An *Inticetus*-like (Cetacea: Odontoceti) postcanine tooth from the Pietra leccese (Miocene, southeastern Italy) and its palaeobiogeographical implications

(Short title: **An *Inticetus*-like cetacean from the Miocene of Italy**)

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With 4 figures

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Abstract:

We report on an isolated cetacean postcanine tooth that was collected close to the village of Melpignano (Lecce Province, Apulia region) from the Miocene 'Pietra leccese' Formation of southeastern Italy. This tooth exhibits a transversely compressed and roughly semi-circular crown featuring several large, broad-based accessory denticles that are arranged radially. Dental enamel ornamentation is limited to faint subvertical grooves, and a slight subvertical incision just below the

base of the crown suggests that it was double-rooted. Our comparisons allow us to identify the Melpignano specimen as belonging to a heterodont dolphin close to *Inticetus vertizi*, the only named member of the archaic odontocete family Inticetidae, which has been recently described from Burdigalian (early Miocene) strata of the Chilcatay Formation of southern Peru. This find highlights the elusive presence of *Inticetus*-like toothed whales in the Mediterranean region during the Miocene. We then review the geographic distribution of fossil remains of *Inticetus*-like cetaceans, which includes records from the Miocene of Peru, North Carolina (eastern U.S.A.), the Atlantic coast of France, and southeastern Italy. We hypothesise that inticetids dispersed via the Central American Seaway, which allowed faunal interchanges between the southeastern Pacific and the northern Atlantic/Mediterranean realms until latest Miocene times. In conclusion, the finding of an *Inticetus*-like tooth in Miocene beds in Italy suggests that our knowledge on the past distribution of inticetid cetaceans is far from being exhaustive.

Key words: Central American Seaway, heterodont, Inticetidae, *Inticetus vertizi*, Mediterranean, Neoceti, palaeobiogeography, *Phococetus vasconum*, Pietra leccese, toothed whales.

1. Introduction

Inticetus vertizi is an extinct heterodont odontocete taxon that has recently been described based on a partially articulated skeleton from the lower Miocene (Burdigalian, 18.8–18.0 Ma) strata of the Chilcatay Formation, Pisco Basin, Peru (LAMBERT et al. 2018). Although the phylogenetic placement of *Inticetus* among archaic odontocetes is still unclear, this large-sized extinct dolphin species was regarded by LAMBERT et al. (2018) as sufficiently different from any other toothed whale to warrant its placement in the new monotypic family Inticetidae. Amongst several other features, the highly autoapomorphic *Inticetus* is characterised by the presence of many large, broad-based accessory denticles in the double-rooted, laterally compressed cheek (i.e., postcanine) teeth.

In the present paper we report on an isolated cetacean cheek tooth from the Miocene 'Pietra leccese' Formation of southeastern Italy that shares several morphological features with the postcanine teeth of *Inticetus*. We address the systematic affinities of this fossil specimen and briefly discuss its palaeobiogeographical significance.

2. Geological and palaeontological framework

The Pietra leccese is a Miocene calcarenite limestone cropping out in the Salento peninsula (Apulia Region, southeastern Italy). This calcareous formation, mostly consisting of poorly stratified yellowish foraminiferal biomicrites and biosparites, ranges chronostratigraphically from the Burdigalian to the Messinian (e.g., FORESI et al. 2002; BOSSIO et al. 2005, 2006; MAZZEI et al. 2009). The Pietra leccese lies on the Aquitanian Lecce Formation and gradually passes upward into the Calcareniti di Andrano Formation, which closes the Miocene sedimentary cycle in Salento (BOSSIO et al. 2005). According to BOSSIO et al. (2005), deposition of the Pietra leccese was repeatedly interrupted by the action of marine currents, which inhibited the accommodation of the sediments and/or remobilised those previously deposited, resulting in significant hiatuses (often marked by the occurrence of glauconite mineralizations) of various durations. The presence of

depositional hiatuses would also explain the relatively limited thickness of the Pietra leccese (few tens of meters; FORESI et al. 2002) despite its 11-million-year-long deposition time (BOSSIO et al. 2006).

