



A new odontocete (Inioidea, Odontoceti) from the late Neogene of North Carolina, USA

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Abstract. A new monotypic genus of Neogene odontocete (*Isoninia borealis*) is named on the basis of a partial skull (CMM-V-4061). The holotype was found on the riverbed of the Meherrin River (North Carolina, USA) and probably originated from the Miocene marine Eastover Formation. Deep interdigitation of the cranial sutures indicates that this individual was mature. The new taxon differs from all other delphinidans in the unique combination of the following characters: anteriorly retracted premaxillae and maxillae; premaxillae not contacting nasals; thick nasals with ventrolateral margins deeply imbedded within corresponding troughs in the frontals (this is an apomorphy); nasals with transversely convex dorsal surface; nearly symmetrical vertex; os suturatum (or interparietal or extra folds of the frontals) at the vertex; large dorsal infraorbital foramen level with the posterior margin of the external bony nares; and a postorbital recess on the ventrolateral face of the frontal below and behind the postorbital process of the frontal. This odontocete exhibits two small but pronounced concavities on the cerebral face of the frontal/presphenoid that are presumed to have held vestigial olfactory bulbs in life. Inioidea is only diagnosed by a single unequivocal synapomorphy: width across nasals and nares subequal. *Isoninia* shares this feature with other inioids and forms the basis for the placement of *Isoninia* within this clade. A relatively high vertex coupled with a supraoccipital that is deeply wedged between the frontals suggests placement of this new inioid species within the family Iniidae. This

is the second inioid described from the Eastover Formation (the other being *Meherrinia isoni*). This new species adds new cranial morphology and a new combination of cranial characters to this taxonomically small but growing group of mostly marine and mostly Western Hemisphere odontocetes (urn:lsid:zoobank.org:pub:E8B817CA-B250-42B3-9365-36EFBFE351C9).

1 Introduction

The extant South American river dolphins (*Inia* and *Pontoporia*) are traditionally grouped in the Inioidea (sensu de Muizon, 1988), a conclusion with which more recent work is in agreement; however, there has been some discussion of whether its sister group is the Yangtze river dolphin (Lipotidae) or modern marine dolphins (Delphinoidea) (Arnason and Guldberg, 1996; Yang and Zhou, 1999; Yang et al., 2005; Cassens et al., 2000; Hamilton et al., 2001; Nikaido et al., 2001; Cozzuol, 2010; Geisler and Sanders, 2003; McGowen et al., 2009; Geisler et al., 2011, 2012; Gatesy et al., 2013; Pyenson et al., 2015; Post et al., 2017; Lambert et al., 2017, 2018, 2020; McGowen et al., 2020). Extant Inioidea are comprised of two monotypic families (Ruiz-Garcia and Shostell, 2010), Iniidae Gray, 1846, and Pontoporiidae Gill, 1871. *Inia* is a strictly freshwater form that includes three living species: *Inia geoffrensis* (de Blainville, 1817) found within the Orinoco and Amazon river basins, *Inia bolivien-*

sis (Banguera-Hinestroza et al., 2002) that inhabits the Beni–Mamoré river basin, and possibly *Inia araguaiaensis* (Hrbek et al., 2014) from the Araguaia–Tocantins river basin. *Pontoporia* is monotypic (*P. blainvillei*; Gervais and d’Orbigny, 1844) and occupies shallow marine and estuarine environments along the southeastern coast of South America, with some entrance into proximal riverine systems including Babitonga Bay, southern Brazil (Cremer and Simões-Lopes, 2005), and the La Plata river of Argentina and Uruguay (Casinos) (Secchi, 2010).

The Pontoporiidae (sensu Geisler et al., 2012) is known from the late middle Miocene to the Holocene. Several authors (Lambert and Post, 2005; Godfrey and Barnes, 2008; Gutstein et al., 2009; Lambert and Muizon, 2013; Pyenson and Hoch, 2007; Pyenson et al., 2015; Post et al., 2017; Lambert et al., 2020) have detailed the geographic and stratigraphic extent of the extinct members of this family, which includes small-bodied, mostly coastal odontocetes with rostra ranging from short to long.

Extinct iniids include *Kwanzacetes khoisani* Lambert et al., 2018, from the Kwanza Basin, Angola; the Argentinian forms *Ischyrorhynchus vanbenedeni* Ameghino, 1891 (Cozzuol, 1985, 1996, 2010; Cione et al., 2011; Pyenson et al., 2015), *Sauroctes argentinus* Burmeister, 1871, and *S. gigas* Cozzuol, 1989, all from the late Miocene Ituzaingó Formation (Cozzuol, 1989, 1996); a Pleistocene species of *Inia* from Brazil (Cozzuol, 2010); *Isthminia panamensis* Pyenson et al., 2015, from the late Miocene Chagres Formation of Panama; *Brujadelpis ankylostris* Lambert et al., 2017, from the late Miocene Pisco Formation, Pisco Basin, in Peru; and *Goniodelphis hudsoni* Allen, 1941, from the late Miocene Bone Valley Formation of Florida, USA (Morgan, 1994).

