A new physeteroid from the late Miocene of Peru expands the diversity of extinct dwarf and pygmy sperm whales (Cetacea: Odontoceti: Kogiidae)

Alberto COLLARETA, Olivier LAMBERT, Christian de MUIZON,
Aldo Marcelo BENITES PALOMINO, Mario URBINA & Giovanni BIANUCCI

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Alberto COLLARETA
Dipartimento di Scienze della Terra, Università di Pisa, via Santa Maria 53, 56126 Pisa (Italy)
alberto.collareta@unipi.it (corresponding author)

Olivier LAMBERT
Institut Royal des Sciences Naturelles de Belgique, D.O. Terre et Histoire de la Vie, rue Vautier
29, 1000 Brussels (Belgium)

Christian de MUIZON
Centre de Recherches sur la Paléobiodiversité et les Paléoenvironnements,
CR2P (CNRS, MNHN, UPMC, Sorbonne Université),
Département Origines et Évolution, Muséum national d'Histoire naturelle,
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)

Aldo Marcelo BENITES PALOMINO
Departamento de Paleontologia de Vertebrados, Museo de Historia Natural de la Universidad
Nacional Mayor de San Marcos, avenida Arenales 1256, Lima 14 (Peru)
and Paläontologisches Institut und Museum, Karl-Schmid-Strasse 4, CH-8006 Zürich (Switzerland)
and Center for Tropical Paleoecology and Archeology,
Smithsonian Tropical Research Institute, Balboa, Ancón, 0843-03092, Panama (Panama)

Mario URBINA
Departamento de Paleontologia de Vertebrados, Museo de Historia Natural de la Universidad
Nacional Mayor de San Marcos, avenida Arenales 1256, Lima 14 (Peru)

Giovanni BIANUCCI
Dipartimento di Scienze della Terra, Università di Pisa, via Santa Maria 53, 56126 Pisa (Italy)

ABSTRACT

Nowadays, the odontocete family Kogiidae is monotypic and only includes two species of diminutive relatives of the great sperm whale *Physeter* Linnaeus, 1758. Conversely, a growing body of extinct species indicates that kogiids were diverse and disparate during the late Neogene. The fossil record of Kogiidae is, to date, represented by several cranial specimens from Mio-Pliocene localities of the Northern Hemisphere, with the significant Southern Hemisphere exception of the Pisco Formation of Peru, from which two genera were known so far, including *Scaphokogia* Muizon, 1988, a highly idiosyncratic form characterised by a distinctly spoon-shaped dorsal surface of the neurocranium and a downturned semicylindrical rostrum, which is even placed in its own subfamily Scaphokogiinae. Here, we report on two skulls of Kogiidae from the Messinian (upper Miocene) portion of the Pisco

KEY WORDS
Scaphokogiinae,
Pisco Formation,
East Pisco Basin,
Messinian,
new genus,
new species.

Formation exposed in the East Pisco Basin. These two skulls are referred to the new taxon *Platyscaphokogia landinii* n. gen., n. sp., which our phylogenetic analysis recovers as sister group of *Scaphokogia*, within the subfamily Scaphokogiinae. Although *Platyscaphokogia* n. gen. shares with *Scaphokogia* a remarkably spoon-like dorsal aspect of the neurocranium, it retains a non-pachyostotic, dorsoventrally thin rostrum that distinctly points anteriorly; as such, *Platyscaphokogia* n. gen. might be regarded as testifying an early stage in the evolution of the scaphokogiine cranial anatomy. Morphofunctional and palaeoecological considerations allow for hypothesising that *Platyscaphokogia* n. gen. was a raptorial physeteroid that foraged along the water column in relatively open-sea palaeoenvironments. In conclusion, our finds expand the palaeodiversity of Kogiidae, as well as our knowledge on the late Miocene sperm whales of the southeastern Pacific, and further suggest that the fossil content of the East Pisco Basin is crucial for reconstructing the Neogene evolutionary history of physeteroids.

RÉSUMÉ
Un nouveau physétéroïdé du Miocène supérieur du Pérou augmente la diversité des cachalots nains et pygmées (Cetacea: Odontoceti: Kogiidae) éteints.
La famille d'odontocètes Kogiidae est de nos jours monotypique et ne comprend que deux espèces, parents de petite taille du grand cachalot *Physeter* Linnaeus, 1758. Inversement, un nombre croissant d'espèces éteintes décrites indique que les kogiidés montraient une diversité et une disparité élevées pendant le Néogène tardif. Le registre fossile des Kogiidae est à ce jour représenté par plusieurs spécimens crâniens de localités mio-pliocènes de l'hémisphère nord, à l'exception australe de la Formation Pisco, au Pérou, de laquelle deux genres étaient connus à ce jour, incluant *Scaphokogia* Muizon, 1988, une forme hautement idiosyncratique caractérisée par une surface dorsale du neurocrâne distinctement en forme de cuillère et un rostre en semi-cylindre renversé, qui est placé dans sa propre sous-famille Scaphokogiinae. Nous rapportons ici deux crânes de Kogiidae de la portion messinienne (Miocène supérieur) de la Formation Pisco exposée dans la partie orientale du Bassin Pisco. Ces deux crânes sont référés au nouveau taxon *Platyscaphokogia landinii* n. gen., n. sp., que notre analyse phylogénétique place comme groupe-frère de *Scaphokogia* au sein de la sous-famille Scaphokogiinae. Bien que *Platyscaphokogia* n. gen. partage avec *Scaphokogia* un aspect dorsal du neurocrâne remarquablement en forme de cuillère, ce nouveau genre conserve un rostre non-pachyostotique, dorso-ventralement aplati, et pointu; *Platyscaphokogia* n. gen. pourrait donc être considéré comme témoignant d'un stade précoce de l'évolution de l'anatomie crânienne des scaphokogiinés. Des considérations morphofonctionnelles et paléoécologiques permettent de supposer que *Platyscaphokogia* n. gen. était un physétéroïdé raptorial qui se nourrissait dans la colonne d'eau, dans des paléoenvironnements relativement ouverts. En conclusion, nos découvertes augmentent la paléodiversité des Kogiidae, ainsi que nos connaissances sur les cachalots du Miocène tardif du Pacifique sud-est, et suggèrent en outre que les fossiles de la partie orientale du Bassin Pisco sont cruciaux pour la reconstruction de l'histoire évolutive des physétéroïdés du Néogène.

MOTS CLÉS
Scaphokogiinae,
Formation Pisco,
partie orientale du Bassin Pisco,
Messinien,
genre nouveau,
espèce nouvelle.

INTRODUCTION

The family Kogiidae (Cetacea: Odontoceti: Physeteroidea) is currently represented by two species of physeteroid toothed whales, namely, *Kogia sima* (Owen, 1866) (the dwarf sperm whale) and *Kogia breviceps* (de Blainville, 1838) (the pygmy sperm whale). These small-sized and largely elusive relatives of the great sperm whale *Physeter macrocephalus* Linnaeus, 1758 are known as deep-diving marine mammals that inhabit tropical to temperate open-sea environments worldwide (McAlpine 2017). The fossil record of kogiids is, to date, represented by several skulls and isolated ear bones from Miocene and Pliocene localities of the Northern Hemisphere (e.g. Barnes 1973, 1998; Bianucci & Landini 1999; Bianucci *et al.* 2011; Collareta *et al.* 2019; Lambert 2008; Lambert *et al.* 2017a; Luo & Marsh 1996; Pilleri 1987; Vélez-Juarbe *et al.* 2015, 2016; Whitmore & Kaltenbach 2008), with the significant Southern Hemisphere exception of the late Neogene record from the coastal desert of Peru (Collareta *et al.* 2017a; Di Celma

et al. 2017; Muizon 1988). Indeed, two genera and species of kogiids – namely, *Koristocetus pescei* Collareta, Lambert, Muizon, Urbina & Bianucci, 2017 and *Scaphokogia cochlearis* Muizon, 1988 – are currently known from the upper Miocene portion of the Pisco Formation of southern Peru; whereas the former has been recognized as an early-branching representative of the extant subfamily Kogiinae (Collareta *et al.* 2017a), the latter is a highly idiosyncratic form, characterised by a downturned semicylindrical rostrum and a spoon-shaped dorsal surface of the neurocranium, assigned to its own subfamily Scaphokogiinae (Muizon 1988).

The present paper reports on two skulls of Kogiidae from the Pisco Formation that are here referred to a new genus and species of Scaphokogiinae. These specimens were discovered in upper Miocene beds exposed at the localities of Cerro Hueco la Zorra and Cerro los Quesos, in the East Pisco Basin. An analysis of the phylogenetic relationships of this new taxon and a discussion of its palaeoecological and evolutionary significance are then undertaken.

GEOLOGICAL FRAMEWORK

The East Pisco Basin is a 180-km-long, NW-SE elongated Andean forearc basin that extends along the narrow coastal plain of southern Peru between the towns of Pisco and Nazca, being located just landward of where the aseismic Nazca Ridge impinges on the Peru-Chile trench (Pilger 1981; Hsu 1992; Macharé & Ortlieb 1992; Hampel *et al.* 2004) (Fig. 1A). The sedimentary basin infill comprises, from the oldest to the youngest, the Eocene Caballas and Paracas formations, the Oligo-Miocene Chilcatay Formation, and the Mio-Pliocene Pisco Formation (DeVries 1998, 2017; Dunbar *et al.* 1990). These units are bounded by regionally extensive angular unconformities demarcated by pavements of igneous, pebble- to boulder-sized clasts, which account for periods of subaerial exposure and represent major breaks of the sedimentary history of the East Pisco Basin (DeVries 1998). Therefore, as highlighted by Di Celma *et al.* (2018a), the aforementioned formations might rather be regarded as alloformations (North American Commission on Stratigraphic Nomenclature [NACSN] 2005).

Remains of the new kogiid taxon described herein were collected from upper Miocene beds of the Pisco Formation exposed in the Ica desert (Ica region, southern Peru) (Fig. 1B). The Pisco Formation is a shallow-marine sedimentary unit comprised of conglomerates, sandstones, diatomites, diatomaceous siltstones, volcanic ash beds, and dolomitic horizons, which testify to deposition in a nearshore environment characterised by strong coastal upwelling and high primary productivity conditions (Suess *et al.* 1988; Dunbar *et al.* 1990; Brand *et al.* 2004). Due to the exceptional abundance of fossil vertebrate remains, high diversity and disparity, and remarkable quality of preservation, the Pisco strata cropping out in the Ica desert are widely known as constituting one of the most impressive Cenozoic marine Fossil-Lagerstätten worldwide (e.g., Muizon & DeVries 1985; Lambert *et al.* 2009, 2010, 2015, 2017a, b, 2020; Bianucci *et al.* 2010, 2016a, b, 2019; Brand *et al.* 2011; Esperante *et al.* 2008, 2015; Collareta *et al.* 2015, 2017b; Gariboldi *et al.* 2015; Stucchi *et al.* 2015, 2016; Gioncada *et al.* 2016, 2018a, b; Marx *et al.* 2017a, b; Ramassamy *et al.* 2018; Bosio *et al.* in press). Recent fieldwork in several localities of the Ica desert have led to recognize that the Pisco Formation is comprised of three allomembers, designated P0, P1, and P2 from oldest to youngest, which progressively onlap a composite basal unconformity from southwest to northeast (Di Celma *et al.* 2017, 2018a) (Fig. 1C). Similar to the transgressive sequences that comprise the geologically older Chilcatay Formation (e.g., Di Celma *et al.* 2018b, 2019; Coletti *et al.* 2018), each Pisco allomember is comprised of a coarse-grained lower portion, reflecting deposition along the inshore, that fines upwards into a package of finer offshore sediments (DeVries & Jud 2018; Di Celma *et al.* 2017, 2018a).

Due to the lack of tephra layers and biostratigraphic markers, the depositional age of the P0 allomember was, until recently, very poorly constrained between 18.02 ± 0.07 Ma and 9.00 ±0 .02 Ma (Di Celma *et al.* 2017, 2018b); now however,

new age estimates obtained via strontium isotope (^{87}Sr/^{86}Sr) stratigraphy place the P0 strata in the middle Miocene (14.8-12.4 Ma) (Bosio *et al.* 2020a). The time of deposition of the overlying P1 and P2 allomembers is better constrained thanks to diatom biostratigraphy and calculated Ar-Ar ages (Bosio *et al.* 2019, 2020b; Di Celma *et al.* 2016a, b; Gariboldi *et al.* 2017). These methods concur in indicating that the beds that constitute the P1 allomember were deposited sometime between 9.5 Ma and 8.9 Ma, whereas those that constitute the P2 allomember are younger than 8.5 Ma and older than 6.71 ± 0.02 Ma (Di Celma *et al.* 2017, and references therein).

