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NASAL COMPARTMENTALIZATION IN KOGIIDAE (CETACEA, PHYSETEROIDEA): INSIGHTS FROM A NEW LATE MIOCENE DWARF SPERM WHALE FROM THE PISCO FORMATION

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Abstract: Facial compartmentalization in the skull of extant pygmy whales (Kogiidae) is a unique feature among cetaceans that allows for the housing of a wide array of organs responsible for echolocation. Recent fossil findings indicate a remarkable disparity of the facial bone organization in Miocene kogiids, but the significance of such a rearrangement for the evolution of the clade has been barely explored. Here we describe *Kogia danomurai* sp. nov., a late Miocene (c. 5.8 Ma) taxon from the Pisco Formation (Peru), based on a partially preserved skull with a new facial bone pattern. Phylogenetic analysis recovers *K. danomurai* as the most basal representative of the extant genus *Kogia*, displaying a combination of derived (incipiently developed and excavated sagittal facial crest) and plesiomorphic features (high position of the temporal fossa, and antorbital notch not transformed into a narrow slit). Furthermore, when

compared with the extant *Kogia*, the facial patterning found in *K. danomurai* indicates differential development among the facial organs, implying different capabilities of sound production relative to extant *Kogia* spp. Different facial bone patterns are particularly notable within the multi-species kogiid assemblage of the Pisco Formation, which suggests causal connections between different patterns and feeding ecologies (e.g. nekton piscivory and benthic foraging). At c. 5.8 Ma, *K. danomurai* was part of a cetacean community composed of clades typical of the late Miocene, and of other early representatives of extant taxa, a mixture probably representing an initial shift of the coastal faunas toward the ecosystem dynamics of the present-day south-eastern Pacific.

Key words: Messinian, marine mammals, Kogiinae, Pisco Formation, Peru, south-eastern Pacific.

PYGMY (*Kogia sima* (Owen, 1866)) and dwarf (*K. breviceps* (Blainville, 1838)) sperm whales (Physeteroidea, Kogiidae) are a group of highly elusive cetaceans that inhabit tropical and temperate ocean regions across the globe, mostly foraging for squids using suction feeding (Bloodworth & Odell 2008). These animals are relatives of the great sperm whale, the physeterid *Physeter macrocephalus* Linnaeus, 1758, from which they differ by the smaller body size and presence of highly derived facial

organs (Thornton *et al.* 2015; Velez-Juarbe *et al.* 2015). Both *Kogia* and *Physeter* and their fossil relatives display a high degree of cranial asymmetry (Coombs *et al.* 2020), with a dorsal excavation known as the supracranial basin, which houses their hypertrophied nasal organs. However, kogiids exhibit a sagittal facial crest that medially splits the supracranial basin into two, thus producing several regions for the attachment of the facial muscles, nasal complex organs, and other soft-tissue structures (Clarke

2003; Thornton *et al.* 2015). These organs and soft-tissue structures are homologous to regions present in the melon of other odontocetes (Norris & Harvey 1972); nevertheless, in *Kogia*, these are independent structures that both fulfil a specific function and occupy a specific region of the forehead. Such a patterning of the facial organs is herein referred to as compartmentalization.

Molecular estimates suggest that kogiids diverged from the rest of the physeteroids during the late Oligocene (McGowen *et al.* 2009, 2019; Geisler *et al.* 2011); however, the large majority of fossil kogiids come from late Miocene – early Pliocene deposits across the world, and as such, they highlight an outstanding diversification during this time span (Collareta *et al.* 2019, 2020). The Pisco Formation exposed in the coastal desert of southern Peru (13°–16°S) has been recognized as a major diversification hotspot of sperm whales. In fact, four species of extinct kogiids have been described so far from the Pisco strata, namely: *Scaphokogia cochlearis* Muizon, 1988; *Koristocetus pescei* Collareta *et al.*, 2017; *Scaphokogia totajpe* Benites-Palomino *et al.*, 2020a; and *Platyscaphokogia landinii* Collareta *et al.*, 2020. Such a broad taxonomic diversity during the late Miocene and Pliocene was not restricted to kogiids, but also applies to other physeteroids (Lambert *et al.*, 2016). ‘Macroraptorial’ sperm whales also attained a great diversity, as highlighted by the presence of three different species of the genus *Acrophyseter*, plus the large *Livyatan melvillei* Lambert *et al.*, 2010 (Lambert *et al.* 2008, 2010, 2016). Here, we describe a new kogiid taxon from upper Miocene strata of the Pisco Formation exposed at the Sacaco locality and perform a comprehensive analysis of the heterogeneous patterns of variation of the craniofacial region in kogiids.

GEOLOGICAL SETTING

The Pisco Formation is a Neogene marine sedimentary unit, cropping out along the southern coast of Peru, which is known as one of the most remarkable Cenozoic marine fossil Lagerstätten worldwide due to the abundance, diversity, and excellent state of preservation of the fossil vertebrates therein contained (Esperante *et al.* 2008; Lambert *et al.* 2015; Gioncada *et al.* 2016). The Pisco Formation consists of conglomerates, sandstones, diatomaceous siltstones, tephra layers, and nodular dolomitic beds that represent a shallow-marine environment characterized by high ocean primary productivity and strong upwelling conditions (Dunbar *et al.* 1990; DeVries 1998; Di Celma *et al.* 2017, 2018). The southernmost deposits of the Pisco Formation occur in the Sacaco area (15°–16°S; Fig. 1) of the Sacaco basin, where five fossil vertebrate-bearing localities have been recognized since the 1980s, namely El

Jahuay, Aguada de Lomas, Montemar, Sud Sacaco (west), and the eponymous Sacaco (Muizon 1984; Muizon & DeVries 1985; Ehret *et al.* 2012).

The holotype of *K. danomurai* sp. nov. described herein was found and collected in 2019 at the Sacaco locality from strata referred to the ‘Sacaco vertebrate level’ (= SAO) of Muizon (1984) and Muizon & DeVries (1985) (Figs 1, 2). The rock record from this locality consists of metre-scale packages of massive to parallel-laminated yellowish sandstones (Fig. 2). These sandstones are mostly fine to medium grained, poorly cemented, and display variable contents of silt and shell fragments. Sandstone packages alternate with shell banks of various thicknesses that mainly contain remains of *Dosinia* sp. and *Anadara* sp. (DeVries & Frassinetti 2003). Three distinct volcanic ash layers, from which radiometric dates have been obtained (Muizon & Bellon 1980; DO unpub. data), also occur at the base of this succession. The depositional environment of the SAO strata has been interpreted as a shallow sea adjacent to a rugged coastline that formed protected bays, peninsulas, archipelagos, and lagoons (Marocco & Muizon 1988).

The age of the SAO deposits has been a subject of debate over the last decades. Muizon & Bellon (1980) proposed an age of 3.9 ± 0.2 Ma based on the K–Ar radiometric dating of one volcanic ash layer. Later, Ehret *et al.* (2012) evaluated the age of the SAO beds at 5.89 Ma based on strontium isotope stratigraphy using mollusc shells. The latter age estimate is, however, in agreement with an unpublished result (5.75 ± 0.05 Ma) obtained from an Ar–Ar radiometric dating of biotite crystals from a nearby tephra horizon (see details in Ehret *et al.* 2012). As consequence of this, there was no consensus on whether the SAO beds were latest Miocene (5.7–5.8 Ma) or Pliocene (3.9 ± 0.2 Ma) in age. However, a recent reassessment of the age through U–Pb radiometric dating of two volcanic ashes, including the ash layer analysed by Muizon & Bellon (1980), yielded reliable and consistent latest Miocene ages (5.74 ± 0.056 and 5.848 ± 0.031 Ma; Fig. 2; DO unpub. data), similar to the one proposed by Ehret *et al.* (2012). We thus regard the geological age of the SAO deposits as latest Miocene (i.e. late Messinian; 5.8–5.7 Ma).

MATERIAL AND METHOD

Specimens analysed for comparison

In addition to MUSM 3888, we have directly examined for comparison the following fossil and extant Physeteroidea: *Acrophyseter deinodon* Lambert *et al.*, 2008 (MNHN SAS 1626); *Acrophyseter robustus* Lambert *et al.*,

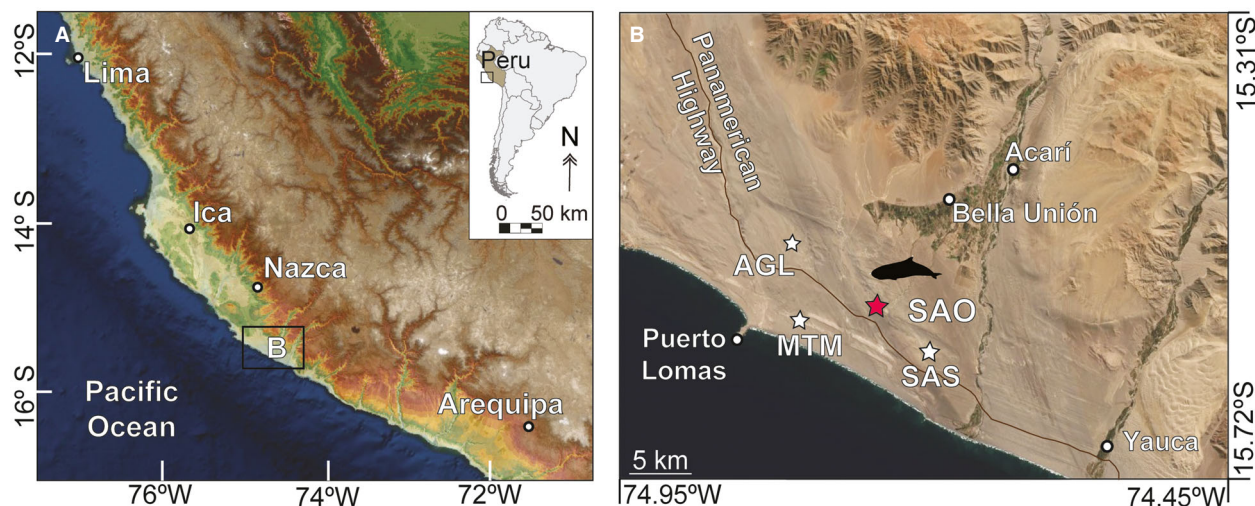


FIG. 1. A, relief map of the southern coast of Peru, showing the location of the Sacaco area (rectangle). B, close-up of the Sacaco area, showing the location of the type locality (SAO, red star) of *Kogia danomurai* sp. nov., along with other vertebrate-bearing localities. Abbreviations: AGL, Aguada de Lomas; MTM, Montemar; SAO, Sacaco; SAS, South Sacaco. Map source: 30 arc-second digital elevation model of South America (Data Basin Dataset), US Geological Survey's Center for Earth Resources Observation and Science (EROS).