Within Inioidea, several taxa move from one family to the other in successive phylogenetic analyses, which indicates that for some species final family attribution is not yet settled. Furthermore, eventually some of those could even fall as stem inioids, branching before the node Iniidae + Pontoporiidae.

The discovery of marine iniids has fostered a discussion about the Mio-Pliocene global distribution of inioids in general and has raised questions about the timing and paleobiology of the origin and diversification of marine forms and of the extinction of most iniids except for the exclusively freshwater South American riverine forms (Cassens et al., 2000; Gutstein et al., 2014; Pyenson et al., 2015).

Odontocetes, including inioids, present a dizzying array of cranial morphologies. Our goal here is to add to that diversity by describing and naming a new genus and species of inioid from the late Neogene of North Carolina (USA).

2 Materials and methods

2.1 CT scanning

The holotype partial skull, CMM-V-4061, was CT scanned in the Department of Anthropology at the National Museum of Natural History, The Smithsonian Institution, Washington, D.C., USA. The 3 mm helical CT scans in the transverse plane were taken at 120 kV and 280 mA.

2.2 Whitening and photography

In its natural state, the holotype skull (CMM-V-4061) is very dark, so to improve contrast in Figs. 2 and 3, the specimen was lightly dusted with sublimed ammonium chloride (a whitening technique described by Cooper, 1935, and Feldman, 1989). After the specimen was photographed with a Nikon Coolpix 510 camera on a black velvet background under fluorescent light, the ammonium chloride was removed by holding the specimen under running water (Shelburne and Thompson, 2016).

2.3 Institutional abbreviations

CMM-V, Calvert Marine Museum fossil vertebrate collection, Solomons, Maryland, USA.

MGUH VP, Geological Museum of Copenhagen University, Copenhagen, Denmark.

NMNH, National Museum of Natural History, The Smithsonian Institution, Washington, D.C., USA.

2.4 Anatomical terminology

For the anatomy of the skull, we follow the terminology proposed by Mead and Fordyce (2009) for the extant delphinid *Tursiops*.

3 Systematic paleontology

CETACEA Brisson, 1762

ODONTOCETI Flower, 1867

DELPHINIDA de Muizon, 1984

Superfamily INIOIDEA de Muizon, 1988

Family ?INIIDAE

Genus *Isoninia* gen. nov.

Figs. 2 and 3

Type species

Isoninia borealis, sp. nov., herein designated.

Etymology

The genus name is a combination of “Ison”, the family (surname) name of Ronald Ison, who found and donated the type specimen to the Calvert Marine Museum, and *Inia*, the feminine generic epithet of the Amazon river dolphin (*Inia geoffrensis*), also known as the boto or pink river dolphin. The species name “borealis” is Latin for “northern”, a reference to the type and only known specimen having been found in the Northern Hemisphere.

Holotype

The holotype is CMM-V-4061 (Figs. 2 and 3). It consists of an incomplete skull, preserving the posterior facial region, from the lateral margins of the bony nares to the supraoccipital, including the vertex. Ventrally, part of the vomer/presphenoid complex is also preserved. This specimen was alluded to by Geisler et al. (2012) prior to it having been assigned a CMM catalogue number: “Other odontocete cranial elements are known from the same locality. However, they cannot be assigned to the present taxon either because they do not overlap with the aforementioned specimens that constitute the hypodigm or because of the presence of at least one other comparably sized but currently undescribed iniod from the same locality” (Geisler et al., 2012, p. 201).

Type locality and horizon

The holotype was recovered by Ronald Ison (from the same location where the type and referred specimens of *Meherrinia isoni* were collected; Geisler et al., 2012) from the bed of the Meherrin River – a tributary of the Chowan River, Murfreesboro, Hertford County, North Carolina, USA (near 36°27' N, 77°5' W). More detailed locality information is available from the authors to qualified individuals upon request. Unfortunately, the specimen was not found in situ and was devoid of entombing sediment, as were all specimens of *Meherrinia* (Geisler et al., 2012). Nevertheless, it is considered to have been locally derived from the Cobham Bay Member of the Eastover Formation (upper Miocene, Messinian) (Lauck W. Ward, personal communication, 30 November 2009) (Fig. 1). Because it was not collected in situ, it is possible that it could have come from the Pliocene Yorktown Formation, but according to Ward (personal communication, 30 November 2009) this derivation is less likely because of where along the river bed the specimen was recovered. Conservatively, the specimen can be considered to have come from a time interval encompassing the upper Tortonian (Miocene, i.e., the Claremont Manor Member of the Eastover Formation) to the lower Piacenzian (Pliocene). As in Geisler et al. (2012), another argument in favor of the derivation of *Isoninia* from the Eastover Formation is the observation that specimens of neither *Isoninia borealis* nor *Meherrinia isoni* have been found in the Yorktown

EPOCH		AGE	NORTH CAROLINA	
PLIOCENE	upper	Piacenzian	Chowan River Formation	
	lower	Zanclean	Yorktown Formation	
MIOCENE	upper	Messinian	Eastover Formation	Cobham Bay Member
		Tortonian		Claremont Manor Member (Possibly Subsurface)

Figure 1. Stratigraphy of the marine late Miocene to Pliocene of North Carolina, USA, showing the Cobham Bay Member of the Eastover Formation, from which CMM-V-4061, the holotype and only known specimen of *Isoninia borealis* (gen. nov., sp. nov.), is thought to be derived. From Geisler et al. (2012), which they modified from Ward and Andrews (2008).