MATERIAL AND METHODS

ABBREVIATIONS
Institutional abbreviations

IGF	Istituto di Geologia di Firenze (= Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università degli Studi di Firenze), Florence;
IRSNB	Institut royal des Sciences naturelles de Belgique, Brussels;
MBMS	Museo Balseros del Mar del Sur, Salango;
MNHN	Muséum national d'Histoire naturelle, Paris;
MSNC	Museo Civico di Storia Naturale di Comiso, Comiso;
MSNUP	Museo di Storia Naturale dell'Università di Pisa, Calci;
MUSM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima;
MUSNAF	Museo di Storia Naturale dell'Accademia dei Fisiocritici, Siena;
UCMP	University of California Museum of Paleontology, Berkeley;
USNM	National Museum of Natural History, Smithsonian Institution, Washington DC;
ZMA	Zoological Museum Amsterdam, Amsterdam.

Additional abbreviation

c.	character state, as described and numbered in the SOM. For example, 'c. 11[2]' refers to state 2 of character 11 (i.e, two large dorsal infraorbital foramina present in the area of the right antorbital notch and posteriorly).

KOGIID SPECIMENS ANALYSED FOR COMPARISON
AND ANATOMICAL TERMINOLOGY

In addition to MUSM 3291 and MUSM 3405, we have directly examined for comparison the following extinct and extant Kogiidae: *Aprixokogia kelloggi* Whitmore & Kaltenbach, 2008 (USNM 187015); *Kogia breviceps* (de Blainville, 1838) (MBMS 4000; MNHN-ZM-AC-1976-37; USNM 22015, 22559, 22893, 270979, 283625, 302041, 395699, 504314; ZMA 14.817, 14.818); *Kogia pusilla* (Pilleri, 1987) (IGF 1540V); *Kogia sima* (Owen, 1866) (MSNC 3450; MUSNAF Mam410; USNM 550482, 550487, 573734; ZMA 14.765); *Koristocetus pescei* Collareta, Lambert, Muizon, Urbina & Bianucci, 2017 (MUSM 888); *Pliokogia apenninica* Collareta, Cigala Fulgosi & Bianucci, 2019 (MSNUP I-17603); *Praekogia cedrosensis* Barnes, 1973 (UCMP 315229); *Scaphokogia cochlearis* Muizon, 1988 (MNHN.F.PPI229, MUSM 971, MUSM 1998, MUSM 3244); *Scaphokogia* sp. (MUSM 972, MUSM 973);
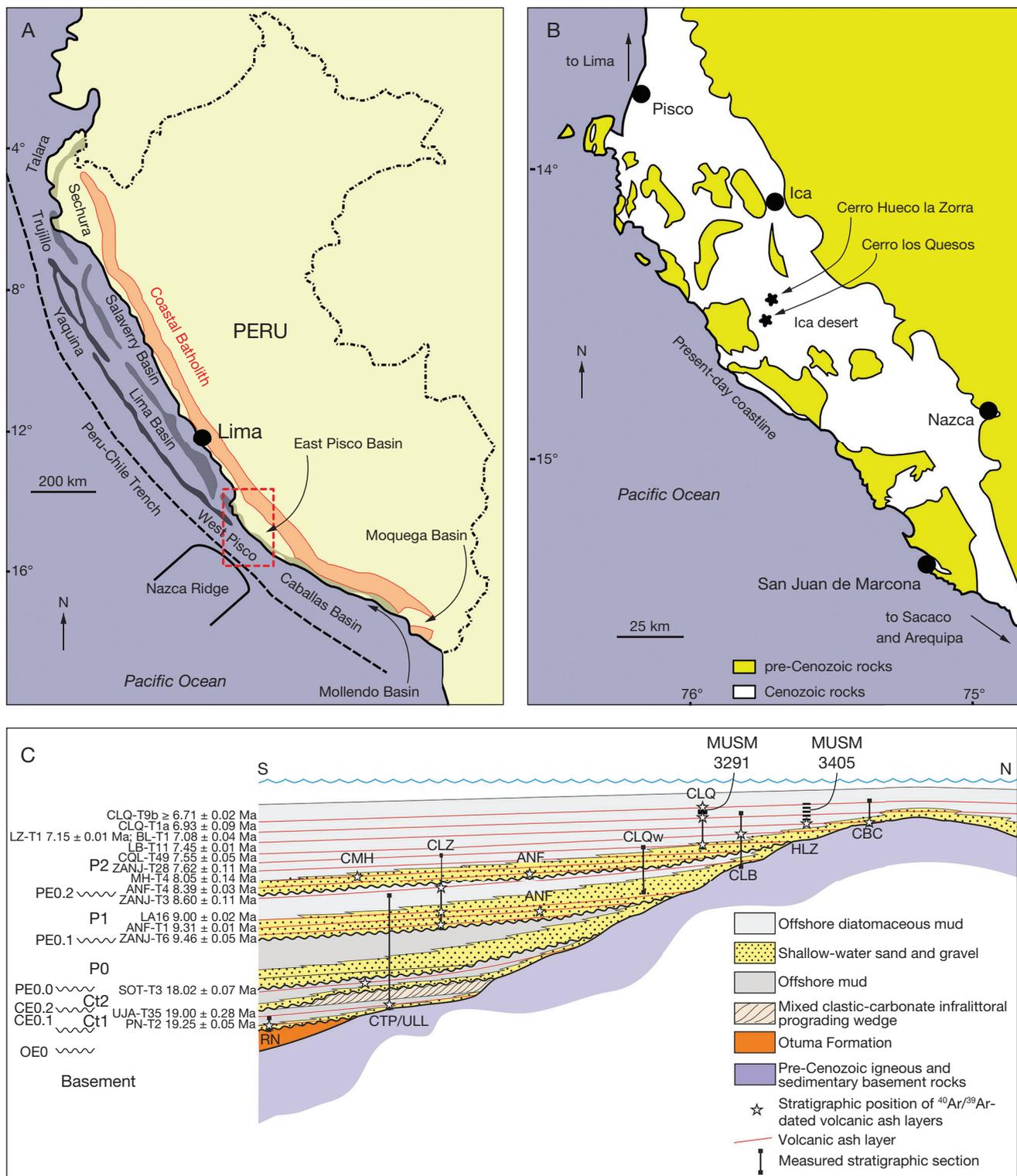
Fig. 1. — **A**, Map of the major structural trends and basins of coastal Peru. The red dashed rectangle outlines the location of the area shown in detail in panel B. Redrawn and modified from Travis *et al.* (1976) and Thornburg & Kulm (1981); **B**, Schematic geological map of the East Pisco Basin, showing the areas of Cenozoic outcrop and the location of the sites where the holotype and paratype of the new physeteroid taxon described herein were found (Cerro Hueco la Zorra and Cerro los Quesos; black stars). Redrawn and modified from DeVries & Schrader (1997); **C**, Schematic, dip-oriented allostratigraphic diagram for the Pisco Formation and the lower Chilcatay and Otuma formations, showing the stratigraphic position of the two kogiid fossils (MUSM 3405 and MUSM 3291) studied in the present work along with ^{40}Ar/^{39}Ar-dated volcanic ash layers (labelled with their field names on the left side of the diagram) and measured stratigraphic sections published in previous works (Bosio *et al.* 2020b, and references therein). The Pisco Formation exhibits pronounced thinning to the northeast, with the allomembers onlapping onto the basal composite surface (PE0.0) and arranged in a retrogradational pattern, progressively offset to northeast. Modified from Bosio *et al.* (2020b).Abbreviations: **RN**, Roca Negra; **CTP**, Cerro las Tres Piramides; **ULL**, Ullujaya; **CMH**, Cerros la Mama y la Hija; **CLZ**, Cerros Cadena de los Zanjones; **ANF**, Anfiteatro; **CLQ**, Cerro los Quesos; **CLQw**, Cerro los Quesos west; **CLB**, Cerro la Bruja; **HLZ**, Cerro Hueco la Zorra; **CBC**, Cerro Blanco.

Thalassocetus antwerpiensis Abel, 1905 (IRSNB M.525). Except when explicitly stated otherwise, the anatomical terminology utilized in the present paper follows Mead & Fordyce (2009).

Phylogenetic analysis
The phylogenetic analysis was undertaken with PAUP* (Swofford 2001), using a modified version of the character/taxon matrix of Collareta *et al.* (2019), where the new kogiid taxon described herein was already present and indicated as "Scaphokogiinae sp." (see the SOM, Supplementary Online Material file, for the list of characters and the character/taxon matrix). Notably, we amended our previous coding for *Diaphorocetus* on the basis of the recent rescoring and redescription provided by Paolucci *et al.* (2019), as well as on further analyses of previous photographs of the holotype. Note also that some undoubtedly valid physeteroid species that are based on fairly incomplete type specimens (e.g., *Ferecetotherium kelloggi* Mchelidze, 1970 and *Albicetus oxymycterus* Boersma & Pyenson, 2015 [Boersma & Pyenson 2015; Mchelidze 1976]) are not included in our character/taxon matrix.

We used the tree-bisection-reconnection algorithm and the heuristic search option for 1000 replicates and one tree saved per replicate. All the characters were considered as unordered and unweighted. We used the definitions proposed by Bianucci & Landini (2006) and then reaffirmed by Lambert *et al.* (2017a) for Physeteroidea, Physeteridae, and Kogiidae. Following Collareta *et al.* (2017a, 2019), we define Kogiinae Gill, 1871, as the most inclusive clade including *Kogia* Gray, 1846 but not *Scaphokogia* Muizon, 1988, whereas we define Scaphokogiinae Muizon, 1988, as the most inclusive clade including *Scaphokogia* but not *Kogia*.

SYSTEMATIC PALAEONTOLOGY

Order CETACEA Brisson, 1762
Clade PELAGICETI Uhen, 2008
Clade NEOCETI Fordyce & Muizon, 2001
Suborder ODONTOCETI Flower, 1867
Superfamily PHYSETEROIDEA Gray, 1821
Family KOGIIDAE Gill, 1871

Subfamily SCAPHOKOGIINAE Muizon, 1988

EMENDED DIAGNOSIS. — Scaphokogiinae are recognized as Kogiidae by the following combination of characters: strongly asymmetric skull in dorsal view; relatively small skull size (i.e., bizygomatic width < 40 cm); presence of a broad supracranial basin that extends over most of the dorsal surface of the neurocranium; external nares greatly asymmetric; absence of both nasals; presence of a sagittal facial crest; and right maxilla reaching the sagittal plane of the skull on the posterior wall of the supracranial basin.
Scaphokogiinae differ from all other kogiids by the following presumed autapomorphies: on the right side of the skull, maxilla-premaxilla suture distinctly anterolaterally directed anterior to the antorbital notch; lateral maxillary crests high, vertical, and plate-like (c. 5[1]); nuchal crest strongly shifted backwards in lateral view; occipital shield flat or concave in lateral view, forming an angle distinctly greater than 90° with the long axis of the rostrum

(c. 30[3]); supracranial basin deep to very deep and spoon-shaped; right anterolateral border of the supracranial basin marked by a distinct supracranial step; absence of distinct premaxillary or peripheral fossae within the supracranial basin; right premaxilla covering a small fraction (i.e., less than ⅓) of the total area of the supracranial basin. They are further diagnosed by the following combination of characters: right premaxilla neither reaching, nor even approaching the occipital crest (shared with *Aprixokogia* Whitmore & Kaltenbach, 2008); presence of discrete dental alveoli on the maxilla (shared with *Aprixokogia*, *Koristocetus* Collareta, Lambert, Muizon, Urbina & Bianucci, 2017 and, possibly, *Pliokogia* Collareta, Cigala Fulgosi & Bianucci, 2019; condition unknown in *Praekogia* and *Thalassocetus* Abel, 1905); antorbital notches not opening onto the supracranial basin (shared with *Aprixokogia* and *Thalassocetus*); antorbital notches forming a narrow slit (shared with *Nanokogia* Vélez-Juarbe, Wood, De Gracia & Hendy, 2015, *Kogia*, *Koristocetus*, *Pliokogia* and, possibly, *Praekogia* Barnes, 1973); lateral maxillary crests mediolaterally thin (shared with *Koristocetus*, *Nanokogia* and *Praekogia*); posterodorsal corner of the lacrimojugal complex shaped as a pointed process that wedges between the maxilla and the frontal (shared with *Kogia*, *Nanokogia*, *Pliokogia*, and *Praekogia*; condition unknown in *Thalassocetus*); and presphenoid not covered by the vomer in ventral view (shared with *Aprixokogia*, *Kogia*, *Nanokogia*, and *Pliokogia*; condition unknown in *Thalassocetus*).

Platyscaphokogia n. gen.

urn:lsid:zoobank.org:act:F764D6F6-9E50-4CA8-8205-941A2E7CE7E9

ETYMOLOGY. — From the combination of the Ancient Greek adjective "platús" (πλατύς), meaning "flat", with "*Scaphokogia*", i.e., the name of the type genus of Scaphokogiinae, for highlighting the dorsoventrally flattened morphology of the rostrum of the new form. Gender feminine.

