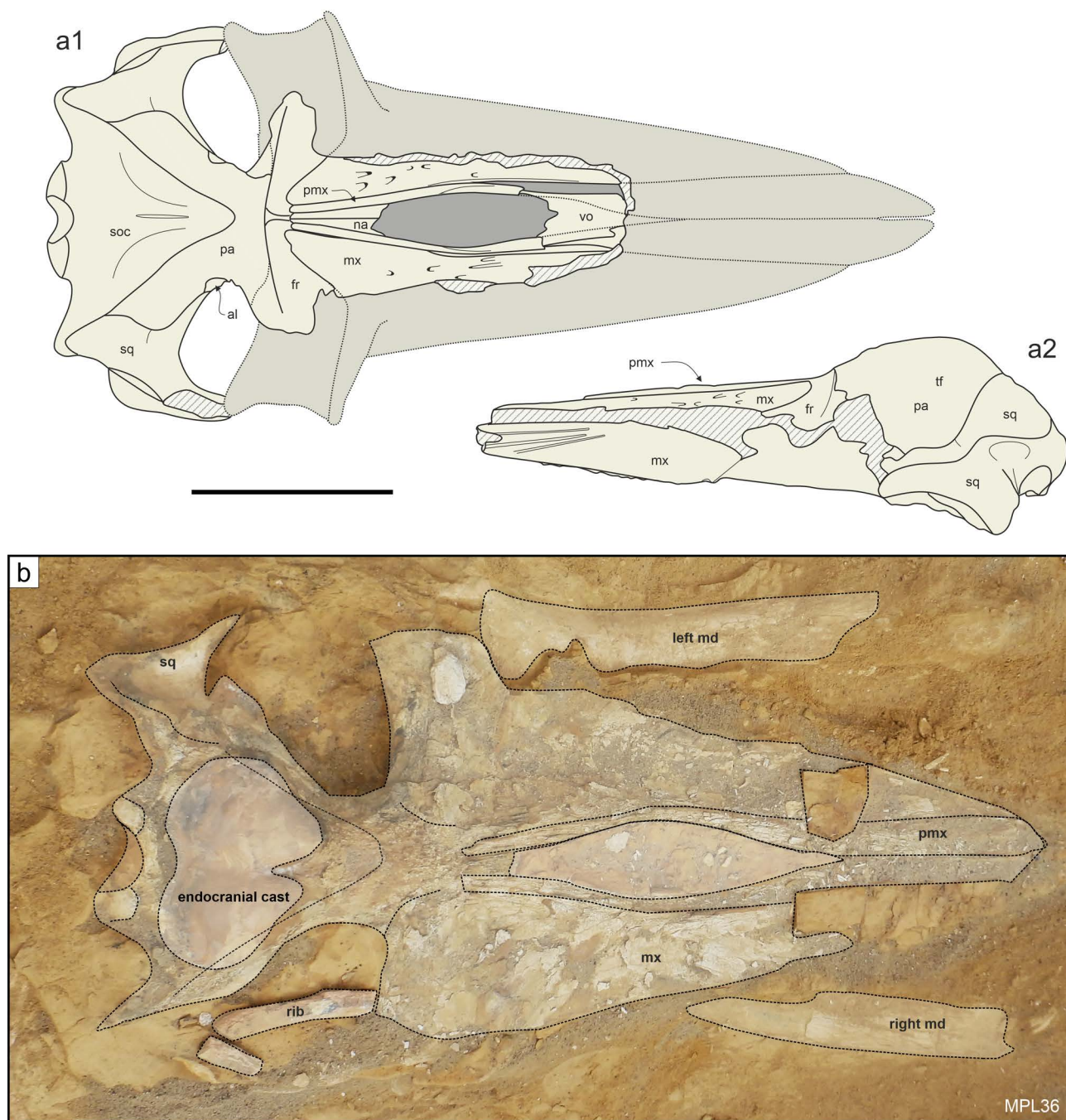
Fig. 9 - Cetotheriids from the P0 beds of the Pisco Formation. a) Cranium of *Tiucetus rosae*, MNHN.F. PPI261 (holotype), in dorsal (a1) and left lateral (a2) views. Stippled lines indicate reconstructed parts (redrawn and modified after Marx et al., 2017b: figs 2, 4). b) Skull of cf. *Tiucetus* sp., field photograph; the field number is reported at the bottom right of the panel. Abbreviations: fr, frontal; md, mandible; mx, maxilla; na, nasal; pa, parietal; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa; vo, vomer. Scale bar is equal to 20 cm.

al., 2021b). Body length estimates for the largest P2 balaenopteroids range between 15.8-18.3 m, once again indicating that the titanic body size standard of most living mysticete clades is firmly rooted in the Miocene (Bianucci et al., 2019b).

Cetotheriids are present in P2 with *Piscobalaena nana*, whose type material comes from Messinian Pisco-equivalent strata exposed in the Sacaco area, south of the East Pisco Basin proper (Pilleri & Siber, 1989; but see Ochoa et al., 2021 for an updated age attribution).

Arguably representing the best-known extinct member of Cetotheriidae (Bouetel & Muizon, 2006), *P. nana* is a small-sized species about four meters in body length (Collareta et al., 2017a), as well as a "typical" non-neobalaenine representative of its family, characterised by a preorbital process of the maxilla prolonged dorsomedially into a crest, a strongly developed occipital sagittal crest, a broad exposure of the vomer on the palate, and a wide and transversely rounded vomerine crest (Bouetel & Muizon, 2006; Marx et al., 2017b) (Fig.
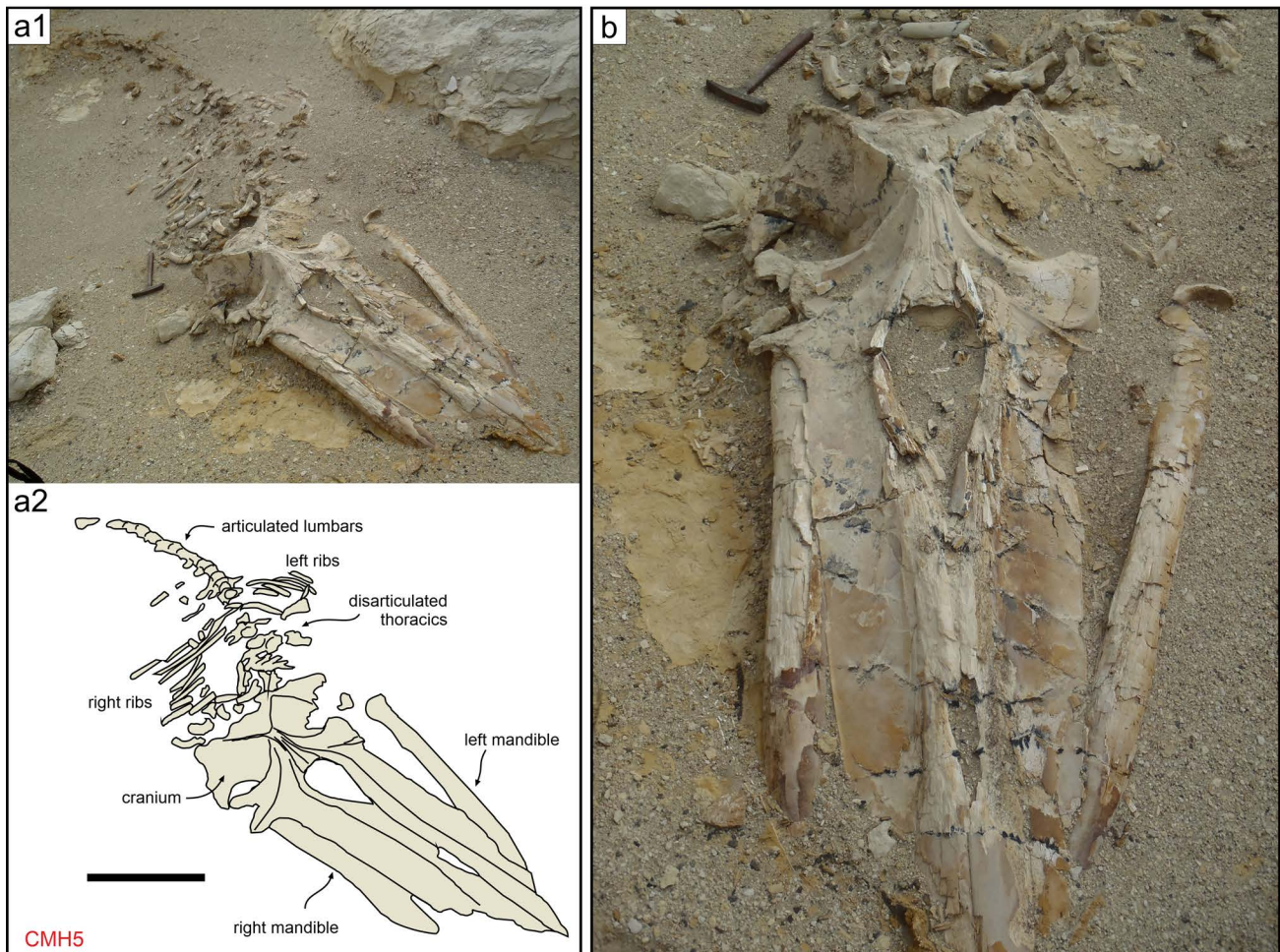
Fig. 10 - Skeleton of Cetotheriidae gen. et sp. indet. from the P1 beds of the Pisco Formation. a1) Field photograph, a2) corresponding schematic drawing and b) close-up of the skull. The field number is reported at the bottom left of panel a2. Scale bar is equal to 50 cm.

12). One skeleton of *Piscobalaena nana* from upper P2 strata exposed at Cerro Ballena was found preserving an exquisitely phosphatised baleen rack, which in turn represents the first record of such apparatus in a major mysticete morphotype no longer present in the modern oceans (Marx et al., 2017b) (Fig. 12c1-2). Similar to the condition observed in the living *Caperea marginata*, the baleen plates of *P. nana* are closely spaced and embed fine tubules. Crucially, the relatively short size of the rack, extending for slightly more than half the rostrum length, matches the distribution of the palatal nutrient foramina and sulci, thus indicating the presence of an unusually conspicuous subrostral gap, which in turn may suggest some kind of (maybe continuous) suction feeding that finds no analogues in extant mysticetes (Marx et al., 2017b). Overall, the trophic habits of *P. nana* largely remain an enigma, with putative target species ranging from zooplankton to schooling fish like sardines (Collareta et al., 2021b).

Puzzlingly, no representatives of the family Balaenidae (right whales) have been recorded so far from the Ica Desert and surrounding areas; in turn, the neobalenines (pygmy right whales) have their best-known fossil representative in *Miocaperea pulchra* Bisconti, 2012, whose holotype and only known specimen comes from upper Tortonian Pisco-equivalent strata of the Sacaco area.

If such a lack of right whale fossils is genuine, it may be suggestive of some sort of competitive exclusion, with neobalaenines locally typifying the ram feeding niches occupied elsewhere by balaenids (see also Tsai & Ando, 2016 and Collareta et al., 2021c for similar case studies).

INTICETUS VERTIZI LAMBERT ET AL., 2018: A WITNESS OF THE HETERODONT ODONTOCETE RADIATION

Among extant neocetes, those belonging to the suborder Odontoceti are characterised by displaying a unique echolocating system (including the odontocetes' signature organ, the melon), a peculiar architecture of the "telescoping" cranial bones (which largely reflects the development of echolocation), and no baleen, with a complete dentition being retained in most species (Hooker, 2018). Since many archaic mysticetes were also provided with teeth, and the soft tissue parts that are implied in echolocation have never been described as fossils, the earliest members of Odontoceti are recognised as such on the basis of their cranial osteoanatomy (e.g., Uhen, 2008; Geisler et al., 2014; Sanders & Geisler, 2015). Interestingly, whereas the discovery of *Mystacodon selenensis* demonstrates that mysticetes are as old as 36.4 Ma, the
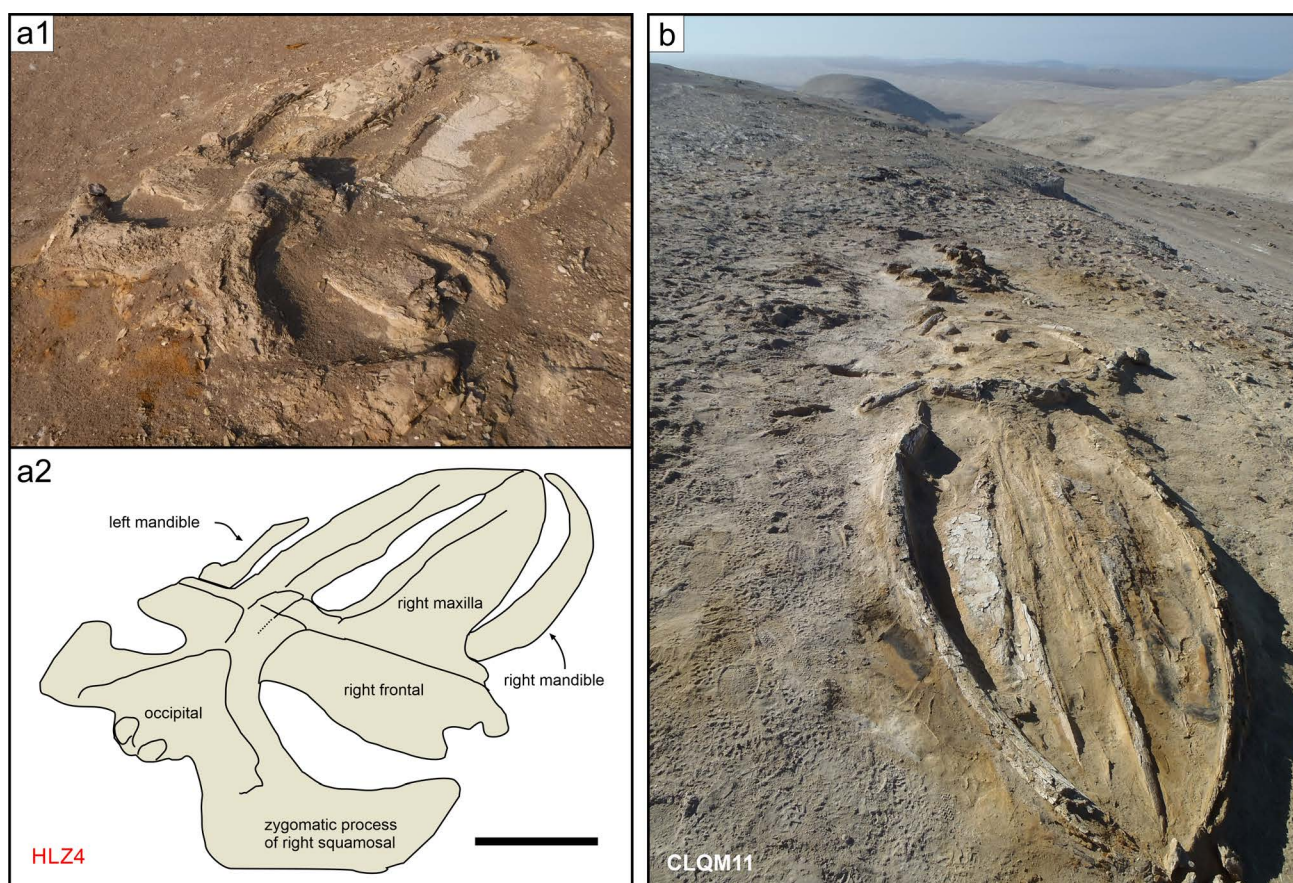
Fig. 11 - Balaenopterids from the P2 beds of the Pisco Formation. a) Skull of Balaenopteridae gen. et sp. indet. 1: field photograph (a1) and corresponding schematic drawing (a2). b) Skeleton of Balaenopteridae gen. et sp. indet. 2, field photograph. The field numbers are reported at the bottom left of panels a1 and b. Scale bar is equal to 50 cm.

fossil record of their closest odontocete relatives only date back to the early Oligocene, around 29 Ma (Sanders & Geisler, 2015) or slightly earlier (Fordyce, 2002).