Formation despite extensive collection and study of the fauna of the Yorktown Formation at the Nutrien Aurora Phosphate Mine (formerly known as the Lee Creek Mine, Aurora, North Carolina) for more than 40 years (Whitmore and Kaltenbach, 2008).

Diagnosis

Isoninia is diagnosed on the basis of the following unique combination of features, most of which are not apomorphic: anteriorly retracted premaxillae and maxillae (i.e., no contact between premaxillae and nasals and maxillae retracted anteriorly from the sides of the frontals below the vertex); large posterior-most dorsal infraorbital foramen at approximately the same level with posterior margin of external bony nares; robust nasals, anteroposteriorly longer than transversely wide in dorsal view with *ventrolateral margins turned ventromedially to form ridges deeply imbedded within corresponding troughs in frontals* (italicized text represents an apomorphy); nasals large; nasals with transversely convex dorsal surface; dorsal surface of nasals not inflated; elevated, bilaterally compressed nearly symmetrical vertex, narrower than external bony nares; frontals form apex of the vertex; presence of os suturarum (or extra folds of the frontals or a projection of the interparietal) at the vertex; in ventral view, pronounced fossa on ventrolateral face of frontal below and behind postorbital process of frontal for the postorbital lobe of the pterygoid sinus (the postorbital recess).

Description

The bones that are preserved are thickened by comparison to a comparably sized *Inia*. These thickened bones along with

Table 1. Cranial dimensions (mm).

Maximum width of bony nares	53
Maximum anteroposterior length of right nasal	43
Maximum width of nasals (combined)	43.5
Maximum width across maxillae (as preserved)	98
Minimum distance between maxillae across the vertex	35
Maximum width between ethmoid foramina (within cranial cavity)	50
Dorsoventral thickness of vertex through cerebral midline of supraoccipital up through frontal	52.5

the degree to which the ventral surfaces of the maxillae and nasals deeply suture to the frontals (Fig. 3c) indicate that the holotype of *Isoninia borealis* was a mature individual (as is also seen in the holotype of the inioid *Stenasodelphis russellae*, Godfrey and Barnes, 2008, and in the holotype of the iniid *Kwanzacetus khoisani*, Lambert et al., 2018).

Vomer: the anterior-most preserved part of the skull is the prenasal process of the vomer (Figs. 2 and 3), which widens conspicuously to the mesorostral canal. Posterior to it is the nasal septum.

Maxilla: only parts of the maxillae adjacent to the nares and nasals are preserved. Here, at least their lateral margins are incomplete. However, with the preserved portion it can be clearly observed that the maxillae are retracted anteriorly such that they do not overlap the frontals immediately adjacent to the vertex (Figs. 2 and 3). Consequently, there is wide exposure of the frontal lateral to the vertex. Deep interdigitating sutures bind the maxillae and frontals (Fig. 3c). A shallow trough on the anterior extremity of the preserved segment of the right maxilla is interpreted as the area that held the posterior extremity of the now-missing premaxilla (Fig. 2). This suture indicates that the premaxillae were retracted rostrally such that the posterior-most reach of the premaxillae was approximately level with the mid-point in the length of the external bony nares. The maxillae form the posterolateral margin of the external nares. The thickened posteromedial margin of the maxilla broadly contacts and underlies the lateral margin of the nasal (Fig. 3a and c).

Nasals: both nasals are well preserved in *Isoninia borealis*. They are robust elements, each sub-rectangular in outline in both dorsal and lateral views. In dorsal view, their conjoined anterior margin forms the essentially straight posterior margin of the external bony nares. From this position, their combined widest point, they slightly narrow gradually along their lateral borders before turning abruptly medially towards the apex of the vertex. The dorsal surface of the nasals slopes conspicuously towards the bony nares (Fig. 3e). The pronounced undercut below the anterior margin of the nasals

(Fig. 3c) may have held the now-missing part of the pre-sphenoid that formed the posterodorsal margin of the nasal septum. The lateral margin of each nasal is deeply imbedded ventromedially into the frontal (Fig. 3c). The frontals are wedged between the posteromedial ends of the nasals.