2016 (MUSM 13399); *Acrophyseter* sp. (MUSM 2182); *Aprixokogia kelloggi* Whitmore & Kaltenbach, 2008 (USNM 187015); *Aulophyseter morricei* Kellogg, 1927 (USNM 11230, LACM 50626, LACM 154100); *Diaphorocetus poucheti* (Moreno, 1892) (MLP 5-6); *Kogia breviceps* (LACM 27082, LACM 95745, UF 13562, UF 14213, UF 14214, UF 15732, UF 18702, UF 18704, UF 19128, UF 25545, USNM 504902, USNM 504921); *Kogia pusilla* (Pilleri, 1987) (IGF 1540V); *Kogia sima* (LACM 47142, LACM 95817; MSNC 3450; MUSNAF Mam410; UF 18705, UF 18706, UF 24629, UF 25573, UF 25575-25578); *Koristocetus pescei* (MUSM 888); *Livyatan melvillei* (MUSM 1676); *Nanokogia isthmia* Velez-Juarbe *et al.*, 2015 (UF 273554, UF 280000); *Platyscaphokogia landinii* (MUSM 3291, 3405); *Praekogia cedrosensis* Barnes, 1973 (UCMP 315299); *Pliokogia appeninica* Collareta *et al.*, 2019 (MSNUP I-17603); *Physeter macrocephalus* (MSNUP I-266); *Scaphokogia cochlearis* (MHN PPI 229, MUSM 978, MUSM 1998); *Scaphokogia totajpe* (MUSM 973); *Scaphokogia* sp. (MUSM 972); *Thalassocetus antwerpiensis* (IRSNB M.525).

Anatomical terminology

The morphological description of the holotype skull was based on Mead & Fordyce (2009), with modifications to the facial region of Kogiidae (soft-tissue organs and other cranial features) by Thornton *et al.* (2015) and Velez-Juarbe *et al.* (2015). Muscular and other soft tissues nomenclature follow Schulte & Forest Smith (1918).

Institutional abbreviations. IGF, Istituto di Geologia di Firenze (= Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università degli Studi di Firenze), Italy; IRSNB, Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium; LACM, Departments of Vertebrate Paleontology and Mammalogy, Natural History Museum of Los Angeles County, Los Angeles, California, USA; MLP, Museo de La Plata, Buenos Aires, Argentina; MNHN, Muséum national d'Histoire naturelle, Paris, France; MSNC, Museo Civico di Storia Naturale, Comiso, Italy; MSNUP, Museo di Storia Naturale dell'Università di Pisa, Italy; MUSM, Departamento de Paleontología de Vertebrados, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru; MUSNAF, Museo di Storia Naturale dell'Accademia dei Fisiocritici, Sienna, Italy; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; UF, Mammalogy Collection, Florida Museum of Natural History, Gainesville, Florida, USA; USNM, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

Additional abbreviation. char., character state; as described and numbered by Lambert *et al.* (2016), with modifications from prior and subsequent works (Boersma & Pyenson 2015; Velez-Juarbe *et al.* 2015; Collareta *et al.* 2017); e.g. 'char. 6[1]' refers to state 1 of character 6.

SYSTEMATIC PALAEOLOGY

CETACEA Brisson, 1762

ODONTOCETI Flower, 1867

PAN-PHYSETEROIDEA Velez-Juarbe *et al.*, 2015

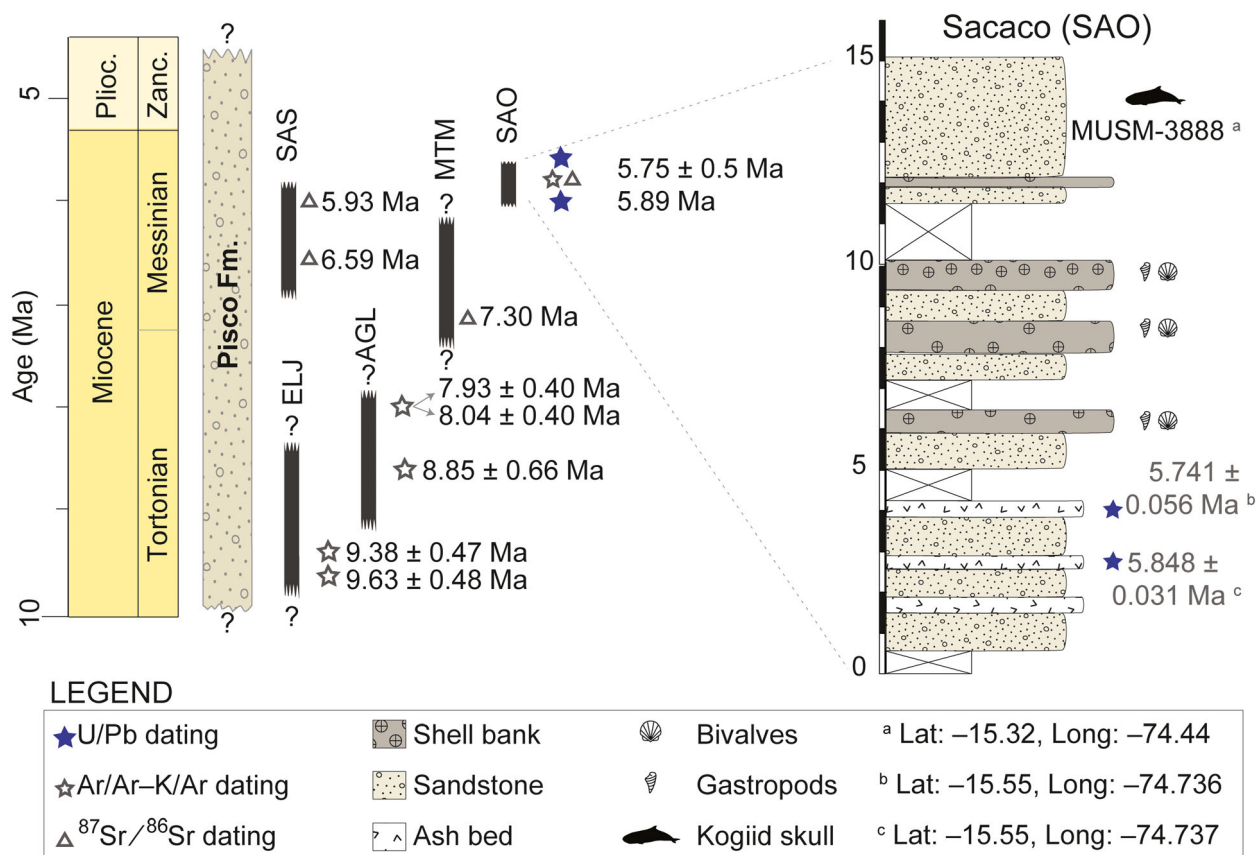


FIG. 2. Schematic representation of the main localities from the Pisco Formation in the Sacaco area: AGL, Aguada de Lomas; ELJ, El Jahuay-Altogrande; MTM, Montemar; SAO, Sacaco; SAS, South Sacaco. New and pre-existing radiometric (stars) and strontium ratio (triangles) age constraints are also indicated for each locality. To the right, stratigraphic column for the locality where MUSM 3888 was found, showing the position of U–Pb radiometric dates. Age data from Ehret *et al.* (2012), Muizon & Bellon (1980) and DO (unpub. data). *Abbreviations:* Plioc., Pliocene; Zanc., Zanclean.

PHYSETEROIDEA Gray, 1821
 KOGIIDAE Gill, 1871
 KOGIINAE Gill, 1871
 KOGIA Gray, 1846

Type species. *Physeter breviceps* Blainville, 1838

Included species. *Kogia breviceps*; *K. sima*; *K. pusilla*; *K. danomurai* sp. nov.

