

A new kogiid sperm whale from northern Italy supports psychrospheric conditions in the early Pliocene Mediterranean Sea

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Among living cetaceans, dwarf and pygmy sperm whales (*Kogia*) are the only members of the family Kogiidae, regarded as diminutive and elusive relatives of the great sperm whale *Physeter*. Kogiids are known as fossils by several skulls, teeth, and ear bones from Neogene deposits of the Northern Hemisphere and Peru. We report on a fossil kogiid specimen collected at Sant'Andrea Bagni (northern Italy) from Zanclean marine mudstone; these deposits also yielded a rich deep-water elasmobranch assemblage depicting the presence of Atlantic-derived psychrospheric waters. The kogiid specimen, consisting of a partial cranium, one detached tooth, one vertebra, and one fragmentary rib, is here referred to *Pliokogia apenninica* gen. et sp. nov. *Pliokogia* is mostly characterised by a long and dorsally flattened rostrum and by the presence of two well-distinct fossae on the right side of the supracranial basin, including an elongated peripheral maxillary fossa on the posterior portion of the right maxilla. Our phylogenetic analysis recovers *Pliokogia* as a member of the subfamily Kogiinae, which includes *Kogia*, *Koristocetus*, *Nanokogia*, and *Praekogia*. A low temporal fossa and the absence of dental enamel suggest that, like extant *Kogia*, *Pliokogia* was a suction feeder. Since living kogiids do not inhabit the Mediterranean waters, and considering that they feed on deep-water prey in open-sea areas, the association of *Pliokogia* with a psychrospheric elasmobranch assemblage with Atlantic affinities is noteworthy. Indeed, in early Pliocene times, the Gibraltar connection was controlled by estuarine dynamics, thus allowing the entrance of deep-water organisms (including the putative prey of *Pliokogia*) in the Mediterranean Basin. The subsequent abandonment of the Mediterranean Sea by kogiids might therefore be related to the definitive establishment of the present-day antiestuarine circulation at Gibraltar, which likely led to a limited deep nutrient supply and resulted in the strong depletion of most Mediterranean deep-water ecosystems.

Key words: Mammalia, Cetacea, Odontoceti, Physeteroidea, Kogiinae, oceanisation, Pliocene, Northern Apennines.

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Introduction

Among modern toothed whales (Cetacea: Odontoceti), pygmy and dwarf sperm whales, *Kogia breviceps* (de Blainville, 1838) and *Kogia sima* (Owen, 1866), respectively, are the only living members of the physeteroid family Kogiidae, known as diminutive relatives of the great sperm whale (Physeteridae: *Physeter macrocephalus* Linnaeus, 1758), with whom they share the presence of a spermaceti organ in the supracranial region of the head (e.g., McAlpine 2002). These small-sized marine mammals are characterised by a square head, small lower jaws, and a short rostrum—the shortest snout among extant cetaceans (Werth

2006). Despite being globally distributed, kogiids are still among the less known families of marine mammals, and most of our understanding of their anatomy and life history comes from isolated and often serendipitous observations on beached individuals.

The fossil record of Kogiidae is currently represented by some skulls, teeth, and more abundant isolated ear bones from Neogene deposits of the Northern Hemisphere (e.g., Barnes 1973, 1998; Pilleri 1987; Whitmore 1994; Bianucci 1996, 1997; Cigala Fulgosi 1996; Luo and Marsh 1996; Bianucci et al. 1998, 2011; Bianucci and Landini 1999; Lambert 2008; Whitmore and Kaltenbach 2008; Vélez-Juarbe et al. 2015, 2016; Lambert et al. 2017b), with the remarkable excep-

tion of the late Miocene record from the Pisco Formation of southern Peru, which includes several skulls of *Scaphokogia* (a highly autapomorphic genus characterised by a pachyostotic, semicylindrical, downwards-deflected rostrum and a spoon-shaped dorsal surface of the neurocranium) besides a few specimens displaying less derived cranial morphologies (Muizon 1988; Bianucci et al. 2016; Collareta et al. 2017b; Di Celma et al. 2017). Although *Kogia* does not inhabit the present-day Mediterranean Sea (e.g., McAlpine 2017), kogiids are known from the Mediterranean region for a few late Neogene fossil specimens, namely: (i) an isolated left periotic from the Tortonian of Melleha (Malta), identified as belonging to Kogiidae indet. (Bianucci et al. 2011); (ii) some teeth, periotics, and tympanic bullae from the Pliocene of Orciano Pisano (Tuscany, central Italy) (Pilleri 1987; Bianucci 1996); and (iii) the holotype and only known specimen of *Kogia pusilla* (Pilleri 1987), consisting of an incomplete skull from the upper Pliocene of Monte Voltraio (Tuscany, central Italy) (Bianucci 1997; Bianucci et al. 1998; Bianucci and Landini 1999). Moreover, a partial kogiid skeleton was collected by one of us (FCF) from lower Pliocene (i.e., Zanclean) mudstone exposed at Sant'Andrea Bagni (Emilia-Romagna, Italy) and cursorily mentioned in a work on the remarkable deep-water elasmobranch assemblage from the same site (Cigala Fulgosi 1996). This cetacean fossil is here fully described, figured, and referred to a new genus and species of Kogiinae, the kogiid subfamily that includes the present-day *Kogia*. We then undertake a parsimony analysis of the phylogenetic relationships of this new taxon and briefly discuss its palaeobiological significance.

Institutional abbreviations.—IRSNB, Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; MAS, Museo Arqueológico de Salango, Salango, Ecuador; MGPUF, Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università degli Studi di Firenze, Firenze, Italy; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MSNC, Museo Civico di Storia Naturale di Comiso, Comiso, Italy; MSNUP, Museo di Storia Naturale dell'Università di Pisa, Calci, Italy; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru; MUSNAF, Museo di Storia Naturale dell'Accademia dei Fisiocritici, Siena, Italy; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

Other abbreviations.—CNPL, Calcareous Nannofossil Plio-Pleistocene zonation of Backman et al. (2012); MNN, Mediterranean Neogene Nannoplankton zonation of Rio et al. (1990); MPL, Mediterranean Pliocene foraminiferal zonation of Cita (1973, 1975) and Sprovieri (1992).

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:D41EA0A5-E65D-48CB-AB8F-0EE1725247EC

Material and methods

Kogiid specimens analysed for comparison and anatomical terminology.—In addition to MSNUP I-17603, we have directly examined for comparison the following fossil and extant Kogiidae: *Aprixokogia kelloggi* Whitmore and Kaltenbach, 2008 (USNM 187015); *Kogia breviceps* (Blainville, 1838) (MAS 4000; MNHN 1976-37; USNM 283625); *Kogia pusilla* (Pilleri, 1987) (MGPUF 1540V); *Kogia sima* (Owen, 1866) (MSNC 3450; MUSNAF Mam410); *Koristocetus pescei* Collareta, Lambert, Muizon, Urbina, and Bianucci, 2017 (MUSM 888); *Scaphokogia cochlearis* Muizon, 1988 (MNHN PPI 229, MUSM 971, MUSM 1998); *Scaphokogia* sp. (MUSM 972); *Scaphokogiinae* sp. (MUSM 3291; MUSM 3405); *Thalassocetus antwerpiensis* Abel, 1905 (IRSNB M.525). The anatomical terminology for the skull follows Mead and Fordyce (2009), except when explicitly stated otherwise.

Phylogenetic analysis.—The phylogenetic analysis was undertaken with PAUP* (Swofford 2001) using a modified version of the character/taxon matrix of Collareta et al. (2017b) (for the list of characters and the character/taxon matrix see the SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app64-Collareta_etal_SOM.pdf). We used the tree-bisection–reconnection algorithm and the heuristic search option, considering all characters as unordered and unweighted. We used the definitions proposed by Bianucci and Landini (2006) and then reaffirmed by Lambert et al. (2017a) for Physeteroidea, Physeteridae, and Kogiidae. Following Collareta et al. (2017b), we define Kogiinae Gill, 1871 as the most inclusive clade including *Kogia* but not *Scaphokogia*, whereas we define Scaphokogiinae Muizon, 1988 as the most inclusive clade including *Scaphokogia* but not *Kogia*.

Geological and stratigraphic setting

The cetacean fossil described in the present work was collected from a small badland area at the margins of the village of Sant'Andrea Bagni (Parma Province, Northern Apennines, northern Italy), a site where lower Pliocene (i.e., Zanclean) marine mudstone (“Argille Azzurre” sensu lato) are exposed along a short section, about 25 m thick (Fig. 1A). The stratigraphy of this exposure, consisting of monotonous silty argillaceous pelites that exhibit indistinct bedding, has been described in detail by Cigala Fulgosi (1986, 1996) and Channel et al. (1994). The kogiid specimen here described was collected a few metres above the base of the section measured by Channel et al. (1994) and figured by Cigala Fulgosi (1996: fig. 2). These sediments have also yielded a rich deep-water elasmobranch assemblage (including teeth and scales attributed to rare squalan sharks such as *Centrophorus squamosus* [Bonnaterre, 1788], *Chlamydoselachus* sp., *Deania*

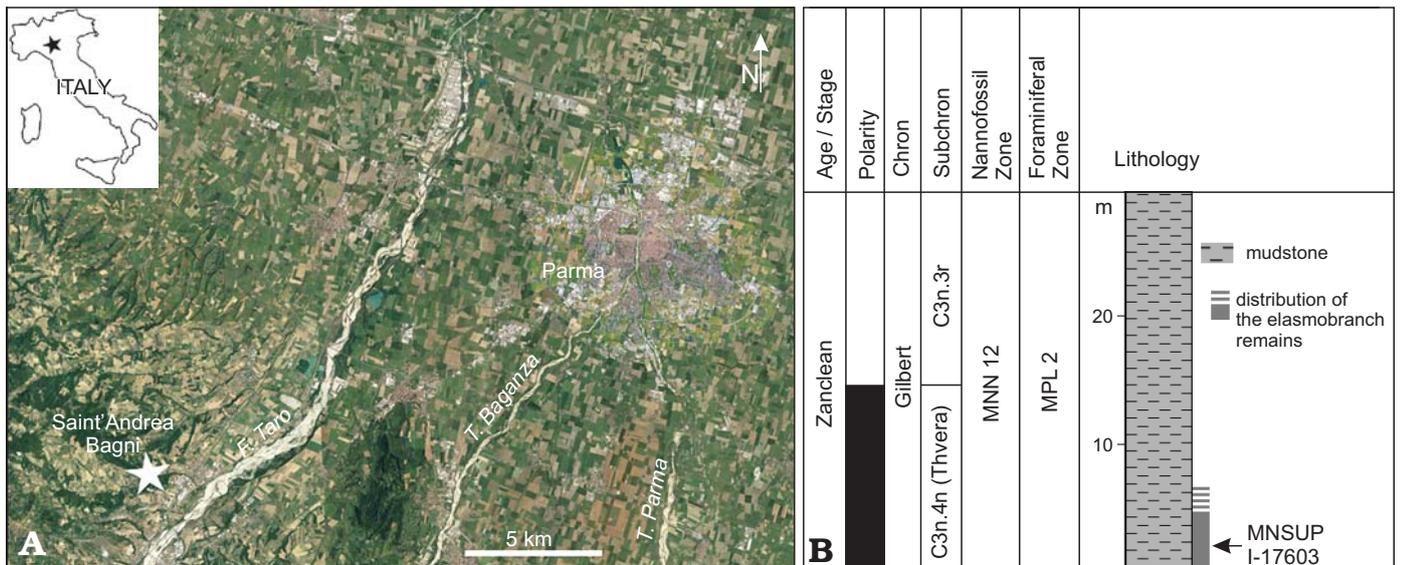


Fig. 1. **A.** Geographical position (star) of the lower Pliocene site of Sant'Andrea Bagni, Northern Apennines, northern Italy, where the holotype of *Pliokogia apenninica* gen. et sp. nov. (MSNUP I-17603) was discovered (image from Google Earth). **B.** Schematic stratigraphic section of the Pliocene succession exposed at Sant'Andrea Bagni (redrawn and modified after Channel et al. 1994).