From a palaeoenvironmental point of view, the microfossil assemblages of the Pietra leccese indicate deposition in the deepest part of the outer neritic zone (BOSSIO et al. 2006), an interpretation that is also supported by the record of fossil vertebrates (CARNEVALE et al. 2001). Indeed, besides being widely appreciated as a building stone (e.g., CALIA et al. 2013), the Pietra leccese is renowned worldwide for its outstanding content of fossil marine vertebrates, which include turtles, bony and cartilaginous fishes, sirenians, and cetaceans (both toothed and baleen-bearing whales) (e.g., BIANUCCI et al. 2016a, and references therein). Cetacean remains are particularly abundant and include the holotypes of *Archaeschrichtius ruggeroi* (Mysticeti: Eschrichtiidae), *Hesperoinia dalpiazi* (Odontoceti: Inioidea?), *Messapicetus longirostris* (Odontoceti: Ziphiidae), *Rudicetus squalodontoides* (Odontoceti: Kentriodontidae), *Zygophyseter varolai* (Odontoceti: Physeteroidea), as well as the remains of several other odontocetes belonging to the extinct families Squalodontidae and Eurhinodelphinidae (MONCHARMONT ZEI 1950, 1956; BIANUCCI et al. 1992, 1994a, 1994b, 2016a; BIANUCCI 2001; BISCONTI & VAROLA 2000, 2006; BIANUCCI & LANDINI 2006).

The isolated cetacean tooth described herein has been collected from the Pietra leccese deposits close to the village of Melpignano (Fig. 1; geographic coordinates: 40°09′ N, 18°18′ E), within the type area of this formation (FORESI et al. 2002). Unfortunately, the exact locality and, consequently, the stratigraphic position of this specimen are uncertain. Samples of the sediment embedding the cetacean tooth have proved not useful for biostratigraphic purposes (RITA CATANZARITI, personal communication, 2018). However, since the Burdigalian and Langhian portions of the Pietra leccese are well exposed in the Melpignano area (FORESI et al. 2002; MAZZEI et al. 2009), and considering that the other finds of marine mammals from the outcrops of the Pietra leccese near Melpignano

come from Burdigalian to Langhian strata (BIANUCCI & LANDINI 2002), a late early Miocene to early middle Miocene age may tentatively be proposed for the fossil tooth described in the present work.

3. Systematic Palaeontology

Cetacea BRISSON, 1762

Pelagiceti UHEN, 2008a

Neoceti FORDYCE & DE MUIZON, 2001

Odontoceti FLOWER, 1867

Inticetidae LAMBERT et al., 2018

cf. *Inticetus* LAMBERT et al., 2018

cf. *Inticetus* sp.

(Figs. 2, 3a)

Referred material: One isolated and partial postcanine tooth, kept at Museo Civico di Storia Naturale di Comiso (= MSNC), Comiso, Ragusa Province, Sicily, under accession number MSNC 4457 (INSACCO 2014).

Occurrence: Miocene calcarenite limestones of the Pietra leccese exposed close to the village of Melpignano (Lecce Province, Apulia Region, southeastern Italy).

Description: MSNC 4457 exhibits a laterally compressed, roughly semi-circular crown that measures 23.8 mm in dorsoventral height and 35.9 mm in basal mesiodistal length. Besides the main cusp, this tooth bears several large accessory denticles; in particular, the ?mesial (i.e., anterior) carina bears four denticles, whereas seven denticles occupy the ?distal (i.e., posterior) carina. The tips of the accessory denticles are gently bowed towards the main cusp; moreover, they are

distinctly arranged radially, so that their tips roughly draw an arc. The height of the accessory denticles gradually decreases moving towards the base of the crown. The labial surface of the crown bears no ectocingulum and dental enamel ornamentation is limited to a few faint subvertical grooves close to the base of the crown; in turn; the lingual surface is locally damaged. The tips of the main cusp and one accessory denticle are fractured, but macroscopic evidence of in vivo wear, such as abrasion or occlusion facets, is not observable. Although most of the tooth root is missing, the presence of a groove along the labial surface just below the base of the crown suggests that the root was originally bilobate.