TYPE AND ONLY KNOWN SPECIES. — *Platyscaphokogia landinii* n. gen., n. sp.

DIAGNOSIS. — Same as for the type species until other species are described.

KNOWN RANGE. — Late Miocene (Messinian) of southern Peru.

Platyscaphokogia landinii n. sp.
(Figs 2-6; 8A)

urn:lsid:zoobank.org:act:FC3BE988-0F09-4262-911C-5B50070D1B97

ETYMOLOGY. — The specific name honours Walter Landini, Italian vertebrate palaeontologist, for his substantial contribution to the knowledge and understanding of both the Miocene vertebrate assemblages of the East Pisco Basin (e.g., Landini *et al.* 2017a, b, 2019) and the Italian fossil record of physeteroids (e.g., Bianucci & Landini 1999, 2006).

HOLOTYPE. — MUSM 3405, an incomplete skull lacking the tip of the rostrum and the basicranium.

PARATYPE. — MUSM 3291, an incomplete skull, preserving only the rostrum and the right portion of the neurocranium.

TYPE LOCALITY. — The holotype was found at Cerro Hueco la Zorra, Ica desert, *c.* 30 km south of the town of Ica, southern coast of Peru (Fig. 1B); geographic coordinates of the finding site: 14°26'44.35"S, 75°42'24.05"W.

Table 1. — Measurements (in mm) of the skulls of *Platyscaphokogia landinii* n. gen., n. sp., from the upper Miocene of the Pisco Formation (East Pisco Basin, southern Peru). Estimated dimensions are preceded by '*e*'.

	MUSM 3405 (holotype)	MUSM 3291 (paratype)
Maximum preserved length of skull	550	395
Length of rostrum	300	270
Width of rostrum at base	158	167
Height of rostrum at base	70	–
Width of rostrum at mid length	106	120
Height of rostrum at mid length	45	53
Width of rostrum at ¾ length, measured from posterior end	70	79
Height of rostrum at ¾ length, measured from posterior end	39	42
Width of mesorostral groove at apex of rostrum	38	37
Maximum width of dorsal opening of mesorostral groove posterior to dorsomedial contact between premaxillae along rostrum	23	28
Distance from tip of rostrum to right external naris	320	e290
Greatest preorbital width	e250	e245
Least supraorbital width	235	e235
Greatest postorbital width	e255	e250
Width of left external bony naris	16	–
Width of right external bony naris	11	–
Greatest width across external bony nares	38	–
Greatest width across premaxillae	89	–
Width across premaxillae at mid length of rostrum	63	62

Type horizon. — The holotype was found in deposits belonging to the silty upper portion of the P2 allomember of the Pisco Formation (as defined by Di Celma *et al.* 2017, 2018a) (Fig. 1B, C). Stratigraphically, MUSM 3405 is located between the P2-8 and the P2-9 horizons of Di Celma *et al.* (2017, 2018a), which are prominent and laterally continuous ledges at the top of sheer cliff faces. At the nearby locality of Cerro Blanco, a tephra layer placed just below the P2-8 horizon has been recently dated to 7.084 ± 0.044 Ma by means of Ar-Ar radiometric analyses (Bosio *et al.* 2020b). An age younger than 7.084 Ma is thus proposed for the horizon from which the holotype was collected. Considering also that no marine deposit younger than the Miocene is known from the western side of the lower Ica valley, MUSM 3405 is here regarded as Messinian (latest Miocene) in age.

Locality and horizon of the paratype. — The paratype was found at Cerro los Quesos (Ica desert, *c.* 50 km south of the town of Ica, southern coast of Peru (Fig. 1B, C); geographic coordinates of the finding site: 14°30'54.00"S, 75°43'08.90"W), in deposits belonging to the P2 allomember of the Pisco Formation. MUSM 3291 was indicated with the field number O14 and identified as belonging to "aff. *Scaphokogia* sp." in the fossil map published by Bianucci *et al.* (2016a). The horizon from which the paratype was collected belongs to the stratal package known as "Member F" (Di Celma *et al.* 2016a), within the silty upper portion of the P2 allomember; it is further located *c.* 35 m above a tephra layer, the Mono key bed of Di Celma *et al.* (2016a), that has been dated to 6.93 ± 0.09 Ma by means of Ar-Ar radiometric analyses. A stratigraphically higher volcanic ash bed, cropping out in the uppermost portion of the Cerro Los Quesos succession (i.e., 17 m above the paratype), has been dated to an age equal or older than 6.71 ± 0.02 Ma (Di Celma *et al.* 2016a). As such, the horizon from which the paratype originates can be constrained to a short time interval within the Messinian, i.e., between 6.93 Ma and 6.71 Ma. Such an age estimate finds support in the biostratigraphic data, which indicate an age younger than 7.35 Ma for this portion of Member F (Gariboldi *et al.* 2017).

Several fossil vertebrates from Cerro Los Quesos were found in strata belonging to Member F, including mysticetes (balaenopterids and cetotheriids), odontocetes (e.g., the holotype of the beaked whale *Chavinziphius maxillocristatus*, the macroraptorial stem physeteroid *Acrophyseter* sp., and the phocoenid cf. *Lomacetus ginsburgi*), pinnipeds, crocodiles, seabirds, and sharks (Bianucci *et al.* 2016a, b; Lambert *et al.* 2017a).

Differential diagnosis. — *Platyscaphokogia landinii* n. gen., n. sp. differs from *Scaphokogia cochlearis* by the following combination of characters: in dorsal view, skull roughly drop-shaped, due to the remarkable tapering of the rostrum towards the anterior tip of the skull; sagittal facial crest longer, less displaced laterally, dividing the supracranial basin in two different sub-basins; supracranial basin moderately shallower and slightly more anterodorsally oriented; in lateral view, rostrum vertically much thinner (i.e., dorsoventrally compressed) and not exceeding in height the lateral maxillary crests at its base; long axis of the rostrum projecting anteriorly rather than anteroventrally; in ventral view, presence of larger, well-individualised, likely functional upper dental alveoli (right maxilla presenting 10 alveoli).

Description, comparisons, and remarks

The following description is based on the holotype, unless otherwise specified.

General outline of the cranium

The holotype skull (MUSM 3405; Figs 2-5) is incomplete, lacking the basicranium, part of the floor of the supracranial basin (coinciding with the circumnarial basin of Mead & Fordyce 2009; the former term is here preferred for consistency with several recent works on the skull anatomy of extinct kogiids), all the ear bones, the mandibles, and all the teeth. Both the dorsal and the ventral aspects of the cranium are generally well preserved, although a few delicate features (e.g., the thin, plate-like lateral maxillary crests and the medial halves of the premaxillae along the rostrum) are locally broken or abraded and some regions of the cranium (e.g., the narrow antorbital notches and most of the mesorostral groove) are covered or infilled by hardened sediment. Unambiguous evidence of diagenetic deformation is not found on MUSM 3405, and even the most delicate features (e.g., thin and salient bony walls such as the lateral maxillary crests and the sagittal facial crest) do not appear to have significantly suffered compaction, displacement, or distorsion. The paratype cranium (MUSM 3291; Fig. 6) is distinctly less complete, only preserving the rostrum, the anterolateral portion of the supracranial basin, and the right supraorbital region. Abrasion and weathering are ubiquitous on this skull, except for the well-preserved supraorbital region; moreover, hardened sediment infills most of the mesorostral groove. Sutures between adjacent bones are generally not distinguishable on this specimen, with the significant exception of the right supraorbital region, where the relationships between the maxilla, lacrimojugal complex, and frontal are clear.

The skull of *Platyscaphokogia* n. gen. is anteroposteriorly elongated and distinctly teardrop-shaped (Figs 2; 3), thus
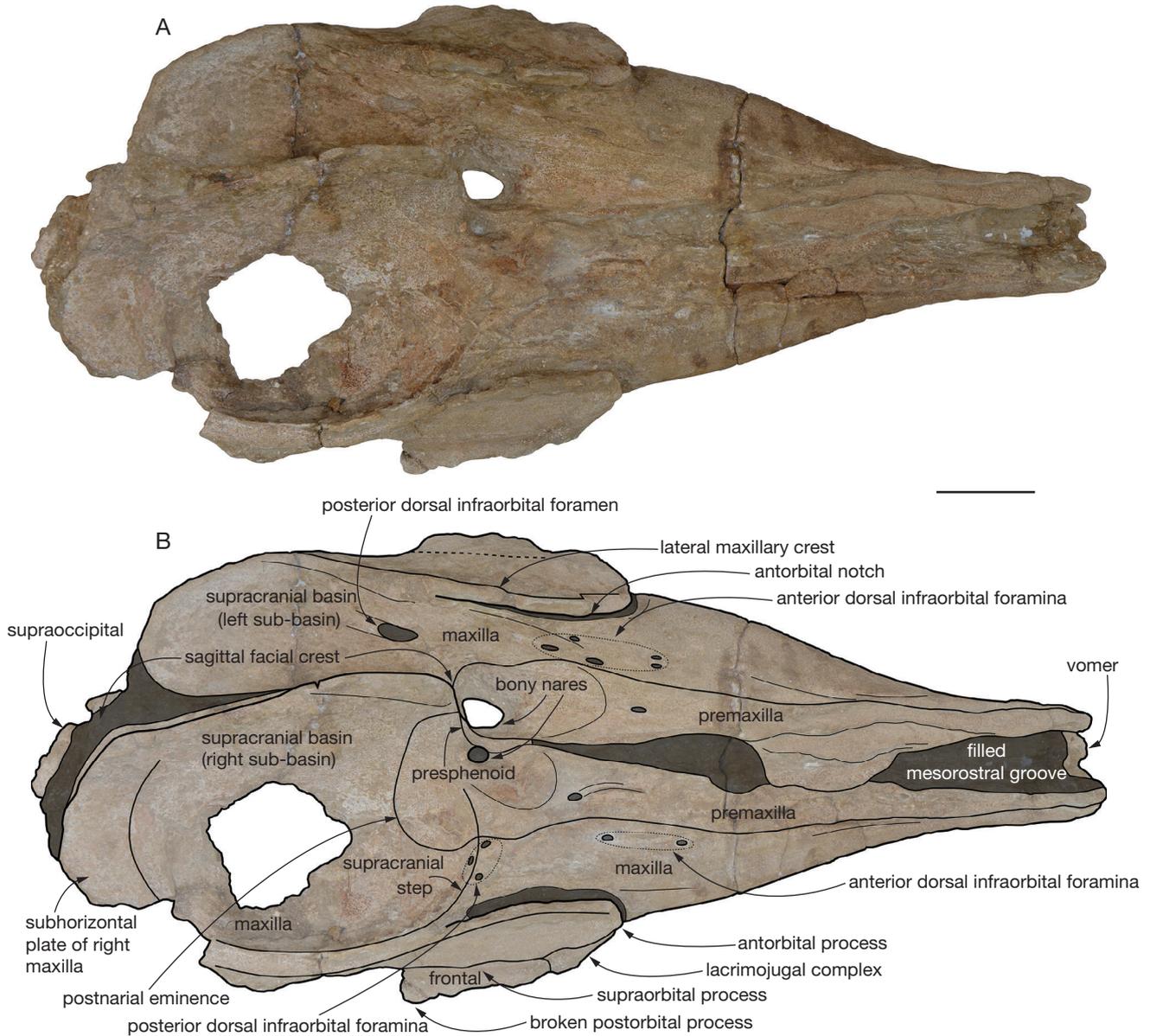
FIG. 2. — Cranium, in dorsal view, of the kogiid sperm whale *Platyscaphokogia landinii* n. gen., n. sp. (MUSM 3405, holotype), from the upper Miocene of the Pisco Formation (East Pisco Basin, southern Peru). **A,** photograph; **B,** corresponding explanatory line drawing. The grey-shaded areas correspond to hardened sediment. The dashed line approximates the position of the maxilla-frontal suture. Scale bar: 5 cm.