sp., *Pristiophorus* sp., *Scymnodalatis* aff. *garricki* Kukuev and Konovalenko, 1988, *Scymnodon ringens* Barbosa du Bocage and Brito Capello, 1864, and *Zameus squamulosus* [Günther, 1877] (Cigala Fulgosi 1986, 1996). On the whole, the chondrichthyan assemblage from Sant'Andrea Bagni depicts the presence of psychrospheric (i.e., belonging to colder, deeper part of the oceans, known as the psychrosphere; Bruun 1957) water masses of Atlantic origin in the Adriatic palaeo-area during an early Pliocene phase of remarkable "oceanisation" of the Mediterranean Basin (Cigala Fulgosi 1996), as already hypothesised on the basis of the fossil record of ostracod crustaceans (Benson 1972a, b, 1975) and scleractinian corals (Russo 1980). Teeth of bony fish, spines of cidaroid urchins, rare very small pyritised molluscs, and scattered remains of solitary corals were also collected at the study site (Cigala Fulgosi 1986, 1996); the latter include small-sized, cup-shaped, relatively flat corallites that might belong to the extant species *Caryophyllia aradasiana* Seguenza, 1864 (= *Caryophyllia calveri* Duncan, 1873; Vertino and Di Geronimo 2003).

Integration of foraminiferal biostratigraphy, calcareous nannoplankton biostratigraphy, and magnetostratigraphy allows a precise and robust bracketing of the time of deposition of the fossiliferous horizons cropping out at Sant'Andrea Bagni (Cigala Fulgosi 1986, 1996; Channel et al. 1994; Fig. 1B). In particular, the foraminiferal assemblage was attributed to the MPL 2 biozone, which is currently referred to the 5.08–4.52 Ma time span (Violanti 2012), whereas the calcareous nannoplankton assemblage was attributed to the MNN 12 biozone, corresponding to the more recently instituted CNPL 4 biozone, whose bounding bioevents have been calibrated at 5.53 Ma and 5.04 Ma, respectively (Backman et al. 2012). Confirming these biostratigraphical results, Channell et al. (1994) assigned the lower

part of the section exposed at Sant'Andrea Bagni to the Thvera Subchron of the Gilbert Chron; the Thvera Subchron is currently referred to the 5.235–4.997 Ma time span (Ogg 2012). All together, these results indicate that the geological age of the cetacean specimen described herein and the co-occurring fish assemblage can be constrained between 5.08 and 5.04 Ma—a surprisingly precise age estimate.

Systematic palaeontology

Cetacea Brisson, 1762

Pelagiceti Uhen, 2008

Neoceti Fordyce and Muizon, 2001

Odontoceti Flower, 1867

Physeteroidea Gray, 1821

Family Kogiidae Gill, 1871

Remarks.—Within the family Kogiidae, Muizon (1988) established the monotypic subfamily Scaphokogiinae for inclusion of the then new highly autoapomorphic genus *Scaphokogia*. In doing so, Muizon (1988) collected the genera *Kogia* and *Praekogia* under the subfamily name Kogiinae (established by Gill 1871 according to the "Principle of Coordination" of the International Code of Zoological Nomenclature; ICZN 1999: article 36.1). For purposes of completeness, the kogiid subfamily Kogiinae, to which the new taxon herein described belongs, is here provided with a diagnosis on the basis of the results of our cladistic analysis (see Phylogeny below).

Subfamily Kogiinae Gill, 1871

Diagnosis.—Kogiids in which the posterior end of the right antorbital notch opens onto the supracranial basin.

Genus *Pliokogia* nov.

ZooBank LSID: urn:lsid:zoobank.org:act:1DEA564E-280B-4E35-A193-655DCE48CE61

Type and only known species: *Pliokogia apenninica* sp. nov.

Etymology: From the combination of Pliocene, in reference to the geological age of the holotype, and *Kogia*, generic name of the extant members of Kogiidae. Gender feminine.

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

Stratigraphic and geographic range.—Early Pliocene (5.08–5.04 Ma, early Zanclean; see above for more details) of northern Italy (palaeo-Adriatic area).

Pliokogia apenninica sp. nov.

Figs. 2–8.

1996 “a fragmented skull of kogiinae (Cetacea: Odontoceti)”; Cigala Fulgosi 1996: 303.

ZooBank LSID: urn:lsid:zoobank.org:act:27C92259-D30E-4F02-BB6F-CB13067302EA

Etymology: From Apennines, the mountain range that includes the type horizon.

Holotype: MSNUP I-17603, a partial cranium, one detached tooth, one vertebra, and one fragment of rib.

Type locality: Sant’Andrea Bagni, about 20 km WSW of the town of Parma, Parma Province, Italy. Indicative geographic coordinates: 44°43’ N, 10°05’ E. Precise locality data are available on request from the authors.

Type horizon: Zanclean marine mudstone (“Argille Azzurre” sensu lato): characterised by the presence of fossilised teeth and denticles of deep-water squalan sharks such as *Centrophorus squamosus*, *Chlamydoselachus* sp., *Deania* sp., *Pristiophorus* sp., *Scymnodalatias* aff. *garricki*, *Scymnodon ringens*, and *Zameus squamulosus* (Cigala Fulgosi 1986, 1996). The geological age of the type horizon has been constrained between 5.08 and 5.04 Ma by means of foraminiferal biostratigraphy, calcareous nannoplankton biostratigraphy, and magnetostratigraphy (Channel et al. 1994; Cigala Fulgosi 1996).

Diagnosis.—*Pliokogia apenninica* is a small-sized physeteroid, similar in skull length to *Kogia breviceps*. It is recognised as a member of Kogiidae based on the following features: estimated bizygomatic width much smaller than 400 mm, presence of a sagittal facial crest, and external nares greatly asymmetric (Lambert et al. 2017a). It is recognised as a member of Kogiinae by the right antorbital notch whose posterior end opens onto the supracranial basin (this work).

The cranium of *Pliokogia apenninica* differs from other kogiids by the following presumed autapomorphies: (i) presence of a proportionally long rostrum, accounting for more than three fifths of the reconstructed total length of the cranium, whose flat dorsal surface is not invaded by the supracranial basin; (ii) presence of two well-distinct fossae on the right side of the supracranial basin, including an elongated peripheral maxillary fossa on the caudal portion of the right maxilla, posterior and posteromedial to the corresponding antorbital notch; and (iii) presence of a sagittal vomerine sulcus, reflected in a V-shaped transverse section of the dorsal surface of the vomer along the mesorostral groove.

Pliokogia apenninica further differs from *Aprixokogia*, *Koristocetus*, *Nanokogia*, and *Scaphokogia* by the thicker and blunter lateral maxillary crest. It further differs from *Aprixokogia* and *Koristocetus* by the presence of a subdivided right posterior dorsal infraorbital foramen and by the lower temporal fossa. It further differs from *Aprixokogia*, *Scaphokogia*, and *Thalassocetus* by the right antorbital notch opening onto the supracranial basin. It further differs from *Aprixokogia* and *Kogia* by the smaller angle between the frontal–maxilla suture line and the coronal plane, along the supraorbital process, with skull in lateral view. It further differs from *Aprixokogia* and *Thalassocetus* by the slit-like geometry of the antorbital notches. It further differs from *Aprixokogia* by the smaller skull length. It further differs from *Kogia*, *Nanokogia*, and *Praekogia* by presenting no lateral expansion of the postnarial eminence of the right premaxilla. It further differs from *Kogia* by the proportionally smaller lacrimojugal complex. It further differs from *Kogia breviceps*, *Kogia sima*, and *Koristocetus* by the absence of any constriction of the right premaxilla at the level of the external bony nares. It further differs from *Kogia breviceps* and *Kogia sima* by the supracranial basin not being laterally expanded, by the thinner and not inflated lateral maxillary crest, and by the higher temporal fossa. It further differs from *Kogia pusilla*, *Kogia sima*, and *Koristocetus* by the greater skull length. It further differs from *Kogia sima* and *Scaphokogia* by the lack of a left premaxillary foramen. It further differs from *Kogia sima* by the presphenoid which does not extend anteriorly within the mesorostral groove. It further differs from *Koristocetus* and *Nanokogia* by the less obliquely oriented frontal groove. It further differs from *Nanokogia* and *Scaphokogia* by having a wider mesorostral groove in the posterior portion of the rostrum. It further differs from *Praekogia* by having the left premaxilla that does not reach the sagittal facial crest. It further differs from *Scaphokogia* by the rostrum having a dorsal surface that is not semicylindrical, the postnarial eminence that significantly contributes to the sagittal facial crest, the sagittal facial crest that is not significantly dislocated towards the left side of the skull, and the supracranial basin that is not spoon-shaped.

Description.—*Cranium*: The skull is incomplete, lacking the basicranium, the left part of the supracranial basin, the left lateral portion of the rostrum, all the ear bones, the mandibles, and all the teeth but one (Figs. 2–7). The dorsal aspect of the cranium is generally well preserved, although some surfaces are moderately abraded and the left part of the supracranial basin is lost (Fig. 2). In ventral and lateral views, the cranium is poorly preserved, which makes the relationships between the different bones locally unclear (Figs. 3, 4). Various fractures, sometimes filled by gypsum, are observed throughout the cranium.