4. Comparisons and identification

We compared MSNC 4457 with the teeth of several extinct cetacean taxa that exhibit a similar dental morphology (Fig. 3). Considering the Miocene age of MSNC 4457, we regarded this tooth (Fig. 3a) as likely belonging to a member of Neoceti (i.e., Mysticeti + Odontoceti; FORDYCE & DE MUIZON 2001).

The greatest similarities were found with the check teeth of the heterodont odontocete *Inticetus vertizi* (Fig. 3b) from the Chilcatay Formation of Peru (LAMBERT et al. 2018). MCSNC 4457 shares with the double-rooted postcanine teeth of *Inticetus* a transversely compressed, semi-circular crown that bears several large and bowed accessory denticles that are distinctly oriented radially. In both MCSNC 4457 and the cheek teeth of *Inticetus*, there is no ectocingulum, dental enamel ornamentation is reduced, with slight subvertical grooves being present above the base of the crown. Moreover, the size of the crown of MCSNC 4457 is comparable with the largest known cheek teeth of the holotype of *I. vertizi* (e.g., C^8 to C^{10} and C_8 to C_{12}; LAMBERT et al. 2018: figs. 16, 17). The sole significant morphological difference between MCSNC 4457 and the postcanine teeth of *Inticetus* is the smaller number of accessory denticles found in the latter (i.e., up to five denticles along the distal carina) (LAMBERT et al. 2018). Moreover, the type horizon of *Inticetus* has been

referred by LAMBERT et al. (2018) to the late early Miocene (i.e., Burdigalian), a chronostratigraphic interval that is consistent with that of the lower vertebrate-bearing portion of the Pietra leccese exposed in the Melpignano area.

LAMBERT et al. (2018) highlighted the similarities between the type specimen of *Phococetus vasconum* (an enigmatic taxon of Cetacea, based on a single cheek tooth from the Burdigalian of southwestern France: DELFORTRIE 1873; KELLOG 1936; FORDYCE & BARNES 1994; UHEN 2008b; FITZGERALD 2010) and the postcanine teeth of *I. vertizi*, concluding that systematic affinities of *P. vasconum* (Fig. 3c) with *Inticetus* cannot be ruled out. Later, BOESSENECKER (2018) reported on two isolated teeth, strongly resembling the holotype of *Phococetus* and the cheek teeth of *Inticetus*, from Lee Creek Mine (North Carolina, eastern U.S.A.); BOESSENECKER (2018) identified these teeth as belonging to cf. *Phococetus* sp. (Fig. 3d) and tentatively recognised *Phococetus vasconum* as an *Inticetus*-like large-sized heterodont odontocete. For the purposes of the present paper, we concur in supporting the affinities of *Inticetus* with the holotype of *Phococetus* and the recently described specimens from North Carolina, as well as with MCSNC 4457, pending the finding of more complete specimens that will hopefully allow more precise taxonomic identifications.

Among basal odontocetes, MSNC 4457 could also be compared with the postcanine teeth of several Squalodontidae (e.g., *Squalodon* and *Eosqualodon*). However, the cheek teeth of squalodontids (Fig. 3e) exhibit more erect and less dorsoventrally high accessory denticles than the Melpignano specimen. In addition, squalodontids typically display a cingulum, strong ornamentation of the dental enamel, and a more triangular and distinctly pointed general shape of the crown of cheek teeth (e.g., DAL PIAZ 1916; ROTHAUSEN 1958, 1961, 1965, 1967). The squalodontid-like heterodont odontocete *Neosqualodon* (Fig. 3f), which is known from Langhian deposits of northern Italy and Sicily (BIANUCCI & LANDINI 2002, and references therein), exhibits proportionally larger accessory denticles (e.g., DAL PIAZ, 1904, 1916; GEMMELLARO 1919; ROTHAUSEN 1968), but they are less numerous (generally three on the distal/posterior carina and

two on the mesial/anterior carina) and less radially oriented than observed in MCSNC 4457. Moreover, the crown of MCSNC 4457 is about three times longer and two times higher than cheek teeth of *Neosqualodon*.