Emended diagnosis. Small to medium-sized physeteroids. In extant species, sexual maturity is observed for individuals over 1.9 m in total body length, whereas the maximum adult length is c. 3.5 m (Bloodworth & Odell 2008). Based on allometric equations for reconstructing the body size (Pyenson & Sponberg 2011), the length of the fossil species would have been similar (see Differential Diagnosis of *K. danomurai* below). The skull of *Kogia* displays a triangular outline, being wider in the facial region and narrowing towards the apex of the rostrum (condition unknown in *K. danomurai*). This blunt rostrum condition is referred to as amblygnathy (Werth 2006), being highly derived

in both the extant species. The rostrum is flat to concave (as highlighted by the rostrum fragment of *K. danomurai*), thus indicating that the supracranial basin extended anteriorly over the dorsal rostral surface (char. 3[2]). The mesorostral groove is open along the rostrum (unknown in *K. danomurai*). Ventrally, the maxillae lack functional, well-individualized dental alveoli (char. 6[1]; unknown in *K. danomurai*). The antorbital notch enters the supracranial basin, extending posteriorly towards the posterior edge of the right bony naris. The external bony nares are located at (or slightly posterior to) the level of the preorbital process. The sagittal facial crest extends posteriorly from the external bony nares and reaches the occipital crest, thus dividing the supracranial basin into a left and a right maxillary fossa and hosting a medially displaced premaxillary fossa. The maxillary crests are moderately to fairly robust and project dorsally above the level of the supracranial basin. In dorsal view, the supraorbital process extends laterally beyond the lateral walls of the cranial vault, a condition enhanced by the relatively low position of the postorbital process (only known in extant *Kogia* spp.) The relative size of the maxillary fossae varies, from being moderately asymmetrical (as in *K. danomurai*) to overall similar in size to each other (as in extant *K. sima* and *K. breviceps*). Posteriorly,

the occipital shield is flat and forms an angle of *c.* 90° with the main body axis (char.30[2]). The surface of the occipital shield is flat to slightly convex. Laterally, the temporal fossa is shallow and proportionally small when compared with the rest of the skull, being notoriously reduced in *K. sima*.

Chronostratigraphic distribution. *Kogia sima* and *K. breviceps* are extant species. The holotype skull of *K. danomurai* sp. nov. was found in the uppermost Miocene Sacaco (SAO, 5.84–5.74 Ma) vertebrate level (as defined by Muizon & DeVries 1985), Sacaco locality, Sacaco basin. The holotype skull of *Kogia pusilla* was recovered from the Monte Voltraio locality (Pisa, Italy) and it has been regarded as late Pliocene (3–2.6 Ma; Bianucci *et al.* 1998) in age. Isolated periotics referred to *Kogia* have been described from the lower Pliocene (*c.* 4.8–3.1 Ma) Yorktown Formation of North Carolina (Vélez-Juarbe *et al.* 2016), as well as from the Pliocene of Italy (Pilleri 1987; Bianucci 1996). Additional fragmentary remains have been attributed to *Kogia* by previous authors, however, given that these reports were based on isolated teeth (e.g. *Kogia prisca* Matsumoto, 1926), their assignment to this living genus (and even to the family Kogiidae) is largely unsupported (Barnes 1973). Therefore, we constrain the presence of the genus *Kogia* from the latest Miocene (5.84 Ma) to the present day.

Kogia danomurai sp. nov.

Figure 3

LSID. urn:lsid:zoobank.org:act:1F6E4C83-FB4D-41BB-B8E0-4D2DFA3F162D

Derivation of name. The specific name honours the Peruvian science professor Dan Omura, in recognition of his contribution to national vertebrate palaeontology, as member of both the Department of Vertebrate Palaeontology of the Natural History Museum of the Universidad Nacional Mayor de San Marcos (UNMSM, Lima) and the Peruvian School La Union.

Holotype. MUSM 3888, a partial cranium, preserving the facial and dorsolateral regions of the cranial vault, but lacking most of the rostrum and basicranium. Collected by Mario Urbina, Rodolfo Salas-Gismondi, Diana Ochoa and Ali Altamirano in 2019.

Differential diagnosis. Small physeteroid with an estimated total body length of *c.* 232 cm (based on the body size equation proposed by Pyenson & Sponberg 2011 for Physeteroidea). Among known kogiids, it is recognized by the following combination of characters: rostrum surface slightly concave, as suggested by the rostral fragment with the supracranial basin of the skull extending onto the dorsal surface of the rostrum (char. 3[2]; shared with *Physeter macrocephalus*, *Aprixokogia* and *Kogia* spp.); antorbital notches transversely widened, but not transformed into narrow slits as in most kogiids (char. 9[1], shared with *Aprixokogia* and *Praekogia*); antorbital processes slightly

thickened, a condition fully developed only in extant *Kogia* spp.; one large maxillary foramen located slightly anterolateral to the right bony naris (char. 11[3]); maxillary crests transversely thickened and high, greatly extending above the level of the supracranial basin; supracranial basin moderately excavated, resembling *Praekogia*, *Pliokogia* and *Nanokogia*, and contrasting with the deeper basin present in *Scaphokogia* and modern *Kogia* spp.; nuchal crest presenting a W-shaped outline in dorsal view (condition shared with extant *Kogia* spp., unknown in *Pliokogia* and *Koristocetus*); relatively short projection of the lacrimojugal complex between the frontal and maxilla (char. 23[0], shared with *Nanokogia* and *S. totajpe*); and temporal fossa located in a relatively high position, its top being observed just below the dorsal level of the maxillary crests (char. 44[0], shared with *Scaphokogia* spp.). *K. danomurai* can be further distinguished from other kogiids by presenting: a blunt outline of the premaxillary processes in the dorsal view of the skull; and a sagittally located premaxillary fossa that is shallowly excavated and located below the average level of the supracranial basin, being well-delimited leftwards but only vaguely delimited rightwards.

Horizon and age. The holotype cranium of *K. danomurai* (MUSM 3888) comes from uppermost Miocene (i.e. upper Messinian) deposits of the Pisco Formation exposed at the Sacaco locality (15.5426°S, 74.7336°W); these deposits have recently been dated at *c.* 5.8–5.7 Ma based on strontium isotope stratigraphy and radiometric dates provided by Ehret *et al.* (2012) and DO (unpub. data) (see Geological Setting, above, for more details).

Description

General features of the cranium. The holotype cranium of *K. danomurai* (Table 1) has a preserved length of 25.9 cm (measured from the anteriormost preserved point of the premaxilla to the posterior end of the nuchal crest) and a greatest supraorbital width of 24.1 cm. The preserved skull region indicates that the original cranium was larger than those of *Koristocetus* and *S. totajpe*, which are known from geologically older layers of the Pisco Formation (Collareta *et al.* 2017; Benites-Palomino *et al.* 2020a), and similar in size to that of modern *Kogia* spp. Most of the cranial sutures are fully closed, indicating that the animal was a full-grown adult (Chen *et al.* 2011). Only a small portion of the rostrum base is preserved. However, it indicates that the rostrum was dorsoventrally flattened, similar to other Kogiinae, and its dorsal region was concave, serving as the base for the facial organs. The external bony nares are located slightly posterior to the antorbital processes, as observed in *Koristocetus*, *Pliokogia* and *Nanokogia*, whereas the external bony nares in modern *Kogia* are much more posteriorly displaced. The supracranial basin resembles that of *Pliokogia appeninica* (Collareta *et al.* 2019) and extant *Kogia* spp. in being divided into three main cavities (i.e. the premaxillary fossa and the left and right maxillary fossae) due to the presence of a more or less longitudinally elongated sagittal facial crest. However, it differs from the condition observed in *Pliokogia* (Collareta *et al.* 2019) and extant *Kogia* spp. by not possessing a complete right wall of the