The maximum preserved length of the cranium is 380 mm, which closely approximates the condylobasal length, here estimated at about 400 mm. Such a reconstructed skull length is similar to that of *Kogia breviceps*, smaller than that of

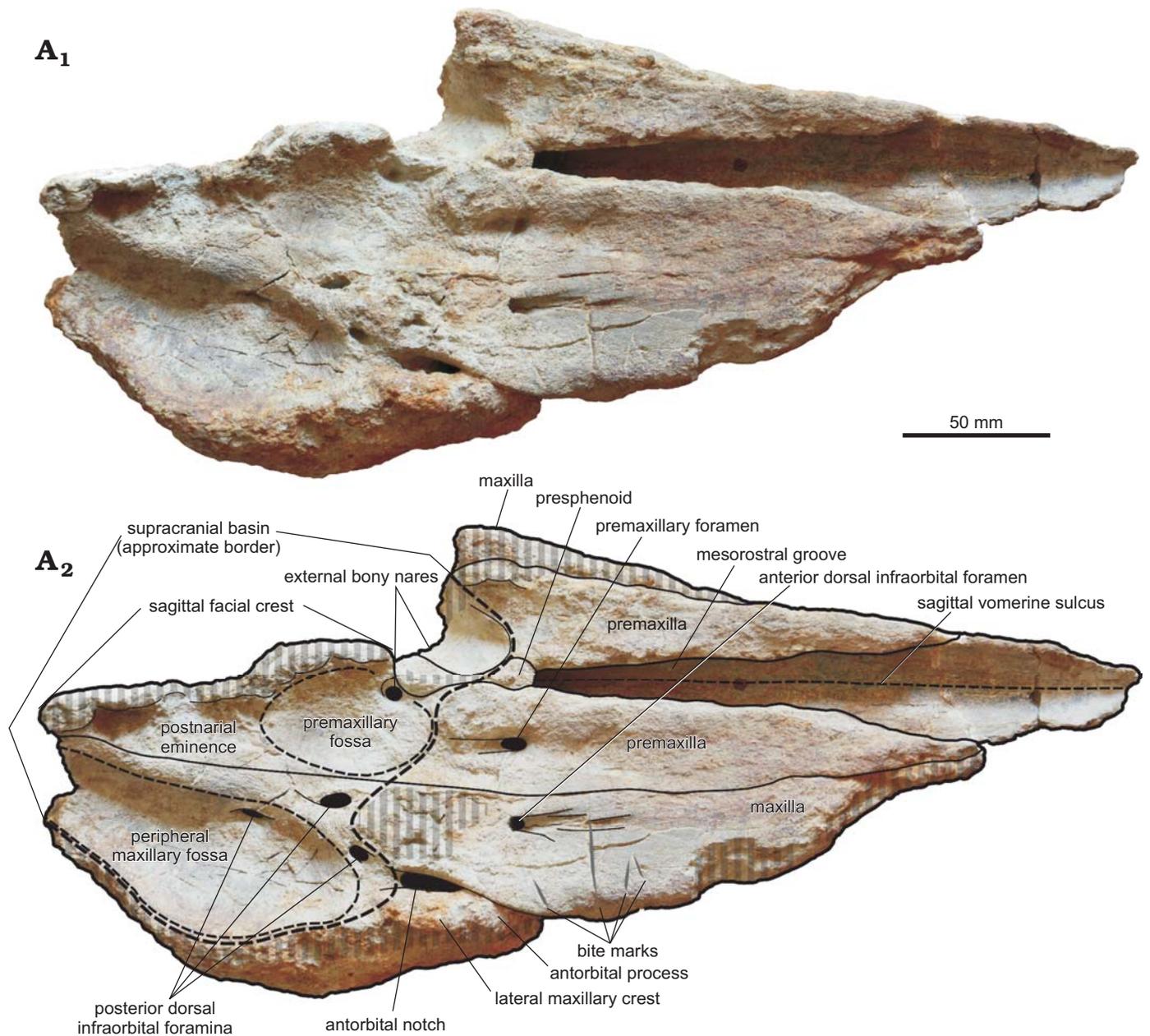


Fig. 2. Cranium, in dorsal view, of the kogiid sperm whale *Pliokogia apenninica* gen. et sp. nov. (MSNUP I-17603, holotype), from the lower Pliocene of Sant' Andrea Bagni (Northern Apennines, northern Italy). Photograph (A₁), explanatory drawing (A₂). The black areas correspond to openings in the skull. The grey vertical stripes denote abraded or broken areas. Dashed lines are for the sagittal vomerine sulcus and the approximate border of the supracranial basin, premaxillary fossa, and peripheral maxillary fossa.

Aprixokogia, and greater than those of *Kogia pusilla*, *Kogia sima*, *Koristocetus*, and possibly *Nanokogia*.

The neurocranium is dorsally concave, forming a wide supracranial basin (a key feature of Physeteroidea); it is also strongly asymmetric, exhibiting strongly uneven bony nares (i.e., the left naris is much wider than the right one) that are significantly displaced leftwards, as well as an obliquely directed sagittal facial crest (a diagnostic character of Kogiidae) (Fig. 2). With respect to extant *Kogia*, the skull of *Pliokogia* appears as strongly elongated antero-posteriorly (Figs. 2–5), due to the presence of a 250 mm long rostrum (measured between the level of the antorbital

notches and the anteriormost tip of the skull). The ratio between the length of the splanchnocranium (i.e., the rostrum) and the condylobasal length is thus estimated at around 0.63 in *Pliokogia*, that is, indistinguishable from that estimated for *K. pusilla* (ca. 0.63, but the sole known skull is strongly distorted by diagenesis), vs. 0.51 in *Nanokogia* and about 0.45–0.50 in living kogiids and *Koristocetus*. As the rostrum of *K. pusilla* is markedly concave dorsally (Bianucci and Landini, 1999), the long and dorsally flat splanchnocranium of *Pliokogia* is unique among the living and extinct kogiids for which this feature is known. Sutures between adjacent cranial bones are fused in MSNUP I-17603, thus

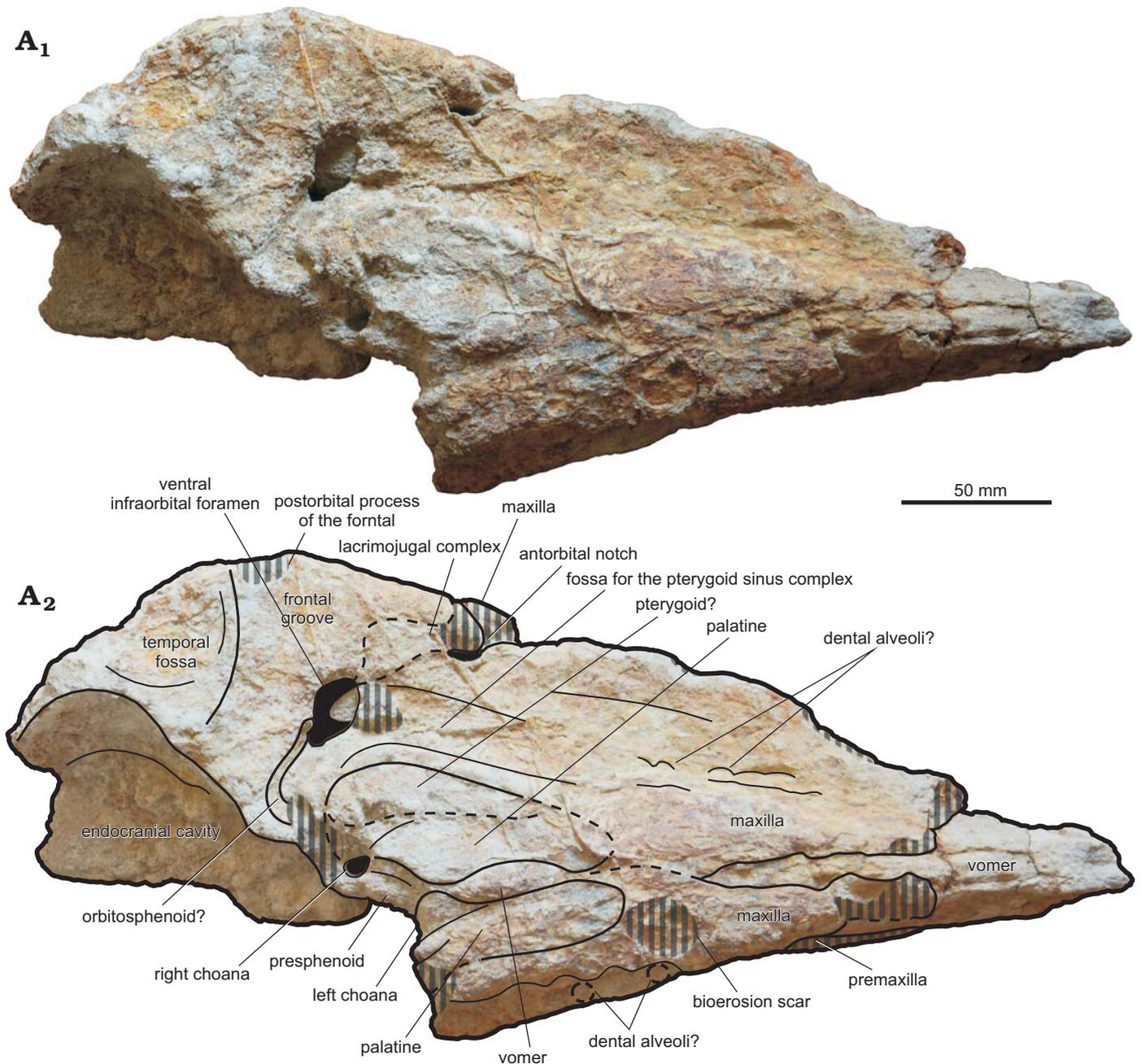


Fig. 3. Cranium, in ventral view, of the kogiid sperm whale *Pliokogia apenninica* gen. et sp. nov. (MSNUP I-17603, holotype), from the lower Pliocene of Sant'Andrea Bagni (Northern Apennines, northern Italy). Photograph (A₁), explanatory drawing (A₂). The black-shaded areas correspond to openings in the skull. The grey vertical stripes denote abraded or broken areas. Dashed lines for approximating the position of several sutures and borders.

indicating that it belonged to a physically adult individual (e.g., Chen et al. 2011).