Among toothed mysticetes, the transversely flattened cheek teeth of the recently described *Coronodon havensteini* (GEISLER et al. 2017) exhibit remarkable morphological affinities with MSNC 4457, including the presence of several broad-based accessory denticles whose tips roughly draw an arc and the substantial lack of dental enamel ornamentation. However, the postcanine teeth of *Coronodon* (Fig. 3g) are distinctly larger than MSNC 4457, their crowns being about twice as tall as the crown of the Melpignano specimen. Moreover, the cheek teeth of *Coronodon* exhibit a seemingly less circular outline of the crown than MSNC 4457, and they even lack the faint longitudinal fluting of the enamel that characterises the labial surface of the Melpignano specimen close to the base of the crown. Finally, *Coronodon* comes from early Oligocene (i.e., Rupelian) deposits, whereas the geologically oldest strata of Pietra leccese are referred to the late early Miocene (i.e., Burdigalian) (FORESI et al. 2002; BOSSIO et al. 2005). Therefore, coupled with the Miocene age of the Melpignano specimen, our morphological observations likely prevent any tentative attribution of MSNC 4457 to *C. havensteini* or other *Coronodon*-like toothed mysticetes.

5. Palaeobiogeographical inferences and concluding remarks

MSNC 4457 represents the first fossil record of an *Inticetus*-like cetacean in the Mediterranean basin, and as such, it expands our knowledge on the Miocene central Mediterranean biodiversity. By reviewing the geographic distribution of fossil remains of *Inticetus*-like cetaceans, some further palaeobiogeographical insights can be highlighted. Indeed, so far, *Inticetus*-like heterodont cetaceans are known from the southeastern Pacific (the holotype of *Inticetus vertizi*, an incomplete skeleton from the Chilcatay Formation, southern Peru), the northwestern Atlantic (two isolated postcanine teeth referred to cf. *Phococetus* sp., likely from the Pungo River Formation, North

Carolina, eastern U.S.A.), the northeastern Atlantic (the holotype of *Phococetus vasconum*, an isolated postcanine tooth from the 'molasse de Saint Médard-en-Jalle', southwestern France), and the central Mediterranean basin (this work). Interestingly, such a distributional pattern (Fig. 4) recalls that of another Pietra leccese toothed whale, the late Miocene beaked whale *Messapicetus*, which is known from southern Peru (as *Messapicetus gregarius*; BIANUCCI et al. 2010, 2016b; LAMBERT et al. 2015; DI CELMA et al. 2017; RAMASSAMY et al. 2018), possibly the eastern U.S.A. (as cf. *Messapicetus* sp.; FULLER & GODFREY, 2007), and southeastern Italy (as *Messapicetus longirostris*; BIANUCCI et al. 1992, 1994, 2016a); as such, it further strengthens the hypothesis of well-developed faunal connections between the southeastern Pacific and the northern Atlantic/Mediterranean realms during the Miocene (DE MUIZON 1984; BIANUCCI et al. 2016a). The presence of *Inticetus*-like cetaceans in the southeastern Pacific Ocean, in the northern Atlantic Ocean, and in the Mediterranean Sea seemingly reflects faunal interchanges through the Caribbean region, similar to what has been proposed by BIANUCCI et al. (2016a) for *Messapicetus* during early late Miocene times: indeed, until the latest Miocene (e.g., JACOBS et al. 2004), the then open Central American Seaway allowed a direct, low-latitude communication between the Pacific and Atlantic oceans. Alternatively, inticetids could have dispersed via the Eastern Tethys Seaway, which was still active (yet vanishing) in late early Miocene times (e.g., REUTER et al. 2009; HAMON et al. 2013). However, the palaeobiogeographical patterns of other marine faunal elements (e.g., molluscs) account for a gradual deterioration of the migration potential across the Eastern Tethys Seaway during the Oligocene and the earliest Miocene (i.e., Aquitanian) which eventually resulted in the collapse of the biogeographical affinities between the Mediterranean Sea and the Indo-western Pacific region in Burdigalian times (HARZHAUSER et al. 2007). Therefore, dispersion of inticetids through the Central American Seaway appears as the most parsimonious hypothesis for explaining the geographical extent of their fossil occurrences.