Differing from their archaeocete precursors, the greatest majority of extant odontocete species display a homodont and polydont dentition, i.e., they bear a great number of single-rooted, largely unornamented teeth that are similar to each other in shape (Lambert et al., 2018b). This condition may have derived from the multiplication of the morphologically simple anterior teeth of their ancestors (Armfield et al., 2013), and likely reflects major shifts in predation techniques and food processing strategies (Lambert et al., 2018b). There is some indication from phylogenetic analyses that homodonty and polydonty were acquired independently in different odontocete clades, and many Oligocene and Miocene toothed whale forms retain the plesiomorphic condition of double-rooted posterior cheek teeth (i.e., postcanines) that bear accessory denticles.

Inticetus vertizi is an extinct heterodont odontocete species known from a single articulated skeleton from the Ct1c strata of the Chilcatay Formation exposed at Roca Negra (Lambert et al., 2018b; Di Celma et al., 2019). Among other features, this large-sized dolphin (total body length around four meters, or slightly greater) is characterised by a long and robust rostrum hosting at least 18 teeth per quadrant, conical anterior teeth

(i.e., incisors to anterior postcanines, the former being unprotruding), the occurrence of many large accessory denticles along the mesial and distal edges of the double-rooted posterior cheek teeth, a reduced ornamentation of the dental crowns, and a remarkably robust styliform process of the jugal (Lambert et al., 2018b) (Fig. 13a1-2). Although the relationships of *I. vertizi* are still unclear, with phylogenetic analyses recovering it either as a stem- or as a crown-group odontocete, this large-sized extinct dolphin species is sufficiently different from any other toothed whale to warrant its placement in the as yet monotypic family Inticetidae (Lambert et al., 2018b).

The posterior postcanines of *Inticetus vertizi* are particularly remarkable: they bear labiolingually compressed, semi-circular crowns, and their accessory denticles are bowed and distinctly deflected radially (Fig. 13b). Such a highly idiosyncratic dentition suggests a similarly peculiar, and currently unparalleled, feeding specialisation: *I. vertizi* may have used its roughly conical, unprotruding anterior teeth to grasp its prey, whereas the posterior postcanines, with their semi-circular outline, coarse denticulations and no attritional tooth wear facets, may have led to an efficient closure of the lateral walls of the posterior buccal cavity, thus favouring suction and allowing for the retention of food items within the posterior oral cavity during water expulsion (Lambert et al., 2018b).
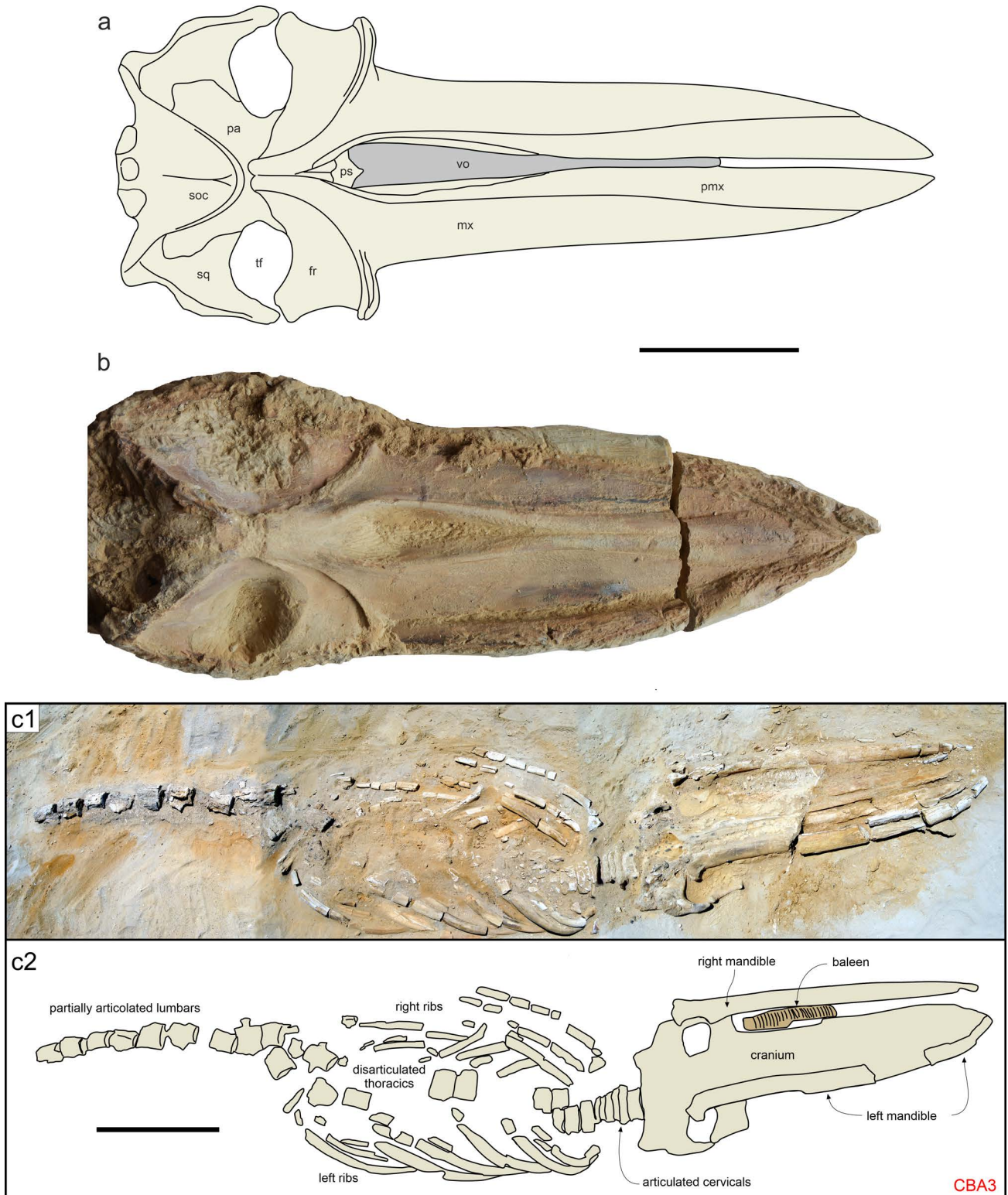
Fig. 12 - *Piscobalaena* from the P2 beds of the Pisco Formation. a) Cranium of *Piscobalaena nana*, MNHN SAS 1617, in dorsal view. b) Skull (partially embedded in the sediment) of *Piscobalaena* cf. *nana*, stored in the palaeontological collections of INGEMMET (Lima, Peru), in dorsal view. c) Skeleton of *Piscobalaena nana*, field number field photograph (c1) and corresponding schematic drawing (c2). The field number is reported at the bottom right of panel c2. Abbreviations: fr, frontal; mx, maxilla; pa, parietal; pmx, premaxilla; ps, presphenoid; soc, supraoccipital; sq, squamosal; tf, temporal fossa; vo, vomer. Scale bars are equal to 20 cm for panels a, b; 50 cm for panels c1, c2.

Teeth similar to those of *Inticetus vertizi* have been recorded from the Miocene of North Carolina (eastern U.S.A.), the Atlantic coast of France and southeastern Italy (Boessenecker, 2019; Peri et al., 2019). Inticetids may have dispersed across the Central American Seaway, which permitted faunal interchanges between the
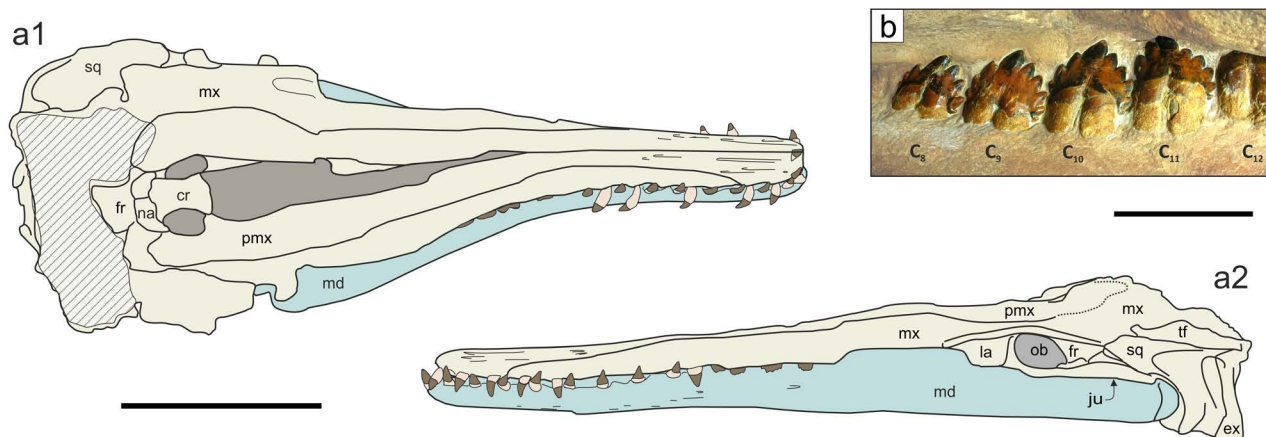
Fig. 13 - *Inticetus vertizi*, MUSM 1980 (holotype), from the Ct1c beds of the Chilcatay Formation. a) Skull in dorsal (a1) and left lateral (a2) views. Dashed areas indicate damaged surfaces. b) Detail of the right mandibular cheek teeth C8-C12 in medial view. Abbreviations: cr, cribriform plate; fr, frontal; ju, jugal; md, mandible; mx, maxilla; na, nasal; ob, orbit; pa, parietal; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa. Scale bars are equal to 20 cm for panels a1, a2; 5 cm for panel b.

PHYSEROIDEA, THE SPERM WHALES

Only three living species of physeteroids (sperm whales) are known, namely, the large-sized *Physeter macrocephalus* Linnaeus, 1758, whose adult males may reach a total body length of 18 m, and two species in the much smaller genus *Kogia* (Caldwell & Caldwell, 1989; Rice, 1989). Both *Physeter* and *Kogia* bear a spermaceti, a mass of waxy material that takes place dorsal to the skull and posterior to the melon, and whose function is still incompletely understood. Crucially, the presence of the spermaceti is reflected, in both extant and extinct physeteroids, by the occurrence of a broad supracranial basin excavating the asymmetric dorsal surface of the skull (Lambert, 2010). Modern physeteroids are deep-divers that feed in open-ocean waters of the continental slope and submarine canyons, with *Physeter macrocephalus* being regularly reported from depths greater than 1000 m (Withehead, 2018). They primarily forage upon squid which they take by means of suction (Werth, 2004). Somewhat reflecting this feeding style, the temporal fossae and dentition of living sperm whales are very reduced, and the latter only includes lower functional teeth (Caldwell & Caldwell, 1989; Rice, 1989).

Except for the highly enigmatic putative physeteroid *Ferecetotherium kelloggi* Mchedlidze, 1976, which comes from the upper Oligocene of Caucasus, sperm whales are known as fossils from the Early Miocene onwards. The oldest physeteroid fossils from the East Pisco Basin occur in Burdigalian deposits of the Chilcatay Formation exposed at the well-prospected localities of Ullujaya (Bianucci et al., 2018b; Di Celma et al., 2018b) and Zamaca (Di Celma et al., 2019; Lambert et al., 2020). Besides indeterminate fragmentary remains, the Chilcatay physeteroids include a skull referred to cf. *Diaphorocetus* sp. and the holotype and only known specimen of *Rhaphicetus valenciae* Lambert et al., 2020. The former comes from the Ct1a strata exposed at Ullujaya and resembles *Diaphorocetus*

poucheti (Moreno, 1892) from the Early Miocene Monte León Formation of Argentina (Bianucci et al., 2018b). By displaying deep dental alveoli that comprise a complete upper dentition, and differing from the suction feeding extant sperm whales, cf. *Diaphorocetus* sp. was likely an actively grasping predator; furthermore, compared to the size of the skull, the diameter of the alveoli is invariantly small, suggesting that this odontocete fed on relatively small prey items (Bianucci et al., 2018b). Originating from Ct1a beds exposed at Zamaca, the *R. valenciae* holotype includes the partial skull, ear bones, mandibles, teeth, sternum, vertebrae and ribs (Lambert et al., 2020). Recovered by phylogenetic analyses as an early branching stem physeteroid, *R. valenciae* was likely about 5 m in total body length. The most striking character of the skull of *R. valenciae* is its extremely long snout provided with a circular cross-section (Fig. 14a1-2); furthermore, both the rostrum and the mandibles bear dental alveoli that housed slender, pointed teeth (Fig. 14b), but the anteriormost upper alveoli are filled by thick bony pads (Lambert et al., 2020). This unusual feature is interpreted as part of a mechanism leading to the loss of upper teeth along a segment of the rostrum that was likely placed anterior to the anteriormost tip of the mandibles (Fig. 14a2). Along with the observation of a long temporal fossa (Fig. 14a2), this peculiar design of the dentition and rostrum suggests that *R. valenciae* used its teeth to grasp relatively small prey, possibly via rapid movements of the head, close to the sea bottom; alternatively, a longer upper jaw could have still been useful to strike and stun fish higher in the water column, in a way similar to extant billfishes (Lambert et al., 2020).

Rhaphicetus valenciae is roughly coeval to several other stem physeteroids and early branching physeterids (e.g., Lambert, 2008); as such, it contributes to depict an Early Miocene phase of radiation of sperm whales, one that also saw the emergence of crown physeteroids.