Bioerosional modifications can be locally observed on MSNUP I-17603. On the dorsal surface of the right maxilla, anterior to the antorbital notch, four prominent elongated incisions are present (Figs. 2, 6). These traces consist of sub-straight gouges with no serrations, disposed roughly orthogonal to the lateral margin of the bone, ranging in length between 11 mm and 32 mm. Their morphology cannot easily match any bioerosional feature originating from the action of marine invertebrates, being in turn perfectly consistent

with the bone modifications due to biting by sharks provided with large, labiolingually flattened, smooth-edged tooth crowns (e.g., Bianucci et al. 2010, 2018; Govender 2015). In the light of the morphological-genetic classification scheme proposed by Cigala Fulgosi (1990) and then emended by Bianucci et al. (2010) and Collareta et al. (2017a), these traces can be interpreted as due to type I (i.e., production of a subrectilinear or weakly curved mark by impact of the tooth edge from above downward) or type II (i.e., production of a more or less elongated incision by dragging of the tooth edge in parallel with the dental axis) biting actions. In

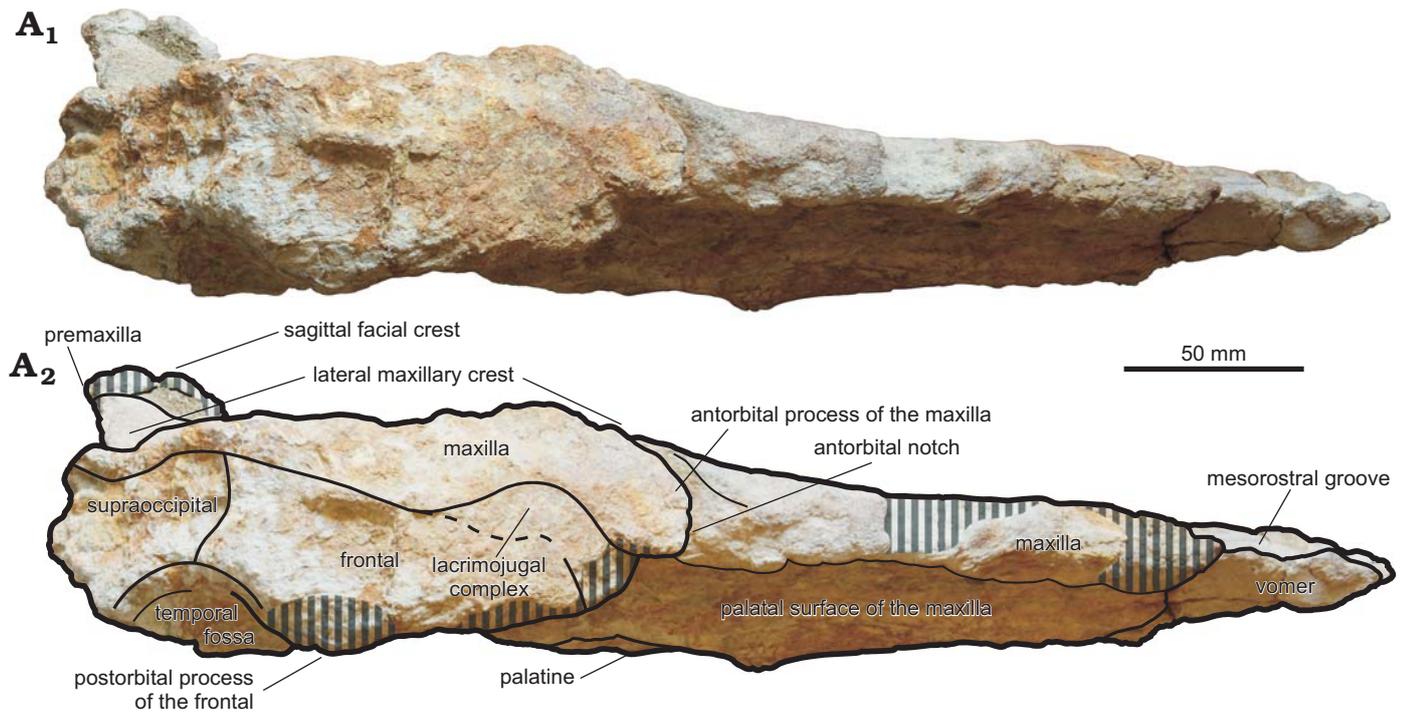


Fig. 4. Cranium, in lateral view, of the kogiid sperm whale *Pliokogia apenninica* gen. et sp. nov. (MSNUP I-17603, holotype), from the lower Pliocene of Sant'Andrea Bagni (Northern Apennines, northern Italy). Photograph (A₁), explanatory drawing (A₂). The grey vertical stripes denote abraded or broken areas. Dashed line for approximating the position of the frontal-lacrimojugal complex suture.



Fig. 5. Cranium of the kogiid sperm whale *Pliokogia apenninica* gen. et sp. nov. (MSNUP I-17603, holotype), from the lower Pliocene of Sant'Andrea Bagni (Northern Apennines, northern Italy); in anterodorsal (A₁) and right anterodorsolateral (A₂) views.

addition, an indeterminate circular bioerosion scar is present on the palatal surface of the left maxilla (Fig. 3).

Premaxilla: Both premaxillae are lost in the anteriormost quarter of the rostrum; moreover, the left premaxilla is not preserved posterior to mid-length of the left bony naris. In dorsal view, the lateral margins of the premaxillae are substraight along the dorsal surface of the rostrum and weakly converge towards the anteriormost tip of the skull (Fig. 2). At the level of the bony nares, the premaxillae are subequal in transverse width; anterior to this level, the right premaxilla is slightly but distinctly wider than the left premaxilla throughout their preserved length along the rostrum. Medial to the premaxillae, and partially overhung on by them, the

mesorostral groove opens approximately 40 mm anterior to the base of the rostrum. The mesorostral groove widens progressively towards the apex of the rostrum as the medial borders of the premaxillae weakly diverge forwards. The posterior half of the mesorostral groove is more widely open dorsally than in *Nanokogia* and *Scaphokogia* (a condition reminiscent of that observed in *Aprixokogia*, *Kogia breviceps*, and *Koristocetus*); however, moderate erosion of the medial margins of the premaxillae may have accentuated this character. In the posterior third of the rostrum, just anterior to the posterior end of the mesorostral groove, the dorsal surfaces of both premaxillae are slightly concave transversely (Fig. 5); they progressively flatten in the cen-

tral third of the rostrum. At about two thirds of the length of the rostrum (measured from its base), the dorsal surface of the left premaxilla is gently convex, whereas the dorsal surface of the right premaxilla is flat; MSNUP I-17603 thus differs from *Aprixokogia* and *Kogia* spp., in which the dorsal surface of the rostrum is distinctly concave throughout. The lateral face of the left premaxilla (i.e., the premaxilla-maxilla suture) can be observed for most of the length of the rostrum thanks to the loss of the adjoining portion of the left maxilla; it is flat and subvertical throughout. As in *Aprixokogia*, *Kogia breviceps*, *K. pusilla*, *Koristocetus*, and *Nanokogia*, there are no foramina on the left premaxilla (Fig. 2). Conversely, a rather large (12 mm long and 8 mm wide) premaxillary foramen is present on the right premaxilla, at the level of the posterior end of the mesorostral groove (Figs. 2, 6); this foramen is followed posteriorly by a 15 mm long groove. Medial and posteromedial to the right premaxillary foramen, the dorsal surface of the right premaxilla is high and bulging. The external bony nares are situated at the level of the antorbital notches. As observed in all physeteroids, they are strongly asymmetrical and distinctly displaced towards the left side of the skull. Only the anterior and medial walls of the large (i.e., more than 20 mm wide) left naris are preserved; they suggest an oval-shaped opening, situated in an anteroposteriorly oriented, funnel-shaped depression (a feature reminiscent of *Kogia* spp. and *Koristocetus*). The right naris is significantly smaller than the left and roughly circular, having a diameter of 9 mm; its anterior, lateral, and posterior walls are formed by the right premaxilla. Differing from *Kogia breviceps*, *K. sima*, and *Koristocetus*, no constriction of the right premaxilla is observable at the level of the external bony nares. Posterior to this level, as observed in all Kogiidae described to date, the right premaxilla is expanded posteromedially as a strip of bone (i.e., the postnarial eminence sensu Whitmore and Kaltenbach 2008) that forms most of the right dorsolateral face of the sagittal facial crest (Figs. 2, 3, 5); in this respect, MSNUP I-17603 markedly differs from *Scaphokogia*, in which the right premaxilla constitutes only a small fraction of the short and strongly leftwards displaced sagittal facial crest. The lateral margin of the postnarial eminence is almost straight and posterodorsomedially oriented, thus differing from the condition observed in *Aprixokogia*, *Kogia breviceps*, *K. sima*, *Nanokogia*, and *Praekogia*. Differing from extant *Kogia*, the postnarial eminence of MSNUP I-17603 does not overhang laterally over the right side of the supracranial basin. The anterior portion of the postnarial eminence, lateral and posterolateral to the right naris, is shaped as a rather deep fossa (i.e., the premaxillary fossa sensu Barnes 1973), whose floor represents the lowest point of the exposure of the right premaxilla within the supracranial basin (see description of the maxilla below) and, more generally, on the whole dorsal surface of the skull. The position and extent of the premaxillary fossa recall a similar depression observed in *Praekogia*; in the latter taxon, however, this depression extends onto the adjoining lateral margin of the right maxilla, whereas in MSNUP

I-17603 it is defined laterally by a steep wall just medial to the premaxilla-maxilla suture. The premaxillary fossa is oval-shaped, rather large (ca. 60 mm longitudinally long and 30 mm transversely wide), and parallels the lateral margin of the postnarial eminence. In our opinion, this depression is homologous to the fossa observed on the right dorsolateral face of the sagittal facial crest of *Kogia* spp., *Koristocetus*, and *Thalassocetus* (but see Barnes 1973 and Whitmore and Kaltenbach 2008 for different interpretations of the premaxillary fossa of *Praekogia*). If this homology is correct, the premaxillary fossa of MSNUP I-17603, being situated close to the sagittal plane of the skull, likely hosted the spermaceti chamber accommodating the fibrous case that surrounds the spermaceti organ of extant Kogiidae (Thornton et al. 2015). The sagittal facial crest is only partially preserved, lacking its dorsal (i.e., subhorizontal) edge; in turn, the lower portion of the anterior (i.e., subvertical) edge of the sagittal facial crest is preserved, being observed at the posterior termination of the dorsal exposure of the presphenoid, medial to the bony nares. The preserved portion of the sagittal facial crest, facing rightwards, is flat and slopes anterodorsally. The posterior termination of the sagittal facial crest reaches (or almost reaches) the nuchal crest, thus differing from the condition observed in *Aprixokogia*. The premaxillae are not exposed on the ventral surface of the cranium (Fig. 3); however, they are not preserved at (and close to) the anteriormost tip of the skull. The premaxilla is observed, in ventral view, on skulls of the extant kogiids *Kogia breviceps* and *K. sima*.