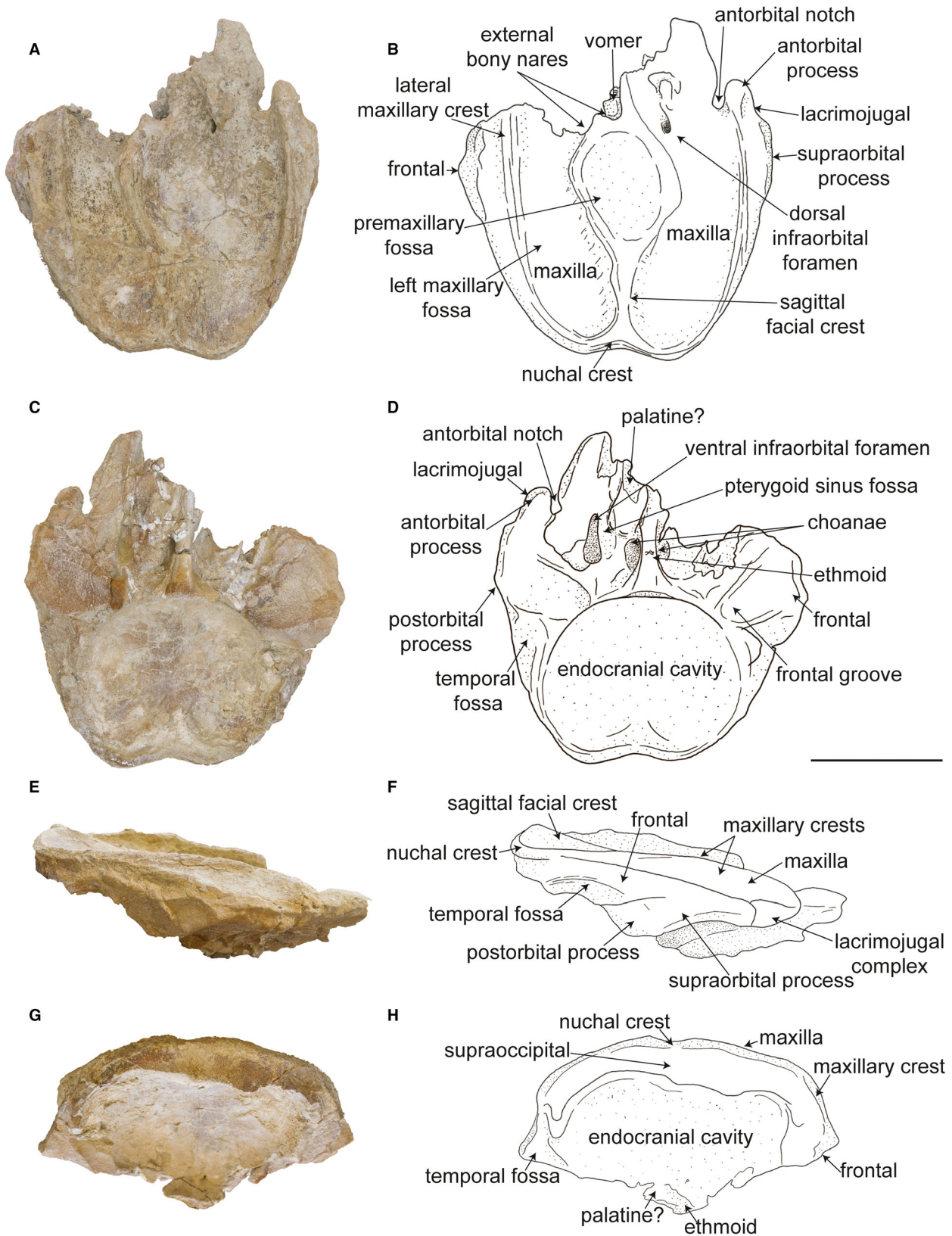


FIG. 3. MUSM 3888, holotype and only known specimen of *Kogia danomurai* sp. nov., photographs and schematic drawings of the holotype skull in: A–B, dorsal; C–D, ventral; E–F, right lateral; G–H, posterior view. Scale bar represents 10 cm.

TABLE 1. Measurements (in mm) of the skull of *Kogia danomurai* sp. nov. (MUSM 3888).

Preserved condylobasal length	261
Length of the preserved portion of the rostrum	74
Width of rostrum at base	151
Maximum width of the external right bony naris	23
Maximum width of the external left bony naris	42
Greatest preorbital width (width across preorbital processes)	201
Greatest postorbital width (width across postorbital processes)	242
Least supraorbital width	221
Maximum width of external nares	55
Greatest parietal width, within post-temporal fossae	154 ^e
Greatest length of temporal fossa	89 [†]
Length of right orbit from apex of preorbital process of frontal to apex of postorbital process	76
Length of antorbital process of left lacrimal taken horizontally	42

Modified from Benites-Palomino *et al.* (2020a, table 1).

e, estimated value; †, measurement taken on incomplete element.

premaxillary fossa of the sagittal facial crest, a condition that is somewhat reminiscent of *Praekogia* (Barnes 1973).

Premaxilla. Only a small portion of the right premaxilla is preserved at the rostrum base, suggesting that the dorsal surface of the premaxillae was shallowly concave upwards. In the neurocranial region, only the right premaxilla is preserved, lateral and posterior to the external bony nares. Anteriorly, the right premaxilla forms the walls of the right bony naris, along with the vomer and the presphenoid. The right bony naris has an approximate anteroposterior length of 2.5 cm and a transverse width of 2.1 cm. Both nasal bones are lacking, as observed in all kogiids for which this region is known. The left naris is preserved only along its posterior edge; however, as in all physteroids, it is clearly larger than the right one. Posterior to the right bony naris, the dorsal surface of the premaxilla forms a step, which is more prominent on the left side. The sagittal facial crest is moderately displaced towards the left side of the skull, being weakly bent leftwards from the level of the antorbital notch to the level of the anterior limit of the temporal fossa, thus slightly overhanging the left maxillary fossa. The posterior portion of the crest runs along the sagittal plane of the skull, joining the nuchal crest posteriorly. Posteromedial to the nares the sagittal facial crest expands transversely to form a large depression that extends onto the right maxilla. Posterior to this depression, the sagittal facial crest tapers transversely, reacquiring a median position. In this region, the depression that is found on the premaxilla is laterally delimited by a keeled prominence that faces the right side of the skull. Considering also that it is significantly deeper than the rest of the supracranial basin (see description of the maxilla below), it is here interpreted as the premaxillary fossa (Barnes 1973). In both the living species *K. sima* and *K. breviceps* the premaxillary fossa is well-defined

and excavated upon a dorsal promontory of the sagittal facial crest. The premaxillary fossa is laterally delimited by the right premaxillary and medial crests (*sensu* Thornton *et al.* 2015; Fig. 3). Ventrolaterally, these crests serve as the attachment sites for the facial muscles on the left side and for the case on the right (Thornton *et al.* 2015). *K. danomurai* displays an incipient, early-stage development of these characteristics, given that the premaxillary fossa is not completely separated from the right maxilla, being anteriorly delimited by a bulging margin of the postnarial eminence at the level of the right posterior dorsal infraorbital foramen.

Maxilla. As for the premaxillae, only a small portion of the right maxilla is preserved on the rostrum. The preserved rostral portion of the maxilla indicates that its dorsal surface was flat to slightly convex. The rostrum is dorsoventrally flattened, and, in anterior view, it presents a slightly V-shaped transverse section, implying that the supracranial basin extended onto the rostrum as observed in *Kogia breviceps*, *K. sima* and *K. pusilla*. On the right maxilla, a single dorsal infraorbital foramen is preserved; it is medially located near the suture with the right premaxilla and at a level posterior to the corresponding antorbital notch, reaching an anteroposterior length of 1.3 cm and a transverse width of 0.8 cm. Due to the loss of more rostral portions of the maxilla, it is not possible to ascertain whether one or more anterior dorsal infraorbital foramina were present in *K. danomurai*. Unlike other kogiids such as *Nanokogia*, *Praekogia*, *Koristocetus* or *Pliokogia*, no posterior dorsal infraorbital foramina are present in the area of the right maxillary fossa. The supracranial basin has an ovoid outline, being longer than wide, but not as deep as in extant *Kogia*. The supracranial basin is anteromedially deeper, being shallower and slightly convex transversely in its posterior portion. Posteriorly, the maxillary fossae are separated from each other by the ridge-like posterior projection of the sagittal facial crest; this condition is somewhat reminiscent of that observed in *Pliokogia* and in modern *Kogia*. The right maxillary fossa is reniform and transversely compressed, only moderately widening posteriorly. The well-preserved right antorbital process is transversely thickened, thus differing from most fossil kogiids that display a transversely compressed antorbital process (e.g. *Aprixokogia*). This condition is even more developed in *K. sima* and *K. breviceps*, where the antorbital process is greatly inflated (i.e. hyperostotic) and displays an overall bulbous aspect. The maxillary crests are transversely narrow and moderately high over the dorsal level of the supracranial basin, as observed in *Nanokogia* and *Koristocetus*. The lateral maxillary crests run roughly parallel to each other along the dorsal surface of the cranium, bending medially on the posterior third of the cranium to form the nuchal crest by coalescence. Posteriorly, the nuchal crest is joined medially by the sagittal facial crest, thus forming a W shape, being slightly asymmetric due to weakly posterior enlargement of the right maxillary fossa. The W-shaped outline of the nuchal crest is found only in taxa in which the sagittal facial crest reaches the nuchal crest, including the extant *Kogia* spp., *Praekogia* and, to a lesser extent, in *Nanokogia*. This condition might have also been present in *Koristocetus*, as suggested by the position of the sagittal facial crest; however, the holotype skull is missing most of the nuchal crest. In ventral

view, the preserved portion of the palatal surface of the maxilla is flat. The preserved ventral portion of the rostrum on the right side of the skull indicates that *K. danomurai* did not present functional posterior alveoli, thus resembling other coeval Kogiinae in which reduced maxillary alveoli (or even a narrow alveolar groove) are retained. Preserved only on the right side of the skull, the ventral infraorbital foramen is anteroposteriorly oriented and opens at a level slightly posterior to that of the corresponding antorbital notch, being shaped as a large furrow that reaches 3.5 cm in anteroposterior length and 1.1 cm in transverse width. The endocranial cavity has a cordiform outline in ventral view. It narrows anteriorly and exhibits a medial notch posteriorly.

Vomer. Only the posteriormost region of the vomer is preserved. Posteriorly, along with the ethmoid, the vomer creates a wall that separates both the left and right internal choanae from each other. The vomer runs anteriorly along with the ethmoid. The posteriormost preserved portion of the vomer flares dorso-laterally, and, as such, it exhibits a triangular outline in transverse section.

Ethmoid. The ethmoid is anteriorly broken, along with the rest of the rostrum. In anterior view, the transversely broken surface of the ethmoid displays an elliptical, mediolaterally elongated outline. The preserved region of the ethmoid has a length of 8.1 cm and narrows medially, thus creating a waist-like compression at mid-length that forms most of the nasal septum. The ethmoid broadens posteriorly, being broken at the level of the cribriform plate. The ethmoid mostly consists of spongy bone and exhibits a thicker periosteum compared with the adjacent bones.

Lacrimojugal complex. The lacrimojugal complex is preserved only on the right side of the skull, lacking the ventral portion of the preorbital process. As in *Scaphokogia totajpe* and *Nanokogia isthmia*, the lacrimojugal complex sends a small, distally tapering projection that wedges between the maxilla and the frontal. Ventrally, the attachment site of the m. masseter is more developed than in *Koristocetus* and *Nanokogia*, but not as transversely widened as in *K. breviceps* and *K. sima*.