A single indeterminate non-kogiid physeteroid is known from the P0 allomember of the Pisco Formation (Collareta et al., 2021a). In turn, the sperm whale record from the P1 and P2 allomembers is utterly rich and makes the Pisco Formation a key unit for reconstructing the
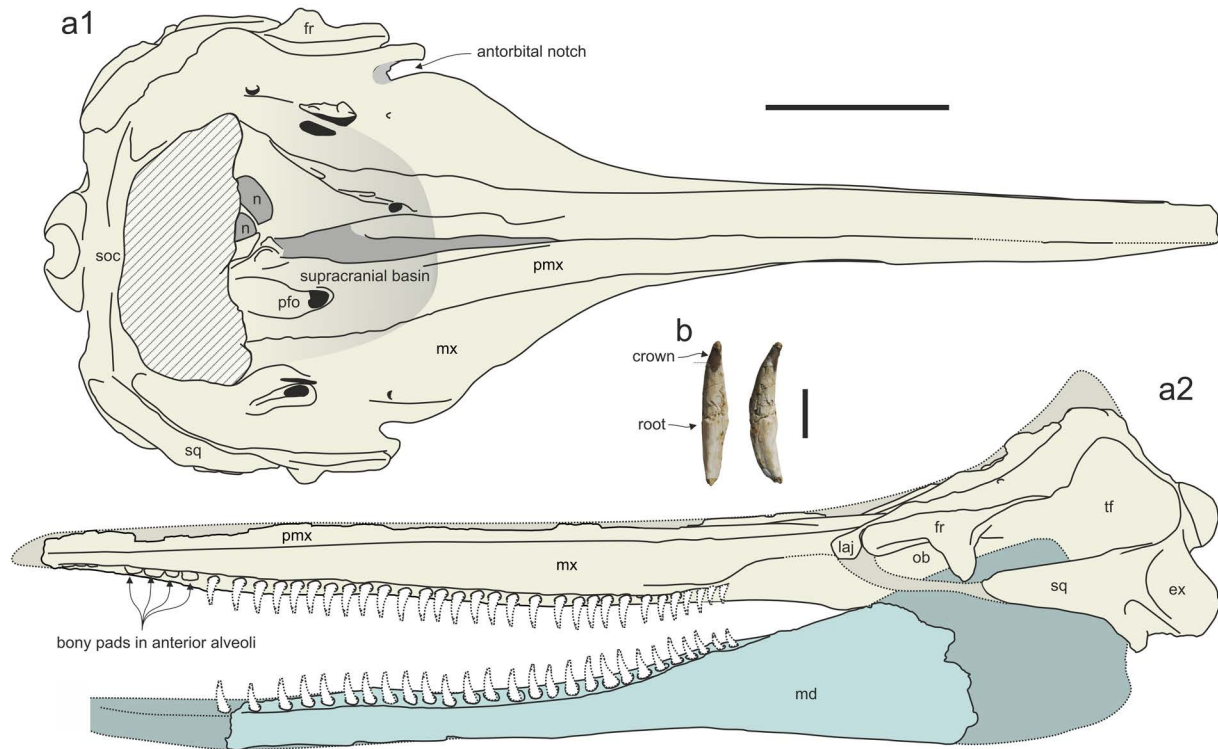
Fig. 14 - *Rhaphicetus valenciae*, MUSM 2543 (holotype), from the Ct1 beds of the Chilcatay Formation. a) Skull in dorsal (a1) and left lateral (a2) views. Dashed areas indicate damaged surfaces; stippled lines indicate reconstructed parts. b) Detached tooth. Abbreviations: ex, exoccipital; fr, frontal; laj, lacrimojugal complex; md, mandible; mx, maxilla; n, external bony naris; ob, orbit; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa. Scale bars are equal to 20 cm for panels a1, a2; 2 cm for panel b.

evolutionary history of sperm whales. In P1, physeteroids are represented by the stem sperm whales *Acrophyseter* sp. and *Livyatan melvillei* (Collareta et al., 2021b). Both *Acrophyseter* and *Livyatan* are widely referred to as "macroraptorial physeteroids", that is, sperm whales that likely used to forage upon large-sized food items by using their conspicuous, enamel-coated teeth and powerful temporal muscles to grab and tear or shear the prey (Lambert et al., 2017a).

Not much is known about the P1 representative of *Acrophyseter*, which has been collected and prepared only recently; however, this genus is well known from highly informative finds from P2 (see below). Described on the basis of a skull with associated teeth and mandibles from the locality of Cerro Colorado (Fig. 1c, d), *Livyatan melvillei* is characterised by a three-m-long cranium, the retention of a complete dentition, robust mandibles, and a temporal fossa considerably larger than in extant physeteroids (Lambert et al., 2010b) (Fig. 15a1-2). The teeth are few (numbering eleven in the maxilla and nine in the dentary) and giant-sized (maximum diameter and apicobasal length of 12 cm and more than 36 cm, respectively) (Fig. 15b). Deep, subvertical wear facets are ubiquitous, suggesting a high degree of interlocking and frequent biting actions; furthermore, the anteriormost teeth distinctly project anteriorly from both the upper and the lower jaws. Interpreted as a stem physeteroid, *L. melvillei* represents one of the largest raptorial predators and, possibly, the biggest tetrapod bite ever found. The body length of *L. melvillei* is evaluated as matching the

range of adult males of *P. macrocephalus*; further recalling the latter, *L. melvillei* displays a long supracranial basin that extends over the whole rostrum length, thus evoking the presence of a similarly elongated spermaceti organ.

The P2 strata are home to two members of *Acrophyseter* (*Acrophyseter robustus* Lambert et al., 2017a and *Acrophyseter* sp.) as well as to some of the oldest representatives of the extant family Kogiidae (*Platyscaphokogia landinii* Collareta et al., 2020 and *Scaphokogia cochlearis* Muizon, 1988a; see below) (Bianucci et al., 2016b; Lambert et al., 2017a; Collareta et al., 2020a, 2021b). The former are medium-sized physeteroids distinguished by a large, bowl-shaped supracranial basin that extends laterally on the right side of the cranium, overhanging the right orbit but not extending on the rostrum, as well as by relatively short and robust upper and lower jaws that are distinctly bent upwards (Fig. 16). Coming from the basal sandstones of P2 exposed at Cerro La Bruja, *A. robustus* (Fig. 16a1-2) mostly differs from the type species of *Acrophyseter*, *A. deinodon* Lambert et al., 2008 from the Sacaco area, based on the less attenuate rostrum, absence of left premaxillary foramina, and more rounded dorsal margin of the supracranial basin and coronoid process of the mandible. *Acrophyseter robustus* also displays two nasals (Fig. 16a1), which seemingly represents a unicum among physeteroids (in which no more than one nasal is usually present), though this may change with the discovery of additional specimens of e.g., *A. deinodon*. Further up along the P2 section, the diatomaceous mudstones occurring at
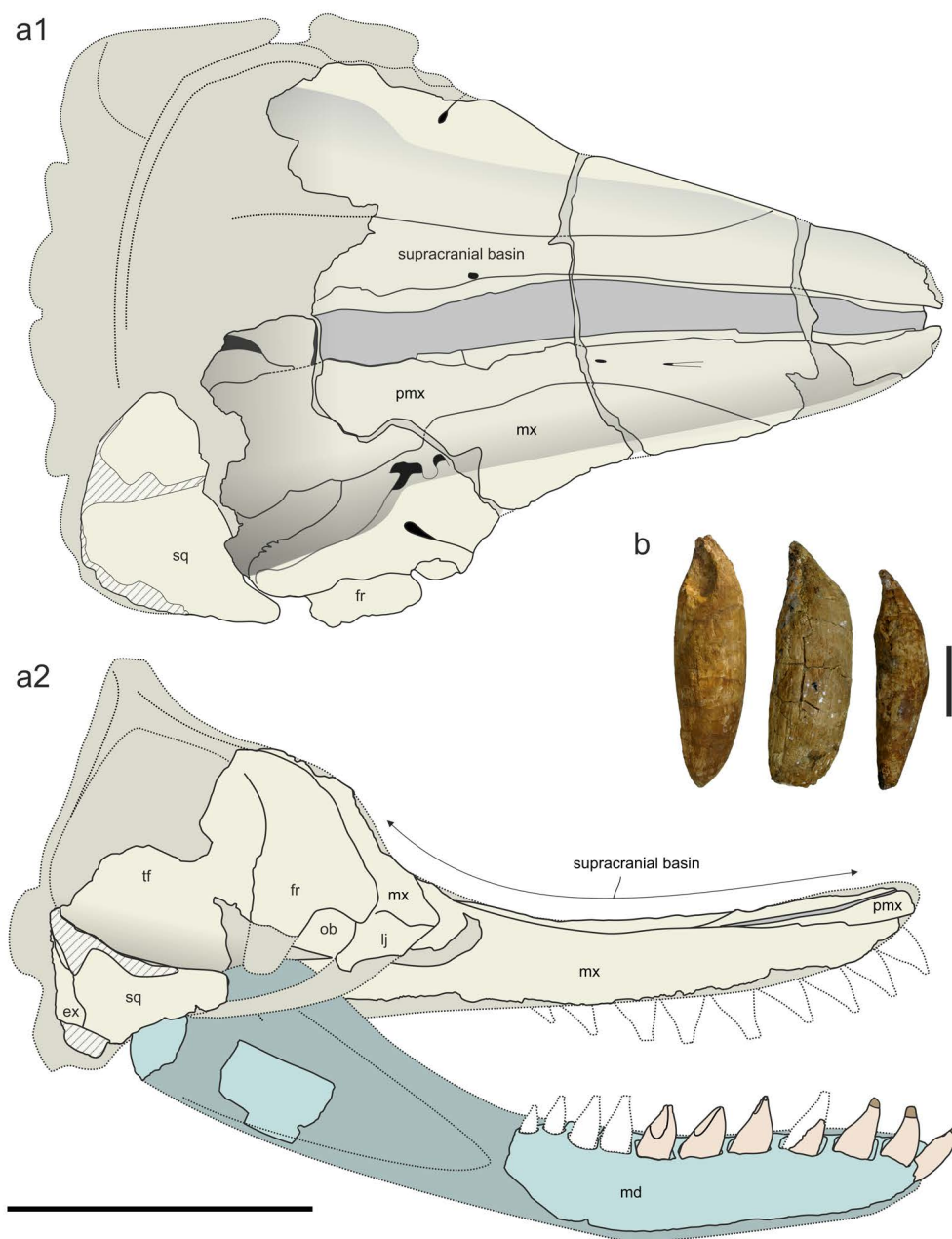
Fig. 15 - *Livyatan melvillei*, MUSM 1676 (holotype), from the P1 beds of the Pisco Formation. a) Skull in dorsal (a1) and right lateral (a2) views. Dashed areas indicate damaged surfaces; stippled lines indicate reconstructed parts. b) Three detached teeth. Abbreviations: ex, exoccipital; fr, frontal; laj, lacrimojugal complex; md, mandible; mx, maxilla; ob, orbit; pmx, premaxilla; sq, squamosal; tf, temporal fossa. Scale bars are equal to 100 cm for panels a1, a2; 10 cm for panel b.

the top of Cerro Los Quesos host an incomplete skull with mandibles that has been referred by Lambert et al. (2017a) to *Acrophyseter* sp. (Fig. 16b-d). While significantly differing from both the geologically older holotype of *A. robustus* and the likely younger holotype of *A. deinodon*, this specimen may either testify to intraspecific variation within the latter species or represent a third, as yet unnamed species of *Acrophyseter* (Lambert et al., 2017a). *Acrophyseter robustus* and *Acrophyseter* sp. consistently cluster with *A. deinodon* in phylogenetic studies, thus unambiguously indicating the monophyly of *Acrophyseter* (Lambert et al., 2017a; Collareta et al., 2017b, 2019, 2020; Paolucci et al., 2020; Alfsen et al., 2021); however,

whether *Acrophyseter* and *Livyatan* belong to the same clade of stem physeteroids is at present unclear.

The ecotrophic role of *Acrophyseter*, *Livyatan* and allied forms has often been investigated by means of functional morphology and biomechanics (Bianucci & Landini, 2006; Lambert et al., 2008, 2010b, 2014a, 2017a; Lambert & Bianucci, 2019; Peri et al., 2020, 2021). All these studies suggested a macrophagous feeding style that involved both biting and shearing (e.g., *Acrophyseter*) or tearing (e.g., *Livyatan*), thus strikingly contrasting with the strong suction feeding specialisation seen in Recent sperm whales (e.g., Bloodworth and Marshall, 2005; Werth, 2006; Hocking et al., 2017). Unfortunately,
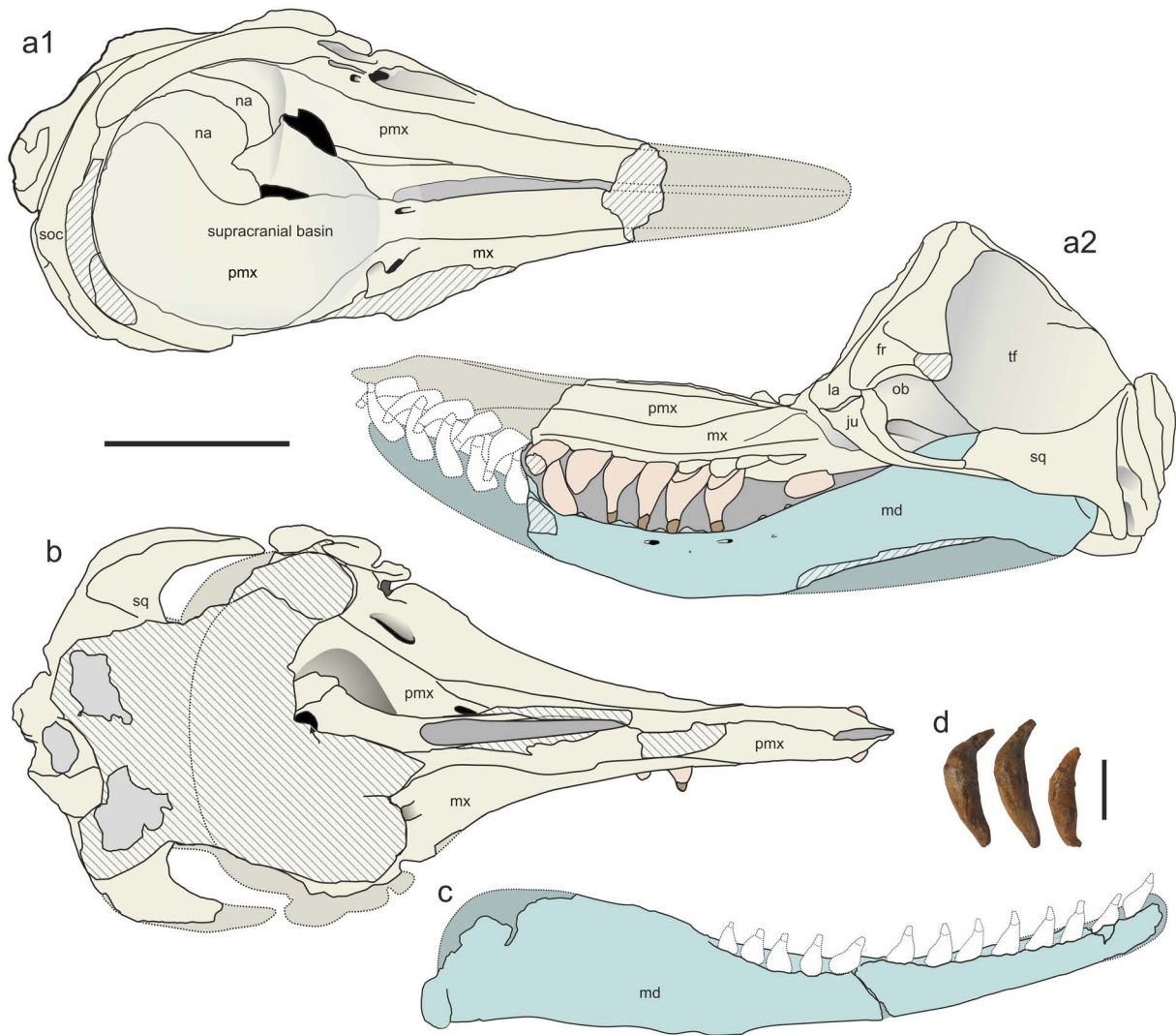
Fig. 16 - *Acrophyseter* from the P2 beds of the Pisco Formation. a) Skull of *Acrophyseter robustus*, MUSM 1399 (holotype), in dorsal (a1) and left lateral (a2) views. b-d) *Acrophyseter* sp., MUSM 2182; b) cranium in dorsal view; c) right mandible in lateral view; d) three teeth. Dashed areas indicate damaged surfaces; stippled lines indicate reconstructed parts. Abbreviations: fr, frontal; laj, lacrimojugal complex; md, mandible; mx, maxilla; na, nasal; ob, orbit; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa. Scale bars are equal to 20 cm for panels a1,a2, b, c; 5 cm for panel d.

no direct evidence for the trophic ecology of these forms (e.g., bite marks or fossilised stomach contents) has emerged from the fossil record to date. During the Late Miocene, the macroraptorial stem physeteroids of the Pisco embayment ranged between medium-sized (*Acrophyseter*, 4-4.5 metres long) and gigantic (*Livyatan*, 13.5-17.5 metres long) forms (Bianucci and Landini, 2006; Lambert et al., 2014a), thus likely foraging on a similarly broad range of potential prey items. As already highlighted elsewhere (e.g., Bianucci & Landini, 2006; Lambert et al., 2017a; Collareta et al., 2021b), only the killer whale *Orcinus orca* (Linnaeus, 1758) could be evoked as a possible extant analogue for *Acrophyseter*, *Livyatan*, and allied stem physeteroids. Killer whales are currently known as the oceans' apex non-human predators (Ford et al., 2010). They are highly sociable organisms, and the cooperation of several of them in hunting makes every inhabitant of the sea potentially suitable as prey, almost regardless for its size (e.g., Jefferson et al., 1991;

Bianucci et al., 2022); however, mammal-eating killer whales are typically found at high latitudes, where they primarily forage on pinnipeds (Corkeron and Connor, 1999), and consequently their predatory impact on low-latitude ecosystems is often poorly studied and understood. Interpreting the impact of macroraptorial sperm whales on the Late Miocene ecosystems of Peru would also need a basic knowledge of their social habits, which in turn are likely impossible to test in such extinct forms. Extant physeteroids exhibit contrasted patterns of sociability (e.g., Caldwell and Caldwell, 1989; Rice, 1989), and as such, cannot shed light on this issue. Under the assumption of solitary hunting, *Acrophyseter* spp. may have been able to prey upon small-sized marine mammals not longer than a couple of metres. In turn, the giant-sized *Livyatan melvillei* may have been able to ordinarily forage on larger prey items such as cetotheriids and ziphiids, thus likely exhibiting a trophic spectrum largely superimposed to that of the giant lamniform shark

Carcharocles megalodon (Agassiz, 1835) (Collareta et al., 2021b).