strongly differing from the shorter and wider skull of extant *Kogia*. It is also strongly asymmetric, as highlighted by the presence of bony nares that are dissimilar in size (i.e., the right naris is much smaller than the left one) and significantly displaced towards the left side of the cranium (Figs 2, 5). Both nasals are absent (Figs 2, 5); the same condition is observed in all kogiids known to date. The dorsal surface of the neurocranium is distinctly concave, forming a wide supracranial basin (a diagnostic character of physeteroids) that is crossed by a sagittal facial crest (a key feature of Kogiidae) formed by the coalescence of the medial margin of the right maxilla with the upturned medial margin of the left maxilla posterior to the bony nares (Figs 2, 5). The dorsal and ventral aspects of the skull are strongly reminiscent of those of *Scaphokogia*, the most obvious differences between these two genera being

in the degree of tapering of the rostrum (almost negligible in *Scaphokogia*, conspicuous in *Platyscaphokogia* n. gen.) and in the length and position of the sagittal facial crest (short and appressed to the left margin of the supracranial basin in *Scaphokogia*, longer and located more medially in *Platyscaphokogia* n. gen.) (Muizon 1988; Figs 2, 3). The lateral view highlights further major differences between the crania of these two genera: for instance, whereas in *Scaphokogia* the rostrum is deflected downwards, dorsoventrally high, and clearly exceeds in height the lateral maxillary crests at its base, the rostrum of *Platyscaphokogia* n. gen. is roughly oriented horizontally, not inflated dorsoventrally, and its dorsalmost portion is located distinctly ventral to the highest point of the lateral maxillary crests (Fig. 4). Nonetheless, even in lateral view, the skulls of these two genera still exhibit clear affinities,
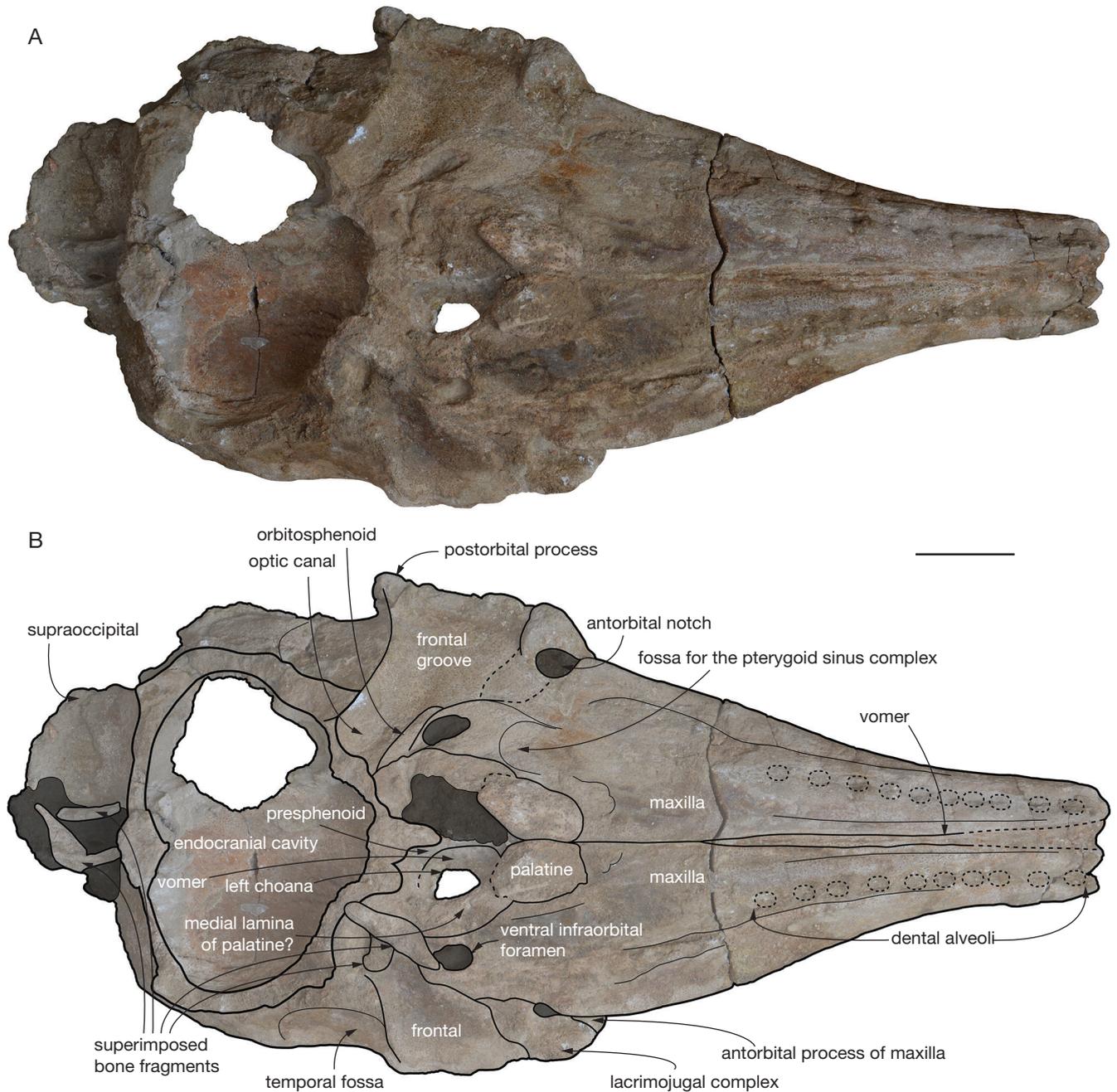
FIG. 3. — Cranium, in ventral view, of the kogiid sperm whale *Platyscaphokogia landinii* n. gen., n. sp. (MUSM 3405, holotype), from the upper Miocene of the Pisco Formation (East Pisco Basin, southern Peru). **A,** photograph; **B,** corresponding explanatory line drawing. The grey-shaded areas correspond to hardened sediment. The dashed line approximates the position of several sutures and borders. Scale bar: 5 cm.

as highlighted by the observation of a concave upper portion of the occipital shield that forms an angle distinctly greater than 90° with the long axis of the rostrum, as well as by the peculiar morphology of the supraorbital region (Figs 4, 6C).

Skull measurements of MUSM 3405 and MUSM 3291 are reported in Table 1.

Premaxilla

In dorsal view (Fig. 2), the premaxillae appear as two bands of bone running subparallel to the long axis of the skull medial to the maxillae. All along the rostrum, the lateral margins of the maxillae are slightly wavy and converge very weakly towards the anterior termination of the skull. Medial to the premaxillae, the mesorostral groove dorsally opens approximately 35 mm anterior to the level of the posterior end of the bony nares. The dorsal opening of the mesorostral groove progressively widens forwards, as the medial borders of the premaxillae weakly diverge from each other. Consequently, in the posterior half of the rostrum, the mesorostral groove is more widely open dorsally than in *Nanokogia* and, especially, *Scaphokogia*. At about mid-length of the rostrum, the left premaxilla contacts and seemingly slightly overhangs the
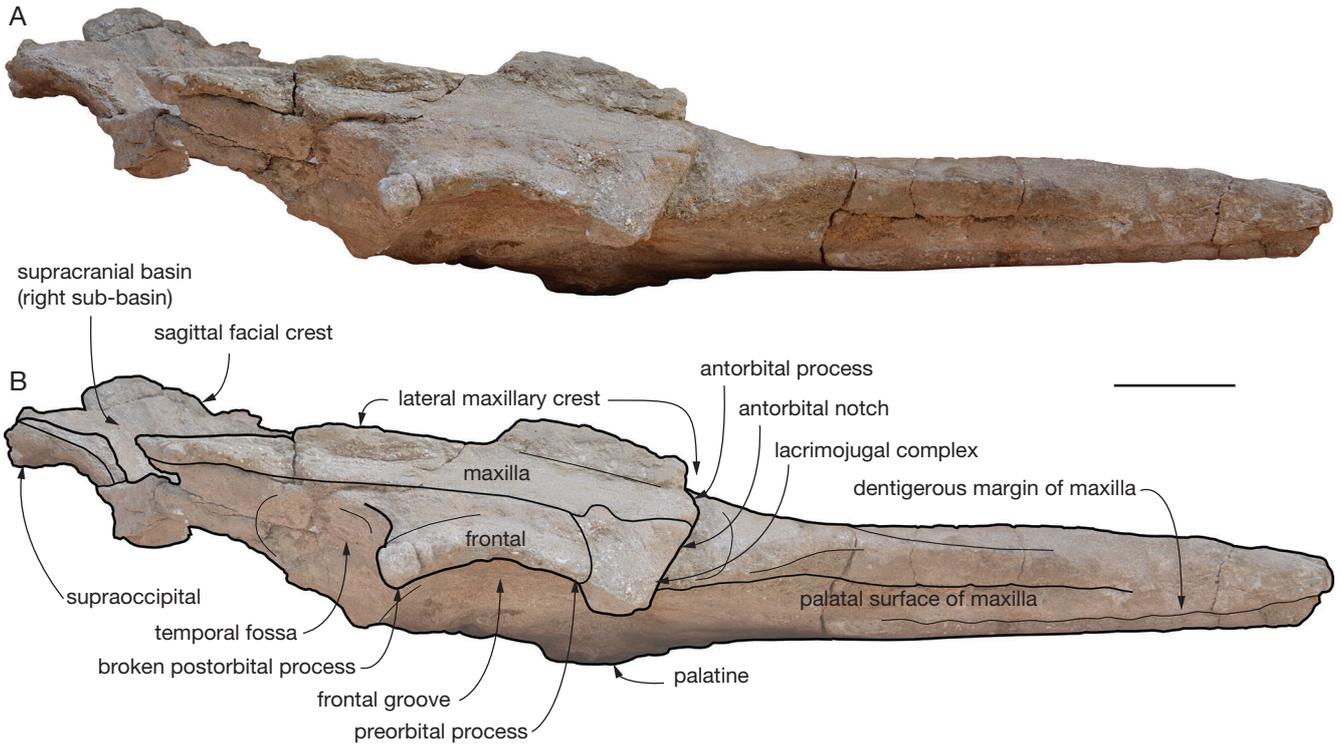
Fɪɢ. 4. — Cranium, in right lateral view, of the kogiid sperm whale *Platyscaphokogia landinii* n. gen., n. sp. (MUSM 3405, holotype), from the upper Miocene of the Pisco Formation (East Pisco Basin, southern Peru). **A**, photograph; **B**, corresponding explanatory line drawing. Scale bar: 5 cm.

medial margin of its right antimere, thus roofing dorsally the mesorostral groove for *c.* 50 mm; this feature is reminiscent of the condition observed in *Scaphokogia*, where overlapping of the premaxillae occurs closer to the base of the rostrum (Muizon 1988). In this region, the transverse width of the left premaxilla is roughly twice that of its right homologue; otherwise, the two premaxillae are subequal in width all along the rostrum. Anterior to the area of overlapping, the medial borders of the premaxillae weakly diverge again, thus causing the mesorostral groove to reach its maximum transverse width (*c.* 40 mm) at the apex of the rostrum. In the posterior half of the rostrum, each premaxilla is transversely narrower than the corresponding maxilla, whereas in the anterior half of the rostrum the width of each premaxilla is equal or greater than that of the corresponding maxilla. Anterior to the antorbital notch, the dorsal surface of the right premaxilla is generally flat, turning gently convex transversely close to the anterior-most tip of the rostrum. A similar condition is observed on the left premaxilla; however, the latter exhibits a transversely concave dorsal surface in proximity of the corresponding naris. Differing from *Aprixokogia, Kogia breviceps, Kogia pusilla, Koristocetus, Nanokogia,* and *Pliokogia,* a premaxillary foramen is present on the left premaxilla, at roughly the same level as the anterior termination of the antorbital notches. The right premaxillary foramen is placed at a slightly more posterior level than the left and is followed anteriorly by a deep, 30 mm long groove extension. Both the left and the right premaxillary foramina are anteroposteriorly elongated, *c.* 8 mm long and 4 mm wide. The external bony nares are located at the level of the posterior end of the antorbital

notches. As observed in all physeteroids, the bony nares are distinctly asymmetrical, dissimilar in size, and displaced leftwards (Figs 2, 5). The left naris is 22 mm long and 16 mm wide; it takes place in a funnel-shaped, anteroposteriorly oriented depression (a condition reminiscent of *Kogia* spp., *Koristocetus,* and *Pliokogia*). The rounded posterior end of the left premaxilla is located just behind the posterior wall of the left naris. The right naris is 13 mm long and 12 mm wide; it is also placed at the bottom of a funnel-like depression and its anterior, lateral, and posterior walls are formed by the right premaxilla. As in all kogiids known to date, posterior and posterolateral to the right bony naris, the right premaxilla exhibits a lobe-shaped expansion (the postnarial eminence, sensu Whitmore & Kaltenbach 2008) that enters the right portion of the supracranial basin (see description of the maxilla below). Differing from most other kogiids but *Scaphokogia,* the postnarial eminence constitutes here a small fraction (i.e., less than $\frac{1}{5}$) of the total area of the supracranial basin (Fig. 2). The right premaxilla does not reach the posterior margin of the supracranial basin, its distal termination being located at the level of the left posterior dorsal infraorbital foramen. As observed in *Scaphokogia,* the posteromedial portion of the postnarial eminence contacts the presphenoid and the right maxilla, thus contributing to the anteriormost part of the sagittal facial crest (see description of the maxilla below); in all other kogiids known to date, a much larger portion of the sagittal facial crest is contributed by the right premaxilla. Differing from all kogiids but *Nanokogia* and *Scaphokogia,* no distinct fossa takes place on the postnarial eminence, either within the borders of the right premaxilla (e.g., *Kogia breviceps,*

Fig. 5. — Cranium, in anterodorsal view, of the kogiid sperm whale *Platyscaphokogia landinii* n. gen., n. sp. (MUSM 3405, holotype), from the upper Miocene of the Pisco Formation (East Pisco Basin, southern Peru); close-up of the dorsal surface of the neurocranium. Scale bar: 5 cm.