Frontal: the frontals are the largest bones preserved in *Isoninia borealis*, occupying most of the dorsal area from the temporo-orbital plate to the back of the vertex (Figs. 2 and 3). The posterodorsal margin of the apex of the vertex may have been slightly eroded postmortem but is otherwise complete. Immediately medial to the preserved lateral margin of the frontal is a conspicuous trough until the margin of the preserved portion of the specimen, interpreted here as homologous to the trough for the posterior-most dorsal infraorbital foramen (the actual foramen is not preserved due to the loss of the lateral portion of the maxilla).

The trough is (dorsal infraorbital canal; Fig. 3f) larger than in any other comparably sized odontocete, so the opening for the posterior-most dorsal infraorbital foramen was also thought to be correspondingly large, most similar to that seen in *Isthminia* (see Pyenson et al., 2015; fig. 3B). Immediately below this trough, ventrolaterally, a fossa for the postorbital lobe of the pterygoid sinus occupies the area on the ventrolateral face of the frontal below and behind the postorbital process of the frontal, (i.e., the postorbital recess in Fig. 3f).

Behind the thickened maxilla, the frontal gains wide dorso-lateral exposure as it ascends the lateral face of the elevated vertex. The frontals form the narrow and pointed vertex posteromedially. Although the suture between contralateral frontals is located along the sagittal plane, below the vertex they are not symmetrical. A CT-scan image through the vertex transversely (Fig. 3d) confirms that the right frontal is thicker than the left and its lateral face is not as concave as is that of its left antimer. A supernumerary ossification is present on the vertex, being similar to structures described in the delphinid *Sotalia guianensis* (Simões-Lopes, 2006) as os suturarum. It is visible both in photos of the partial skull and in CT scans (Figs. 2, 3a and d). The CT images appear to indicate that it is a separate ossification distinct from the frontals, but lack of clarity engenders caution; it may simply be a fold in the left frontal. This separate ossification could represent an interparietal also present in *Kwanzacetus* and *Inia* (Lambert et al., 2018), as well as *Samaydelphis* (Lambert et al., 2020).

Below the vertex beyond the reach of the maxillae is a cluster of foramina that pass posteriorly and sub-horizontally through the frontal into the body of the supraoccipital (Fig. 2). The course of at least one larger foramen on either side of the vertex can be followed through the supraoccipital where it turns medially towards the midline of the latter.

The ventral sides of the frontals preserve some of the endocranial cavity (Fig. 3f). The ethmoid foramen passes from the anterior face of the cranial cavity anterolaterally towards the orbit. The dorsal rim of the optic canal is preserved posteroventral to the ethmoid foramen (Fig. 3e and f).