Maxilla: Both maxillae are incompletely preserved. The right maxilla is not preserved in the anteriormost fourth of the rostrum, and the ventral tip of the antorbital process is also lost (Figs. 3, 4). The left maxilla is mostly lost, except for part of its palatal surface. In dorsal view, the dorsal exposure of the maxilla tapers transversely towards the anterior termination of the skull (Fig. 2). Through the rostrum, the lateral margin of the right maxilla is anteromedially directed; it is not substraight as seen in *Kogia breviceps* and *K. sima*, but rather exhibits a marked constriction at about three fifths of the rostrum length, thus recalling the condition observed in *Koristocetus* and, especially, *Nanokogia*. The right maxilla is slightly but constantly wider than the adjoining premaxilla along the rostrum; however, the former bone is not preserved at (and close to) the anterior end of the rostrum, a region where the right maxilla is wider than the premaxilla in some extinct kogiids (e.g., *Nanokogia*). Medial and posteromedial to the right antorbital notch, the dorsal surface of the right maxilla is high, bulging, and rugose; then it flattens progressively forwards. The antorbital notch is deep, narrow, teardrop-shaped, and slit-like in its anterior portion, thus recalling *Kogia* spp. in this respect. The posterior end of the right antorbital notch opens onto the supracranial basin, a condition reminiscent of that observed in *Kogia* spp., *Koristocetus*, *Nanokogia*, and *Praekogia*. Lateral to the antorbital notch, the right lateral maxillary crest reaches its maximum height and width (Figs. 4, 5); it is high and transversely thick, not as inflated as in *Kogia breviceps* and *K. sima*, but in contrast to

the thin lateral maxillary crest of *Aprixokogia*, *Koristocetus*, *Nanokogia*, and *Scaphokogia*. The right lateral maxillary crest does not overhang either the supracranial basin or the orbital region; it points towards the apex of the rostrum and forms part of the right lateral margin of the supracranial basin. Due to the loss of the left maxilla and premaxilla posterior to the left bony naris, only the right portion of the supracranial basin (i.e., right to the sagittal facial crest), is preserved in MSNUP I-17603. As in all Kogiidae except for *Scaphokogia*, the supracranial basin generally faces antero-dorsally (Fig. 5). Similar to *Koristocetus*, *Nanokogia*, and *Scaphokogia*, the supracranial basin does not extend into the region above the rostrum (Fig. 2); conversely, in *Aprixokogia* and *Kogia* spp. the anterior part of the supracranial basin is open onto the dorsal surface of the rostrum. Similar to *Nanokogia*, the right posterolateral edge of the supracranial basin slightly overhangs the underlying temporal region (see description of the frontal bone below). The preserved lateral and posterolateral margins of the ascending process of the right maxilla suggest a roughly oval outline for the supracranial basin, thus recalling the condition observed in *Nanokogia* and *Praekogia* rather than the more circular and posterolaterally expanded supracranial basin of extant *Kogia*. Posterior and posteromedial to the right antorbital notch, and posterolateral to the premaxillary fossa, a major depression is observed on the facial surface of the right maxilla, in the right posterolateral region of the supracranial basin (Figs. 2, 5). This depression, for which the name “peripheral maxillary fossa” is here proposed, is limited anteriorly by the bulging region of the maxilla medial to the right antorbital notch, medially by a broad and substraight ridge running just lateral to the right border of the postnarial eminence, and laterally by the right lateral maxillary crest. The peripheral maxillary fossa is almost completely preserved, its posteromedial termination (sited where the sagittal facial crest and the nuchal crest likely joined to each other) being lost; it is lobe-shaped, larger than the premaxillary fossa (i.e., ca. 110 mm long and 55 mm wide), and deeply excavated. The floor of this depression, which displays a fibrous aspect, includes the lowest point of the exposure of the right maxilla within the supracranial basin. The peripheral maxillary fossa of MSNUP I-17603 is strongly reminiscent of a similar kidney-shaped depression located in the right posterolateral region of the supracranial basin of *Aprixokogia*. The latter was interpreted by Withmore and Kaltenbach (2008) as homologous to the larger right maxillary fossa of modern kogiids, which occupies most of the facial aspect of the right maxilla and expands onto the caudal termination of the right antorbital notch (thus differing from the condition observed in *Pliokogia*). In extant *Kogia*, this fossa hosts the vocal chamber where the phonic lips and vocal caps (two soft-tissue structures, part of the echolocating system of *Kogia breviceps* and *K. sima*) are situated (Thornton et al. 2015). If this homology and the above interpretation of the premaxillary fossa of MSNUP I-17603 are correct, then the topology of the echolocating system of this fossil kogiid would have been

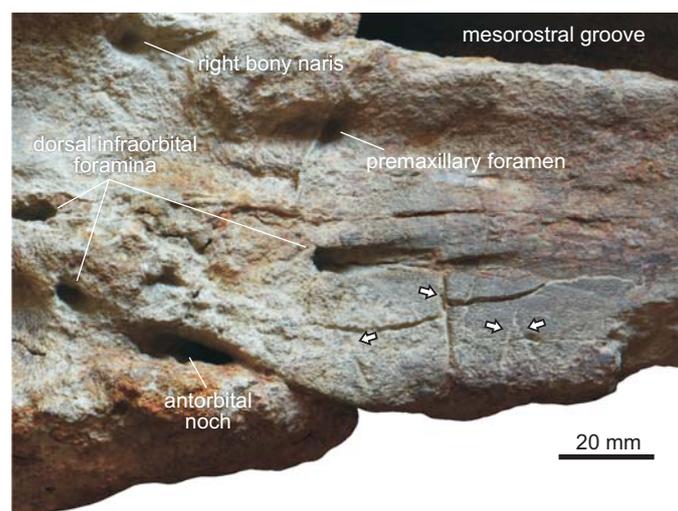


Fig. 6. Close-up of the dorsal surface of the cranium of the kogiid sperm whale *Pliokogia apenninica* gen. et sp. nov. (MSNUP I-17603, holotype), from the lower Pliocene of Sant’Andrea Bagni (Northern Apennines, northern Italy), showing the shark bite marks that affect the right maxilla (arrows).

likely similar to that of the extant species *K. breviceps* and *K. sima* (see e.g., Thornton et al. 2015: figs. 2–5). Several dorsal infraorbital foramina are observed on the right maxilla (Figs. 2, 6). The right anterior dorsal infraorbital foramen is located 40 mm anterior to the posteriormost end of the right antorbital notch, near the maxilla-premaxilla suture; it is anteroposteriorly elongated, 5 mm wide, and followed anteriorly by a deep, 45 mm long groove extension. As observed in *Kogia breviceps*, *K. sima*, *Nanokogia*, *Praekogia*, *Scaphokogia*, and *Thalassocetus*, the right posterior dorsal infraorbital foramen is subdivided, and at least three large openings are observed on the supracranial basin posteromedial to the right antorbital notch. The anteriormost opening is located 10 mm posteromedial to the right antorbital notch; it is elliptical, anterolaterally oriented, 8 mm long and 4 mm wide, and bears no groove extension. Medial and slightly posterior to this foramen, another elliptical foramen is observed 5 mm lateral to the maxilla-premaxilla suture, close to the lateral-most margin of the premaxillary fossa. This foramen is anteroposteriorly elongated, 11 mm long and 7 mm wide, and is followed posteromedially by a short and wide groove; it is connected by a wide branch of the infraorbital canal with the underlying right ventral infraorbital foramen (see below). The posteriormost opening observed on the dorsal surface of the right maxilla is located 60 mm posterolateral to the right bony naris. It opens into the left portion of the peripheral maxillary fossa, 5 mm lateral to its medial border. This foramen is anteroposteriorly elongated, 15 mm long and 5 mm wide, and is not followed by a groove. Medial to the right antorbital notch, where the poorly preserved dorsal surface of the maxilla is rough and bulging, the strong abrasion of the cortical portion of the bone prevents the unambiguous detection of foramina, but three or four small (i.e., smaller than 5 mm in diameter) additional openings might be present in

this area. In lateral view (Figs. 4, 5), the right lateral maxillary crest exhibits a high and subvertical face that comprises the supraorbital and antorbital processes of the maxilla (the anteroventral tip of the latter is missing). Medial to the anterior portion of the lateral maxillary crest, the lateral surface of the rostral portion of the right maxilla is high and adpressed to the right antorbital process. Anterior to this level, the lateral margin of the maxilla becomes slightly thinner dorsoventrally and regularly rounded. In ventral view (Fig. 3), the palatal surface of the maxilla is poorly preserved. Throughout the rostrum, the ventral surface of the maxilla is significantly convex transversely in its medial part, whereas it becomes flat to weakly concave close to the margins of the rostrum. A few badly defined circular depressions, having a mean diameter of ca. 8 mm, are locally observed on both maxillae, where the bone surface is better preserved. These depressions are reminiscent of shallow dental alveoli such as those observed on the bony palate of *Koristocetus*; in turn, deeper and large upper dental alveoli are present in *Aprixokogia*, whereas a relict alveolar groove is observed in *Kogia* spp., *Nanokogia*, and *Scaphokogia*. Along the right maxilla, these putative alveoli are situated roughly at mid distance between the lateral edge of the rostrum and the sagittal plane of the skull, where the flat and convex portions of the palatal surface of the maxillae meet each other. Among the individuated depressions, the posteriormost ones are observed on the left maxilla, in the posterior third of the rostrum. It is unclear, however, whether these putative alveoli were well distinct from each other all along the rostrum. Moreover, although the preservation state of the palatal surface of the rostrum might partially obliterate their original depth, it seems unlikely that, in the living animal, the maxillary dental alveoli would have been deep enough to bear functional teeth, especially when considering the slender and elongated morphology that characterises the sole preserved tooth of *Pliokogia* (see below). The right and left maxillae are separated medially by the ventral exposure of the vomer, except for the mid part of the palate, where the maxillae contact each other medially for about 50 mm, thus recalling the condition observed in *Nanokogia*. Due to the poor preservation state of the ventral surface of the skull, the presence of palatine foramina and sulci could not be ascertained. In ventral view, the right antorbital notch penetrates less posteriorly than observed in dorsal view, i.e., the notch itself is shorter posteriorly than it appears on the dorsal view. Posterior to the base of the rostrum, the maxilla projects lateral to the palatine and medial to the lacrimojugal complex and frontal to form the anterior and anteromedial walls of the ventral infraorbital foramen. The latter is elliptical, anterolaterally directed, and very large (i.e., 29 mm long and 15 mm wide), although its size could have been exaggerated by peripheral erosion of its walls. Anterior to the ventral infraorbital foramen and medial to the antorbital notch, a rather deep depression is observed on the posterior portion of the right maxilla. This fossa is anteroposteriorly stretched, ca. 55 mm long, and parallels the adjoining palatine, thus recalling

the condition observed in *Scaphokogia*. Similar depressions, located anterior or anterolateral to the ventral infraorbital foramen, have also been observed in *Kogia breviceps*, *K. sima*, *Koristocetus*, and *Nanokogia*. Following the interpretation proposed by Vélez-Juarbe et al. (2015) and Collareta et al. (2017a), we regard this fossa as related to the anteriormost portion of the pterygoid sinus complex.

Nasal: The right nasal is absent. The same condition is observed in the vast majority of physeteroids, with the significant exception of the late Miocene Peruvian species *Acrophyseter robustus* (Lambert et al. 2017a). Due to the loss of the posterior wall of the left bony naris (Fig. 2), it is not possible to ascertain whether MSNUP I-17603 possessed the left nasal (absent in all kogiids known to date).

Palatine: Because of the loss of most of the pterygoids, both palatines are largely exposed on the ventral surface of the skull, located posteromedially to the maxillae and anterolaterally to the choanae (Fig. 3). They are long, anterolaterally bent (i.e., reniform), gently convex transversely, and almost contact each other medially. Their medial margin is provided by the ventral exposure of the vomer. The left palatine contributes to the anterior border of the left choana. Otherwise, the palatines are not well defined.