In conclusion, coupled with the recent results of Boessenecker (2018), the find of MCSNC 4457

highlights the elusive presence of *Inticetus*-like heterodont dolphins in the northern Atlantic and Mediterranean region during the Miocene, thus suggesting that our knowledge on the past distribution of inticetid cetaceans and, more generally, Miocene heterodont odontocetes is far from being exhaustive.

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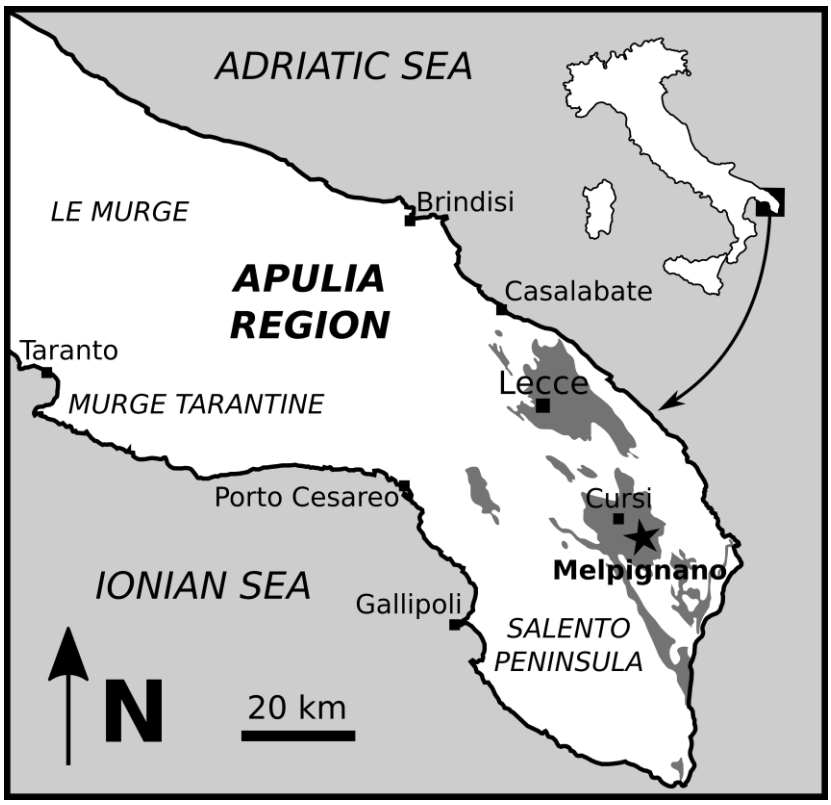
Figure captions

[*Possible position for the three figures: Fig. 1, possibly 1½ columns wide, between lines 67 and 68; Fig. 2, possibly 2 columns wide, between lines 121 and 122; Fig. 3, possibly 1½ columns wide, between lines 141 and 142; Fig. 4, possibly 1½ columns wide, between lines 212 and 213]*

Fig. 1. Location of the site where the fossil cetacean specimen MCSNC 4457 was found (Melpignano, black star) and schematic regional geological map. Grey-shaded areas indicate the exposures of the Pietra leccese, the Miocene calcarenite limestone from which the fossil originates. Redrawn and modified after CALIA et al. (2013).

Fig. 2. MCSNC 4457, postcanine tooth of cf. *Inticetus* sp., in a) labial and b) lingual view.

Fig. 3. Comparison of MCSNC 4457 with other cheek teeth of Miocene heterodont neocetes. All in labial view and reduced to the same basal mesiodistal length of the crown. Scale bars equal 1 cm. a) cf. *Inticetus* sp. (specimen MCSNC 4457), b) *Inticetus vertizi*, c) *Phococetus vasconum*, d) cf. *Phococetus* sp., e) *Squalodon bellunensis*, f) *Neosqualodon assenzae*, g) *Coronodon havensteini*.