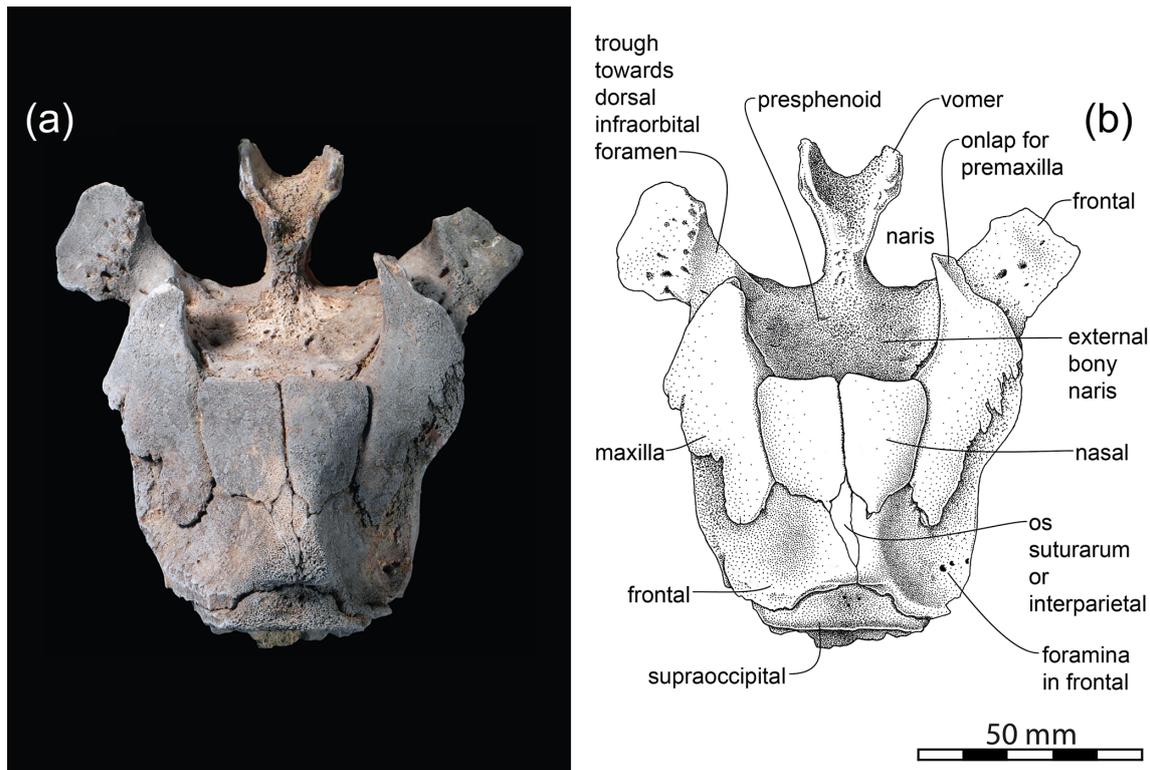


Figure 2. *Isoninia borealis* (gen. nov., sp. nov.). (a) Partial skull CMM-V-4061 in dorsal view lightly coated with sublimed ammonium chloride. (b) Interpretative drawing of (a).

Presphenoid and cribriform plate: most of the presphenoid (Ichishima, 2016) is preserved in *Isoninia borealis* (Figs. 2 and 3). On the posterior cerebral face of the cribriform plate dorsomedial to the ethmoid foramina are two small ovoid depressions, the long axis of which has an anteroventral–posterodorsal orientation. They may have held small olfactory bulbs (or their vestigial remnants) in life; in any case, these cavities are less well developed as compared to the tiny olfactory bulb cavities preserved in the platanistoid *Araeodelphis natator* (Godfrey et al., 2017). Extending from each of these depressions is a trough that merges into a single one dorsomedially. Minute foramina pass from these depressions and conjoining troughs through the cribriform plate to the nasal cavity (Fig. 3b and f). Nevertheless, it is not known whether these tiny foramina through the cribriform plate actually conducted olfactory axons to olfactory receptor tissue within the nasal cavity (see Ichishima, 2016, p. 6). Unlike MGUH VP 3338 (an unnamed platanistoid odontocete from the latest Oligocene of Denmark; Hoch, 2000) and *Squalodon* sp. (Godfrey, 2013), there is no development of crescentic foramina or ethmoturbinals on the anterior side of the ectethmoid in *Isoninia*. Therefore, *Isoninia borealis* seems to be more derived in the complete loss of these structures over the two aforementioned osmatic odontocetes. Although the derived condition in *Isoninia* does not pinpoint its geological age, it does suggest a younger Miocene or

Pliocene age – a time when most, if not all odontocetes were anosmatic.

Supraoccipital: a robust supraoccipital is wedged deeply between and behind the frontals (Fig. 3). In dorsal view, the supraoccipital gains wide exposure behind the vertex (Fig. 3a). Posterodorsally, the top of the supraoccipital is a step down from the top of the vertex formed by the frontals (Fig. 3e). In a posterior view of *Isoninia*, the broken bone suggests the presence of an external occipital crest just below the top of the supraoccipital. A transverse CT scan image through the vertex (Fig. 3d) shows that the supraoccipital was wedged dorsally between the thickened frontals. In ventral view, the supraoccipital abuts the frontals along their posteromedial margins. Posteriorly, within the brain cavity, the medial part of the supraoccipital becomes increasingly ridge-like (i.e., the internal occipital protuberance; Fig. 3d and f) and in life is presumed to have partially separated the cerebral hemispheres posteriorly.

4 Phylogenetic position

In an attempt to test the phylogenetic position of *Isoninia* within modern and extinct odontocetes, we coded the specimen and conducted three experimental phylogenetic analyses using the morphological character matrix employed by Pyen-