Frontal. The frontal is dorsoventrally compressed and appressed to the overlying maxilla. In lateral view, the suture between the maxilla and the frontal is straight and forms a 25° angle relative to the horizontal plane. In dorsal view, the supraorbital processes protrude laterally beyond the level of the maxillary crests, thus exposing a small strip of each frontal, as in other kogiids. Ventrally, the frontal grooves are excavated and progressively bend laterally, thus approaching the condition observed in extant *Kogia*, whereas other members of Kogiinae such as *Koristocetus* display more anteriorly oriented frontal grooves.

PHYLOGENETIC ANALYSIS

The anatomical characters of *K. danomurai* were coded into the matrix of Benites-Palomino *et al.* (2020a).

Subsequent amendments on *Kogia pusilla* were based on direct observations of the holotype cranium. The final matrix includes 34 taxa and 57 characters and was edited using Mesquite 2.75 (Maddison & Maddison 2011; Benites-Palomino *et al.* 2020b). A preliminary heuristic search was performed using PAUP (version 4.0a [build 167]) (Swofford 2002), using the tree bisection and reconnection (TBR) algorithm, with equal weights for all characters. Because of the poor resolution of this analysis (Fig. 4A), and in order to further evaluate the matrix consistency and the character performance, a series of subsequent parsimony analyses was performed. With the aim of focussing only on the relationships among extant and fossil pygmy sperm whales, the ingroup was restricted to Kogiidae on the following analyses, leaving the outgroup composed of non-kogiid sperm whales, stem odontocetes, and archaeocetes. For our second analysis, all characters were also treated as unordered, but we down-weighted homoplastic characters by using the implied weighting method (Fig. 4B), with the default value of 2 for the constant *k* (Goloboff 1993). Two additional analyses were performed using the same methodology as the previous analyses (Fig. 4C, D), but considering the characters 1, 3, 4, 10, 12, 18, 22, 25, 26, 30, 32, 34, and 38 as ordered, in agreement with the approach that has recently been proposed by Paolucci *et al.* (2020). Following previous works (Lambert *et al.* 2010; Paolucci *et al.* 2020) that combined implied weighting with the use of ordered characters, we prefer the fourth analysis (Fig. 4D) by virtue of its overall better node resolution. The fourth analysis strongly supports the monophyly of Kogiidae on the basis of 13 synapomorphies, namely: maxillae, premaxillae, and vomer reaching the tip of the rostrum (char. 2 [1]); maximum width of the skull, bizygomatic or postorbital width, less than 40 cm (char. 8[0]); three to four dorsal infraorbital foramina in the area of the right antorbital notch or posterior to it (char. 11[0]); right premaxilla not widened posteriorly (char. 13[0]); sagittal crest present and shaped as a shelf covered by the pointed right premaxilla (char. 14[1]); both nasals absent (char. 19[2]); right maxilla reaching the sagittal plane of the skull on the posterior wall of the supracranial basin (char. 21[1]); long projection of the lacrimojugal complex between the frontal and the maxilla (char. 23[1]); temporal fossa anteroposteriorly longer than the distance between the preorbital process of the maxilla and the anterior wall of the temporal fossa (char. 26[0]); posterior extension of the petiotic parallel to the general plane of the bone, and not ventrally oriented (char. 33[1]); lack of contact between the jugal and the zygomatic process of the corresponding squamosal (char. 45[2]); short dorsal process of the petiotic (char. 48[2]); and symphyseal angle on the mandibles greater than 55° (char. 51[2]). Previous work (Benites-Palomino *et al.* 2020a; Collareta *et al.* 2020)

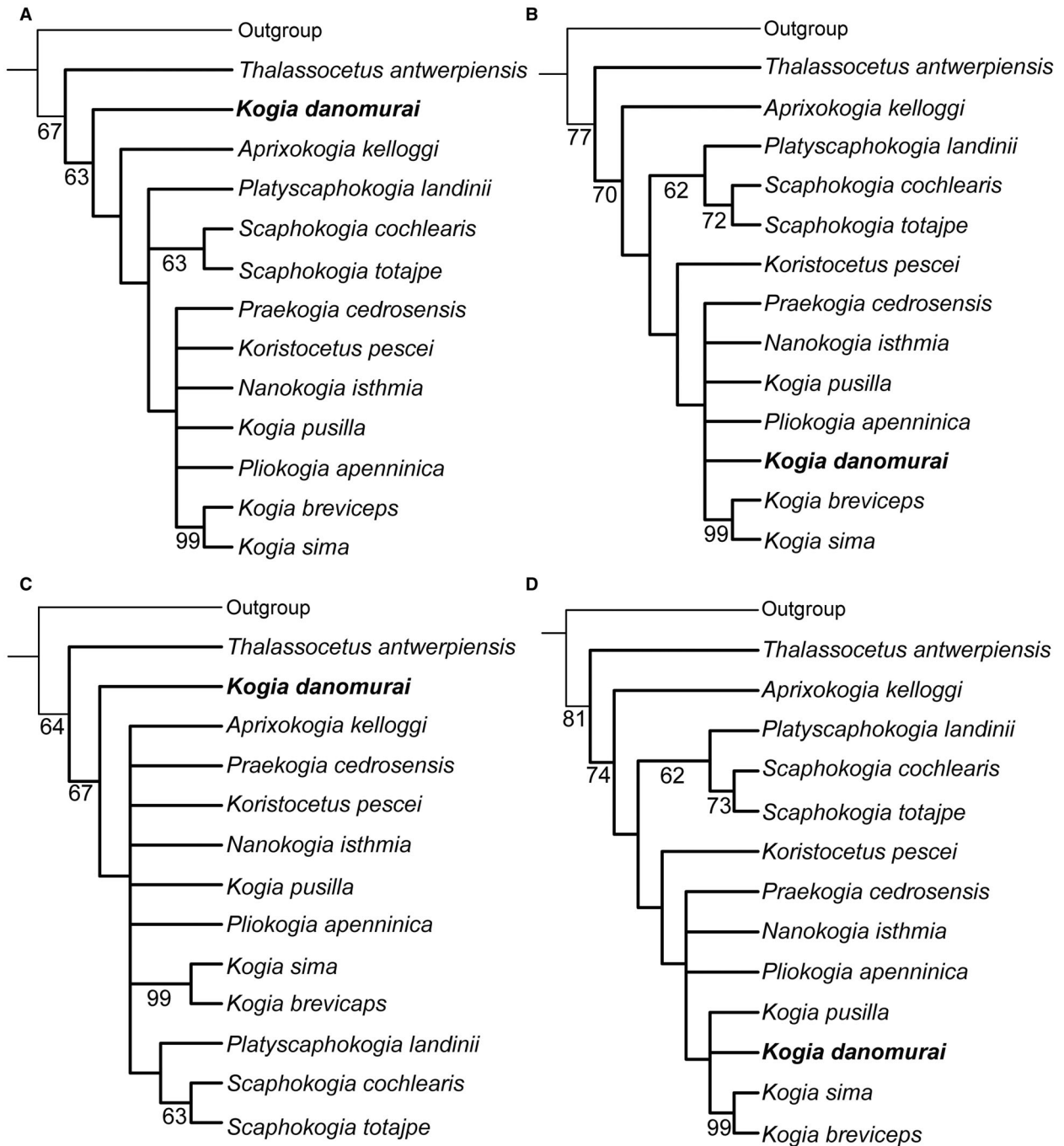


FIG. 4. Phylogenetic relationships of *Kogia danomurai* sp. nov. with other kogiids. A, strict-consensus tree of the full heuristic search resulting from 576 trees, each 178 steps long, with retention index (RI) = 0.743 and consistency index (CI) = 0.494. B, strict-consensus tree of the implied weights (k = 2) search resulting from 90 trees, each 182 steps long, with RI = 0.731 and CI = 0.484. C, strict-consensus tree of the heuristic search with ordered characters weighting resulting from 17 784 trees, each 206 steps long, with RI = 0.753 and CI = 0.539. D, strict-consensus tree of the implied weights analysis with ordered characters resulting from 135 trees, each 211 steps long, with RI = 0.740 and CI = 0.526.

supported the presence of two conspicuous clades among Kogiidae, namely, Scaphokogiinae and Kogiinae. The former are recovered on the basis of the following

characters: suture between the premaxilla and maxilla distinctly anterolaterally directed anterior to the antorbital notches (char. 5[1]); right premaxillary foramen posterior