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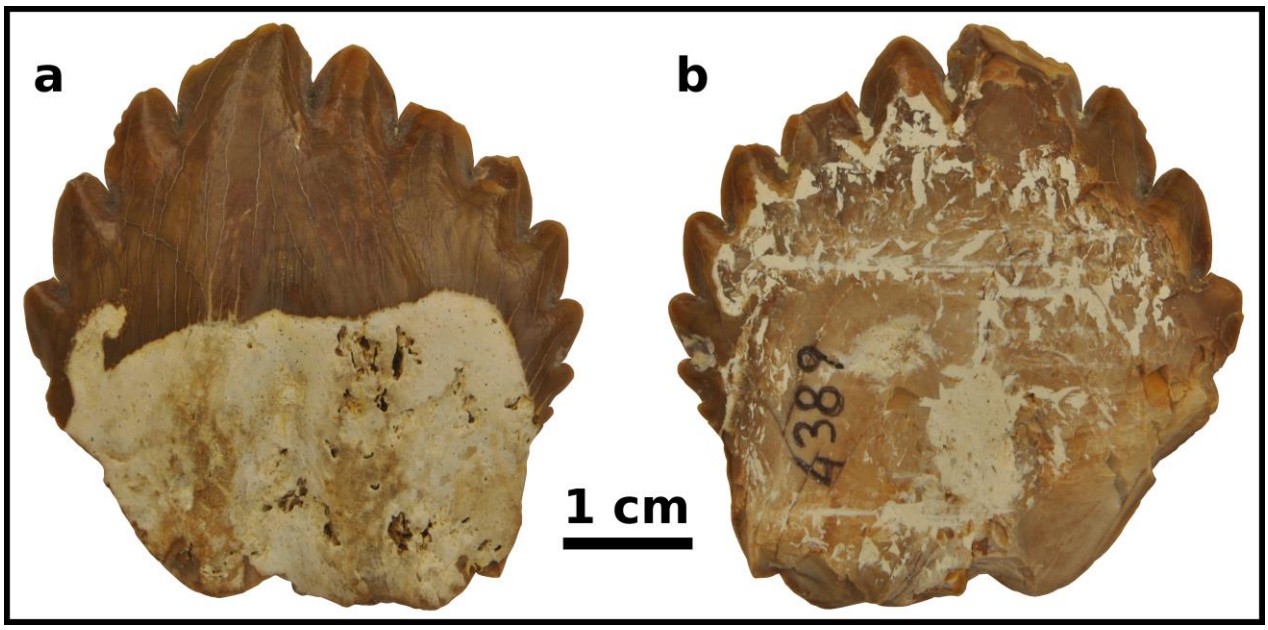