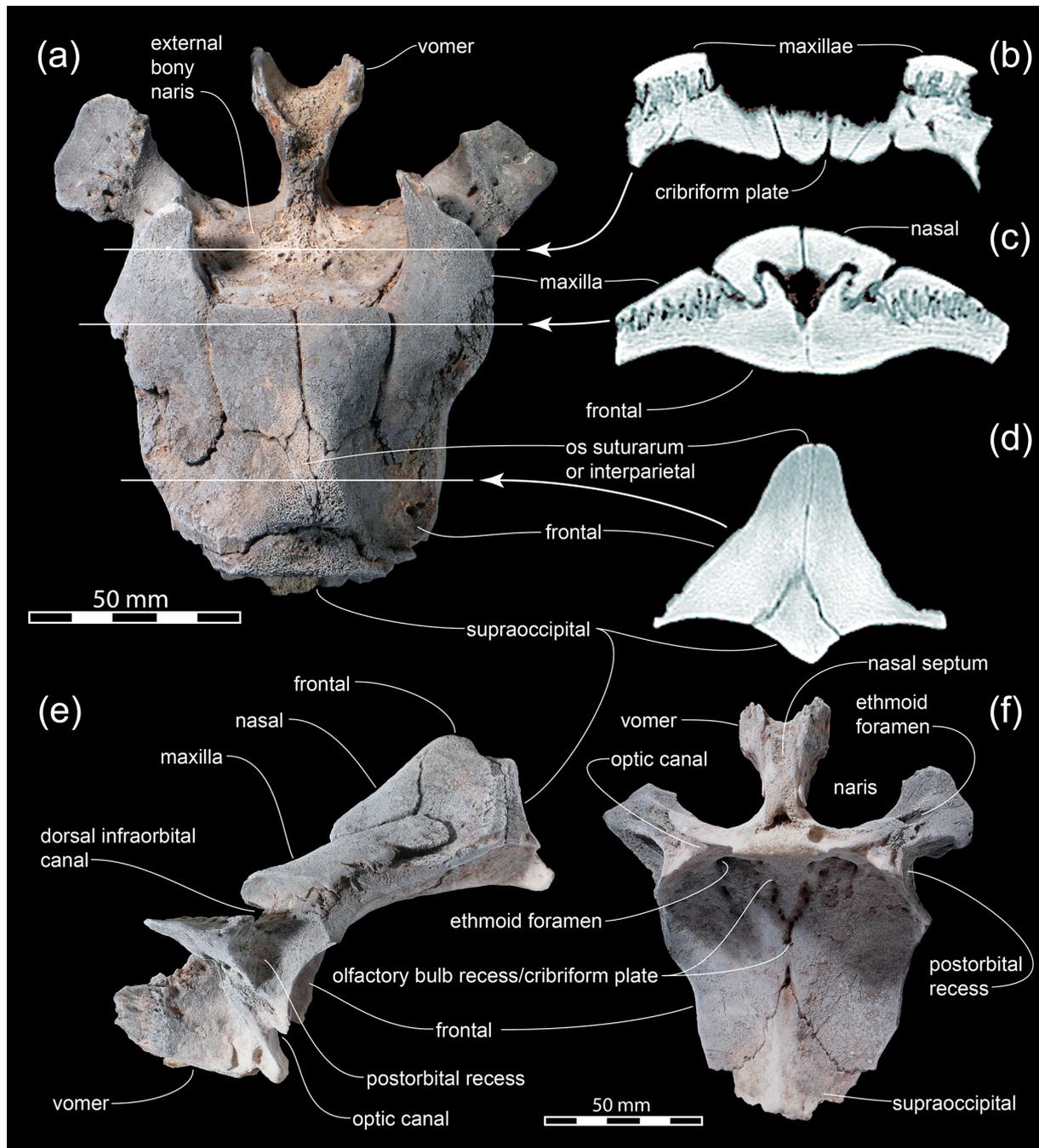


Figure 3. *Isoninia borealis* (gen. nov., sp. nov.). (a) CMM-V-4061 in dorsal view; anterior to top of figure. (b) Single CT-scan image through CMM-V-4061 in posterior view as indicated by the transverse white line in (a) to which the corresponding arrow is pointing. (c) Single CT-scan image in posterior view through the anterior part of the nasals as indicated by the white line in (a). (d) Single CT-scan image in posterior view through the vertex showing the os suturarum or a fold in the frontals as indicated by the white line in (a). (e) CMM-V-4061 in left lateral view. (f) CMM-V-4061 in ventral view; anterior to top of figure. Specimen lightly coated with sublimed ammonium chloride. CT-scan images (b–d) are adjusted to the scale bar to the left below (a). The scale bar for (e) and (f) is to the left below (f).

son et al. (2015) and Lambert et al. (2020). In every analysis, the results differed widely, and Bremer support was very low. This kind of volatility and low support are to be expected when the analyses include fragmentary/poorly known taxa, (see also Post et al., 2017, and Lambert et al., 2018, 2020, for comments to this effect). Only when a more complete specimen of *Isoninia* with ear bones is found will the results of a phylogenetic analysis be trustworthy. Consequently, we have opted not to present a potentially misleading phylogenetic analysis here (however, the results of our analyses are presented in the Supplement).

Comparisons

Lambert et al. (2017) found that Inioidea is only diagnosed by a single unequivocal synapomorphy: width across nasals and nares subequal. *Isoninia* shares this feature with other inioidea and forms the basis for our placement of *Isoninia* within this clade. Of the 14 equivocal synapomorphies for Inioidea, unfortunately because the holotype skull of *Isoninia* is so incomplete, it only preserves one – maxilla between premaxilla and nares edge.

We now compare *Isoninia* with some other inioidea (listed alphabetically). *Isoninia* shares anteriorly retracted premaxillae with *Auroracetus*. *Auroracetus* differs from *Isoninia* in that its nasals appear to be more slender bilaterally than they are in *Isoninia*. *Auroracetus* is from the Nutrien Aurora Phosphate Mine in Aurora, North Carolina, USA. It derives from the Sunken Meadow Member of the Yorktown Formation and is therefore early Pliocene in age (Gibson and Geisler, 2009).