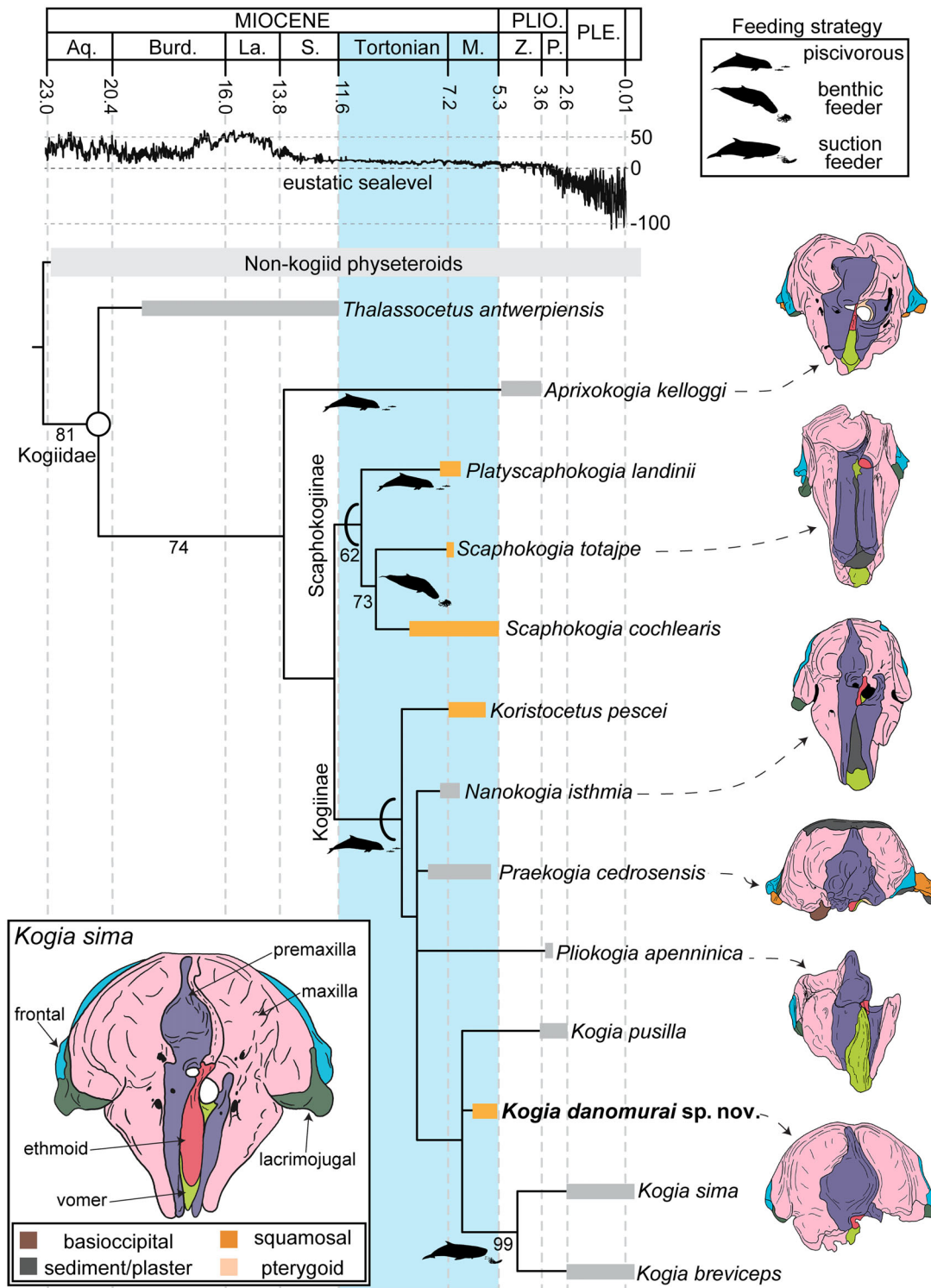


FIG. 5. Time-calibrated phylogenetic relationships of Kogiidae and cranial variations among different genera. Strict-consensus tree of Kogiidae based on 135 most parsimonious trees, each 211 steps long, with retention index (RI) = 0.740 and consistency index (CI) = 0.526 (see Fig. 3D). Arcs denote branch-based clades, circle denotes node-based clade, numbers at nodes indicate bootstrap values. The time scale is based on Cohen *et al.* (2020), eustatic sealevels are after de Boer *et al.* (2010). *Abbreviations:* Aq., Aquitanian; Burd., Burdigalian; La., Langhian; M., Messinian; P., Piacenzian; Ple., Pleistocene; Plio., Pliocene; S., Serravallian; Z., Zanclean.

to the corresponding antorbital notch (char. 17[1]); occipital shield flat or concave, forming an angle greater than 90° with the horizontal (char. 30[3]); hypertrophy of the mesorostral canal, in which the canal occupies more than 50% of the rostrum diameter (char. 57[1]). The members of the second clade, Kogiinae, are recognized by the following synapomorphies: short rostrum, ratio of the rostrum length to skull width <0.95 (char. 1 [2]); dorsal exposure of the maxilla on the rostrum wider than the premaxilla all along (char. 4[2]); right antorbital notch entering the supracranial basin (char. 10[1]); in lateral view, presence of a well-developed, wide notch posterior to the postglenoid process of the squamosal for the enlarged posterior process of the tympanic (char. 29[2]); occipital shield convex and forming an angle of *c.* 60° with the long axis of the rostrum (char. 30[1]).

The clade including the four species of *Kogia* is supported by the following synapomorphies: supracranial basin extended onto the whole surface of the rostrum (char.3[2]); occipital shield flat or slightly concave, forming an angle of *c.* 90° (char. 30[2]); and mandible curved in lateral view, with its ventral margin concave (char. 50 [2]; known only in extant taxa). *Kogia pusilla* is diagnosed by two derived characters: anteroposterior level of the last upper alveoli or posterior vestigial alveolar groove placed at the level of the antorbital notch or slightly anterior (char. 41[1]); and postorbital process of the frontal moderately extended posteroventrally (char. 43[0]). *Kogia danomurai* differs from other species of *Kogia* by these four characters: antorbital notch not transformed into a narrow slit (char. 9[1]); one large dorsal infraorbital foramen present in the area of the right antorbital notch (char. 11[3], shared with *Koristocetus*); short projection of the lacrimojugal between the frontal and the maxilla (char. 23[0], shared with *Nanokogia*); and dorsal margin of the temporal fossa at the top of skull or somewhat lower (char. 44[0]). The monophyly of the clade formed by *Kogia breviceps* and *Kogia sima* is supported by two characters: frontal–maxilla suture forming an angle greater than 35° with the skull in lateral view (char. 25 [2]); and temporal fossa distinctly shorter than the distance between the preorbital process of the maxilla and the anterior wall of the temporal fossa (char. 26[2]).

DISCUSSION

Phylogenetic relationships of K. danomurai within Kogiidae

Kogia danomurai is geologically the oldest species of the genus *Kogia* known so far. As such, it significantly extends the chronostratigraphic range of *Kogia* into the upper Miocene while further enriching the taxonomically diverse physeteroidea assemblage of the Pisco Formation.

Previous work has already stressed the presence of several species of physeteroids, including macroraptorial taxa (Lambert *et al.* 2008, 2016), large suction feeders (Muizon 1988; Benites-Palomino & Urbina 2020), small piscivorous animals and benthic feeders in the Pisco strata (Benites-Palomino *et al.* 2020a; Collareta *et al.* 2020). So far, seven physeteroid species have been described from the Pisco Formation, but the relationships among species-level sperm whale taxa as well as those between the major physeteroid clades are constantly changing as new fossils allow for testing of new phylogenetic hypotheses. The only well-supported clade in most recent phylogenetic reconstructions is Kogiidae.

The monophyly of Kogiidae has indeed been widely supported by both molecular (McGowen *et al.* 2009, 2019; Geisler *et al.* 2011) and morphological analyses (Velez-Juarbe *et al.* 2015; Collareta *et al.* 2017, 2019, 2020; Benites-Palomino *et al.* 2020a; Lambert *et al.* 2020). According to the morphological assessments proposed in the present study (Fig. 5), one of the earliest branching kogiids was the early Pliocene *Aprixokogia kelloggi* from North Carolina, south-eastern USA (Whitmore & Kaltenbach 2008), known from a skull that retains several primitive physeteroid characteristics. This indicates that stem kogiids retaining plesiomorphic characters were able to survive until fairly recent times, with their chronostratigraphic ranges overlapping those of derived forms such as *Kogia* (Velez-Juarbe *et al.* 2016). Two conspicuous clades of morphologically derived kogiids, Scaphokogiinae and Kogiinae, have been recovered by recent phylogenetic analyses, highlighting the role of the Pisco Formation as a hotspot for kogiid diversification during the late Miocene (Benites-Palomino *et al.* 2020a; Collareta *et al.* 2020). Scaphokogiinae are, so far, restricted to the Pisco Formation of southern Peru (12°–16°S). The skeletal morphology of the rostrum of these animals greatly contrasts with that of other kogiids due to the hypertrophied mesorostral canal that occupies more than half of the inner region of the rostrum. Additionally, the facial region of the skull is mostly occupied by the large, deeply excavated supracranial basin, which displaces the sagittal facial crest laterally; this supracranial basin is nonetheless not extended onto the rostrum as in other kogiids (Muizon 1988; Benites-Palomino *et al.* 2020a). Three species, clustered in two genera, are recognized in this clade: *Platyscaphokogia landinii*, characterized by its relatively narrow and transversely compressed rostrum; and *Scaphokogia*, which includes the sister taxa *Scaphokogia cochelaris* and *Scaphokogia totajpe*, diagnosed by a tube-like rostrum. Scaphokogiines have been interpreted as benthic feeders because of their anteroventrally deviated rostrum and the pachyostotic growth of the cranial bones on the rostrum (Benites-Palomino *et al.* 2020a; Collareta *et al.* 2020).