Whereas the crown physeteroid family Physeteridae is known from finds as old as the Burdigalian, its putative sister group, the family Kogiidae, has a fossil record that is limited to the Upper Miocene and Pliocene (Alfsen et al., 2021). Kogiids are promptly characterised by their small, strongly asymmetric crania whose dorsal surface bears a laterally displaced sagittal facial crest (Barnes, 1973; Muizon, 1988a). The absence of kogiid fossils in Lower and Middle Miocene deposits worldwide remains puzzling, and the earliest members of the family (most of which come from the Pisco and Pisco-equivalent strata exposed along the southern coast of Peru) are not representative of the archaic kogiids but rather show full subfamilial derivation within the extant kogiines and extinct scaphokogiines (Muizon, 1988a; Collareta et al., 2017b, 2020a; Benites-Palomino et al., 2019, 2021). In particular, the East Pisco kogiids belong to the scaphokogiines, a monophyletic group characterised by high, plate-like lateral maxillary crests, a nuchal crest that is strongly shifted backwards in lateral view, and a supracranial basin that is deep and spoon-shaped (Collareta et al., 2020a). Skulls of two scaphokogiine genera and species, *Platyscaphokogia landinii* and *Scaphokogia cochlearis*, are currently known from the localities of Cerro Hueco la Zorra, Cerro Los Quesos and Las Antenas (Collareta et al., 2020) (Fig. 17). First described from the Sacaco area, *Scaphokogia cochlearis* is the geologically oldest kogiid known to date; it consists of a highly idiosyncratic form, characterised by a pachyostotic, downwards-deflected, semicylindrical rostrum that bears discrete yet likely relic dental alveoli (Muizon, 1988a) (Fig. 17b1-2). This suggests a peculiar trophic specialisation that is not paralleled by any extant odontocete and has still to be properly investigated and understood, but some kind of benthic foraging in shallow-water, nearshore settings has been proposed (Collareta et al., 2017b, 2020a; Benites-Palomino et al., 2019). In turn, the similarly sized *P. landinii* retains a somewhat more conventional rostrum that distinctly points anteriorly
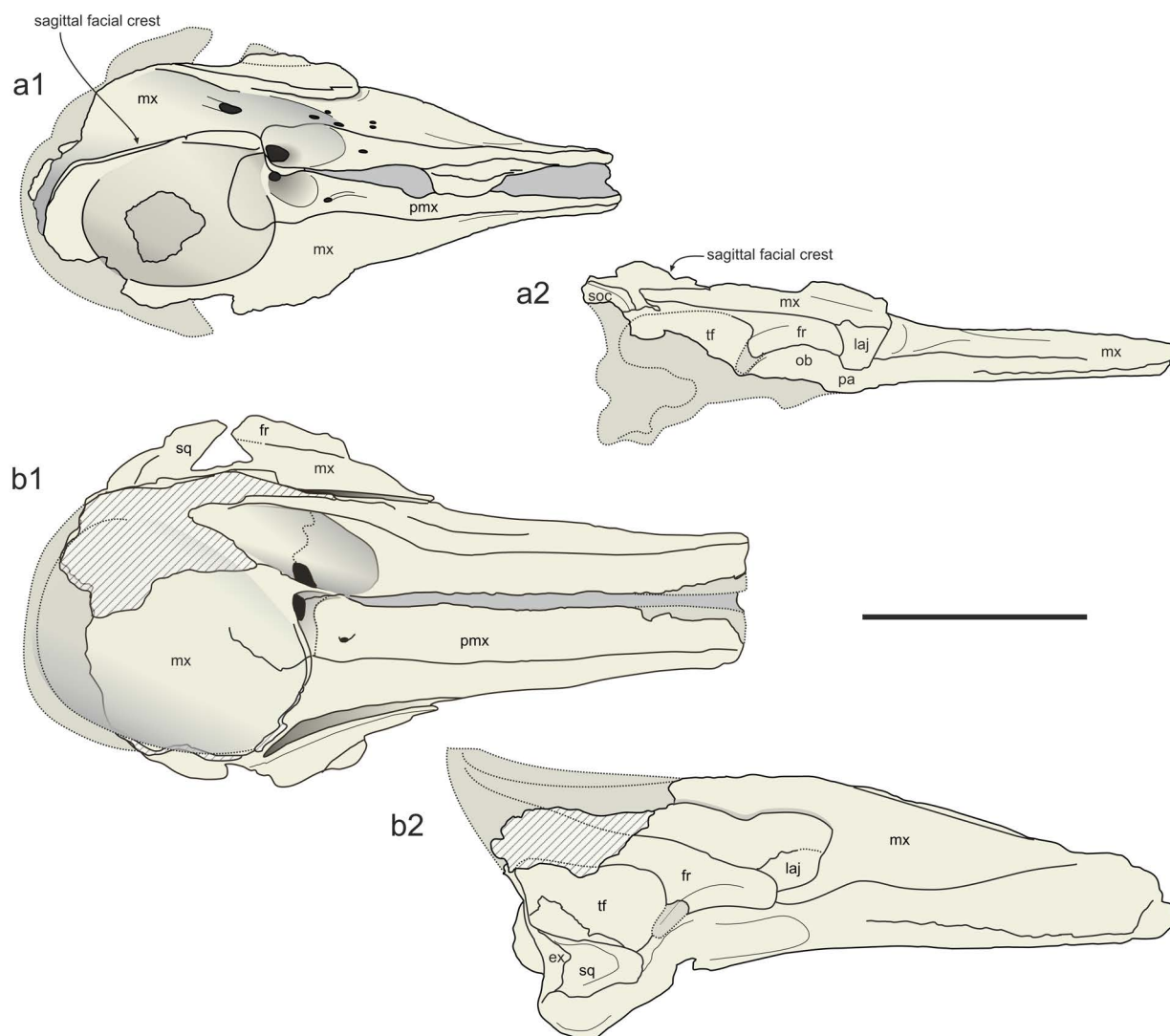

Fig. 17 - Scaphokogiines from the P2 beds of the Pisco Formation. a) Cranium of *Platyscaphokogia landinii*, MUSM 1399 (holotype), in dorsal (a1) and right lateral (a2) views. b) Cranium of *Scaphokogia cochlearis*, MUSM 3244, in dorsal (b1) and right lateral (b2) views. Dashed areas indicate damaged surfaces; stippled lines indicate reconstructed parts. Abbreviations: ex, exoccipital; fr, frontal; laj, lacrimojugal; mx, maxilla; ob, orbit; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa. Scale bar is equal to 20 cm.

and bears fully developed dental alveoli (Fig. 17a1-2); as such, *P. landinii* has been reconstructed as a small-bodied raptorial sperm whale that foraged along the water column in relatively open-sea palaeoenvironments (Collareta et al., 2020a, 2021b).

THE EXPLOSIVE RADIATION OF PLATANISTOIDEA

As redefined by Bianucci et al. (2020), the superfamily Platanistoidea (including Allodelphinidae, Platanistidae and Squalodelphinidae, but not Squalodontidae and Waipatiidae) is a monophyletic group of nearly homodont odontocetes that had its greatest radiation in late Oligocene-Early Miocene times and is nowadays represented only by the South Asian freshwater dolphins (*Platanista gangetica* [Lebeck, 1801] and *Platanista minor* Owen, 1853; Braulik et al., 2021). Platanistoids are odontocetes with single-rooted teeth characterised by the combination of several morphological characters, some of which are peculiar of this clade (synapomorphies) and mainly concern the ear bones, while others are shared with other odontocetes, e.g., the elongated hamular fossa of the pterygoid sinus extending anteriorly on the palatal surface of the rostrum (also present in Ziphiidae). Except for *Allodelphis* and *Ninjadelphis*, the cranium of the platanistoids is markedly asymmetric, having the vertex distinctly displaced to the left of the sagittal plane (Bianucci et al., 2020).

The high diversity of this clade during the Early Miocene is demonstrated by the odontocete assemblage of the Chilcatay Formation as known from strata exposed at Ulluyaja, Zamaca and south of Cerro Colorado. Indeed, three new genera and species of squalodelphinids (*Furcacetus flexirostrum* Bianucci et al., 2020, *Huaridelphis raimondii* Lambert et al., 2014b and *Macrosqualodelphis ukupachai* Bianucci et al., 2018a) and a new genus and species of platanistoid basal to the clade formed by the squalodelphinids and the platanistids (*Ensidelphis riveroi* Bianucci et al., 2020) have been described from these localities; in addition, the squalodelphinid *Notocetus vanbenedeni* Moreno, 1893, a platanistid close to *Araeodelphis natator* Kellogg, 1957 and another unnamed platanistoid have also been reported (Lambert et al., 2014b; Bianucci et al., 2015, 2018a, 2020). The high diversity of platanistoids of the Chilcatay Formation (Figs 18, 19) correlates with a high disparity in the size and shape of the skulls. Considering that all the Chilcatay platanistoids lived in a limited area as well as during a short time span (~19-18 Ma), such a high disparity could be related to a high degree of trophic partitioning (Bianucci et al., 2020).

Ensidelphis riveroi (Fig. 18a1-2) has been described on the basis of a skull and associated cervical vertebrae found in Ct1c strata exposed at Zamaca. It is characterised by extremely elongated rostrum and mandibles; both the former and the latter are flattened in their anterior portions and bear some 250 small teeth. Moreover, the temporal
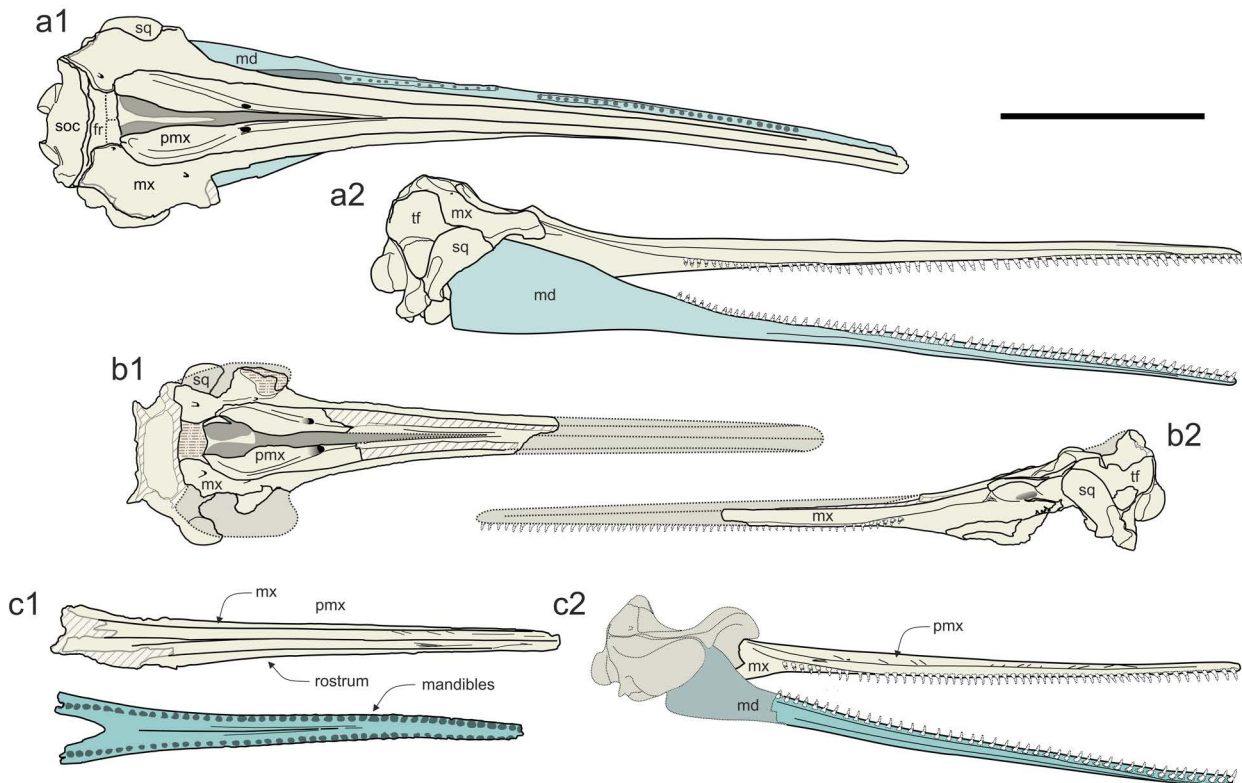