K. sima, *Koristocetus*, and *Thalassocetus*) or affecting both the right premaxilla and maxilla (e.g., *Praekogia*). Differing from the condition observed in the living species of *Kogia*, the premaxillae are not exposed on the ventral surface of the skull.

Maxilla

Both maxillae reach the anterior end of the skull. In dorsal view (Fig. 2), throughout the rostrum, the lateral margins of the maxillae point anteromedially, with a marked constriction at about three fifths of the total rostrum length, thus recalling the condition observed in *Koristocetus* and *Nanokogia*. Along the rostrum, the dorsal surfaces of both maxillae are flat to

weakly convex and roughly subhorizontal. In dorsal view, the antorbital notch is deep and narrow (i.e., slit-like), and *c.* 75 mm long on both sides of the skull; in extent and morphology, it is strongly reminiscent of the condition in *Scaphokogia*. Both antorbital notches are set completely outside of the supracranial basin (Figs 2, 5), thus differing from the derived condition that characterises all the members of the subfamily Kogiinae. Lateral to the antorbital notch, the lateral maxillary crest is shaped as a transversely thin, dorsally high, plate-like stripe of bone that runs almost parasagittally. On the right side of the holotype skull, the lateral maxillary crest has a thickness ranging from *c.* 5 to 10 mm and reaches a maximum
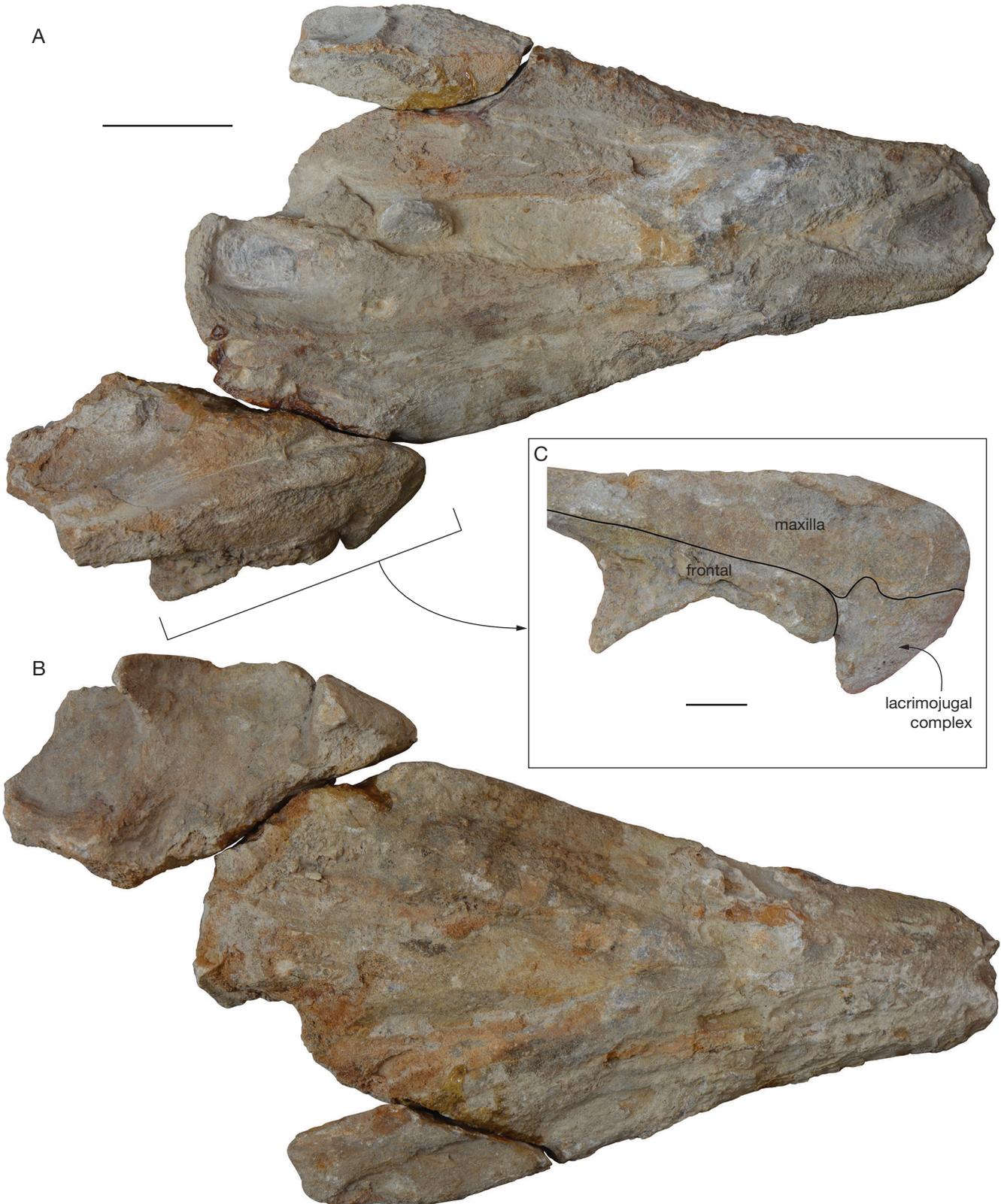
FIG. 6. — Cranium of the kogiid sperm whale *Platyscaphokogia landinii* n. gen., n. sp. (MUSM 3291, paratype), from the upper Miocene of the Pisco Formation (East Pisco Basin, southern Peru): **A**, dorsal view; **B**, ventral view; **C**, right lateral view (close-up of the supraorbital region, with indication of bones and sutures). Scale bars: A, B, 5 cm; C, 2 cm.

height of 22 mm at mid length of the corresponding antorbital notch. The vertical, sharp maxillary crest of *Platyscaphokogia* n. gen. contrasts with the greatly thickened crest of extant

Kogia, being in turn strongly reminiscent of the condition observed in *Scaphokogia*. At the level of the bony nares, similar to *Scaphokogia*, the dorsal surface of the right maxilla

exhibits a very abrupt change in steepness, forming an almost right angle along an anteromedially oriented line. For this feature, which extends to the lateral half of the right premaxilla, the name "supracranial step" is here proposed. A supracranial step is also present in *Scaphokogia* and constitutes a synapomorphy of Scaphokogiinae. Just posterior to the supracranial step, the dorsal surface of the right maxilla faces posterodorsally: therefore, the supracranial step marks the right anterolateral border of the supracranial basin, the latter not extending into the rostrum (a condition reminiscent of *Koristocetus*, *Nanokogia*, *Pliokogia*, and *Scaphokogia*). Similar to *Scaphokogia*, the supracranial basin is large, spoon-shaped, floored by the maxillae (except for a small area that comprises the postnarial eminence of the right premaxilla), and expanded posteriorly (so that its posterior border overhangs the occipital region) and towards the left side of the cranium; with respect to the supracranial basin of *Scaphokogia*, however, the supracranial basin of *Platyscaphokogia* n. gen. is shallower and faces slightly more anterodorsally. The supracranial basin is divided in two parts, hereinafter referred to as the right and the left sub-basins, by the presence of a sagittal facial crest, which represents a synapomorphy of Kogiidae. The right and left sub-basins of *Platyscaphokogia* n. gen. are clearly homologous to similar depressions observed on the dorsal surface of the neurocranium of living kogiids and known as the right and left maxillary fossae (Thornton *et al.* 2015), which correspond to the right and left facial fossae of Mead & Fordyce (2009). However, the facial fossa is defined as the concave surface of the ascending process of the maxilla that lies between the nasal process of the premaxilla and the supraorbital margin of the maxilla (Mead & Fordyce 2009, and references therein). As the depression that comprises the right portion of the supracranial basin of the scaphokogiines extends also over part of the right premaxilla, here we prefer to refer to this feature and to the corresponding depression of the left half of the skull using the term sub-basin. Differing from the condition observed in extant *Kogia*, however, the right sub-basin of *Platyscaphokogia* n. gen. also extends over the posterodorsal portion of the right premaxilla; therefore, for purposes of clarity, here we prefer not to use the term "maxillary fossa". The posterior termination of the sagittal facial crest is placed where the posterior border of the supracranial basin meets the sagittal plane; from this level forwards, the sagittal facial crest runs anterolaterally to end anteriorly at the posteriormost level of the bony nares. In this respect, *Platyscaphokogia* n. gen. thus differs from *Scaphokogia*, where the sagittal facial crest is much shorter, more strongly displaced leftwards (thus strongly limiting the areal extent of the right sub-basin), and distinctly anteromedially oriented. Both the anterior (i.e, subvertical) and the dorsal (i.e. subhorizontal) edges of the sagittal facial crest are sharp, thin and straight; in dorsal view, they form a rounded angle of *c.* 90° at their junction. Throughout its length, the sagittal facial crest dips rightwards and partially overhangs the left sub-basin. The latter is anteroposteriorly elongated, tongue-shaped, and its floor is located at a higher dorsoventral level than the floor of the right sub-basin. The deeper right sub-basin has a roughly

oval outline, its medial and lateral boundaries being made by the flat, rightwards dipping dorsolateral surface of the sagittal facial crest and the vertical medial surface of the right maxillary crest, respectively. Posteriorly, the border of the right sub-basin is marked by a subhorizontal bony plate, displaying a maximum anteroposterior breadth of *c.* 20 mm, formed by the posteriormost portion of the ascending process of the right maxilla. The function of such an idiosyncratic feature is substantially obscure, as it might be interpreted either as an area of origin for some facial muscles or as providing insertion for the organs of the forehead. Interestingly, in *Physeter* Linnaeus, 1758, Heyning (1989) described a large right longitudinal muscle originating from the right portion of the occipital crest and inserting on the "museau de singe" (i.e., the phonic lips region) and right blowhole. It seems thus reasonable to hypothesise that the subhorizontal bony plate that comprises the posterior border of the right sub-basin of *Platyscaphokogia* n. gen. was the area from which a powerful and efficient right longitudinal muscle originated – an interpretation that evokes the presence of a highly specialized echolocation system. Although the central portion of the floor of the right sub-basin is missing, the lowermost point of the dorsal exposure of the maxillae should have been located in this area, thus recalling *Scaphokogia* in this respect. Similar to *Scaphokogia*, but differing from all other kogiids known to date, no distinct premaxillary/supracranial fossa (sensu Barnes 1973 and Vélez-Juarbe *et al.* 2015) or peripheral maxillary fossa (sensu Collareta *et al.* 2019) is observed within the borders of the supracranial basin; this condition represents a synapomorphy of Scaphokogiinae. In the light of the interpretation of the above fossae proposed by Thornton *et al.* (2015) and Collareta *et al.* (2019), the position of the melon and spermaceti organs that take place above these structures cannot be resolved for *Platyscaphokogia* n. gen. and *Scaphokogia*; it is likely, however, that the spermaceti organ of Scaphokogiinae was larger than that of extant Kogiinae and displaced backwards, as suggested by the posterior extension of the supracranial basin (Muizon 1988). On the left maxilla, a single posterior dorsal infraorbital foramen is observed within the left sub-basin, at the level of the base of the postorbital process (preserved on the right side). Similar to *Scaphokogia*, this foramen is large, elliptical, 19 mm long and 8 mm wide, and roughly parallels the left border of the supracranial basin; it is followed posterolaterally by a 15 mm long groove extension. In extant *Kogia*, the left posterior dorsal infraorbital foramen is commonly subdivided (e.g., duplicated), and a similar condition is observed in *Aprixokogia* and *Nanokogia*. Five left anterior dorsal infraorbital foramina are also observed anterolateral to the bony nares (Fig. 2). They are small, fissure-like (i.e., they range between 6 and 11 mm in length and between 2 and 4 mm in width), elongated parallel to the suture between the maxilla and the premaxilla, and are in the medial half of the dorsal surface of the bone. Three of these foramina are located medial to the lateral maxillary crest and, out of them, two take place within the funnel-shaped depression that hosts the left bony naris, close to the maxilla-premaxilla suture. The remaining two left anterior dorsal
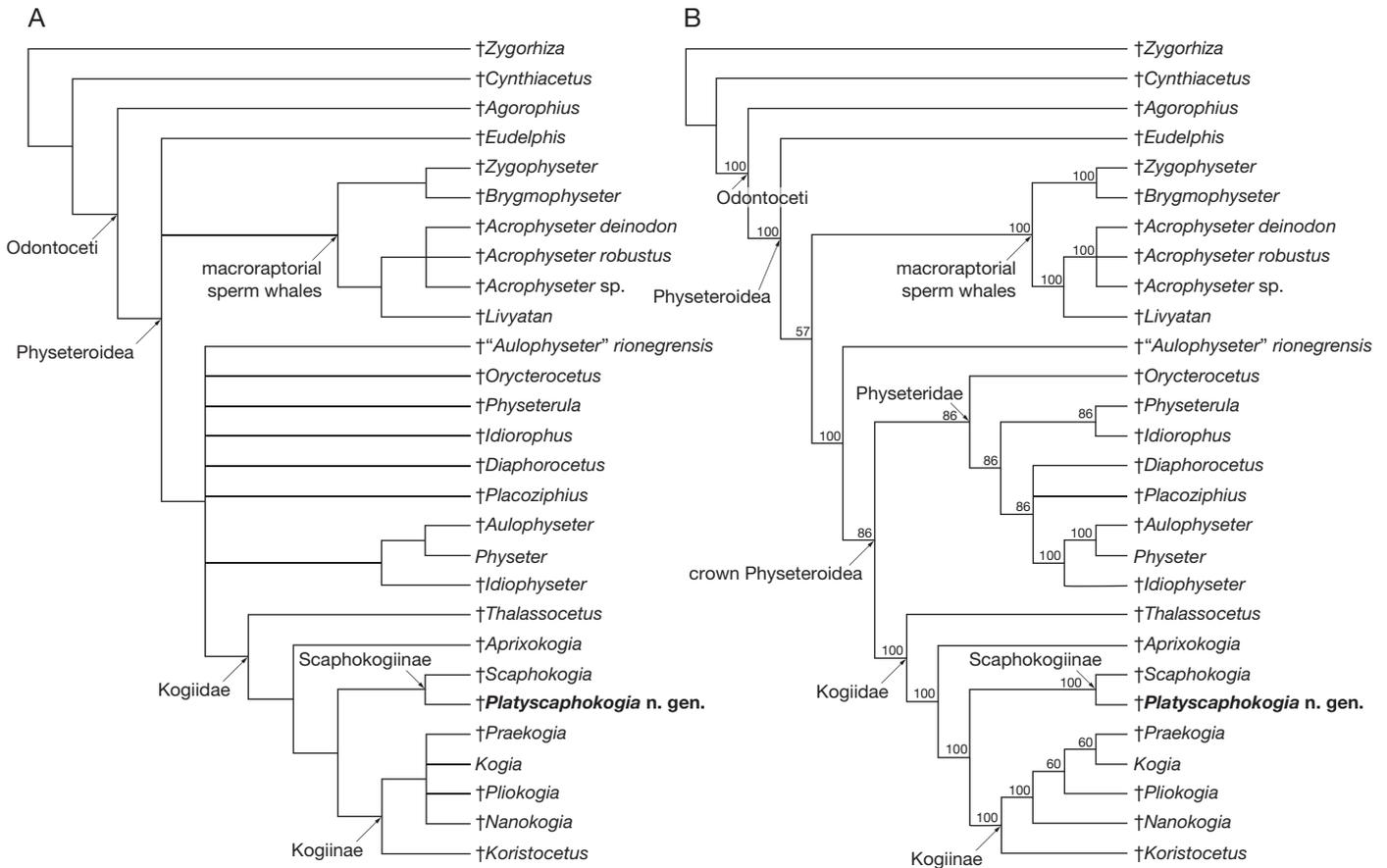
F<small>IG</small>. 7. — Phylogenetic relationships of *Platyscaphokogia landinii* n. gen., n. sp. with other physeteroid odontocetes. **A**, strict consensus tree; **B**, 50% majority-rule consensus tree (the numbers associated with the nodes show the frequencies of occurrence). *Acrophyseter* sp. refers to MUSM 2182, a partial skull from the site of Cerro Los Quesos (upper Miocene, Pisco Formation, Peru) resulting from our cladistic analysis. Extinct genera and species are marked by a dagger (†). See the SOM, Supplementary Online Material file, for further details.