The second clade, Kogiinae, includes an array of several taxa that display different evolutionary stages of their suction-feeding capabilities. Ranging from taxa that either retained functional upper teeth, such as *Koristocetus*, or lack an upper dentition, such as extant *Kogia* spp. Furthermore, these species display a great variability in terms of the arrangement of the nasal organs placed over their foreheads, as revealed by the dorsal aspect of their skulls (see below). Nevertheless, the general aspect of the skull in kogiines, and in scaphokogiines, can be distinguished by the overall triangular outline of the skull, proportional reduction in size of the temporal fossa, the lack of a deep spoon-shaped supracranial basin and the presence of three cavities in the supracranial basin (left and right maxillary fossae and a medially located premaxillary fossa). Within Kogiinae, relationships between taxa have been mostly consistent in recent analyses (Collareta *et al.* 2017, 2019; Benites-Palomino *et al.* 2020a). The earliest branching Kogiinae is *Koristocetus*, a taxon that displays several plesiomorphic characteristic such as the retention of a proportionally larger temporal fossa and the presence of functional upper dentition. The external bony nares of *Koristocetus* are also found in the anteriormost position among the clade. The next node includes *Pliokogia* and *Nanokogia*, characterized by the reduction in size of the temporal fossa and the lack of a supracranial basin extended into the rostrum (Collareta *et al.* 2019). In the case of *Praekogia*, because the rostrum and the anteriormost left facial region are missing, it is not possible to assess whether the supracranial basin extended into the rostrum or not. However, the overall shape of the basin and its extension indicates that it was smaller than in *Kogia*. This condition is more evident in dorsal view, because both the postorbital region of the frontal and the zygomatic process are well-laterally projected.

Differing from the rest of Kogiinae, *Kogia* are characterized by an evident extension of the supracranial basin into the rostrum. This condition is partly developed on the rostrum of *K. pusilla*, due to its narrower profile anteriorly. In *K. danomurai* it is not possible to assess if this was as well-developed as in extant *Kogia* or partly developed as in *K. pusilla*. However, based on the concave surface of the preserved portion of the rostrum, the supracranial basin should have been well-extended into the rostrum. Furthermore, in both *K. pusilla* and *K. danomurai* the orbital region is not as laterally projected as in *Praekogia*, indicating that the supracranial basin occupied most of the dorsal region of the skull as in extant *Kogia* spp. Additionally, extant *Kogia* spp. displays the most derived suction-feeding skull morphology of extant odontocetes (Werth 2006), characterized by a short triangular rostrum (i.e. amblygnathy). Specific development of the masticatory muscles also provides evidence for this: in *Kogia*, the m. masseter is the main

mandibular adductor (Schulte & Forest Smith 1918; Benites-Palomino *et al.* 2020a), contrasting with raptorial taxa such as *Acrophyseter*, in which mandible adduction is done by the m. temporalis (Lambert *et al.* 2014, 2016). Because of its longer rostrum and the size reduction of the m. masseter attachment site, in *K. pusilla* these suction-feeding capabilities were not as developed as in extant *Kogia* spp., and therefore *K. pusilla* should have retained some raptorial feeding capabilities, such as those of *Nanokogia* or *Pliokogia* for ram prey capture (Hocking *et al.* 2017; Fig. 2D). In *K. danomurai* most of the rostrum is not preserved, thus making it impossible to reconstruct its overall shape. However, the ventral area of the lacrimojugal of *K. danomurai* is proportionally the largest among fossil kogiids, thus indicating that the m. masseter was already playing an important role in the mandibular adduction for suction feeding, as in extant *Kogia* spp.

Patterns of compartmentalization of the facial region of the skull

Unlike *Physeter*, which exhibits greatly hypertrophied spermaceti and melon organs (Clarke 1970), the living species of *Kogia* bear additional soft structures, the roles of which are still not fully understood. Because of their greatly developed facial asymmetry (highlighted also by the sound production pathways of the forehead; Goold & Clarke 2000) and proportionally smaller size, the function of the soft-tissue structures in *Kogia* might have undergone a secondary adaptation or compartmentalization, in which functions were split into specific structures. Such a differentiation in the role of certain regions of the forehead has been suggested in early works based on myology and cranial anatomy (Schulte 1917; Schulte & Forest Smith 1918). Modern descriptions of the organs and other soft-tissue structures indicate that there are four main anatomical structures that form the nasal complex of extant *Kogia* (Thornton *et al.* 2015): (1) the phonic lips, which produce the sound via phonation when the air from the right nasal passage passes through; (2) the spermaceti organ, which is restricted to the facial region of the skull, highly influenced by the skeletal muscles in the region of the premaxillary fossa (Schulte & Forest Smith 1918), and believed to take an active part in sound propagation and transmission; (3) the ‘vocal’ cap, or ‘cushion’ (Clarke 2003), which lies on the right maxillary fossa and has been suggested to modulate the sound via muscular control; and (4) the melon, which extends dorsally onto the rostrum and, as in other toothed cetaceans, is responsible for focusing and emitting the sound waves that are involved in echolocation (Cozzi *et al.* 2016). Furthermore, several air sacs and muscles are attached to the

nasal complex, which rests in the left maxillary fossa, and within the anterodorsal region of the inflated lateral maxillary crests (Clarke 2003; Thornton *et al.* 2015). As in *Physeter*, these complex structures are modulated by highly vascularized surrounding muscles that act as a pneumatic sound generator (Norris & Harvey 1972). This is evidenced by the homologous attachment regions for the facial muscles found in the forehead of *Kogia* (Schulte & Forest Smith 1918). All of the non-muscular structures have different densities, acoustic impedances and sound velocity responses, thus evoking specific roles in the sound production system of kogiids. Computed tomography has confirmed the presence of a fifth structure, the theca (*sensu* Song *et al.* 2015), which covers the entire nasal complex of modern *Kogia*, being mostly constituted by dense connective tissue. Based on this characterization, this structure might be homologous to the 'case' described by Clarke (1978) for *Physeter macrocephalus*.

Fossil Kogiidae display several evolutionary stages of these structures, along with different feeding strategies, as suggested by their cranial anatomy. In *Aprixokogia kelloggi*, one of the earliest diverging kogiids (Fig. 5), the supracranial basin is partially divided by a robust, transversely broad, sagittal facial crest, which ends some 5 cm anterior to the nuchal crest. The reduced sagittal facial crest is also found in Scaphokogiinae, in which it is also displaced leftwards. The dorsal surface of the sagittal facial crest is shallowly concave, probably indicating the position of the base of the spermaceti organ. Furthermore, the sagittal facial crest exhibits a slightly developed lateral right premaxillary crest and a medial crest; in modern *Kogia*, these structures delimit the receptacle-like premaxillary fossa (*sensu* Thornton *et al.* 2015, fig. 4). Because of the poor development of the lateral walls of the premaxillary fossa and shallowness of the latter, the spermaceti organ of *Aprixokogia* could have been proportionally smaller than in other kogiids. A small spermaceti organ would have limited the high-frequency sound production capabilities of this extinct species, thus implying that its preying strategies greatly differed from its extant relatives. This is also highlighted by the retention of well-developed functional upper teeth, which suggest a raptorial ecology, rather than the less active suction feeding, for *Aprixokogia*. Further insights into the paleoecology of *Aprixokogia* could derive from the study of periotics referable to this taxon. A periotic (LACM 37258) from the Yorktown Formation that is likely to represent *A. kelloggi* (Vélez-Juarbe *et al.* 2016), has a cochlear morphology that resembles that of macroraptorial odontocetes (e.g. *Acrophyseter*) and lacks the specializations observed in extant *Kogia* (Galatius *et al.* 2019).

In Scaphokogiinae, the facial bone patterning is not as disparate as in their sister group (Kogiinae), given that scaphokogiines do not possess a true premaxillary fossa.

In turn, the enlarged right maxillary fossa (*sensu* Benites-Palomino *et al.* 2020a) is very large, deep, and occupies most of the dorsal region of the skull, thus displacing leftwards the overly reduced left maxillary fossa (Fig. 6). Because of this, it is not possible to ascertain whether the spermaceti organ or the vocal cap were largely developed on the right maxillary fossa. It seems reasonable to hypothesize that the spermaceti organ occupied most of this cavity and was dorsally covered by the vocal cap (Muizon 1988), given that most of the attachment sites of the facial muscles that modulate this organ are dorsally or anteriorly displaced (as in *Scaphokogia totajpe*). Despite occupying most of the facial region, the spermaceti organ of Scaphokogiinae was not hypertrophied, as in those non-kogiid physeteroids (Velez-Juarbe *et al.* 2015) in which it extends onto the dorsal surface of the rostrum (Lambert *et al.* 2016). In *Scaphokogia*, both the enlarged spermaceti organ and the massive tubular rostrum have been proposed to be adaptations for benthic feeding in shallow environments (Benites-Palomino *et al.* 2020a).