Fig. 18 - Longirostrine platanistoids from the Chilcatay Formation. a) Skull of *Ensidelphis riveroi*, MUSM 3898 (holotype) from the Ct1c beds, in dorsal (a1) and right lateral (a2) views. b) Cranium of Platanidelphidi indet., MUSM 3899 from the Ct1a beds, in dorsal (b1) and left lateral (b2) views. c) Fragmentary skull of aff. *Araeodelphis* sp., MUSM 3899 (referred specimen), in dorsal (c1) and right lateral (c2) views. Stippled lines indicate reconstructed parts. Abbreviations: fr, frontal; md, mandible; mx, maxilla; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa. Scale bar is equal to 20 cm.
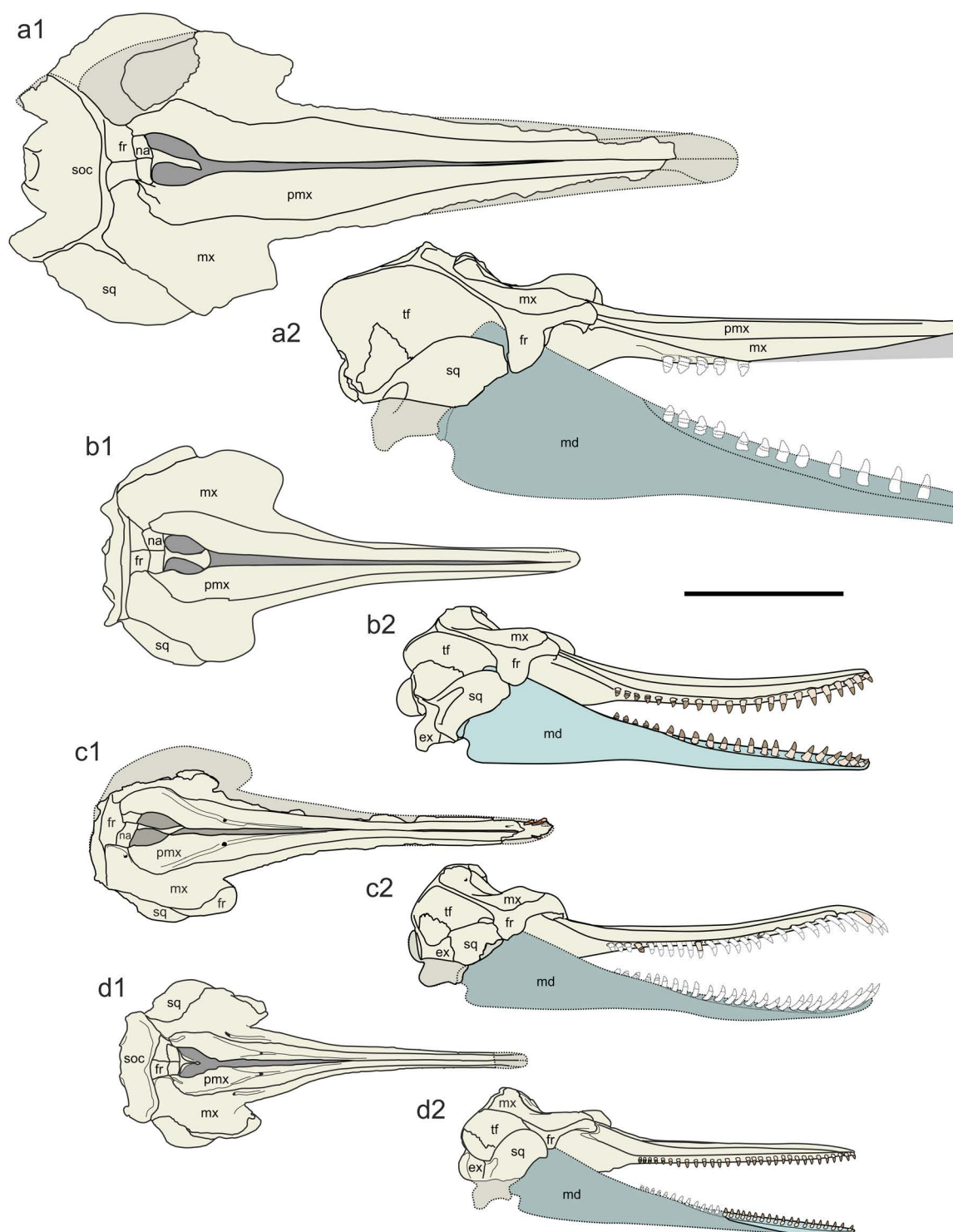
Fig. 19 - Squalodelphinids from the Chilcatay Formation. a) Skull of *Macrosqualodelphis ukupachai*, MUSM 2545 (holotype), in dorsal (a1) and right lateral (a2) views. b) Skull of *Notocetus vanbenedeni* (reconstruction based on MUSM 1395 and MUSM 3896), in dorsal (b1) and right lateral (b2) views. c) Skull of *Furcacetus flexirostrum*, MUSM 487 (holotype), in dorsal (c1) and right lateral (c2) views. d) Skull of *Huaridelphis raimondii*, MUSM 1396 (holotype) (the fragmentary mandible is from MUSM 1403), in dorsal (d1) and right lateral (d2) views. Stippled lines indicate reconstructed parts. Abbreviations: ex, exoccipital; fr, frontal; md, mandible; mx, maxilla; na, nasal; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa. Scale bar is equal to 20 cm.

fossa is small, and the posterior portion of the oral cavity is tube-shaped, having the long post-symphyseal portion of the mandible dorsally heightened and associated to a relatively short tooth row (Bianucci et al., 2020). This peculiar buccal apparatus supports the hypothesis that *E. riveroi* foraged via some kind of suction-assisted raptorial feeding which may have started with 1) stunning the prey with lateral oscillations of the rostrum, mainly

along the horizontal plane, like the extant swordfish *Xiphias gladius* Linnaeus, 1758; 2) grasping the prey while laterally sweeping through the water like the Indian gharial (*Gavialis gangeticus* Gmelin, 1758); or 3) flushing the prey out of soft sediment along the sea bottom as already proposed for the ziphiid *Ninoziphius platyrostris* Muizon, 1893 (Bianucci et al., 2020). Another peculiar character of the skull of *E. riveroi* relies in the right-side torsion of the rostrum (Fig. 18a1); this, however, could be due to an anomaly of the holotype and only known specimen, being also observed in some skulls of extant river dolphins.

A fragmentary skull (rostrum and associated mandibles) from Zamaca (exact locality and horizon unknow) exhibits affinities with the small-sized platanistid *Araeodelphis natator* from the Lower Miocene of Maryland (USA). Characters shared between the Zamaca skull and *A. natator* are, for instance, the narrow rostrum and very elongated, firmly ankylosed symphyseal portion of the mandibles, each of which bears a deep ventrolateral longitudinal groove and a similar number of teeth (Bianucci et al., 2020) (Fig. 18c1-2). Based on some analogies with the extant *Pontoporia blainvillei* Gervais & d'Orbigny, 1844 (including a narrow, elongated and dorsoventrally flattened rostrum), this odontocete could have fed on bottom-dwelling fish, squids and shrimps.

The four squalodelphinid species from the Chilcatay Formation exhibit the distinctive characters of this family, namely, a moderately elongated and tapered rostrum, single-rooted posterior teeth retaining ornamented crowns, and a markedly asymmetric skull.

In particular, *Furcacetus flexirostrum* (represented by a cranium from an unknow locality and horizon at Zamaca) further shows a moderately wide temporal fossa as well as a dorsoventrally flat and delicate sinusoidal rostrum that bears procumbent and large incisors (Fig. 19c1-2). All these characters could be related to bottom feeding, allowing *F. flexirostrum* to grasp with quick bites small and elusive prey such as shrimps and small fish (Bianucci et al., 2020). Interestingly, the peculiar combination of a sinusoidal rostrum with procumbent large premaxillary teeth is reminiscent of the rosette structure observed in the Indian gharial (*Gavialis gangeticus*), the West African slender-snouted crocodile (*Mecistops cataphractus* [Cuvier, 1825]), the pterosaur *Cearadactylus atrox* Leonardi & Borgomanero, 1985, some muraenosocid anguilliform fishes and the spinosaurid *Baryonyx walkeri* Charig & Milner, 1986 (Bianucci et al., 2020).

Notocetus vanbenedeni is recorded from the Chilcatay Formation thanks to taxonomically significant specimens from Ct1c and Ct1a strata exposed at Zamaca and Ulluyaja (Bianucci et al., 2015, 2020) (Fig. 19b1-1). Previously described on the basis of material from the Monte León Formation of Argentina, this squalodelphinid closely resembles *Furcacetus flexirostrum* in size. However, the more robust skull, more voluminous temporal fossa, lower tooth count and larger teeth concur in suggesting that *N. vanbenedeni* performed quick grasping actions to capture larger and tougher prey than those targeted by *F. flexirostrum*. *N. vanbenedeni* may have used its interlocking posterior teeth provided with low, triangular, carinated crowns to cut its prey into smaller pieces before swallowing, thus recalling the foraging style of the extant

Amazon River dolphin, *Inia geoffrensis* (Blainville, 1817) (Bianucci et al., 2020).

Huaridelphis raimondii is based on two well-preserved specimens from Ct1a strata exposed at Ullujaya as well as from fragmentary remains from an unknow locality and horizon at Zamaca (Lambert et al., 2014b) (Fig. 19d1-2). Given its smaller and more gracile skull, slender and more pointed rostrum, less voluminous temporal fossa, and smaller and more numerous teeth, *H. raimondii* may have fed on smaller prey compared to the other Chilcatay squalodelphinids (Bianucci et al., 2020).

Known from a partial skeleton (including the cranium) from the lower Chilcatay strata exposed south of Cerro Colorado, *Macrosqualodelphis ukupachai* is the largest squalodelphinid and platanistoid in the Chilcatay assemblage (estimated total body length around 3.5 m). Besides this large size, the robust rostrum, large teeth, voluminous temporal fossa, and well-developed temporal and nuchal crests (Fig. 19a1-2) concur in suggesting that *M. ukupachai* targeted larger prey than the other Chilcatay platanistoids (Bianucci et al., 2018a, 2020).

THE LONGIROSTRINE HOMODONT ODONTOCETES

During the Early and Middle Miocene, several independent lineages of homodont odontocetes developed a remarkably long and narrow rostrum bearing numerous small teeth. In addition to the above described *Ensidelphis riveroi*, other platanistoids (including all the members of Allodelphinidae and most of Platanistidae) exhibit the same characters, and the same is true for the extinct Eurhinodelphinidae, Eoplatanistidae and other similar long-snouted dolphins forming the so-called "*Chilcacetus* clade" (sensu Lambert et al., 2015b). These extinct odontocetes could be regarded as the ecological analogues of the extant river dolphins, from which they nonetheless differ by reaching even greater values of rostrum length and, with a few exceptions, by their marine habits. As reported for *Ensidelphis* and aff. *Araeodelphis*, the elongated rostrum may be related to the feeding behaviour, and especially to different strategies of prey capture at the seafloor or in the water column.

The presence of longirostrine homodont odontocetes is also well documented in the Lower Miocene layers of Chilcatay Formation. In addition to the aforementioned platanistoids, significant remains of Eurhinodelphinidae and an *Argyrocetus*-like dolphin have been described from the Chilcatay exposures at Ullujaya and Zamaca (Lambert et al., 2015b, 2021b; Bianucci et al., 2018b; Di Celma et al., 2019). In particular, two partial skulls display two peculiar characters of eurhinodelphinids: 1) an extensive anterior portion of the rostrum, formed solely by the premaxillae; and 2) the mandibles (preserved in one of the two specimens) being significantly shorter than the rostrum (Lambert et al., 2021b) (Fig. 20b1, b2).

It is worth underlining that a rostrum significantly longer than the mandibles is regarded as exclusive of eurhinodelphinids among cetaceans (Abel, 1901; Kellogg, 1925; but see also the description of *Rhaphicetus valenciae* above). It recalls the analogous long "swords" of the xiphiid and istiophorid billfishes, pristid sawfishes
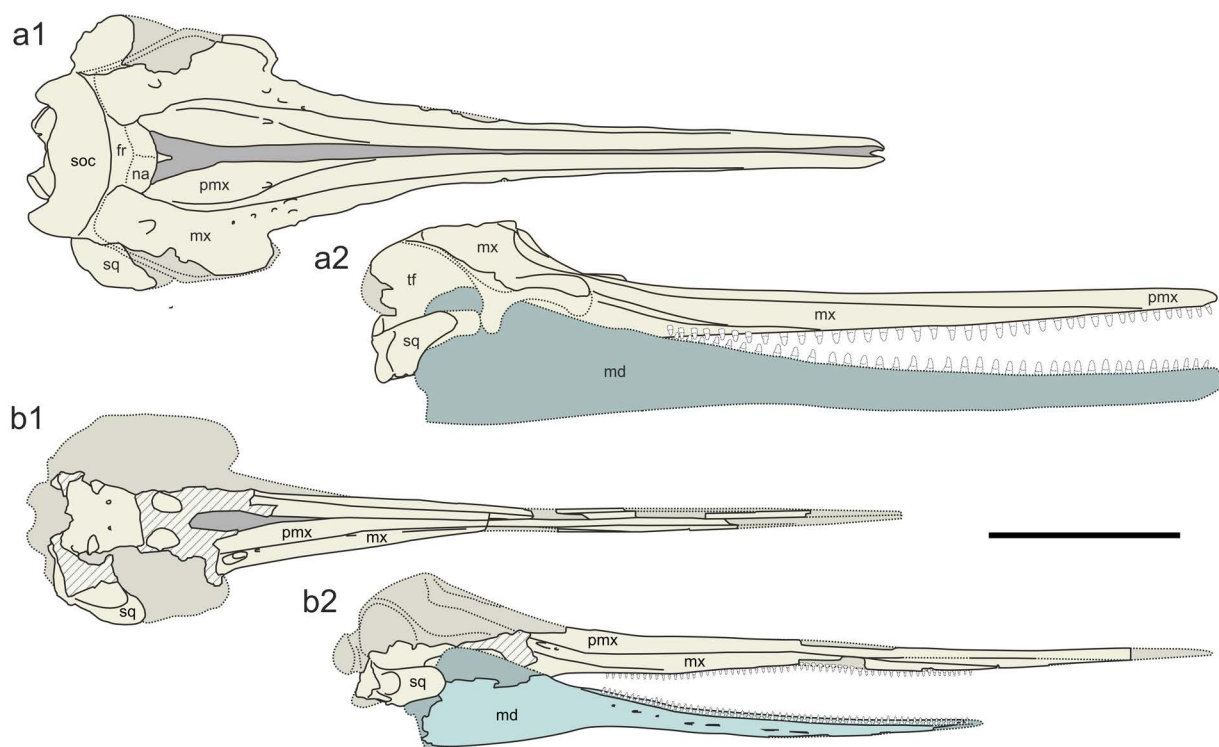
Fig. 20 - Longirostrine homodont odontocetes from the Chilcatay Formation. a) Skull of *Chilcacetus cavirhinus*, MUSM 1401, in dorsal (a1) and right lateral (a2) views; the reconstruction of the mandible is based on the MNHN.F.PRU11 (holotype) and on undescribed material. b) Skull of Eurhinodelphinidae indet., MUSM 632, in dorsal (b1) and right lateral (b2) views. Dashed areas indicate damaged surfaces; stippled lines indicate reconstructed parts. Abbreviations: fr, frontal; md, mandible; mx, maxilla; na, nasal; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa. Scale bar is equal to 20 cm.

and, among other extinct marine vertebrate groups, the leptonectid ichthyosaurs and ganopristid batoids. Due to the incompleteness of the eurhinodelphinid skulls from the Chilcatay Formation, a systematic assignment of these fossils is not possible below the family level, although some similarities with *Schizodelphis* and *Xiphiacetus* have been observed (Lambert et al., 2021b).

The discovery of eurhinodelphinid remains in Peru documents the first unambiguous evidence for the presence of this family in the whole Pacific Ocean as well as in the Southern Hemisphere. Indeed, before the discovery of the Peruvian skulls, and excluding dubious and erroneous records, the geographical range of the eurhinodelphinids was limited to the Northern Atlantic Ocean (including the North Sea) and Mediterranean Sea. The presence of eurhinodelphinids in the Lower Miocene of Peru can be explained by recalling again the open communications that occurred between the Atlantic and Pacific realms during the Early Miocene through the Central American Seaway.