infraorbital foramina are located anteromedial to the anteriormost point of the left antorbital process. No groove extensions are associated to the left anterior dorsal infraorbital foramina. In *Scaphokogia*, the left anterior dorsal infraorbital foramen lies anterior to the antorbital notch, whereas several openings are present in the same region in the skull of extant *Kogia*. On the right maxilla, across the supracranial step, a cluster of three small posterior dorsal infraorbital foramina is observed. One of these openings is located just posterior to the supracranial step, where the maxilla exhibits a posterodorsally oriented surface; it is roughly circular, with a diameter of *c.* 8 mm. On the anterior side of the supracranial step, one circular foramen having a diameter of *c.* 5 mm is observed at mid width of the exposure of the maxilla medial to the lateral maxillary crests. A third foramen of similar size is present, at approximately the same anterodorsal level, appressed to the locally concave lateral margin of the right premaxilla. Two anterior dorsal infraorbital foramina are also observed on the rostral surface of the right maxilla. Both these foramina are ellipitical, anteroposteriorly elongated, *c.* 7 mm long and 4 mm wide, and located in proximity of the maxilla-premaxilla suture. None of the right dorsal infraorbital foramina exhibits a groove extension. The pattern of the right dorsal infraorbital foramina of *Platyscaphokogia* n. gen. closely

resembles that of *Scaphokogia*, in which multiple small-sized openings are observed, along the right maxilla, between the anterior portion of the supracranial basin and a level slightly anterior to the base of the rostrum.

In lateral view (Fig. 4), the ventral margin of the maxilla on the rostrum is substraight and not deflected downwards, thus departing from the clinorhynchy that characterises the skull of *Scaphokogia*. The maxillary flange, which is laterally hidden by the adjoining lateral maxillary crest, parallels the long axis of the rostrum. Anterior to the antorbital notch, the lateral surface of the maxilla is high, appressed to the right antorbital process, and dips laterally, whereas the ventral surface of the maxilla is regularly convex. From a short distance from the antorbital process forwards, the lateral margin of the maxilla is thinner dorsoventrally and somewhat keeled. In the anteriormost third of the rostrum, the lateral margin of the maxilla becomes regularly rounded in cross section.

In ventral view (Fig. 3), ten well-individualised dental alveoli are observed on the palatal surface of each maxilla, starting 90 mm anterior to the anterior margin of the palatines forwards. They are located roughly at mid distance between the lateral margin of the rostrum and the suture between the maxilla and the vomer. Medial to the alveolar row, the palatal surface of the maxilla is distinctly convex

transversely, thus forming a keel that tapers forwards; lateral to the alveolar row, the palatal surface of the maxilla is flat and dips ventromedially. Each dental alveolus is elliptical, anteroposteriorly elongated, *c.* 9 mm long and 6 mm wide, with a depth around 5-6 mm. The presence of well-individualised dental alveoli on the maxillae of *Platyscaphokogia* n. gen. is shared with *Aprixokogia* and, to some extent, to *Pliokogia* and *Scaphokogia* (in which discrete yet likely relic dental alveoli are present), whereas just a faint alveolar groove is present in *Kogia* and *Nanokogia*. Given their size and depth, we regard the dental alveoli of *Platyscaphokogia* n. gen. as most likely bearing functional teeth. The left alveolar row is followed posteriorly by a 55 mm long sulcus that seemingly bears no distinct alveoli. In ventral view, the right antorbital notch is shorter posteriorly than it appears on the dorsal view, as well as distinctly teardrop-shaped. Posterior to the antorbital notch, the ventral exposure of the maxilla wedges between the lacrimojugal complex and the palatine towards the large ventral infraorbital foramen. The latter is elliptical and anterolaterally directed; it measures 25 mm in length and 13 mm in width. Anterior to the ventral infraorbital foramen and medial to the lacrimojugal complex, a shallow fossa excavates the ventral surface of the maxilla, paralleling the palatine. This depression is strongly reminiscent of a similar, yet deeper and longer, fossa observed in the same region of the skull of *Scaphokogia*; furthermore, as in *Scaphokogia*, this depression is deeper and better defined on the right side of the skull than on the left. Similar fossae have also been reported on skulls of *Kogia breviceps*, *K. sima*, *Koristocetus*, *Nanokogia*, and *Pliokogia*. Following the interpretation proposed by Vélez-Juarbe *et al.* (2015), this fossa is here regarded as related to the anteriormost portion of the pterygoid sinus complex (see Fraser & Purves 1960, for data on the extent of the pterygoid sinus and corresponding osteological features in extant *Kogia*).

Palatine
Due to the loss of the pterygoids, both palatines are widely exposed on the ventral surface of the cranium, posteromedial to the maxillae (Fig. 3). Each palatine displays a roughly oval, anteromedially oriented, blocky, and distinctly bulging (i.e., strongly transversely convex) anterior portion that is located anterior to the corresponding choana. Here the palatines contact each other medially, being separated anteromedially by a cusp-like wedge of the maxillae (a condition reminiscent of that of *Scaphokogia*). Two anterolaterally elongated bands of bone lying lateral to the choanae are also identified as belonging to the palatines, possibly representing their medial laminae. They are gently bowed laterally (i.e., roughly C-shaped); they contact the orbitosphenoid posterolaterally and the presphenoid posteriorly. Alternatively, these bands of bone might be interpreted as representing shreds of the pterygoids.

Lacrimojugal complex
As in all physeteroids for which these elements are known, the lacrimal and the jugal are fused in a compound lacrimojugal complex. The latter is rather large and, in lateral view,

it appears as roughly triangular (Fig. 4). As in *Kogia*, *Koristocetus*, *Nanokogia*, *Pliokogia*, *Praekogia*, and *Scaphokogia*, the posterodorsal corner of the lacrimojugal complex is shaped as a pointed posterodorsal process (*sensu* Muizon 1988) that wedges between the maxilla and the frontal; this process is slightly shorter than observed in the holotype of *Scaphokogia cochlearis* (specimen MNHN.F.PPI229). As observed in *Kogia*, *Koristocetus*, *Nanokogia*, *Pliokogia*, and *Scaphokogia*, the suture between the lacrimojugal complex and the maxilla is somewhat wavy, thus recalling also the condition observed in the stem sperm whales *Acrophyseter robustus* and *Livyatan*, among other physeteroids; in particular, this suture is substraight in its anterior half and distinctly sigmoidal in its posterior half. The ventralmost tip of the lacrimojugal complex is preserved on the right side of the paratype skull (Fig. 6B, C). It is robust, rounded, awl-shaped, and points slightly posteroventrally. When viewed ventrally, the lacrimojugal complex wedges between the frontal and the maxilla, tapering posteromedially (Fig. 3). Differing from extant *Kogia*, where the ventral surface of the lacrimojugal complex is bulbous and creates a large attachment site for the masseter muscle (Schulte & Smith 1918: fig. 8), the lacrimojugal complex of *Platyscaphokogia* n. gen. appears as somewhat transversely compressed in ventral view, thus recalling most other extinct kogiids in this regard.

Frontal
The frontals are mainly exposed in lateral and ventral views, their dorsal surfaces being largely hidden by the overlying maxillae. In lateral view (Fig. 4), the suture between the frontal and the maxilla along the supraorbital process slopes, with respect to the coronal plane, at a lower angle than observed in *Scaphokogia*, being reminiscent instead of the condition observed in *Pliokogia* and *Thalassocetus*. Similar to *Scaphokogia*, when viewed laterally, the preorbital process is blunt and globose. In turn, in lateral view, the postorbital process is more slender and distinctly projects posteroventrally in the paratype skull (Fig. 6C; the distal tip of the postorbital process is not preserved in the holotype skull); it is much less ventrally extended than observed in *Aprixokogia* and *Kogia*. In lateral view, the frontal also comprises the preserved upper portion of the temporal fossa. The highest point of the latter appears as distinctly higher than the highest point of the orbit, thus contrasting with the low temporal fossa of extant *Kogia* and recalling instead the condition observed in *Scaphokogia*. The ventral surface of the frontal (Fig. 3) displays a wide frontal groove that represents the distal extension of the optic canal departing from the optic foramen (not preserved). The frontal groove runs anterolaterally, thus contrasting with the almost mediolaterally directed frontal groove of extant *Kogia*. Towards the roof of the orbit, the frontal groove flattens and widens progressively in a way reminiscent of *Scaphokogia*.