Isoninia shares the following features with *Brachydelphis*: nasals that narrow posteriorly and frontals wedged anteromedially between the nasals. *Brachydelphis* differs from *Isoninia* in that its frontals are only narrowly exposed on the vertex and the supraoccipital is not wedged forward between the frontals. Furthermore, in *Brachydelphis*, the premaxillae contact the nasals (although there is some intrageneric variation of that feature in *Brachydelphis jahuayensis*; see Lambert and Muizon, 2013), and the maxillae are not retracted anteriorly to the same extent as they appear to be in *Isoninia*. Two species of *Brachydelphis* are known (*mazeasi* and *jahuayensis*), both from Miocene localities in Chile and Peru (Gutstein et al., 2009; Lambert and Muizon, 2013).

Isoninia shares the following features with *Brujadelphis*: a moderately elevated vertex with wide nasals anteriorly that taper posterodorsally. *Brujadelphis* differs from *Isoninia* in that its frontals are very narrowly exposed on the vertex, it does not have a supraoccipital that is wedged between the frontals, nor does it have an interparietal, and the premaxillae and maxillae are not retracted anteriorly to the same extent as they appear to be in *Isoninia*. *Brujadelphis* is from the late Miocene Pisco Formation in Peru (Lambert et al., 2017).

Isoninia shares the following features with *Inia*: an elevated vertex in which the frontals are wedged between the posterior margins of the nasals, possibly an interpari-

etal (Lambert et al., 2018), and a dorsomedial margin of the supraoccipital that is positioned between the frontals behind the vertex. The vertex of *Inia* differs from that of *Isoninia* in that the premaxillae and maxillae are not retracted anteriorly to the same extent as they appear to be in *Isoninia*, and the vertex is not so abruptly elevated and does not show a frontal boss as seen in *Inia*. Furthermore, the nasals in *Inia* have a reduced dorsal exposure due to their position on the elevated anterior wall of the frontals on the vertex.

Isoninia shares the following features with *Ischyrorhynchus*: its premaxillae are retracted anteriorly so that they do not contact the nasals, and it possesses an elevated vertex, the top of which is formed by the frontals, and nasals that slope anteroventrally towards the external bony nares. *Isoninia* differs from *Ischyrorhynchus* in that its nasals are robust by comparison, and its frontals on the vertex are bilaterally compressed as opposed to being much wider and wider than long in *Ischyrorhynchus*. *Ischyrorhynchus* is known from the Miocene of Argentina, Brazil, and Venezuela (Pilleri and Gihl, 1979).

Isoninia shares the following features with *Isthminia*: a moderately elevated vertex in which the nasals taper posterodorsally, premaxillae and maxillae that are retracted anteriorly, and a large posterior dorsal infraorbital foramen. *Isthminia* differs from *Isoninia* in that the dorsal surface of the nasal slopes less steeply anteroventrally, and its right premaxilla appears to be longer posteriorly. Furthermore, the medial portion of the nasals is more elevated in *Isthminia* compared to the lateral part, and it does not seemingly have a supraoccipital that is wedged between the frontals. *Isthminia* is from the late Miocene Chagres Formation of Panama (Pyenson et al., 2015).

Isoninia shares the following features with *Kwanzacetus*: nasals that narrow posteriorly and an elevated vertex, possibly also preserving an interparietal. *Kwanzacetus* has a medially and undercut abruptly elevated vertex as in other inioidea, which is not observed in *Isoninia*, that has a more gradually sloped and not so elevated vertex. The frontal boss present in *Kwanzacetus*, as in *Inia* and *Ischyrorhynchus*, is not present in *Isoninia*. The right premaxilla is also most likely longer posteriorly in *Kwanzacetus*. Furthermore, the lateral margin of the nasal is much more rounded, and there is a shallow internasal fossa in *Kwanzacetus*. *Kwanzacetus* is known from the late Miocene Kwanza Basin of Angola (Lambert et al., 2018).

Isoninia shares the following features with *Meherrinia*: a smooth and moderately elevated vertex, in which the frontals are wedged between the posterior margins of the nasals, and a supraoccipital that is also wedged between the posterior margins of the frontals. The vertex of *Meherrinia* differs from that of *Isoninia* in that it is proportionately narrower, the nasals are not pinched posteriorly, and the premaxillae and maxillae are not retracted anteriorly to the same extent as they appear to be in *Isoninia*. *Meherrinia* is probably from

the late Miocene Eastover Formation in North Carolina, USA (Geisler et al., 2012).

Isoninia shares the following features with *Pliopontos*: frontals that are wedged anteromedially between the nasals and a supraoccipital that is wedged between the posteromedial margins of the frontals. *Pliopontos* differs from *Isoninia* in that it does not have as elevated a vertex, wide nasals throughout their length, and premaxillae and maxillae that are not retracted anteriorly to the same degree. In *Pliopontos*, the nasals are proportionately elongated, extending posteriorly almost making contact with the supraoccipital (de Muizon, 1984; fig. 1). Consequently, the frontals gain only very limited exposure on the vertex, to which the nasals rise to the same level as the frontals. *Pliopontos* derives from the Pliocene Pisco Formation of Peru (de Muizon, 1983).