Another longirostrine dolphin is known from the Chilcatay Formation on the basis of some diagnostic remains that comprise the holotype of *Chilcacetus cavirhinus* Lambert et al., 2015b (Bianucci et al., 2018b; Di Celma et al., 2019) (Fig. 20a1-2). This homodont odontocete shares several characters with some species of *Argyrocetus* and *Macrodelphinus*, two genera represented by Lower Miocene fossil remains from California (USA) and Argentina. These affinities are supported by a phylogenetic analysis that places these

two genera besides *Chilcacetus* within the aforementioned "*Chilcacetus* clade". The latter represents the earliest diverging branch of homodont odontocetes (Lambert et al., 2015b; Lambert et al., 2018a). Peculiar characters of *C. cavirhinus* rely in the observation of dental alveoli on the anterior premaxillary portion of the rostrum, the lack of a lateral groove along the rostral segment of the maxillary-premaxillary suture, the anterodorsally elevated nasals, the presence of a cavity between the nasals and presphenoid on the posterior wall of the bony nares, the high temporal fossa, and the non-ankylosed mandibular symphysis (Fig. 20a1-2).

ZIPHIIDAE, THE BEAKED WHALES

The extant members of the family Ziphiidae (beaked whales) are known as medium- to large-sized, open-ocean cetaceans that display remarkable adaptations for diving into deep waters, detecting the prey (predominantly squid) by using their sonar system, and finally capturing their food items by means of suction. Due to their elusive behaviour that largely prevents direct observations in natural habitats, little is known about beaked whales in spite of their being the second most diverse family of cetaceans after Delphinidae (ocean dolphins) (Mead, 2018; Yamada et al., 2019; Carroll et al., 2021). Distinctive cranial characters of the ziphiids include an elevated vertex that is anterolaterally bordered by well-distinct premaxillary crests, a wide and elongated
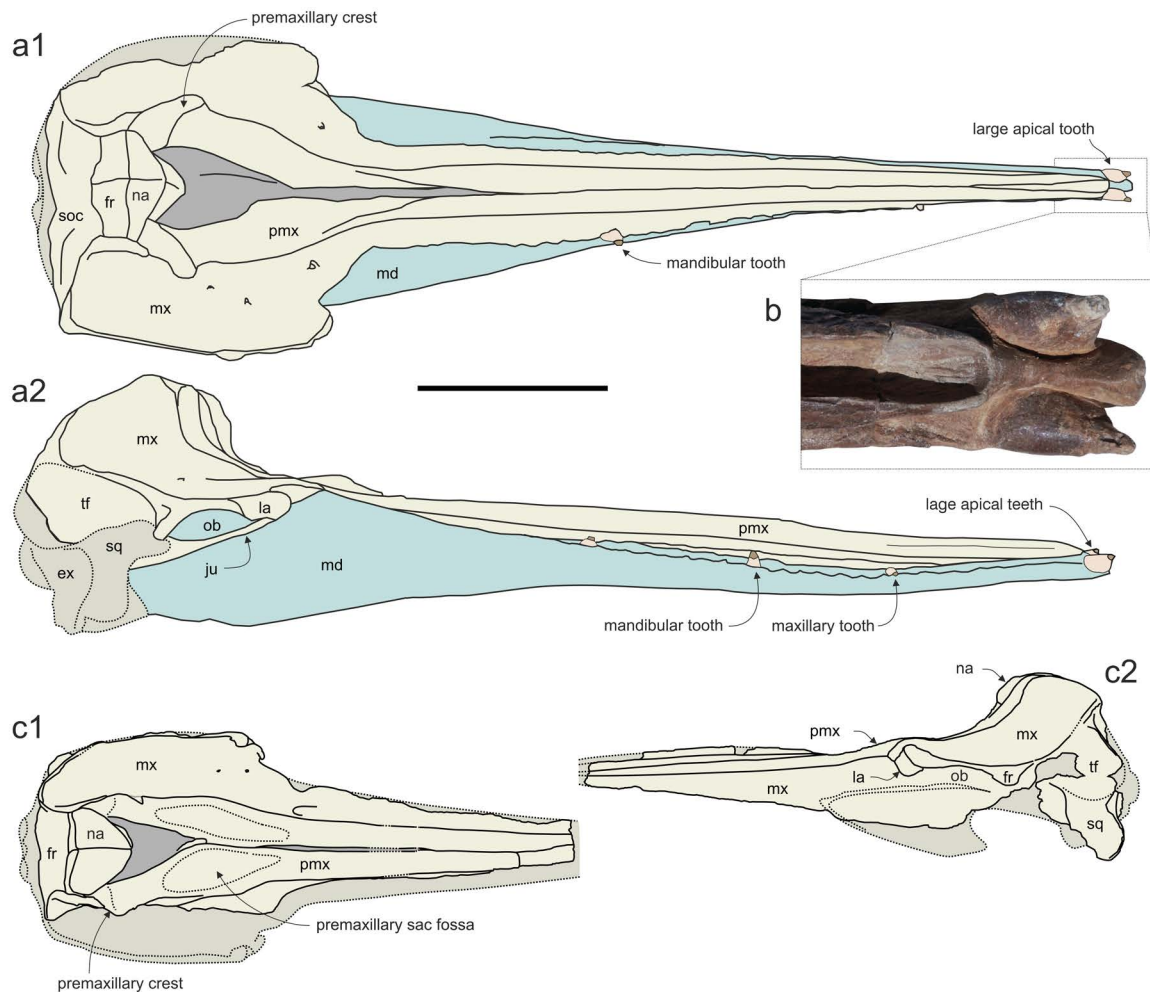
Fig. 21 - Ziphiids from the P1 beds of the Pisco Formation. a-b) Skull of *Messapicetus gregarius*, MUSM 1037 (holotype), in dorsal (a1) and right lateral (a2) views; b) close-up of the apex of rostrum and mandibles, and anterior tusks in dorsal view. c) Cranium of *Chimuziphius coloradensis*, MUSM 2548 (holotype), in dorsal (c1) and right lateral (c2) views. Stippled lines indicate reconstructed parts. Abbreviations: ex, exoccipital; fr, frontal; ju, jugal; la, lacrimal; md, mandible; mx, maxilla; na, nasal; ob, orbit; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa. Scale bar is equal to 10 cm.

hamular process of the pterygoid, and the presence, in male individuals, of one or two (sub)apical tusks on each mandible (Heyning, 1989; Bianucci et al., 2016d).

Scarce and fragmentary up to a few years ago, the fossil record of Ziphiidae greatly increased recently thanks to the unexpected discovery of high specimen concentrations in phosphorites cropping out at deep seafloors (Bianucci et al., 2007, 2008, 2013; Ichishima et al., 2017; Lambert et al., 2018a) as well as to significant finds from the Pisco Formation (Lambert et al., 2009, 2010, 2013, 2015a; Bianucci et al., 2010, 2016d; Ramassamy et al., 2018). Indeed, in the Pisco strata, the remains of ziphiids are among the most significant of the entire cetacean assemblage, being represented by four distinct genera and species: *Chavinziphius maxillocristatus* Bianucci et al., 2016d, *Chimuziphius coloradensis* Bianucci et al., 2016d, *Messapicetus gregarius* Bianucci et al., 2010 and *Nazcacetus urbinai* Lambert et al., 2009. Moreover, another fossil representative of the beaked whale clade, *Ninoziphius platirostris*, was described on the basis of an incomplete skeleton from the uppermost Miocene of the Sacao area (Muizon, 1993, 1994; Lambert et al., 2013).

Interestingly, the holotypes and all the referred materials of the five aforementioned species (Figs 21, 22a1-b2) and genera (except *Messapicetus*) come from Pisco or Pisco-equivalent deposits of southern Peru. Furthermore, more fragmentary remains indicate the presence of at least two additional genera of beaked whales in the Pisco Formation (Bianucci et al., 2016d) (Fig. 22c-f).

Messapicetus is a peculiar beaked whale, characterised by an extremely elongated and narrow rostrum strengthened by the dorsomedial fusion of the premaxillae (Figs 1a, 21a1-2). Its upper and lower jaws bear functional teeth in addition to the mandibular apical tusks (Fig. 21b). The genus *Messapicetus* was originally described from Upper Miocene layers of the Pietra leccese formation (southern Italy) with the type species *Messapicetus longirostris* Bianucci et al., 1992 (Bianucci et al., 1994, 2016a). The osteological characters separating the Peruvian and Italian species were recently outlined by Bianucci et al. (2016a). Thanks to both the high number and the good preservation state of the referred specimens, nowadays *Messapicetus* represents the best known fossil beaked whale genus. Indeed, while all other ziphiid species from the East

Pisco Basin are represented by a single specimen each, *Messapicetus gregarius* is known from 14 partial skeletons (mostly isolated skulls), 13 of which were found at Cerro Colorado and one south of Cerro La Bruja, in strata that invariantly belong to the P1 allomember (Bianucci et al., 2010, 2016c, 2016d; Lambert et al., 2015a; Bosio et al., 2021). Such a large sample of *M. gegarius* specimens from a restricted stratigraphical interval allowed for recognising
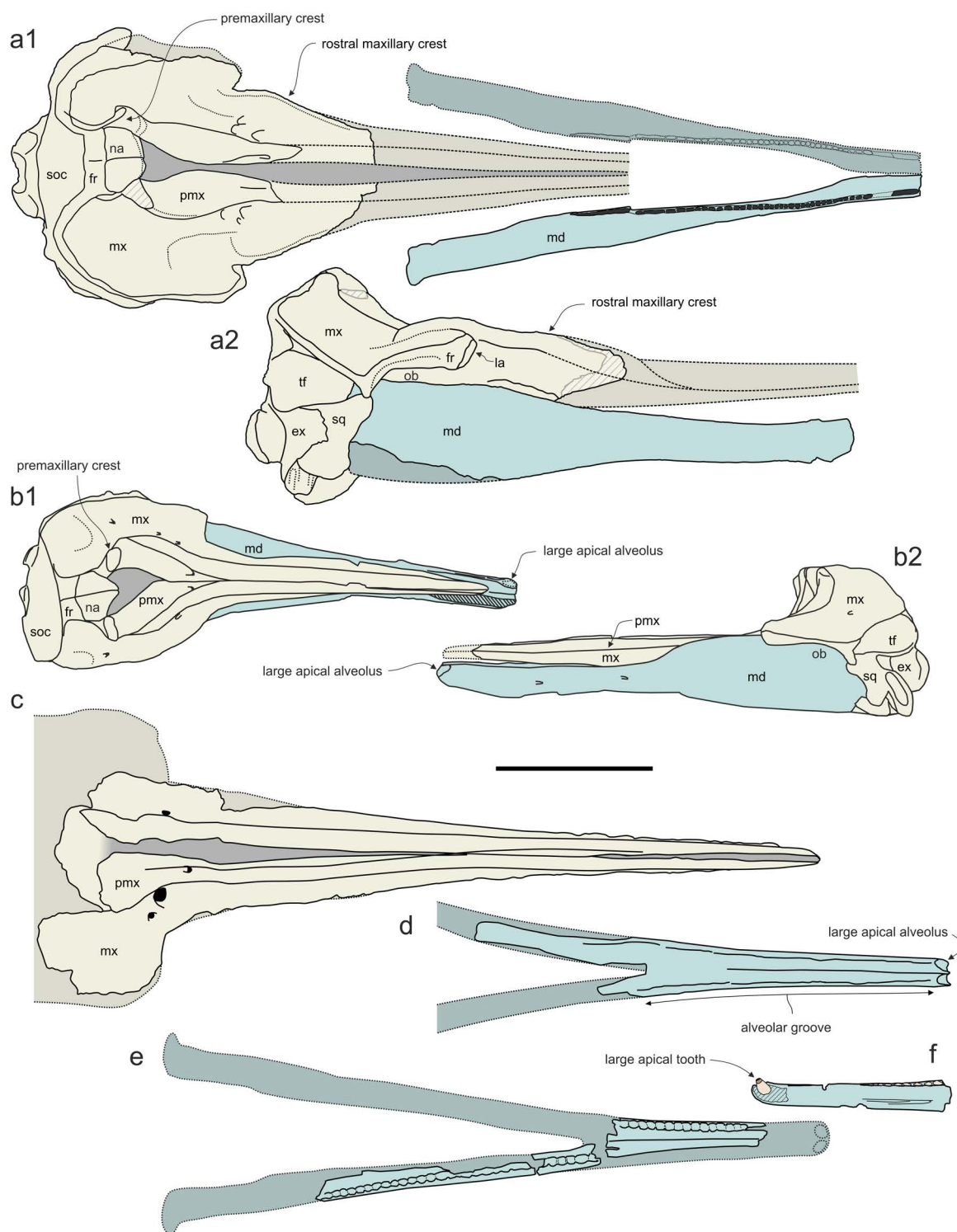

Fig. 22 - Stem ziphiids from the P2 beds of the Pisco Formation. a) Skull of *Chavinziphius maxillocristatus*, MUSM 2538 (holotype), in dorsal (a1) and right lateral (a2) views. b) Skull of *Nazcacetus urbinai*, MUSM 949 (holotype), in dorsal (b1) and left lateral (b2) views. c-d) Fragmentary skull of Ziphiidae gen. et sp. indet. 2 (sensu Bianucci et al., 2016b), MUSM 1609; c) cranium in dorsal view; d) mandibles in dorsal view. e-f) Fragmentary mandibles of Ziphiidae gen. et sp. indet. 1 (sensu Bianucci et al., 2016b); e) MUSM 3237, dorsal view; f) MUSM (uncatalogued), lateral view (with apical tusk in place). Dashed areas indicate damaged surfaces; stippled lines indicate reconstructed parts. Abbreviations: ex, exoccipital; fr, frontal; la, lacrimal; md, mandible; mx, maxilla; na, nasal; ob, orbit; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa. Scale bar is equal to 10 cm.

intraspecific variations that have been interpreted in terms of sexual dimorphism and ontogeny. In particular, skulls with larger mandibular apical tusks are referred to adult males that, similar to some extant ziphiids, may have used these teeth for intraspecific combat (Lambert et al., 2010). Moreover, one of the *M. gregarius* specimens from Cerro Colorado was found associated with numerous skeletons of a clupeiform fish (*Sardinops* cf. *sagax*) interpreted as representing the regurgitated stomach content of the beaked whale (Lambert et al., 2015a). On the whole, the Cerro Colorado assemblage of *M. gregarius* consists of adults (including both males and females) and one calf, and one skeleton even includes evidence of the cetacean's last meal, thus supporting the hypothesis of site fidelity: this extinct ziphiid species lived, bred and foraged in the Pisco embayment, and this situation likely lasted for a relatively long period (Bianucci et al., 2010; Collareta et al., 2021b).

Chimuziphius coloradensis (Fig. 21c1-2), another ziphiid from the P1 strata exposed at Cerro Colorado, displays some morphological affinities with *Messapicetus*, including e.g., the closure of the mesorostral canal due to the medial fusion of the premaxillae. This character represents a synapomorphy of the so-called *Messapicetus* clade, a group of stem ziphiids including both *Messapicetus* and *Chimuziphius* (Bianucci et al., 2016d).

The two other ziphiids of the East Pisco Basin, *Chavinziphius maxillocristatus* and *Nazcacetus urbinai*, come from geologically younger layers of the P2 allomember exposed at Cerro los Quesos. The former, regarded as the basalmost beaked whale, bears robust rostral maxillary crests, similar to those of the extant *Berardius*, and distinct alveoli on the mandible, suggesting the retention of functional lower teeth (Bianucci et al., 2016d) (Fig. 22a1-2). Nested within the crown ziphiids, *N. urbinai* is a small cetacean that exhibits a reduced upper and lower dentition and a small temporal fossa, possibly related to suction feeding (Lambert et al., 2009) (Fig. 22b1-2).