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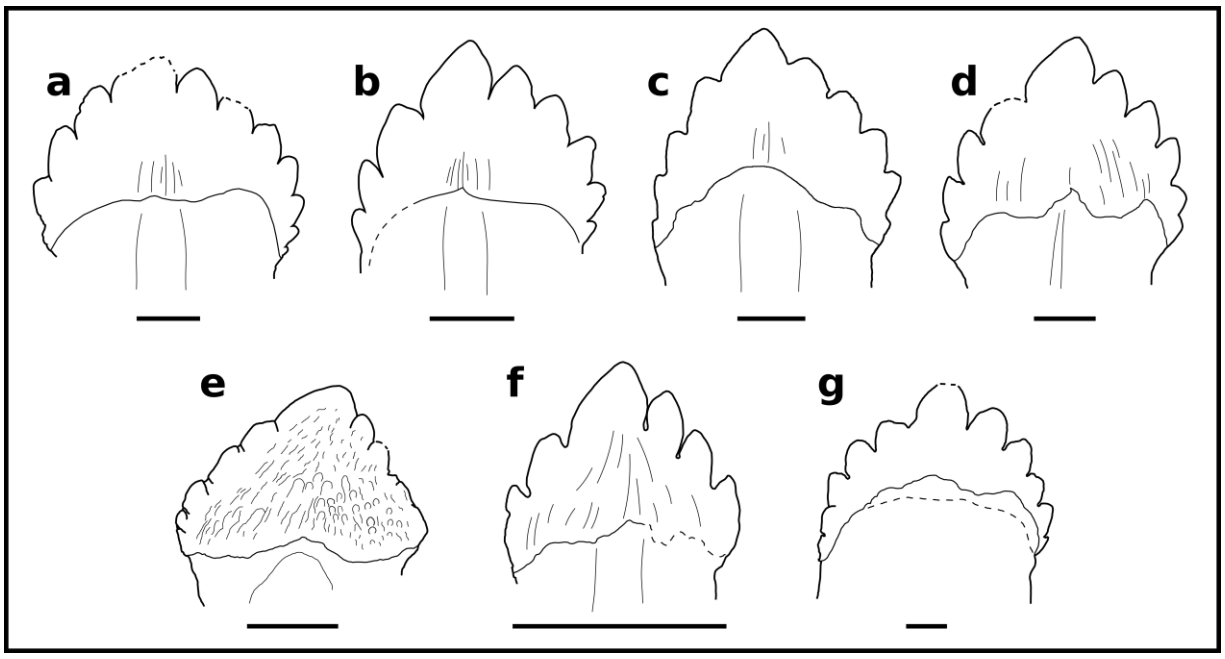

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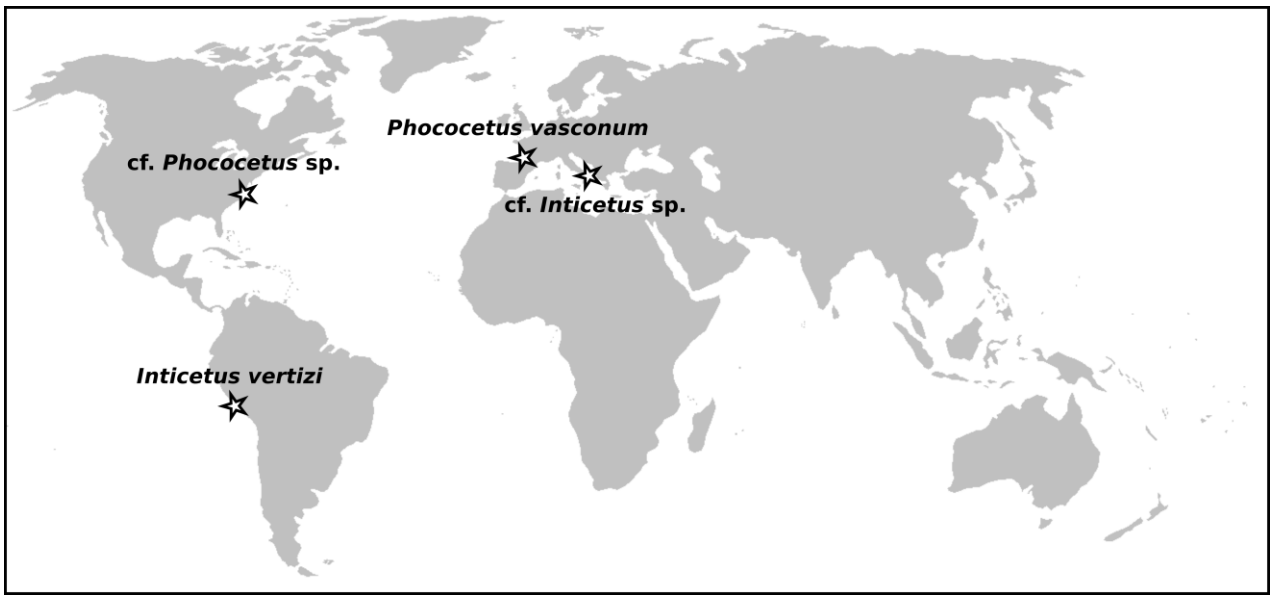

Fig. 4. Geographic distribution of fossil remains of *Inticetus*-like odontocetes from Miocene deposits worldwide. See main text for data sources.