Lacrimojugal complex: Only the right lacrimal is partly preserved (Figs. 3–5). In lateral view (Fig. 4), the lacrimal is large and roughly hook-shaped: indeed, it exhibits an elongate posterodorsal corner (posterodorsal process sensu Muizon 1988) that is wedged between the frontal and the maxilla; a similar feature has been observed, more or less pronounced, in all Kogiidae except for *Aprixokogia* (condition unknown in *Thalassocetus*). The posterodorsal process of the lacrimal is long and slender; it apparently extends more posteriorly than in *Kogia*, *Koristocetus*, and *Nanokogia*, thus recalling the condition observed in *Praekogia*. As observed in *Kogia*, *Koristocetus*, *Nanokogia*, and *Scaphokogia*, the lacrimal-maxilla suture is sigmoidal: it is distinctly convex dorsally in its anterior half and gently concave dorsally in its posterior half, thus roughly paralleling the dorsal profile of the right lateral maxillary crest. The anteroventral tip of the lacrimal bone is not preserved. In ventral view (Fig. 3), as observed in *Nanokogia* and *Praekogia*, the lacrimojugal complex extends posteromedially, towards the anterolateral termination of the ventral infraorbital foramen, but its boundaries are not well defined.

Frontal: Only the right frontal is partly preserved. This bone is mostly exposed in lateral and ventral views (Figs. 3, 4), its dorsal surface being indeed covered by the right maxilla. When viewed laterally (Fig. 4), the frontal-maxilla suture along the supraorbital process is inclined at about 20° with respect to the coronal plane, thus strongly differing from *Aprixokogia* and *Kogia* (in which much higher angles are observed) and resembling instead *Thalassocetus* in this respect. The preorbital and postorbital processes are not preserved, and only a central segment of the orbit roof is preserved. The frontal also comprises the upper portion of the roof of the temporal fossa. The latter is only incompletely

preserved; its higher point is situated slightly higher than the highest point of the orbit but ca. 40 mm lower than the overlying margin of the supracranial basin, thus contrasting with both the high temporal fossa of *Aprixokogia* and *Koristocetus* and the low temporal fossa of extant *Kogia*, recalling instead the condition observed in *Nanokogia*. The outline of the preserved portion of the temporal crest could suggest that the temporal fossa did not strongly differ from that of *Nanokogia*. When viewed ventrally (Fig. 3), the supraorbital process displays a wide frontal groove (representing the distal extension of the optic canal) running from the unpreserved optic foramen towards the lateral termination of the supraorbital process of the frontal (i.e., the roof of the orbit). The frontal groove moderately widens towards its distal end; it is oriented anterolaterally at a smaller angle than observed in *Koristocetus* and *Nanokogia*.

Vomer: The vomer reaches the anterior end of the skull (Figs. 2–5). In dorsal view (Fig. 2), the vomer is widely exposed along the rostrum and forms the floor of the mesorostral groove. The dorsal surface of the vomer consists of two flat to slightly convex bony walls, facing dorsomedially, whose medial junction forms a straight, anteroposteriorly oriented sulcus, for which the name “sagittal vomerine sulcus” is here proposed; as such, the transverse section of the dorsal surface of the vomer along the mesorostral groove is V-shaped (Figs. 2, 5). The presence of such a sagittal vomerine sulcus appears to be unique of *Pliokogia* among Kogiidae. In ventral view (Fig. 3), the vomer is exposed as a narrow but distinctly carinated slit running between the maxillae for most of the rostrum length. At the base of the rostrum, the vomer is exposed between the palatines, where it displays a prominent, anteroposteriorly elongated ventral keel. As in most kogiids except *Praekogia*, the vomer does not cover the ventral surface of the presphenoid medial to the choanae.

Sphenoid: Following Ichishima (2016), we identify the bony septum that separates the external nares medially as belonging to the presphenoid. This septum (Fig. 2) is transversely thin but flares mediolaterally at the posterior termination of the mesorostral groove, where it is exposed for about 20 mm between the premaxillae. Differing from most physically mature specimens of *Kogia sima* and some specimens of *K. breviceps*, the presphenoid does not further extend anteriorly within the mesorostral groove. In ventral view (Fig. 3), the presphenoid is partially exposed between the choanae. A long and thin slice of bone, running parallel and contiguous to the anteromedial margin of the right frontal groove towards the posterior wall of the right ventral infraorbital foramen, is here regarded as possibly representing the orbitosphenoid, following the interpretation proposed by Collareta et al. (2017b) for a similar feature in *Koristocetus*.

Pterygoid: Only a small fraction of the pterygoids is tentatively identified on MSNUP I-17603. An anteroposteriorly elongated stripe of bone, taking place between the right palatine and the adjoining portion of the maxilla lateral and anterolateral to the right bony naris, is here interpreted as a



Fig. 7. Detached tooth of kogiid sperm whale *Pliokogia apenninica* gen. et sp. nov. (MSNUP I-17603, holotype), from the lower Pliocene of Sant'Andrea Bagni (Northern Apennines, northern Italy), in four different views (A₁–A₄). The dashed line denotes the extent of the wear facet.

portion of the right pterygoid (Fig. 3). This bone seems also to cover the lateral margin of the right palatine.

Occipital: A small portion of the supraoccipital is preserved, posterior to the apex of the temporal fossa and below the posterolateral margin of the supracranial basin (Fig. 4). It contacts the frontal anteriorly; the supraoccipital-frontal suture runs roughly subvertical.

Dentition: The only preserved tooth (Fig. 7) is slender, streamlined, delicate, and almost complete, lacking only the basalmost tip of the elongated root; it measures 35 mm in maximum preserved dorsoventral height and 5 mm in maximum transverse diameter. It displays a very weak curvature, weaker than generally observed in the teeth of extant *Kogia* and in more robust isolated fossil teeth, possibly belonging to Kogiidae, described and figured by Pilleri (1987: pl. 15) from the Italian Pliocene locality of Orciano Pisano. The uppermost 7 mm of the tooth are comprised of a dark-coloured cusp, having a roughly circular base (with a mean diameter of ca. 4 mm) and a conical outline. As in most extant adult individuals of *Kogia breviceps* and *K. sima* (Plön 2004), the sole preserved tooth of *Pliokogia* completely lacks enamel. The tooth apex exhibits a small, barely convex, slightly polished facet that is here interpreted as due to abrasive wear. This wearing facet is subvertically oriented, and as such, it provides the tooth apex with a spatula-like appearance.

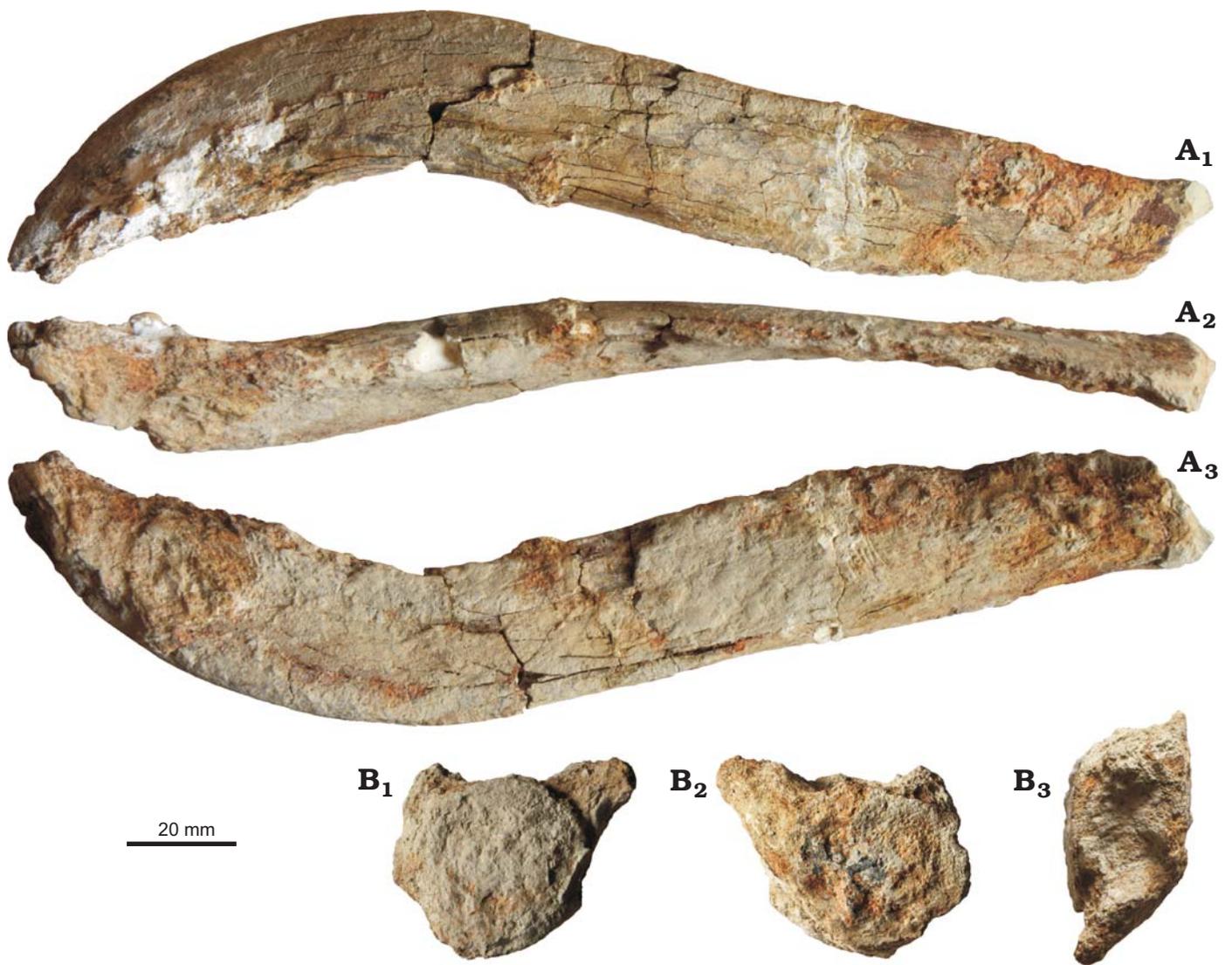


Fig. 8. Postcranial bones of the kogiid sperm whale *Pliokogia apenninica* gen. et sp. nov. (MSNUP I-17603, holotype), from the lower Pliocene of Sant' Andrea Bagni (Northern Apennines, northern Italy). **A.** Fragmentary right rib in dorsal (A₁), posterior (A₂), and ventral (A₃) views. **B.** Fragmentary thoracic vertebra in anterior (B₁), posterior (B₂), and dorsal (B₃) views.

Similar abrasion surfaces, sometimes tilted medially or laterally, are often observed on the teeth of the great sperm whale *Physeter macrocephalus*, where they are explained by the repeated passage of water laden with prey items (Lambert et al. 2013); tooth wear modifications, mostly resulting in the loss of the neonatal enamel cap, have also been reported for extant kogiids, but their origin is still not clear (Plön 2004; Stephanie Plön, personal communication 2018).