Vomer
In dorsal view (Fig. 2), the vomer is observed forming the floor of the mesorostral groove at the apex of the rostrum. In ventral view (Fig. 3), the vomer is exposed along the rostrum as a narrow slit that runs parallel to the long axis of the skull
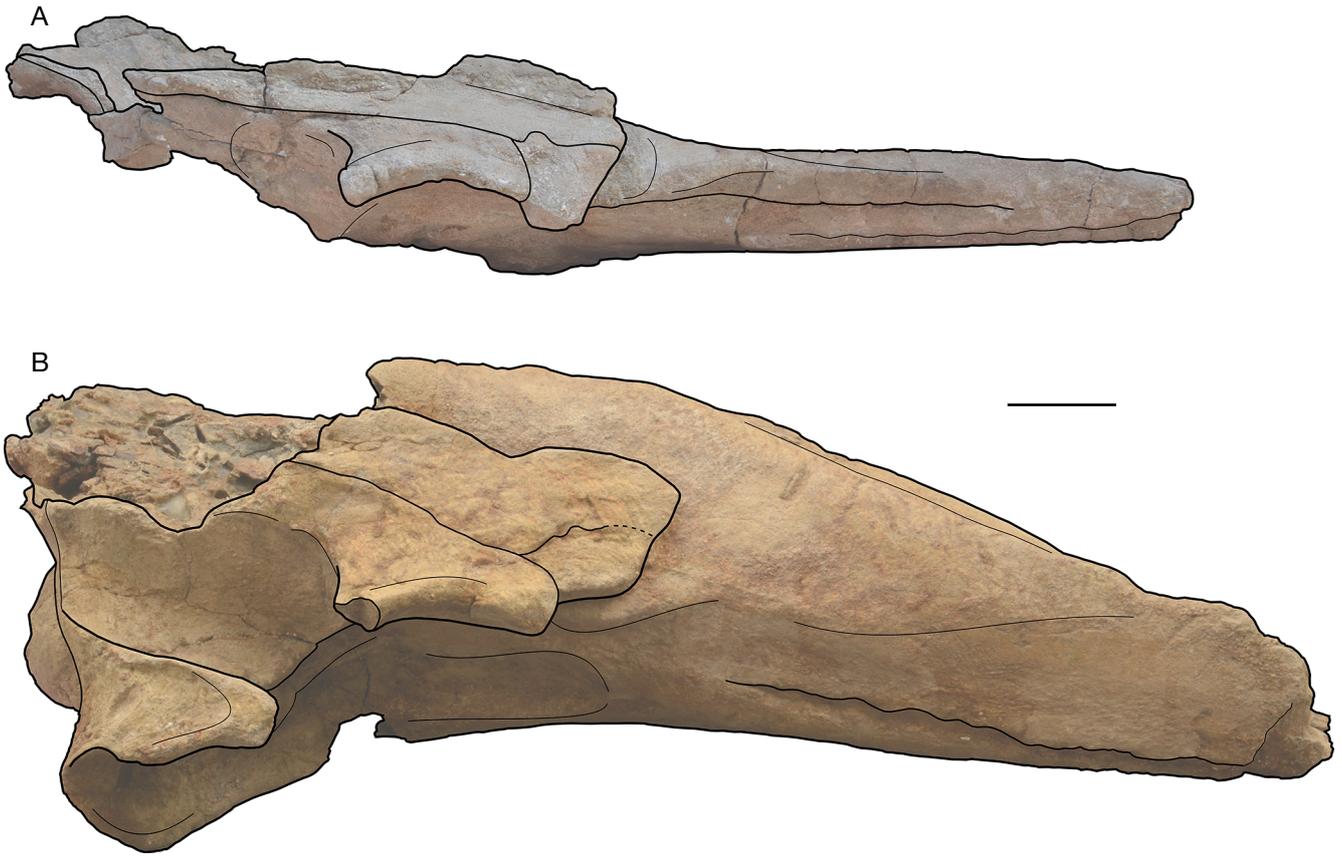
FIG. 8. — Schematic comparison between the cranial morphologies of the two scaphokogiine genera known to date. **A**, Right lateral view (photograph and superimposed line drawing) of MUSM 3405, holotype cranium of *Platyscaphokogia landinii* n. gen., n. sp., from the upper Miocene of the Pisco Formation (East Pisco Basin, southern Peru). **B**, Right lateral view (photograph and superimposed line drawing) of MUSM 3244, unpublished cranium of *Scaphokogia cochlearis*, from the upper Miocene of the Pisco Formation (East Pisco Basin, southern Peru). Note the strong differences existing between the two taxa in terms of height and slope of the rostrum. Scale bar: 5 cm.

between the maxillae. In this region, the vomer is not keeled, thus differing from the condition observed in *Pliokogia*. Reflecting the flattened morphology of the rostrum, the vomer of *Platyscaphokogia* n. gen. is dorsoventrally compressed along the splanchnocranium (Figs 3, 4); this greatly contrasts with the condition observed in *Scaphokogia*, the vomer of which is greatly pachyosteosclerotic and exhibits a wedge-shaped transverse section along the rostrum. The vomer of *Platyscaphokogia* n. gen. is also exposed posterior to the palatines, as a slice-like bony projection that coats the left surface of the presphenoid, thus contributing to the medial wall of the left choana. This condition resembles that observed in most kogiids except for *Praekogia*, in which the ventral surface of the presphenoid is partially wrapped by the vomer.

Sphenoid

In dorsal view, as in all kogiids, the presphenoid forms the sharp septum that separates the bony nares (Figs 2, 5). Differing from *K. sima* and some specimens of *K. breviceps*, the presphenoid does not extend anteriorly to partially fill the mesorostral groove (Fig. 2). In ventral view (Fig. 3), the presphenoid is partially exposed between the choanae, where it forms an anteroposteriorly elongated, strongly carinated bony septum that is bordered laterally by the vomer. Posterior to

the choanae, the presphenoid is robust and flares posterolaterally. A thin, elongated plate of bone running anterior and parallel to the anteromedial margin of the frontal groove is here identified as part of the orbitosphenoid.

Occipital and endocranial cavity

Only the uppermost portion of the supraoccipital is preserved in the holotype skull. In lateral view (Fig. 4), the preserved portion of the occipital shield is concave and forms an angle of *c.* 140° with the long axis of the rostrum. Although this value might have been slightly accentuated by diagenetic compression (the evidence for which is otherwise lacking), this angle would have surely been distinctly greater than 90° – a character that, among Kogiidae, is only observed in *Scaphokogia*. Posterior to the temporal fossa, the suture between the occipital and the frontal is concave backwards and runs roughly subvertical. When viewed ventrally, the holotype skull allows for observing the roof of the endocranial cavity (Fig. 3). The latter is gently concave on its left half but distinctly convex on its right half, thus evoking strongly asymmetrical cerebral hemispheres, much more dissimilar from each other than reported by Marino *et al.* (2003) in extant *Kogia sima*. Different from the condition observed in *Koristocetus*, no ossified falx cerebri is present within the endocranial cavity.

PHYLOGENY

Our phylogenetic analysis resulted in 105 most parsimonious trees having tree length of 147, consistency index (CI) of 0.5306, and retention index (RI) of 0.7240. The strict consensus tree and the 50% majority-rule consensus tree are presented in Figure 7. The relationships within physeteroids found in the former (Fig. 7A) are close to those observed in the strict consensus trees provided by Collareta *et al.* (2017a, 2019), the observed differences being most likely due to the partial rescoring of *Diaphorocetus* and the higher number of replicates undertaken in the present analysis. Indeed, in both trees, the base of Physeteroidea is marked by a polytomy involving: i) the early-middle Miocene genus *Eudelphis*; ii) a clade formed by the four Miocene genera of macroraptorial stem sperm whales (i.e., *Acrophyseter*, *Brygmophyseter*, *Livyatan*, and *Zygophyseter*); and iii) a clade that includes the living physeteroid families (namely, Physeteridae and Kogiidae) besides more archaic-looking taxa such as "*Aulophyseter*" *rionegrensis* (note however that, in our strict consensus tree, the relationships between several taxa of physeterid-like physeteroids are not resolved). Also in agreement with the results provided by Collareta *et al.* (2017a, 2019), our strict consensus tree recognises three groups among kogiids: i) a paraphyletic group including the early branching genera *Aprixokogia* and *Thalassocetus*; ii) a clade (subfamily Scaphokogiinae) consisting of *Scaphokogia* + *Platyscaphokogia* n. gen.; and iii) a clade (subfamily Kogiinae), sister group to Scaphokogiinae, whose members are *Kogia* spp., *Koristocetus*, *Nanokogia*, *Pliokogia*, and *Praekogia*. The three clades corresponding with Kogiidae, Scaphokogiinae, and Kogiinae, respectively, have a branch (Bremer) support of 1 each; however, the monophyly of the scaphokogiines is strongly supported by a large number of apomorphies (see the emended diagnosis above). Although, in the strict consensus tree, *Koristocetus* is recovered as the earliest branching member of Kogiinae, the relationships among *Kogia*, *Nanokogia*, *Pliokogia*, and *Praekogia* are still unresolved, possibly reflecting the relatively minor nature of the osteological differences between the above-mentioned genera. Similar to what was found by Collareta *et al.* (2019), our 50% majority-rule consensus tree (Fig. 7B) fully resolves the relationships among the five genera of Kogiinae: indeed, *Koristocetus*, *Nanokogia*, *Pliokogia*, *Praekogia*, and *Kogia* are here recognised as subsequently branching genera. Furthermore, in the same tree, Physeteridae are recovered as a large clade that includes *Aulophyseter*, *Diaphorocetus*, *Idiophyseter*, *Idiorophus*, *Orycterocetus*, *Physeter*, *Physeterula*, and *Placoziphius*.

GENERAL DISCUSSION

PALAEOECOLOGY OF *PLATYSCAPHOKOGIA* N. GEN.

Besides *Platyscaphokogia* n. gen., two genera of Kogiidae are known from the upper Miocene strata of the Pisco Formation of southern Peru: *Scaphokogia*, the type genus of Scaphokogiinae (Muizon 1988), and *Koristocetus*, an early

branching member of Kogiinae (Collareta *et al.* 2017a). Osteoanatomical evidence clearly associates *Platyscaphokogia* n. gen. and *Scaphokogia*, and the two genera share a sister group relationship in our phylogenetic reconstruction of physeteroids (Fig. 7). At the same time, conspicuous differences exist between *Platyscaphokogia* n. gen. and *Scaphokogia* in terms of cranial morphology, mostly regarding the height and slope of the rostrum (Fig. 8), allowing for a clear separation between the two taxa.

The cranium of *Scaphokogia* (Fig. 8B) is mostly characterised by a spoon-shaped dorsal surface of the neurocranium, as well as by a dorsoventrally elevated, semicylindrical, downwards-deflected rostrum. The peculiar architecture of the dorsal surface of the neurocranium of *Scaphokogia*, with its posterior extension of the supracranial basin, is likely related to the presence of a large, backwards-displaced spermaceti organ (Muizon 1988), which would impact substantially on the functioning of the whole echolocating system. The massive, semicylindrical, clinorhynchous (i.e., anteroventrally directed in lateral view) splanchnocranium of *Scaphokogia* indicates a peculiar feeding/foraging specialization that presents no analogues in extant odontocetes and has still to be properly investigated and understood. That said, in terms of robustness and orientation of the rostrum, *Scaphokogia* is broadly reminiscent of the rostral architecture of extant sirenians (e.g., Domning 2017) – an observation that seemingly suggests benthic habits and foraging at shallow, marginal-marine seafloors. This might be also supported by noting that several skulls of *Scaphokogia*, either collected and stored in museum collections or still in the field, are known from the shallow-marine, nearshore deposits exposed at Aguada de Lomas – an observation that evokes an intense ecospace use of this coastal palaeo-area by members of the genus *Scaphokogia* (Collareta *et al.* 2017a). *Platyscaphokogia* n. gen. closely approaches *Scaphokogia* in terms of neurocranial morphology (Figs 2, 4, 5) while displaying a much more conventional rostral osteoanatomy (Figs 2-4, 6); therefore, *Platyscaphokogia* n. gen. might have been more similar to *Scaphokogia* in terms of topology and functioning of the echolocating system, while departing from the type genus of Scaphokogiinae in terms of feeding/foraging habits. In this respect, it is interesting to note that *Platyscaphokogia* n. gen. differs from extant *Kogia* by displaying a higher temporal fossa, a proportionally longer rostrum, a non-enlarged ventral surface of the lacrimojugal complex, and well-individualised upper dental alveoli that are most likely indicative of a functional maxillary dentition. Overall, these features contrast with those that characterise extant suction-feeding odontocetes (Werth 2006), hinting instead towards the retention of a more active predation mode (for some notes on the macroraptorial habits of several stem physeteroid taxa see also Bianucci & Landini 2006; Lambert *et al.* 2010, 2017a; Peri *et al.* 2020). It is thus reasonable to hypothesise that *Platyscaphokogia* n. gen. was capable of raptorial feeding, similar to what has recently been proposed for the basal kogiine *Koristocetus* (Collareta *et al.* 2017a). Taking into account that the holotype and paratype of *Platyscaphokogia* n. gen. come from offshore mudstones, and considering
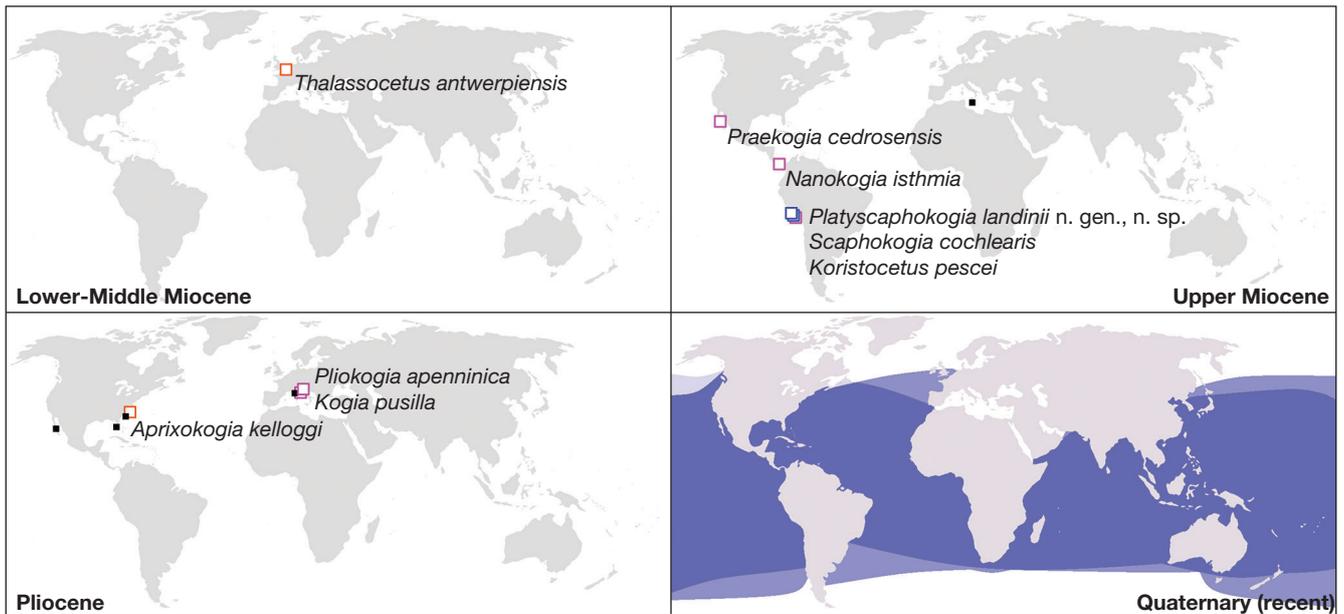
Fig. 9. — Diversity and distribution of kogiids through space and time. Red-border squares indicate fossil early-branching kogiids (i.e., *Thalassocetus* Abel, 1905 and *Aprixokogia* Whitmore & Kaltenbach, 2008); blue-bordered squares indicate fossil scaphokogiines; purple-bordered squares indicate fossil kogiines; small black squares indicate fossil records consisting of isolated ear bones; pale blue-shaded areas indicate the range of extant *Kogia breviceps* (de Blainville, 1838); azure-shaded areas indicate the range of extant *Kogia sima* (Owen, 1866); indigo-shaded areas indicate the range shared by both living kogiid species. See the main text for data sources. The world maps reproduced in the four panels are after wikimedia.org. The distribution of extant *Kogia* Gray, 1846 species shown in the bottom right panel is in very good agreement with the distributional data reported by Taylor *et al.* (2012a, b).