Pontistes differs from *Isoninia* in that it has premaxillae that contact the nasals, a low cranial vertex, maxillae that extend posteriorly to the level of the supraoccipital, and a supraoccipital that does not wedge deeply between the frontals. *Pontistes* is from the Miocene Entrerriana Formation of Argentina (Cozzuol, 2010).

Isoninia shares the following features with *Pontoporia*: nasals that taper posteriorly, frontals that are wedged between the nasals posteriorly, and a supraoccipital that is wedged between the poster margins of the frontals. (However, in one skull of *Pontoporia* that Stephen J. Godfrey has seen, the posterior margins of the nasals are wedged between the frontals.) The vertex of *Pontoporia* differs from that of *Isoninia* in that it is much lower, and the premaxillae and maxillae are not retracted anteriorly to the same extent as they appear to be in *Isoninia*.

Isoninia shares the following features with *Samaydelphis*: a moderately elevated vertex, in which the nasals become narrower posteriorly, frontals that are wedged between the nasals, and possibly a dorsally exposed interparietal. The vertex of *Samaydelphis* differs from that of *Isoninia* in that the nasals rise to the same level as the frontals, the frontals are more deeply wedged between the nasals than in *Isoninia*, and the premaxillae and maxillae are not retracted anteriorly to the same extent as they appear to be in *Isoninia*. *Samaydelphis* originates from within the late Miocene marine deposits of the Pisco Formation of the East Pisco Basin, Peru (Lambert et al., 2020).

Isoninia shares the following features with *Scaldiporia*: a moderately elevated vertex and nasals that narrow posteriorly. *Scaldiporia* differs from *Isoninia* in that it has an internasal fossa, its frontals are very narrowly exposed on the vertex, it does not seemingly have a supraoccipital that is wedged between the frontals, nor does it have an interparietal, and the premaxillae and maxillae are not retracted anteriorly to the same extent as they appear to be in *Isoninia*. *Scaldiporia* is from marine deposits of the Breda Formation – Late Miocene to earliest Pliocene of the Westerschelde estuary (the Netherlands) (Post et al., 2017).

Isoninia shares the following features with *Stenasodelphis*: a moderately elevated vertex, in which the nasals become narrower posteriorly, frontals that are wedged between the nasals, and possibly a shared dorsally exposed interparietal. *Stenasodelphis* differs from *Isoninia* in that its premaxillae and maxillae are not retracted anteriorly to the same degree. *Stenasodelphis* probably derives from the late Miocene Little Cove Point Member of the St. Marys Formation in Maryland, USA (Godfrey and Barnes, 2008).

In most of the aforementioned inioids, the posterior ends of the premaxillae are retracted anteriorly so that they do not contact the nasals (and consequently, the premaxillae are widely separated from the posterior margin of the external bony nares). This feature characterizes all inioids (and many extant delphinoids) except *Pontistes rectifrons* (Burmeister, 1885; de Muizon, 1983, 1984) and *Brachydelphis* (Gutstein et al., 2009, although it is variable). *Isoninia* differs from other inioids in that its nasals are robust. The development of an incipient frontal boss in *Isoninia* and that its supraoccipital is deeply wedged forward between the frontals suggest the placement of this new species within the family Iniidae.

North American inioids include *Auroracetus bakerae* Gibson and Geisler, 2009; *Goniodelphis hudsoni* Allen, 1941; *Meherrinia isoni* Geisler, Godfrey, and Lambert 2012; *Stenasodelphis russellae* Godfrey and Barnes, 2008; and *Isoninia borealis*. All of these taxa are poorly known. Assigning *Isoninia* to the Inioidea increases the morphological diversity exhibited by this clade during the late Miocene and Pliocene outside South America.

5 Conclusion

Although *Isoninia borealis* presents a combination of features that warrant the naming of a new genus and species within the Odontoceti, unfortunately, because the holotype is incomplete, phylogenetic analyses are highly volatile and very weakly supported (see Supplement). Nevertheless, describing another Miocene inioid from North America, as suggested by the shared characters established through comparisons to other inioids, further testifies to the morphological diversity found in this clade.

The present new record from the Atlantic Coastal Plain of the United States, together with inioid genera found in Angola (Lambert et al., 2018), the Caribbean (Cozzuol and Aguilera, 2008; Pyenson et al., 2015; Aguirre-Fernandez et al., 2017), Japan (Murakami, 2016), the North Sea (Lambert and Post, 2005; Pyenson and Hoch, 2007; Post et al., 2017), and Peru (Lambert et al., 2017, 2020), reinforces the hypothesis that extant inioids have a relictual distribution (Cassens et al., 2000; Gutstein et al., 2014; Pyenson et al., 2015).

Data availability. All data and results are presented in the main text, tables, figures, and the Supplement.

Supplement. The supplement related to this article is available online at: <https://doi.org/10.5194/fr-24-275-2021-supplement>.

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