Although the only preserved tooth of *Pliokogia* was found in close proximity of the tip of the rostrum of MSNUP I-17603 (personal observation by AC and FCF), the absence of deep alveoli on the ventral surface of the maxillae suggests its identification as a mandibular tooth; only mandibular teeth are observed in extant Kogiidae, but functional maxillary teeth were presumably present in *Koristocetus* (Collareta et al. 2017b). *Pliokogia apenninica* represents the first extinct kogiid species based on significant cranial material for which at least one tooth is known.

Ribs: A single fragmentary and slightly distorted anterior rib is preserved (Fig. 8A). The head, neck, tubercle, and distal termination of the rib are unfortunately lost. The shaft has a minimum preserved width of 30 mm and ranges from 7 mm to 12 mm in thickness. Based on its general shape and curvature at the angle, this bone is tentatively identified as the second right rib.

Vertebrae: Only one 21 mm long partial vertebra is preserved (Fig. 8B). This vertebra appears to have been deformed by diagenetic compression, and consequently its centrum is shaped as an oblique circular cylinder. The proximal portions of both pedicles are preserved: the left pedicle is relatively more complete than the right and points anterodorsolaterally. The position of the pedicles indicates that, originally, the neural arch was rather wide transversely. The general proportions and size of this vertebra, as well as its moderate anterolateral thickness and the presence of pedicles, suggest its identification as a thoracic. Both the ante-

rior and the posterior vertebral epiphyses are fused with the centrum. Given that, in extant odontocetes, the progression of vertebral epiphyseal ankylosis seemingly terminates in the thoracic and lumbar regions (Galatius and Kinze 2003), this observation confirms that MSNUP I-17603 represents a full-grown cetacean individual.

Stratigraphic and geographic range.—Type locality and horizon only.

Phylogeny

Our phylogenetic analysis resulted in thirty most parsimonious trees having tree length of 145, consistency index of 0.5379, and retention index of 0.7287. The strict consensus tree and the 50% majority-rule consensus tree are presented in Fig. 9. The former (Fig. 9A) displays basically the same relationships within physeteroids as the tree of Collareta et al. (2017a). In this tree, the base of Physeteroidea is marked

by a polytomy involving: (i) *Eudelphis* from the Berchem Formation of Belgium; (ii) a clade including the four genera of macroraptorial stem physeteroids (namely, *Acrophyseter*, *Brygmophyseter*, *Livyatan*, and *Zygophyseter*); and (iii) a clade formed by “*Aulophyseter*” *rionegrensis* plus the crown-group physeteroids (i.e., Physeteridae + Kogiidae). The recovery of the macroraptorial sperm whales (sensu Lambert et al. 2017a) as a monophyletic group might suggest to erect a new family for them, pending further analyses. The strict consensus tree supports the referral of *Pliokogia* to the family Kogiidae. Also in agreement with the results of Collareta et al. (2017a), the strict consensus tree recognises three groups among kogiids: (i) a paraphyletic group including two early diverging forms from the North Atlantic realm, i.e., *Aprixokogia* and *Thalassocetus*; (ii) a clade coinciding with the extinct subfamily Scaphokogiinae, formed by *Scaphokogia* and two undescribed partial skulls from the Pisco Formation of southern Peru; (iii) a clade sister group to Scaphokogiinae and coinciding with the extant subfamily

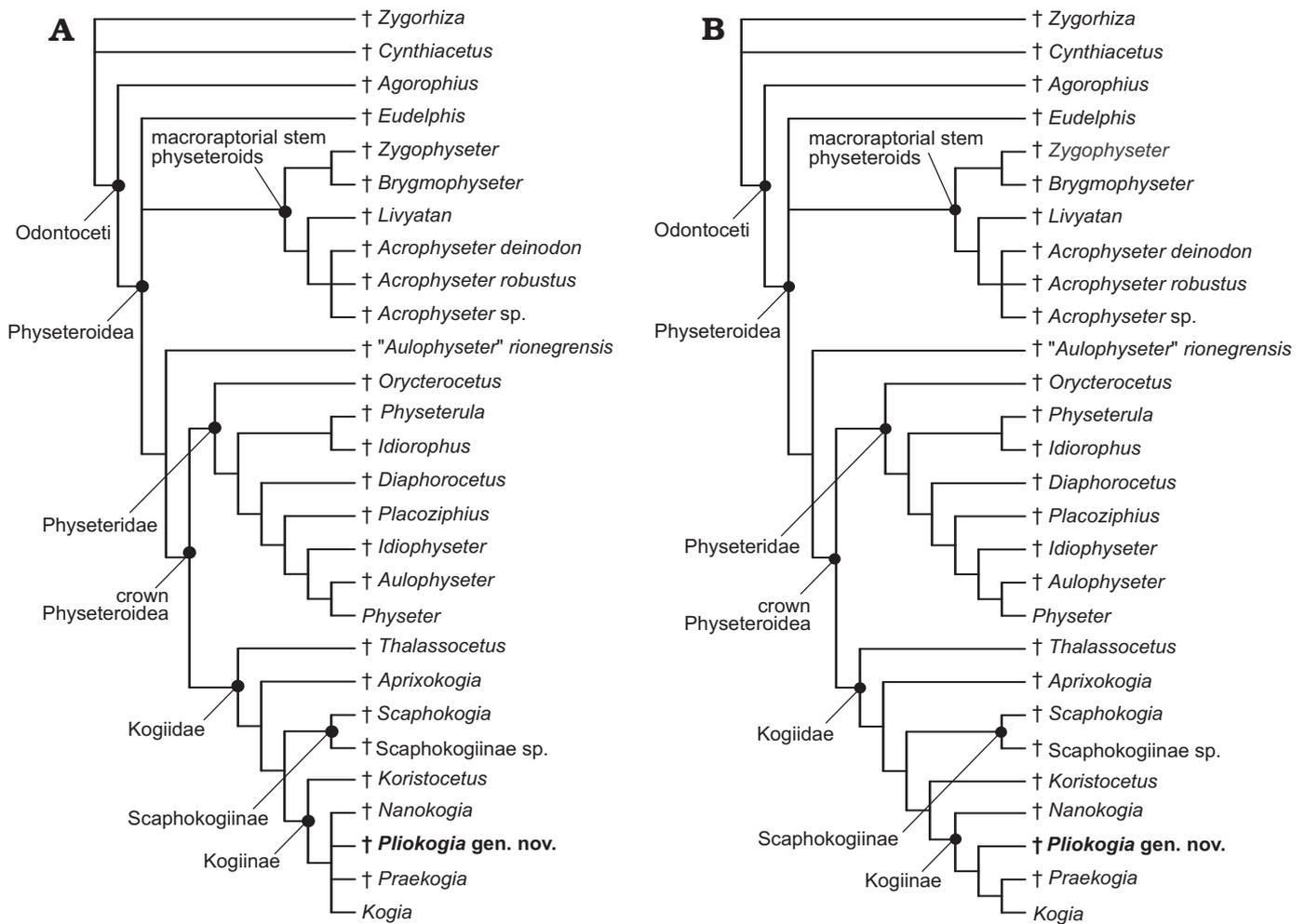


Fig. 9. Phylogenetic relationships of *Pliokogia apenninica* gen. et sp. nov. with other physeteroids. **A.** Strict consensus tree. **B.** 50% majority-rule consensus tree. *Acrophyseter* sp. refers to MUSM 2182, a partial skull from the site of Cerro Los Quesos (upper Miocene, Pisco Formation, Peru); *Scaphokogiinae* sp. refers to MUSM 3291 and MUSM 3405, two partial skulls from the sites of Cerro Los Quesos and Cerro Blanco, respectively (upper Miocene, Pisco Formation, Peru), representing a new form of Kogiidae sharing similarities with *Scaphokogia cochlearis* (see the SOM file for further details). Extinct genera and species are marked by a dagger (†).

Kogiinae, which includes *Koristocetus*, *Nanokogia*, *Praekogia*, *Kogia*, and the newly described genus *Pliokogia*. The subfamily Kogiinae is thus comprised of all the members of Kogiidae in which the posterior end of the right antorbital notch opens onto the supracranial basin (character 10, state 1). Although *Koristocetus* is recovered as the earliest branching member of Kogiinae, the relationships among *Kogia*, *Nanokogia*, *Praekogia*, and *Pliokogia* are unresolved in the strict consensus tree, possibly reflecting the rather minor nature of the anatomical differences between these closely allied genera. The 50% majority-rule consensus tree (Fig. 9B) provides a more satisfactory result, being indeed able to fully resolve the relationships among the five genera of Kogiinae: *Koristocetus*, *Nanokogia*, *Pliokogia*, *Praekogia*, and *Kogia* are here recognised as subsequently branching genera. Therefore, the 50% majority-rule consensus tree recovers *Pliokogia* crownward of *Koristocetus* and *Nanokogia*, as sister group to *Praekogia* + *Kogia*, with which it forms a clade of Plio-Quaternary kogiids that includes the extant representatives of this family.

Palaeoecology

Extant kogiids inhabit tropical to temperate pelagic environments outside the Mediterranean Basin (e.g., McAlpine 2002). Dwarf sperm whales (*Kogia sima*) appear to be widely distributed in the offshore waters of tropical and warm-temperate regions, seemingly preferring low-latitude open-ocean areas (Caldwell and Caldwell 1989). Pygmy sperm whales (*Kogia breviceps*) are known from deep waters (outer continental shelf and beyond) in tropical to temperate zones of all oceans (McAlpine 2002); this species might prefer somewhat cooler waters than the dwarf sperm whale does. Dwarf and pygmy sperm whales are nevertheless sympatric species on large portions of their ranges; evidence for sympatric habits in extinct kogiids has also arisen from the fossil record of the Pliocene Yorktown Formation of North Carolina, USA (Vélez-Juarbe et al. 2015) and the upper Miocene strata of the Pisco Formation of Peru (Collareta et al. 2017b). Three modern records of *K. sima* exist for the Mediterranean region, all from the coasts of Italy (Baccetti et al. 1991; Bortolotto et al. 2003; Maio et al. 2017). All these records, consisting of strandings of isolated individuals, are interpreted as resulting from the entrance of Atlantic vagrants into the Mediterranean Basin; therefore, the latter is still considered outside the range of living kogiids (e.g., McAlpine 2017: fig. 2). By contrast, the Italian fossil record of Kogiidae (Pilleri 1987; Bianucci 1996, 1997; Cigala Fulgosi 1996; Bianucci et al. 1998; Bianucci and Landini 1999; this work) demonstrates that, during the Pliocene, kogiids were part of the Mediterranean cetacean fauna, both during the Zanclean and the Piacenzian. Interestingly, the fossil occurrence reported in the present paper comes from a palaeoenvironmental setting characterised by a high degree of “oceanisation”, that is, by the abundance of Atlantic-derived,

strongly oceanic vertebrate taxa, which indicate strong and well-structured connections between the northern Atlantic ocean and the Adriatic palaeo-area (Cigala Fulgosi 1986, 1996). Therefore, even in the light of the habitat preferences of present-day *Kogia*, the recovery of a fossil kogiid from such a palaeoenvironmental setting is not entirely surprising. Although floating cetacean carcasses can suffer substantial transport by marine or riverine currents before deposition on the seafloor (e.g., Schäfer 1972), it seems indeed reasonable to hypothesise that *Pliokogia* inhabited offshore, several hundred-metres-deep palaeoenvironmental settings such as the Sant’Andrea Bagni area during deposition of the mudstone from which MSNUP I-17603 was collected.