also that their rostra are flat and distinctly pointed anteriorly, *Platyscaphokogia* n. gen. can thus be tentatively interpreted as a raptorial sperm whale that foraged along the water column in relatively open-sea palaeoenvironments rather than at or close to shallow, nearshore seafloors (as hypothesised in turn for *Scaphokogia*).

At Cerro los Quesos, the locality of the paratype of *Platyscaphokogia landinii* n. gen., n. sp., a rich and diversified vertebrate assemblage takes place in a sedimentary succession whose stratigraphy has been finely resolved (Bianucci *et al.* 2016a; Di Celma *et al.* 2016a); this allows for further palaeoecological considerations. The same stratal package that hosts the paratype of the new physeteroid kogiid taxon described herein also provided at least one specimen of the macroraptorial stem physeteroid *Acrophyseter* sp. (Lambert *et al.* 2017a). This observation suggests sympatric habits for the late Miocene sperm whales, as observed nowadays for *Physeter* and *Kogia* spp., and elsewhere in the fossil record (e.g., Vélez-Juarbe *et al.* 2016), including the Pisco beds exposed at Aguada de Lomas (Collareta *et al.* 2017a). Skull measurements (Lambert *et al.* 2017a: table 1) reveal that *Acrophyseter* sp. is distinctly larger than *Platyscaphokogia landinii* n. gen., n. sp. (Table 1); moreover, the former taxon displays clear adaptations for preying upon large-sized prey (e.g., other marine mammals; Lambert *et al.* 2017a), including a remarkably expanded temporal fossa and enlarged maxillary teeth and dental alveoli, that are absent in the latter. The late Miocene Cerro los Quesos physeteroids thus likely occupied different ecological and trophic niches, with *Acrophyseter* sp. hunting larger food items that *Platyscaphokogia* n. gen. used to do.

EVOLUTIONARY SIGNIFICANCE OF *PLATYSCAPHOKOGIA* N. GEN.
As highlighted above, the skull morphology of *Platyscaphokogia* n. gen. appears as intermediate between that of a generalized non-scaphokogiine kogiid other than *Kogia* and the highly autapomorphic morphology of *Scaphokogia*. It is thus reasonable to hypothesise that *Platyscaphokogia* n. gen. illustrates an early stage in the evolution of the scaphokogiine cranial anatomy – a stage characterised by the acquisition of a spoon-shaped dorsal surface of the neurocranium and the retention of likely functional upper dental alveoli coupled with a non-pachyostotic, dorsoventrally thin rostrum that does not point anteroventrally. Therefore, it might be tempting to speculate that *Platyscaphokogia* n. gen. represents the ancestor of *Scaphokogia*, i.e., to interpret Scaphokogiinae as an anagenetic lineage, similar to what has been proposed for the aquatic sloth genus *Thalassocnus*, which is also known from the Pisco Formation (Muizon & McDonald 1995). The five species of *Thalassocnus* display stratigraphically congruent phylogenetic relationships and a gradual adaptation to the marine environment via a progressive accretion of characters related to an aquatic lifestyle that are absent or incipient in the earliest members but fully developed in the latest species (Amson *et al.* 2016). Current stratigraphic and geochronological data, however, do not bring support to this interpretation for the *Platyscaphokogia* n. gen.-*Scaphokogia* sample. Indeed, an age of 7.5-7 Ma was at first tentatively assigned to the Aguada de Lomas (= AGL; Muizon & DeVries 1985) level of the Sacaco Basin, from which the holotype and geologically oldest specimen of *Scaphokogia cochlearis* was collected

(Muizon 1988); this age estimate has been substantially confirmed by recent U-Pb dating on zircon grains from tuff layers and Sr-isotope analyses on marine mollusc shells that bracketed the age of the AGL level between 7.46 and 7.30 Ma, in the Tortonian (Ehret *et al.* 2012). In turn, *Platyscaphokogia landinii* n. gen., n. sp. seemingly represents a geologically younger taxon: indeed, the holotype of this new form comes from Messinian sediments younger than 7.084 Ma, whereas the paratype comes from a Messinian stratal package that deposited between 6.93 Ma and 6.71 Ma. That said, although *Platyscaphokogia* n. gen. appears chronostratigraphically later than *Scaphokogia* in the fossil record of the Pisco Formation, preservational and ecological biases might also explain the absence of *P. landinii* n. gen., n. sp. from the lower (i.e., Tortonian) Pisco strata exposed in the Sacaco Basin, and finer correlations are definitively needed between the Sacaco and East Pisco outcrops to draw definitive conclusions about the chronology of faunal successions over the entire Pisco Formation (Lambert *et al.* 2017a; Marx *et al.* 2017b). Nevertheless, the paratype and holotype of *Platyscaphokogia* n. gen. represent key discoveries for reconstructing how and from where the unique cranial anatomy of *Scaphokogia* evolved.

SOME NOTES ON THE DIVERSITY OF KOGIIDS THROUGH SPACE AND TIME

Thalassocetus antwerpiensis, the geologically oldest member of Kogiidae known to date, comes from uppermost lower or middle Miocene deposits of the North Sea (Lambert 2008) (Fig. 9). *Thalassocetus* is also the sole kogiid known from sediments older than the late Miocene, as well as the earliest branching member of this family; as such, it suggests an Atlantic location for the origin of kogiids.

In the upper Miocene, kogiids are represented by significant cranial remains belonging to at least five distinct species, including two scaphokogiines (i.e., *Scaphokogia cochlearis* and *Platyscaphokogia landinii* n. gen., n. sp.) and three kogiines (i.e., *Nanokogia isthmia* Vélez-Juarbe, Wood, De Gracia & Hendy, 2015, *Praekogia cedrosensis*, and *Koristocetus pescei*) (Fig. 9). Of all the late Miocene kogiid species, three are known from the Pisco beds of Peru, namely, the two scaphokogiines and *K. pescei* (Muizon 1988; Collareta *et al.* 2017a; Di Celma *et al.* 2017; this work); a fourth species, *P. cedrosensis*, also comes from the Southeastern Pacific margin, having been found in northwestern Mexico (Barnes 1973), whereas *N. isthmia* comes from the Central American Seaway palaeo-area (Vélez-Juarbe *et al.* 2015). Whilst the above distributional data evoke the origin of the scaphokogiines and kogiines along the Southeastern Pacific margin, the presence of kogiids in the North Atlantic realm (here regarded as including also the Mediterranean cul-de-sac) during the late Miocene is testified by the occurrence of a periotic of Kogiidae indet. in the Tortonian of Malta (Bianucci *et al.* 2011) (Fig. 9). As highlighted elsewhere, the late Miocene kogiids explored a relatively broad range of body sizes, skull morphologies, and trophic adaptations, including forms that likely shared the ecological preferences

of the extant members of *Kogia* (i.e., *Nanokogia*; Vélez-Juarbe *et al.* 2015), marginal-marine putative benthic feeders (such as *Scaphokogia*; this work), and taxa that retained characters that are regarded as more or less strongly related to raptorial predation along the water column (i.e., *Koristocetus* and *Platyscaphokogia* n. gen.; Collareta *et al.* 2017a; this work). The late Miocene seems therefore to have been a time span of high diversity and disparity for kogiids.

The post-Miocene fossil record of Kogiidae concentrates in Pliocene strata and includes one early branching species from the eastern USA (i.e., *Aprixokogia kelloggi*) besides two Mediterranean kogiines from Italy (i.e., *Kogia pusilla* – the earliest member of the extant genus *Kogia* – and *Pliokogia apenninica*) (Fig. 9). Whereas the relatively large-sized *A. kelloggi* exhibits evident adaptations for macroraptorial feeding, such as huge upper dental alveoli and high temporal fossa (Whitmore & Kaltenbach 2008), *K. pusilla* and *P. apenninica* might have been similar to their living relatives in terms of ecological and trophic preferences (Bianucci & Landini 1999; Collareta *et al.* 2019). Besides these species, the Pliocene record of Kogiidae features several isolated ear bones from Italy, the southeastern United States, and the Mexican portion of California (Pilleri 1987; Luo & Marsh 1996; Barnes 1998; Vélez-Juarbe *et al.* 2016).

Nowadays, the two living species *Kogia breviceps* and *Kogia sima* can be distinguished from each other on the basis of only minor osteoanatomical differences (e.g., Baccetti *et al.* 1991); they inhabit warm and temperate pelagic environments worldwide, being however absent from the Mediterranean Sea (McAlpine 2017: fig. 2), possibly beacuse of the depleted present-day deep-water fauna of this semi-enclosed basin (Collareta *et al.* 2019). Although pygmy and dwarf sperm whales might prefer slightly different seawater temperatures, these two species are sympatric on large portions of their ranges, including the Peruvian offshore (Fig. 9).

CONCLUDING REMARKS

The findings reported in the present paper represent significant additions to the still fragmentary fossil history of Kogiidae that expand the palaeodiversity of this extant family of diminutive sperm whales and provide new insights into the early steps of the anatomical evolution of the extinct, highly autapomorphic subfamily Scaphokogiinae. Furthermore, they expand our knowledge on the late Miocene cetacean assemblages off the Pacific coastline of South America and support the notion that the fossil content of the East Pisco Basin is crucial for reconstructing the Neogene evolutionary paths and patterns of physeteroid odontocetes. Not least, our results stress out the importance of building up an integrated stratigraphic framework for the Pisco Formation deposits, encompassing the outcrops of both the East Pisco and Sacaco basins, in order to further elucidate the evolutionary significance of the faunal assemblages found in this outstanding Cenozoic marine Fossil-Lagerstätte.

NOTES ADDED IN PROOFS

During the production of the present paper, another contribution (Benites Palomino *et al.* 2020) dealing with the description of a new species of *Scaphokogia* was published in an international journal. We refer to this paper for further investigations on the palaeodiversity and evolutionary history of Scaphokogiinae.

A second recent contribution, with part of us as co-authors (Alfsen *et al.* in press), revised the systematic affinities and phylogenetic relationships of *Thalassocetus antwerpiensis*, considerably changing the context of Kogiidae's origin and early evolution.

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