In *Praekogia*, *Koristocetus*, *Kogia pusilla*, *Kogia danomurai*, *Nanokogia* and *Pliokogia*, conspicuous differences in the skull architecture of the supracranial basin reveal a corresponding disparate organization of the soft-tissue structures. In the recently described *Pliokogia apenninica*, the premaxillary fossa is located slightly posterior to the right external bony naris, and it rests well-separated from both the left and right maxillary fossae, the latter being moderately shallow and transversely compressed (Collareta *et al.* 2019; Fig. 6). In *Kogia danomurai*, the premaxillary fossa is not fully separated from the right maxillary fossa; however, posteriorly, the sagittal facial crest partially projects to the right, which partly separates these two depressions (Fig. 6). This condition is similar to the one observed in *Praekogia* (Barnes 1973; Velez-Juarbe *et al.* 2015); however, the projection of the sagittal facial crest is more developed on *K. danomurai* than in the former. Furthermore, the premaxillary fossae of both *K. danomurai* and *Praekogia* extends laterally onto the right maxilla, being much rounder and robust anteriorly and expanding posteriorly over the postnarial eminence of the right premaxilla. Laterally, *K. danomurai* also displays an early stage of the transversal thickening of maxillary crests. In extant *K. sima* and *K. breviceps* (Fig. 6B), this thickening greatly enlarges the dorsal attachment sites for the muscles that modulate the nasal complex. This is evident in the anterodorsally rounder tip of the antorbital notch in *K. danomurai*. One of the main differences between *Kogia* spp. and the rest of the kogiids is the extension of the supracranial basin into the rostrum, an area occupied by the largest organ of the nasal complex: the melon (Fig. 6A, B). In fossil taxa such as *Koristocetus* or *Nanokogia* the rostrum is convex and narrow, indicating that the basin did not extend into the rostrum and

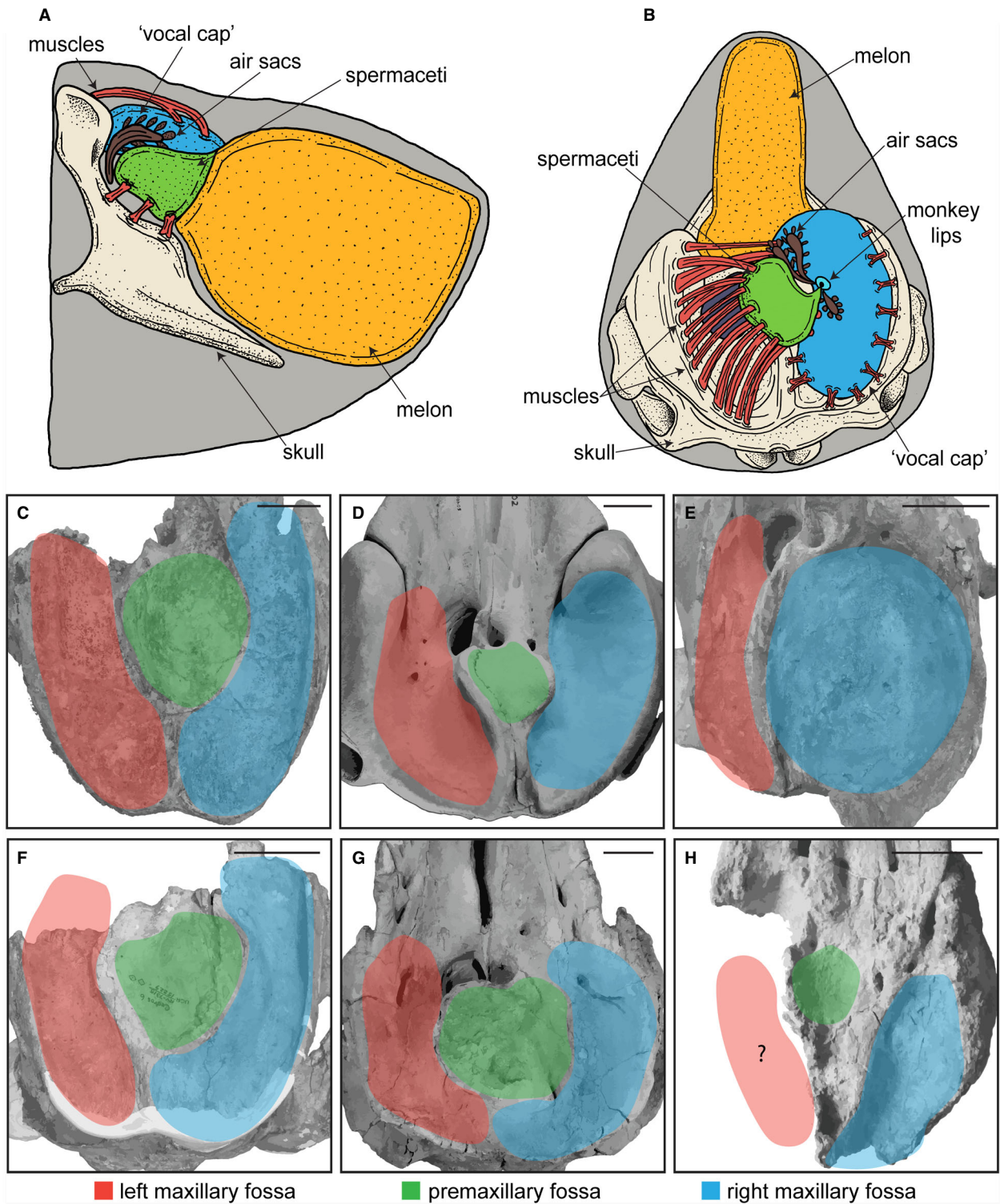


FIG. 6. A–B, schematic representation of the soft-tissue structures present in the facial region of the head of modern *Kogia breviceps*, modified from Thornton *et al.* (2015). C–H, variation of the facial region of the skull region in several modern and fossil kogiid species: C, *Kogia danomurai* MUSM 3888; D, *Kogia breviceps* USNM 504902; E, *Scaphokogia totajpe* MUSM 973; F, *Praekogia cedrosensis* UCMP 315299; G, *Aprixokogia kellogi* USNM 187015; H, *Pliokogia appeninica* MSNUP I 17603. Scale bars represent 5 cm.

therefore held a smaller melon. Both *K. danomurai* (based on the preserved rostral fragment) and *K. pusilla* already displayed a relative extension of the basin into the rostrum, as previously discussed (see above). This larger extension of the supracranial basin and the overall development of the muscle attachment sites for modulating the nasal complex, indicate that *Kogia danomurai* already had a sound production system as in extant *Kogia* spp., but developed to a lesser extent.

The hyperdiverse physeteroid community of Sacaco

The discovery of *Kogia danomurai* highlights that members of the extant genus *Kogia* co-occurred along with other highly derived kogiids such as *Scaphokogia cochlearis*, the craniofacial patterning of which greatly differs from that of *Kogia*. Along with these, the community of physeteroids also included raptorial sperm whales as *Acrophyseter deinodon*, and taxa related to extant *Physeter* (Benites-Palomino & Urbina 2020). Such a multi-species sperm whale community indicates the presence of a wide array of available prey items, and, as such, a niche partitioning within the physeteroid community. This hyperdiversification pattern of odontocete taxa has also been recorded in early Miocene layers, in which a large diversity of platanistoids coexisted within the Pisco basin (Bianucci et al. 2020). However, unlike other previous groups of odontocete taxa, physeteroids occupied a wide array of ecological niches ranging from raptorial to suction feeding, including several transitional forms between both mechanisms (Hocking et al. 2017).

In addition, *K. danomurai* was recovered from levels that also document the oldest records of some extant delphinid and balaenopterid genera (Muizon & DeVries 1985). The cetacean community at Sacaco, featuring both late Miocene and extant genera, probably represents the initial shift of the coastal faunas towards the ecosystem dynamics of the present-day south-eastern Pacific. The late Miocene and early Pliocene marine conditions found in Sacaco indicate that this was a transitional time for the south-eastern Pacific (DO unpub. data). Warmer conditions typical for the Miocene were still present, as evidenced by global data (Dekens et al. 2007; de Boer et al. 2010), along with typical Humboldt conditions such as the presence of a coastal upwelling (Dunbar et al. 1990; Di Celma et al. 2017; DO unpub. data). These conditions could have promoted the proliferation of a wide array of prey, thus benefiting the heterogeneous cetacean assemblage (DO unpub. data).

Finally, the presence of *Kogia danomurai* in Sacaco indicates that the modern genus *Kogia* might have originated in the coastal environments of the south-eastern Pacific; as well as Kogiinae, as evidenced by the presence

of the late Miocene *Koristocetus* (Collareta et al. 2017). The patterning of the facial region of *K. danomurai* indicates that the overall configuration of the forehead organs and soft-tissue structures that are found in extant *Kogia* were already present, although probably less developed in this fossil species. The derived facial configuration of extant *Kogia* spp. could mostly reflect their deep-diving foraging habits, in which they are fully dependent on their echolocating system, or (as a result of evolving narrow-band high-frequency biosonar), a means to escape predation by macroraptorial sperm whales (Galatius et al. 2019) and, more recently, killer whales (Morisaka & Connor 2007).

CONCLUSION

We have described *Kogia danomurai*, a new species of pygmy sperm whale (Kogiidae), on the basis of a fragmentary cranium from the uppermost Miocene (5.8–5.7 Ma) in deposits of the Pisco Formation exposed at the Sacaco locality (southern coast of Peru). Phylogenetic analyses suggest that *Kogia danomurai* is a sister taxon of the Pliocene Italian species *Kogia pusilla* and of the clade formed by the extant dwarf and pygmy sperm whales (*Kogia breviceps* and *Kogia sima*). As such, it constitutes the oldest known record of the genus *Kogia*, thus extending its range into the late Miocene. *Kogia danomurai* is diagnosed on the basis of the following osteological characters: blunt, not transversely compressed antorbital processes; antorbital notch present, but not transformed into a narrow slit; moderately excavated supracranial basin; sagittal crest located medially, but displaced leftwards; and premaxillary fossa located medially, deeper than the rest of the supracranial basin and provided with both a well-defined left wall and a partially developed right one. Our interpretation of the disposition of the facial bony structures indicates that *K. danomurai* and the other fossil kogiids (including the four other extinct species of Kogiinae and Scaphokogiinae that have been described so far from the Pisco Formation), display distinctive arrangement patterns of the bones of the facial region (and, consequently, of the soft-tissue structures as well). Coupled with the different degree of development of several cranial muscles (as highlighted by the attachment sites of the skull), this observation might indicate that these animals evolved different feeding strategies to forage in the shallow water environments of the Peruvian coast during the late Miocene.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural act it contains, have been registered in ZooBank: <http://zoobank.org/References/817802d2-97c5-4f71-b77d-0a0f76e908e4>. Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bzkh1896w>.

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