On the whole, the beaked whale assemblage from the East Pisco Basin (Figs 21, 22) supports the hypothesis that, in the past, ziphiids comprised the richest cetacean family in terms of numbers of species and genera. From a palaeobiogeographic point of view, by combining the Peruvian record with those from other palaeontological localities worldwide, ziphiids appear to have originated somewhere in a broad area including the southeastern Pacific and North Atlantic oceans as well as the Mediterranean Sea during the Middle Miocene, when the Central America Seaway was still open. This scenario is well supported by the geographical distribution of the finds of *Messapicetus*, which include Peru, Italy, North Carolina (USA) and Menorca (Spain) (Fuller & Godfrey, 2007; Bianucci et al., 2010, 2016d, 2019a). In particular, the Peruvian *Messapicetus gregarius* and the Italian *M. longirostris* are regarded as sister species with an antitropical distribution, similar to the extant genera (Bianucci et al., 2016a, c, 2019a). Moreover, both the phylogeny and the palaeoecological data support the hypothesis that the nutrient-rich coastal waters of Pacific South America represented an important area of radiation for the basal ziphiids. Indeed, the earliest diverging

stem ziphiids (*Chavinziphius* and *Ninoziphius*) and two early branches of the *Messapicetus* clade (*Chimuziphius* and *Messapicetus*) have been recorded from Peru, and, at least for *Messapicetus*, robust evidence indicates a coastal habitat (Lambert et al., 2015a; Collareta et al., 2021b). Finally, the phylogenetic analyses support a convergent evolution in the stem *Messapicetus* clade and crown ziphiids, both showing similar evolutionary trends involving body size as well as skull and dental characters, possibly testifying to a convergent ecological shift to deep diving and suction feeding habits (Bianucci et al., 2016d).

DELPHINIDA: A LONG JOURNEY TOWARD THE MODERN DOLPHINS

The infraorder Delphinida includes small- to medium-sized, roughly to fully homodont odontocetes sharing a reduced posterior extension of the premaxilla, a posteriorly elongated lateral lamina of the palatine and some peculiar ear bone characters (Muizon, 1988b; Marx et al., 2016b).

The fossil record shows that delphinidans originated in the late Oligocene, diversified moderately during the Early and Middle Miocene with several representatives of the paraphyletic Kentriodontidae, and significantly radiated starting from the Late Miocene, when the two modern branches originated: 1) Inioidea (including the Recent Lipotidae, Iniidae, and Pontoporiidae, whose living members are commonly grouped together with *Platanista* among the "river dolphins"); and 2) Delphinoidea (including the extant Delphinidae, Monodontidae and Phocoenidae, and the extinct Albireonidae and Odobenocetopsidae) (Marx et al., 2016b).

Delphinidan remains are known from both the Chilcatay and Pisco formations. A kentriodontid belonging to an as yet undescribed species of the genus *Kentriodon* is the most common cetacean in the Lower Miocene beds of the Chilcatay Formation exposed at Ullujaya and Zamaca (Bianucci et al., 2018a; Di Celma et al., 2019). This small-sized basal delphinidan shares some characters with *Kentriodon pernix* Kellogg, 1927, the type species of the genus, including a flat and wide vertex, a deep internasal fossa, a well-developed narial process of the frontal, and a knob-like posterior end of the premaxilla (Kellogg, 1927).

In the Middle Miocene P0 allomember of the Pisco Formation, delphinidans are known from Santa Rosa (with the fragmentary holotype skeleton of *Incacetus broggii* Colbert, 1944), as well as from Cerro Submarino and nearby localities (with collected but as yet undescribed remains) (Fig. 23a1-2). First attributed to the family Ziphiidae by Colbert (1944), *Incacetus broggi* was later revised and assigned to Delphinida by Muizon (1988a). The same author referred *I. broggi* to the kentriodontids due to the absence of evident characters of other delphinidan families rather than to the observation of diagnostic traits of Kentriodontidae. New material of *I. broggi* is therefore needed to better define the systematic position of the first cetacean taxon that has ever been described from the East Pisco Basin.

Belenodelphis peruanus Muizon, 1988a is a longirostrine kentriodontid sensu lato, known from a
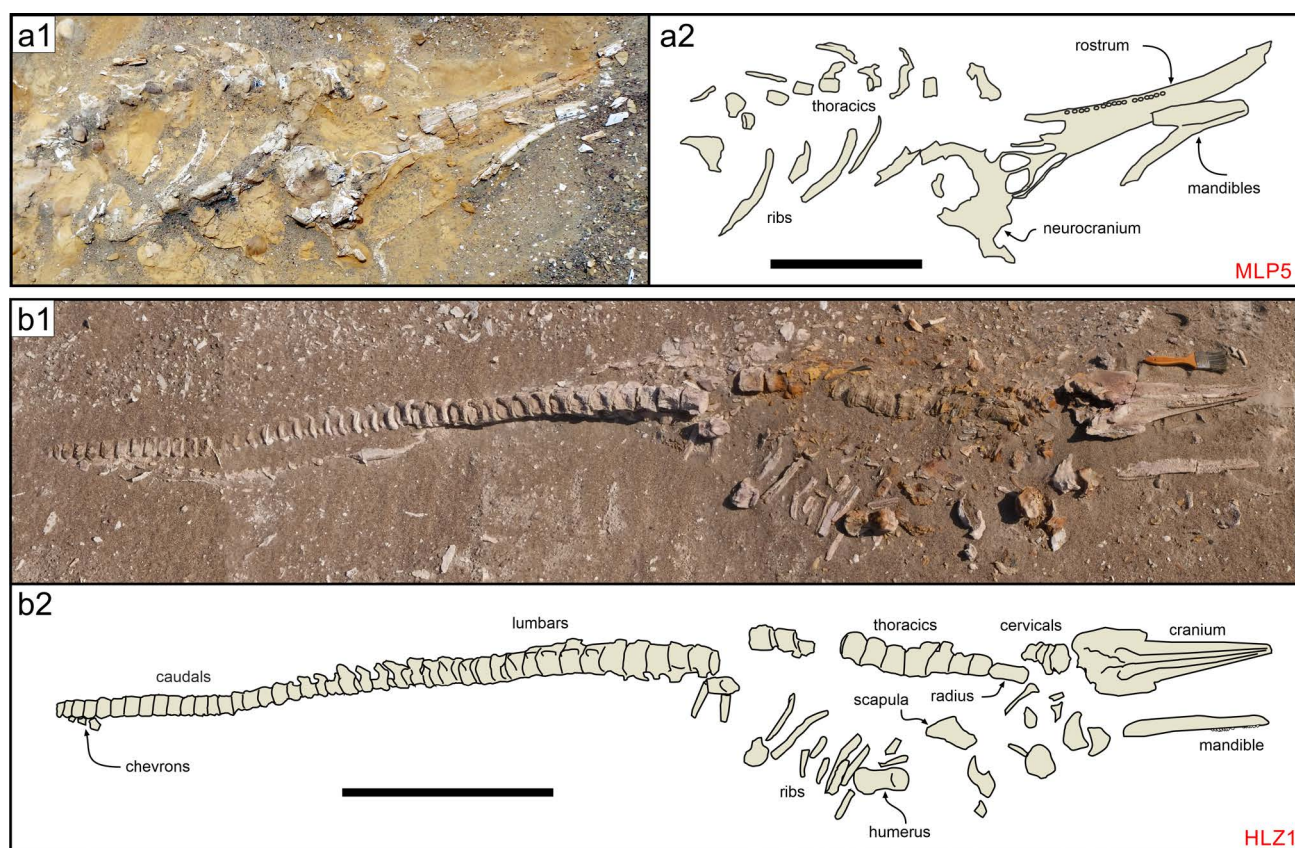
Fig. 23 - Delphinidans from the Pisco Formation. a) Skeleton of Delphinida indet. from the P0 beds: field photograph (a1) and corresponding schematic drawing (a2). b) Skeleton of Phocoenidae indet. from the P2 beds: field photograph (b1) and corresponding schematic drawing (b2). The field numbers are reported at the bottom right of panels a2 and b2. Scale bars are equal to 20 cm for panels a1, a2; 50 cm for panels b1, b2

fragmentary skull (Fig. 24b1-2) and associated postcrania from the so-called "CLB vertebrate level" (Muizon, 1988a), which in turn has recently been identified with the basal P2 strata exposed at Cerro la Bruja (Di Celma et al., 2017). That said, since this species is only known from the holotype specimen, whose exact stratigraphic position is unknown, its assignation to the lowermost strata of P2 allomember should be regarded as tentative. Indeed, although fossil vertebrates are rather common at the base of P2, we cannot exclude that *B. peruanus* was collected from the uppermost beds of P1 exposed at Cerro la Buja. It should also be noted that at least three undescribed kentriodontid-like delphinidan taxa are known from P1 strata exposed at Cerro Colorado and Cerros Cadenas de los Zanjones (Bianucci et al., 2016c; Bosio et al., 2021).

The stem delphinidan *Atocetus iquensis* Muizon, 1988a was described on the basis of a partial skeleton including the skull (Fig. 24a1-2) and referred material belonging to five additional specimens, all of which originated from the CLB vertebrate level. The provenance of this "kentriodontid" from the basal P2 strata is supported by an as yet undescribed, well-preserved partial skeleton found at Cerro la Bruja, in the P2 allomember, near to the contact with the uderlying P1 allomember. *Atocetus iquensis* is a small dolphin that, like other Kentriodontidae s.l. that were referred in the past to the subfamily Pithanodelphininae, displays large and inflated nasals bearing a longitudinal medial depression (i.e., an internasal fossa) that is followed posteriorly by a narrow exposure of the frontals (Muizon, 1988a, b; Marx et al., 2016b) (Fig. 24a1).

Inioids are present in the P1 and P2 allomembers with at least two pontoporiid and one inioid species. The former is currently represented by the sole franciscana, *Pontoporia blainvillei*, living along the eastern coast of South America (Brownell, 1989). Among the synapomorphies of the pontoporiids are the anteroposteriorly long nasals, the low skull vertex, the presence of premaxillary eminences and the lacrimal wrapping itself around the anterior edge of the frontal (Marx et al., 2016b). In the Pisco fossil record, pontoporiids are represented by two small dolphins: the brevirostrine *Brachydelphis mazeasi* Muizon, 1988a and the mesorostrine *Samaydelphis chacaltanae* Lambert et al., 2021a (Muizon, 1988a; Lambert & Muizon, 2013; Bianucci et al., 2016c; Bosio et al., 2021; Lambert et al., 2021a).

The holotype of *Brachydelphis mazeasi* (Fig. 25a1-2) was collected from the CLB vertebrate level (Muizon, 1988a), whereas other well-preserved specimens referred to this species and fragmentary remains assigned to *Brachydelphis* sp. are recorded from both P2 and P1 as well as at several localities (P2: Cerro los Quesos, Cerro Hueco la Zorra, Corre Viento, Cerro Toro Chico and Laguna Seca; P1: Cerro Colorado, Cerros Cadenas de los Zanjones and Cerro la Bruja) (Gutstein et al., 2009; Bianucci et al., 2016c; Gioncada et al., 2018; Bosio et.
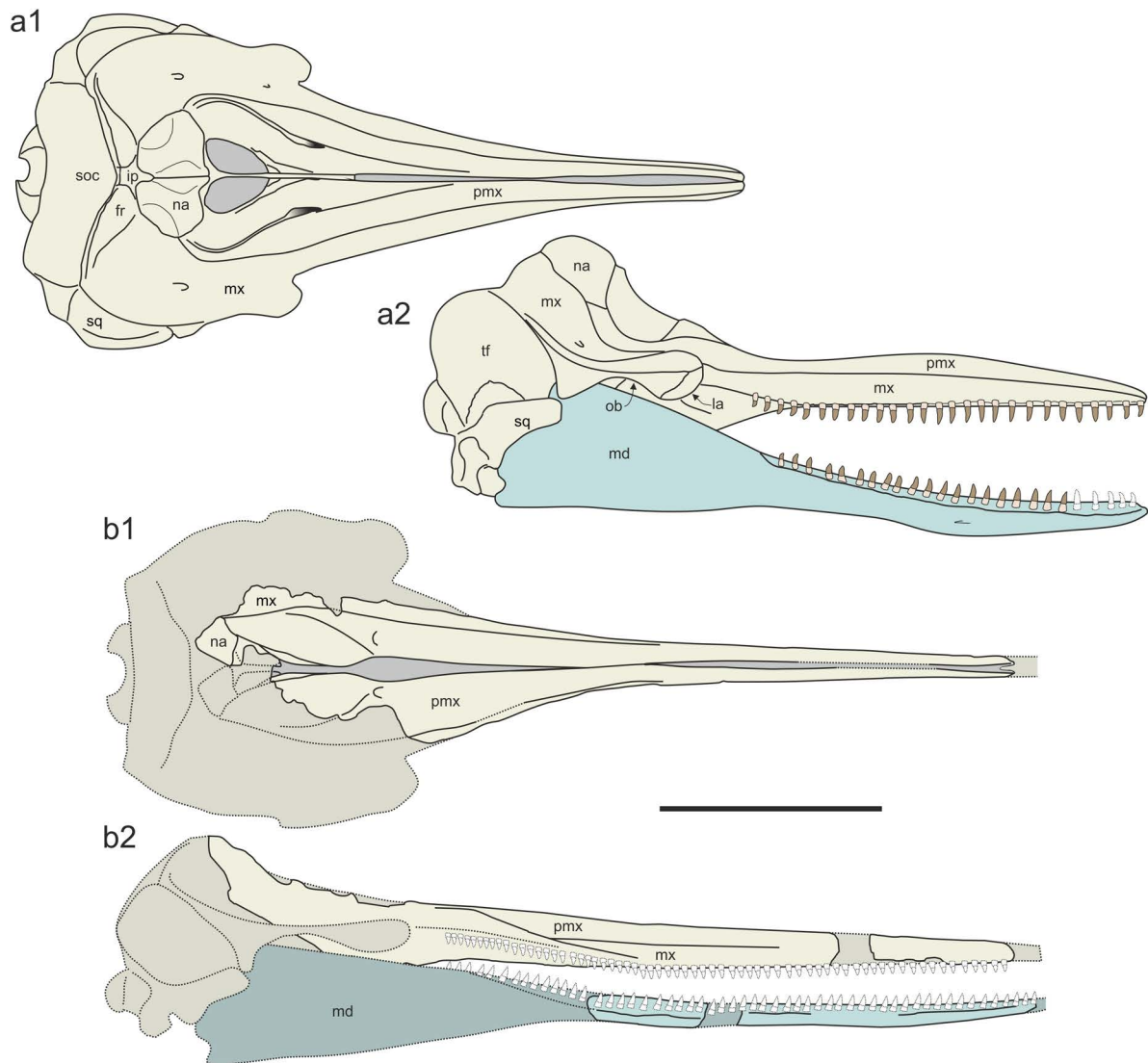
Fig. 24 - Stem delphinidans from the Pisco Formation. a) Skull of *Atocetus iquensis* (reconstruction based on the holotype MNHN PPI 113, modified after Muizon, 1988a: fig. 66) from the base of the P2 beds, in dorsal (a1) and right lateral (a2) views. b) Skull of *Belonodelphis peruvianus*, MNHN PPI 231 (holotype) tentatively referred to the base of the P2 beds, in dorsal (b1) and right lateral (b2) views. Stippled lines indicate reconstructed parts. Abbreviations: fr, frontal; md, mandible; mx, maxilla; na, nasal; ob, orbit; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa. Scale bar is equal to 10 cm.

al., 2021). Indeed, this pontoporiid species is the most common odontocete from the Pisco Formation along with the ziphiid *Messapicetus gregarius*.

Samaydelphis chacaltanae (Fig. 25b1-2) is known on the basis of six crania, five of which come from P1 strata exposed at three localities (Cerros Cadenas de los Zanjones, Cerro Colorado and south of Cerro la Bruja) and one from an unknown horizon exposed at Corre Viento (Lambert et al., 2021a).