As already observed, the dorsal surface of the rostrum of MSNUP I-17603 displays some unambiguous shark bite marks. Similar traces are known from several Pliocene cetacean specimens from the central Mediterranean region (e.g., Portis 1883; Cigala Fulgosi 1990; Bianucci et al. 2002, 2010; Freschi 2017). Due to their remarkable maximum length, unserrated nature, and substraight geometry, these bite marks are most likely referable to a large-sized lamniform such as *Cosmopolitodus plicatilis* (Agassiz, 1843), a possible synonym of *Cosmopolitodus hastalis* (Agassiz, 1838), which in turn is sometimes placed in the extant genus *Carcharodon* (e.g., Ehret et al. 2012; Kent 2018). Interestingly, teeth of *Cosmopolitodus plicatilis* are rather common in lower Pliocene deposits of Italy (see e.g., Marsili 2007a for a review), and evidence for *Cosmopolitodus* preying upon the extinct dolphin *Astadelphis gastaldii* (Brandt, 1874) from the Pliocene of Piedmont has been provided by Bianucci et al. (2010). As highlighted elsewhere (e.g., Cigala Fulgosi 1990; Ehret et al. 2009; Bianucci et al. 2010, 2018; Collareta et al. 2017a; Godfrey et al. 2018), it is virtually impossible to discriminate between active predation and scavenging when dealing with fragmentary fossil specimens such as the holotype of *Pliokogia*. Interestingly, the extant *Carcharodon carcharias* (Linnaeus, 1758) is known to include the pygmy sperm whale *K. breviceps* (which is similar to *Pliokogia* in body size) among its prey items (e.g., Long 1991). Moreover, Marsili (2007a) pointed out that *Cosmopolitodus plicatilis* thrived in the Mediterranean Sea at the Miocene–Pliocene transition, when marine mammals also boomed, and he proposed that the trophic spectrum of this extinct lamniform species was similar to that of the extant great white shark *C. carcharias*, that is, primarily focused on pinnipeds and small-sized cetaceans. In the light of these considerations, a predator-prey relationship between *Cosmopolitodus* and *Pliokogia* does not appear unlikely. At the same time, the placement of the bite marks affecting MSNUP I-17603 (i.e., on the cranium) does not compare favourably with the body regions of small-sized odontocetes primarily targeted by extant white sharks during their predatory attacks (e.g., the dorsum or the caudal peduncle); indeed, *Carcharodon* is believed to avoid detection by both the lateral visual field and the anteriorly directed biosonar of their odontocete prey (Long and Jones 1996).

Overall, extant Kogiidae appear to feed mostly on mid- and deep-water prey, thus recalling the diet habits of their much larger relative *Physeter* (McAlpine 2017). Studies of feeding habits, based on stomach contents of stranded animals, suggest that *K. breviceps* feeds in deep water, primarily on cephalopods and, less often, on deep-sea fish and shrimps (Dos Santos and Haimovici 2001; McAlpine et al. 1997). In Hawaiian waters, pygmy sperm whales appear to engage in foraging activity between 600 m and 1200 m, spanning both the mesopelagic and bathypelagic zones (West et al. 2009). Dwarf sperm whales may prefer to forage in slightly shallower waters of the continental shelf and slope (McAlpine 2017); for instance, stomach contents of *K. sima* from South African waters suggest that this species routinely dives to about 600 m, and possibly even deeper, to feed (Plön and Relton 2016, and references therein). Nevertheless, the feeding ecologies of the pygmy and dwarf sperm whales are similar, and both species occupy roughly equivalent trophic niches, at least off the US mid-Atlantic coast (Staudinger et al. 2014). In *K. breviceps* and *K. sima*, foraging relies on a strong suction feeding specialization based on a highly apomorphic craniomandibular architecture (featuring the proportionally shortest rostrum among living cetaceans) and hyoid apparatus (Caldwell and Caldwell 1989; McAlpine 2002; Bloodworth and Marshall 2005; Werth 2006; Bloodworth and Odell 2008; Hocking et al. 2017). With respect to extant *Kogia*, *Pliokogia* exhibits a distinctly longer rostrum, which can be interpreted in two ways: it could suggest that the foraging technique of this extinct form differed somewhat from that of the extremely short-snouted modern kogiids; alternatively, it might be related to a different extension of the melon (a lipid-rich structure located in the forehead of all odontocetes; Hooker 2018) with respect to *K. breviceps* and *K. sima*. Interestingly, the elongated rostrum of *Pliokogia* recalls that of *Physeter*, thus evoking the possibility that the feeding technique of the former genus integrated some elements of the highly derived suction feeding technique of the latter; however, the length of the rostrum might not be relevant to this feeding strategy, as *Physeter* sucks its prey directly into the oropharyngeal opening, i.e., at the posterior end of the oral cavity (Werth 2004, 2006). As a matter of fact, MSNUP I-17603 shares with the three living species of physeteroids a low temporal fossa, the lack of dental enamel, and the likely absence of functional maxillary teeth; coupled with the extremely slender and delicate aspect of the sole preserved tooth, these characters suggest that, similar to the dwarf and pygmy sperm whales, *Pliokogia* was a suction feeder rather than an active raptorial predator. Moreover, as already highlighted, the arrangement of the premaxillary fossa and peripheral maxillary fossa on the dorsal surface of the neurocranium of *Pliokogia* supports the hypothesis that the echolocating system of this extinct genus was well-developed and overall similar to that of extant kogiids, thus suggesting a similar specialization for deep diving and foraging at great depths. Given these observations, and considering also the palaeobathymetry estimates for the offshore mudstone ex-

posed at Sant'Andrea Bagni (at least 400–900 m; Cigala Fulgosi 1996), we hypothesise that the diet of *Pliokogia* included deep-water prey, thus not substantially departing from that of *Kogia* and, possibly, *Nanokogia* (Vélez-Juarbe et al. 2015). Interestingly, the Sant'Andrea Bagni palaeo-environment was characterised by oxygenated sea bottom conditions, as well as by an abundant and diverse benthic and benthomesopelagic fauna (Cigala Fulgosi 1986, 1996).

Since modern kogiids do not inhabit the Mediterranean Sea, and considering also that they are believed to forage on deep-water cephalopods and fish at or beyond the edge of the continental shelf, the association of *Pliokogia* with a psychrospheric elasmobranch assemblage with strong Atlantic affinities, such as that described by Cigala Fulgosi (1996) from Sant'Andrea Bagni, could stimulate some broader palaeoecological considerations. During the early Pliocene, the Gibraltar connection was likely deep and, at least at times, controlled by estuarine dynamics (e.g., Benson 1975; Van Harten 1984; Thunell et al. 1987; McKenzie et al. 1990; Iaccarino et al. 1999). This situation likely allowed the passage of deep-water organisms (some of which constitute the core of the diet of extant Kogiidae, being possibly important also in the trophic spectrum of the Pliocene genus *Pliokogia*) from the Atlantic Ocean to the Mediterranean Sea and led to the establishment of rich deep-water ecosystems, supported by well-structured trophic systems, in the Mediterranean Basin (Cigala Fulgosi 1996, and references therein). Similar episodes of extensive “oceanisation” of the Mediterranean Basin, characterised by the presence of psychrospheric waters of Atlantic origin due to estuarine circulation in the Gibraltar area, apparently occurred again (if not continuously) during the late Pliocene and early Pleistocene, as indicated by a well-established fossil record of vertebrates and invertebrates (e.g., Di Geronimo and La Perna 1996, 1997a, b; Marsili 2007b; Cigala Fulgosi et al. 2009; Borghi et al. 2014; Sciuto 2014; Collareta et al. 2018). The eventual establishment of present-day antiestuarine circulation at Gibraltar, characterised by deep homothermy and a limited deep nutrient supply, likely led to the eradication of most Atlantic-derived deep-water ecosystems from the Mediterranean Sea (see also Cigala Fulgosi 1996, Marsili 2007b, and Borghi et al. 2014 at this regard). Although several modern Mediterranean toothed whales (e.g., *Physeter macrocephalus* and *Ziphius cavirostris* Cuvier, 1823) forage at mesopelagic and bathypelagic depths, the current diversity of Mediterranean deep-diving odontocetes might be smaller than in Pliocene times, and the absence of kogiids from the present-day Mediterranean Sea has been proposed to reflect a strong, basin-wide depletion of the teuthophagous trophic resource—an interpretation that highlights the prime importance of food availability in controlling the structure and composition of cetacean communities (Bianucci et al. 1998). In the light of these hypotheses, and if our reconstruction of the ecological preferences of *Pliokogia* is correct, the eventual disappearance of Kogiidae from the Mediterranean Basin could be related to the defini-

tive establishment of threshold basin conditions at Gibraltar, resulting in a physical and biological barrier to the entrance of deep-water Atlantic species, including the putative prey of the Pliocene Mediterranean kogiids.

Conclusions

We describe MSNUP I-17603, a partial physeteroid skeleton from the early Pliocene (ca. 5 Ma) of northern Italy (Northern Apennines, Adriatic palaeo-area). This fossil specimen is designated as the holotype of *Pliokogia apenninica*, a new genus and species of Kogiidae. *Pliokogia* is mostly characterised by a long and dorsally flattened rostrum and by the presence of two well-distinct fossae on the right side of the supracranial basin, including an elongated peripheral maxillary fossa (here interpreted as accommodating the vocal chamber) on the posterior portion of the right maxilla. Our phylogenetic analysis recovers *Pliokogia* as a member of the subfamily Kogiinae, which also includes *Kogia*, *Koristocetus*, *Nanokogia*, and *Praekogia*. The palaeoecology of *Pliokogia* is then discussed with reference to its cranial features, the embedding sediments and associated faunal assemblage (which includes a number of deep-water elasmobranch taxa with strong Atlantic affinities), and relevant ecological literature on extant pygmy and dwarf sperm whales. We propose that the eventual disappearance of Kogiidae from the Mediterranean Basin might be related to the definitive establishment of threshold basin conditions at Gibraltar, which possibly resulted in the strong depletion of their putative prey (e.g., deep-sea squids and fish). In conclusion, while significantly expanding our knowledge on the early Pliocene Mediterranean biodiversity, the finding of *Pliokogia* suggests that our understanding of the past diversity, disparity, and distribution patterns of kogiid sperm whales is still far from being exhaustive.

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