The family Iniidae is at present comprised of the pink river dolphins, one or more species of *Inia* inhabiting the Amazon-Orinoco and Araguaia-Tocatins river systems (Best & Silva, 1989). The Pisco Formation has yielded a single, medium-sized longirostrine skull collected from P1 strata exposed south of Cerro la Bruja and described under

the name *Brujadelphis ankylorostris* Lambert et al., 2017b (Fig. 25c1, c2). *Brujadelphis ankylorostris* differs from *Inia* by its larger, inflated nasals and the partial ankylosis of the premaxillae along rostrum (Lambert et al., 2017b).

Interestingly, based on their stratigraphical distribution, the three aforementioned inioid species appear to have shared the same habitat during the deposition of the P1 strata. Differences in some morphological traits suggest trophic partitioning between these coeval, sympatric species. In particular, the shorter rostrum and smaller tooth count suggest that suction was more important in feeding for *Brachydelphis mazeasi* than for *Brujadelphis ankylorostris* and *Samaydelphis chacaltanae* (Lambert & Muizon, 2013). By contrast, the longer and more robust rostrum of *B. ankylorostris*, as well as its larger teeth,

suggest that this dolphin foraged on larger prey, likely by means of a raptorial feeding strategy (Lambert et al., 2017, 2021a).

The P2 strata also record the appearance of the superfamily Delphinoidea in the East Pisco Basin thanks to several undescribed specimens that are unequivocally
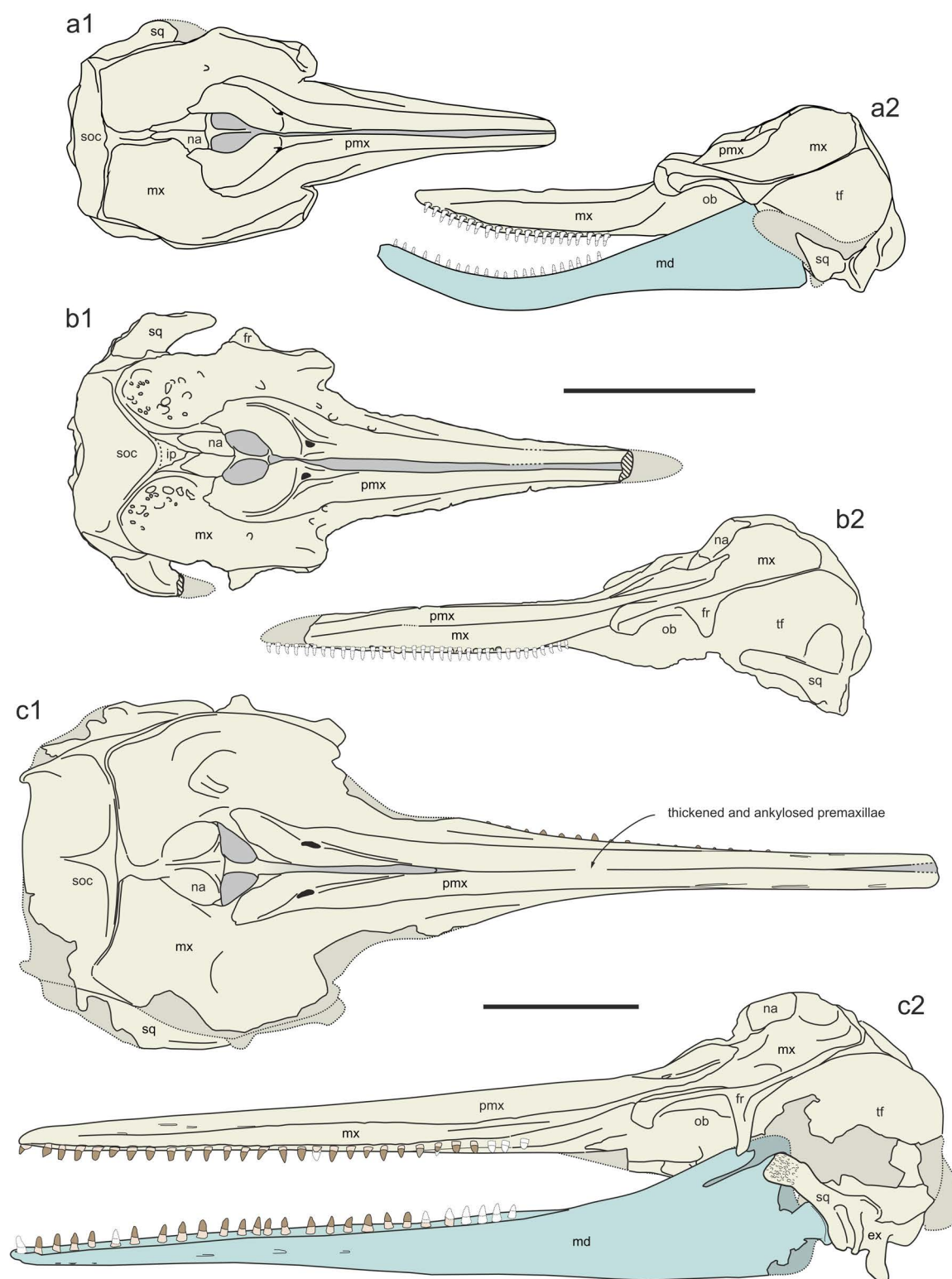

Fig. 25 - Inioids from the Pisco Formation. a) Skull of *Brachydelphis mazeasi*, MUSM 887 from the P2 beds, in dorsal (a1) and left lateral (a2) views. b) Cranium of *Samaydelphis chacaltanae*, MUSM 566 (holotype) from the P1 beds, in dorsal (b1) and left lateral views (b2). c) Skull of *Brujadelphis ankylorostris*, MUSM 1400 (holotype) from the P1 beds, in dorsal (c1) and left lateral (c2) views. Abbreviations: ex, exoccipital; fr, frontal; ip, interparietal; md, mandible; mx, maxilla; na, nasal; ob, orbit; pmx, premaxilla; soc, supraoccipital; sq, squamosal; tf, temporal fossa. Scale bars are equal to 10 cm.

referable to the family Phocoenidae (porpoises) in light of the observation of some synapomorphies of this family (including e.g., high premaxillary eminences anterior to the external nares and spatulate teeth). Significant phocoenid remains have been recorded from Cerro los Quesos East, Cerro Hueco la Zorra and Laguna Seca (Bianucci et al., 2016b; Bosio et al., 2021; Collareta et al., 2021b). In particular, three partial skeletons including crania of a porpoise similar to *Lomacetus ginsburgi* Muizon, 1986 are known from the eastern part of Cerro los Quesos (Bianucci et al., 2016b), whereas two almost complete and articulated skeletons possibly belonging to an undescribed basal phocoenid occur at Cerro Hueco la Zorra (Fig. 23b1, b2).

CONCLUSIONS

Fifteen years of scientific research have considerably increased our knowledge of the cetacean assemblages of the East Pisco Basin, one of the most important palaeontological sites in the world, preserving a plethora of extraordinarily preserved marine vertebrate fossils of Cenozoic age. Our studies have led to the discovery of several hundreds of fossil skeletons, the most significant of which have been collected, prepared and partly studied. In the meantime, interdisciplinary studies have been carried out for 1) placing all the vertebrate finds within an accurate chronostratigraphic framework; 2) reconstructing the taphonomic processes that led to the conservation of these fossils; and 3) elaborating comprehensive palaeoenvironmental and palaeoecological reconstructions. In particular, the systematic description of several new taxa, coupled with the elaboration of a new stratigraphic model of the East Pisco Basin, provided us with an enormous amount of information that have been used herein to detail more than 40 million years of evolutionary history of cetaceans, in Peru as well as on a global scale. The most salient chapters of this history can be summarised as follows.

During the middle Eocene, a quadrupedal cetacean crossed the Central American Seaway and, swimming for the first time in the Pacific Ocean, arrived in Peru ∼42.6 Ma. This story is witnessed by the discovery of an archaeocete skeleton, the holotype of *Peregocetus pacificus*, in the Yumaque strata of the Paracas Formation. This well-preserved specimen suggests that *P. pacificus*, an amphibious whale, was likely provided with a paddle-shaped tail that was used in combination with the hindlimbs for swimming.

The presence of archaeocetes in the Eocene Pisco Basin is also documented by numerous remains of basilosaurids, fully marine cetaceans retaining vestigial hindlimbs. The most significant basilosaurid skeleton from the Pisco Basin is represented by the holotype of *Cynthiacetus peruvianus* from upper Eocene (Priabonian) deposits of the Otuma Formation. This was characterised by a dolphin-like body reaching nine meters in total length. Equipped with large, triangular and multicusped postcanine teeth, *C. peruvianus* was an impressive apex predator in the middle Eocene seas.

The Priabonian strata of the East Pisco Basin also yielded the geologically oldest mysticete specimen ever found. This remarkable fossil takes its place in Yumaque strata dated to ∼36.4 Ma and comprises the holotype of *Mystacodon selenensis*. This baleen whale ancestor retained some plesiomorphic characters such as a full set of teeth and vestigial hindlimbs. *Mystacodon selenensis* was a medium-sized cetacean that probably fed near the seafloor by means of suction.

The chaeomysticetes (baleen-bearing whales) make their first appearance in the East Pisco Basin deposits in strata of the Chilcatay Formation (19-18 Ma). Here, however, chaeomysticetes are very uncommon, as generally observed in other Miocene assemblages worldwide. Baleen whales become the most common vertebrate fossils in the Pisco Formation, starting from the Middle Miocene P0 allomember (14.8-12.4 Ma), where they represent the greatest majority of the entire cetacean assemblage. P0 is home to one of the oldest cetotheriids, *Tiucetus rosae*, as well as to a large, as yet undescribed *Pelocetus*-like balaenopteroid that documents an early origin for the signature gigantism of modern baleen-bearing whales. Another undescribed cetotheriid is very frequent in the P1 strata (9.5-8.5 Ma). This species is similar to but larger than *Piscobalaena nana*, another cetotheriid that occurs in P2 strata (8.4-6.7 Ma). Balaenopteroids from P1 include a specimen featuring exquisitely preserved baleen structures. In P2, balaenopterids are dominant, being represented by various undescribed taxa with different body shapes and sizes.

The odontocetes (echolocating toothed whales) do also first appear in the East Pisco Basin fossil record in the Chilcatay strata. The almost complete skeleton described under the name of *Inticetus vertizi* comes from these deposits. This peculiar heterodont cetacean, referred to its own family (Inticetidae), is mainly distinguished from other toothed whales by its posterior postcanine teeth having semicircular crowns equipped with numerous accessory denticles. In light of this and other characters, *I. vertizi* may have been a suction feeder.

The physeteroids (sperm whales) are well-documented from both the Chilcatay and Pisco formations. The most representative sperm whale from the Chilcatay strata is *Rhaphicetus valenciae*, which features a peculiar, elongated, cylindrical rostrum that bears numerous pointed teeth (except for its edentulous anterior portion). Based on the rostrum shape and other skull characters, *R. valenciae* fed by grasping small prey, possibly via rapid movements of the head. The Pisco Formation preserves several impressive fossils of macroraptorial sperm whales, e.g. the medium-sized *Acrophyseter* spp. from both P1 and P2 strata and the titanic physeteroid *Livyatan melvillei* from the P1 beds. By displaying a three-m-long skull as well as teeth reaching 36 cm in length, the latter is one of the largest macroraptorial predators and, possibly, the biggest tetrapod bite ever found. The P2 beds have yielded some of the earliest representatives of the extant family Kogiidae in the form of two scaphokogiines, namely, *Platyscaphokogia landinii* and *Scaphokogia cochlearis*. The former displays a triangular rostrum bearing fully developed dental alveoli, whereas the latter is characterised by a pachyostotic, downwards-deflected, semicylindrical rostrum that likely hosted no functional teeth. These major cranial differences suggest different feeding strategies, i.e., raptorial feeding in the water

column for *P. landinii*, versus suction near the sea bottom for *S. cochlearis.*

The cetacean assemblage from the Chilcatay Formation further highlights the high disparity and diversity of platanistoids during the Early Miocene, an observation that starkly contrasts with the present-day situation, which sees the Asian river dolphins (*Platanista* spp.) as the sole extant members of Platanistoidea. Indeed, the Chilcatay beds have so far yielded specimens referred to the basal Platanidelphidi *Ensidelphis riveroi*, five squalodelphinids (*Furcacetus flexirostrum*, *Huaridelphis raimondii*, *Macrosqualodelphis ukupachai* and *Notocetus vanbenedeni*), a platanistid close to *Araeodelphis natator* and an unnamed platanistoid. The wide variation of skull morphologies (e.g., rostra index ranging from 0.81 in *Ensidelphis* to 0.62 in *Notocetus*) and body sizes (estimated body length spanning between ~2 m in *Huaridelphis* to 3.5 m in *Macrosqualodelphis*) suggests a high degree of trophic partitioning among these significant components of the Early Miocene cetacean palaeocommunitity of the East Pisco Basin.

In addition to the platanistoids *Ensidelphis* and aff. *Araeodelphis*, other homodont longirostrine odontocetes come from the Chilcatay Formation, namely, an indeterminate eurhinodelphinid and *Chilcacetus cavirhinus*. The eurhinodelphinids are bizarre hyper-longirostrine cetaceans having the rostrum longer than the mandibles, and their record from the East Pisco Basin represents the only unambiguous evidence of the presence of this family in the whole Pacific Ocean and Southern Hemisphere. The elongated rostrum shared by *Ensidelphis*, *Chilcacetus* and the eurhinodelphinids could be related to the feeding behaviours of these odontocetes, which used different strategies for capturing prey at the seafloor or in the water column.

The beaked whales (family Ziphiidae) first appear in the East Pisco Basin fossil record in the P1 allomember of the Pisco Formation. In these strata, skeletons of the stem ziphiid *Messapicetus longirostris* are the most common odontocete remains. The wide sample of fossils of this longirostrine beaked whale provides information on ontogenetic and sexual variations within this species, and allows to hypothesise a diet based on epipelagic fish. The most representative ziphiids from the P2 allomember are the stem beaked whale *Chavinziphius maxillocristatus* and the crown beaked whale *Nazcacetus urbinai*, the former being characterised by robust rostral maxillary crests and the latter by several skull characters that are possibly related to suction feeding.

The East Pisco Basin fill has also yielded remarkable fossils that shed light on some significant steps of the long evolutionary history of Delphinida. The small-sized dolphin *Kentriodon* is common in the Chilcatay strata, whereas the Pisco beds are home to other stem delphinidans (Kentriodontidae s.l.) as well as to several crown delphinidans (Inioidea and Delphinoidea). The partly described kentriodontid-like specimens include the fragmentary skeleton of *Incacetus broggii* from the P0 allomember, the longirostrine *Belenodelphis peruanus* from the base of P2 (or top of P1), and the small-sized dolphin *Atocetus iquensis* from the base of P2. The Late Miocene radiation of the inioids is well documented, with finely preserved remains from both the P1 and P2 strata.

In particular, Pontoporiidae include two small dolphins, the brevirostrine *Brachydelphis mazeasi* (P1 and P2) and the mesorostrine form *Samaydelphis chacaltanae* (P1), whereas Iniidae are represented by the medium-sized longirostrine form *Brujadelphis ankylorostris* (P1). Differences in some morphological traits suggest trophic partitioning of these coeval, sympatric inioid species during the deposition of the P1 strata. The appearance of Delphinoidea in the Pisco Basin is witnessed in P2 by several undescribed skeletons of Phocoenidae, including some *Lomacetus ginsburgi*-like crania.

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