New records of *Hemisyntrachelus* (Odontoceti, Delphinidae) from the late Pliocene or early Pleistocene of the southern North Sea

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Rostral fossils of large dolphins are identified as belonging to the genus *Hemisyntrachelus* Brandt, 1873. They reconfirm and corroborate the presence of this genus in the late Pliocene or early Pleistocene of the North Sea. Comparison of these fossils with the holotypes of the known species of *Hemisyntrachelus* (*H. cortesii* (Fisher, 1829)*, H. pisanus* Bianucci, 1996 and *H. oligodon* (Pilleri & Siber, 1989)) indicates that the North Sea specimens represent a different species which shows a peculiar morphology of the presphenoid. The incompleteness of the key fossils urges the authors to classify these finds temporarily as *Hemisyntrachelus* sp. until more, and more complete specimens are identified or discovered.

KEY WORDS: Cetacea, palaeontology, dolphin, Globicephalinae, presphenoid, The Netherlands

Introduction

Cuvier (1823) noted that some Italian Pliocene fossil dolphin skulls, interpreted as *Tursiops* Montagu, 1821, showed characteristics intermediate between *Tursiops* and *Orcinus* Fitzinger, 1860. Brandt (1873) coined the subgenus *Hemisyntrachelus* for these fossils, assigned *Delphinus cortesii* as the type species and included it – without morphological or systematic arguments - within the Delphinapteridae Slijper, 1936. This caused controversy and several authors did not agree with Brandt's classification (Van Beneden and Gervais, 1880; Capellini, 1882; Sacco, 1891, 1893; Del Prato, 1898; Trouessart, 1898 and Simonelli, 1911). However due to the unusual articulation of the ribs and a distinctive morphology of thoracic and lumbar vertebrae, Slijper (1936) resurrected *Hemisyntrachelus* and created a separate family for these dolphins (Hemisyntrachelidae Slijper, 1936). Some authors followed Slijper (Simpson, 1945), but others disagreed (Pilleri, 1979, 1980, 1985; Pilleri & Pilleri, 1982), or expressed the need for further study (Barnes *et al.*, 1985; Barnes, 1990). Slijper (1936) also included *Lophocetus calvertensis* (Harlan, 1842) from the Miocene of Maryland in this new family. This assignment was followed by Simpson (1945), but rejected by Barnes (1978) who identified *Lophocetus* Cope, 1867 as a kentriodontid. Bianucci (1996), describing the diverse Pliocene cetacean assemblages of Italy, noted in this relevant Italian delphinid a character mix of *Tursiops, Pseudorca* Reinhardt, 1862 and *Orcinus* and observed morphological characteristics of the skull to retain *Hemisyntrachelus* as a valid genus within the Delphinidae Gray, 1821. Bianucci limited the genus to two clearly identified and illustrated species (*H. cortesii* Fisher, 1829*, H. pisanus* Bianucci, 1996) thereby erasing many older synonyms (for details see Bianucci, 1996). Besides *H. cortesii* and *H. pisanus* Post & Bosselaers (2005) reported – based on mandible fragments – the presence of *Hemisyntrachelus* in the late Pliocene and/or early Pleistocene of the North Sea (North Atlantic), doubted the validity of *H. pisanus* and concluded that *Tursiops oligodon* (Pilleri & Siber, 1989) of the Pliocene of Peru should be included in the genus. The latter suggestion was followed by Murakami *et al.* (2014) and Berta (2018).

Evolutionary relationships among Delphinidae remain complicated. During the last century various revisions where proposed by a great number of authors based on both morphological and molecular considerations, often opposing and conflicting with each other (as early as Flower, 1883 to more recent LeDuc *et al.*, 1999 and Horreo, 2018). None of the authors reached a solid classification of the fossil and living members of the family Delphinidae, they all express the need for more research focusing on basic taxonomy. Bianucci (1996) presented three hypotheses on the position of *Hemisyntrachelus*. In his morphology based phylogenetic analysis the hypothesis presenting *Hemisyntrachelus* as sister taxon to *Pseudorca*, *Orcinus* and other Globicephalinae Le Duc, 1997, was considered the most parsimonious. The cladogram of Bianucci (2005) reports *Hemisyntrachelus* to be close to *Arimidelphis* Bianucci, 2005, *Orcinus* and *Pseudorca*. But Aguirre-Fernandez *et al.* (2009) placed *Hemisyntrachelus* inside a clade consisting of broad-headed genera: *Protoglobicephala* Aguirre-Fernández,

Barnes, Aranda-Manteca, Fernández-Rivera, 2009, *Orcinus*, *Feresa* Gray, 1870, *Globicephala* Lesson, 1828, *Pseudorca* and *Grampus* Cuvier, 1812. Murakami *et al.* (2012) allied *Eodelphinus kabatensis* Horikawa 1977, *Orcinus orca* (Linnaeus, 1758) and *H. cortesii* in one clade, which they presumed to be a sister clade to *Orcaella brevirostris* Gray, 1866 and the Globicephalinae. In a more recent phylogeny *H. cortesii* appears as a sister taxon to the entire Globicephaline clade and *Steno bredanensis* Cuvier in Lesson, 1828 (Lanzetti, 2013). The phylogenetic position of the genus *Hemisyntrachelus* is clearly still subject of debate; future studies will have to resolve this controversial issue.
We describe in this article new rostral fossils from *Hemisyntrachelus* from the North Sea. These fossils broaden the knowledge on the morphology, dispersal and diversity of the genus.

Stratigraphic background

Fossils from the bottom of the North Sea were historically and traditionally collected without stratigraphic background (Mol et al., 2008). However during the last decades, research has resulted in detailed geological maps of the bottom of the North Sea and this fact, combined with the collection of precise coordinates of fishing vessels, resulted in some clearly defined areas were fossils of specific (and sometimes unmixed) mammal faunae sub crop at the seafloor (Kortenbout van der Sluijs, 1971; Funnell, 1996; Mol *et al*., 2008; Post & Reumer, 2016; Phillips *et al*., 2017). Fossils from a late Pliocene – early Pleistocene marine mammal fauna (including the walrus *Ontocetus* Leidy, 1859 and the globicephalid *Platalearostrum* Post & Kompanje, 2010) have been harvested only at two specific sites. At these sites the upper Pliocene to lower Pleistocene Westkapelle Ground Formation is present at the seafloor (for more detailed reports see Post & Bosselaers, 2005 and Post & Kompanje, 2010). The fossils described in this article originate from the same sites and show the same conservation and mineralisation. They are always found together with fossils of the walrus *Ontocetus*. *Ontocetus* was present in the North Sea from *ca.* 3 Ma (the oldest find: Belgium – *pers. comm.* L. De Waele) to 1.8 Ma (fossils of Easton Bavents, East Coast UK - *pers. comm.* Nigel Larkin). Since no fossils of *Hemisyntrachelus* have been reported from Belgium, but have been reported from Easton Bavents, the age of the described fossils must be considered - with reasonable certainty - between 3 Ma-1.8 Ma.

Collection acronyms

B	Ecomare, Texel, The Netherlands
NMR	Natuurhistorisch Museum Rotterdam, Rotterdam, The Netherlands
RMHN	Rijksmuseum van Natuurlijke Historie, now part of Naturalis Biodiversity Center, Leiden, The Netherlands
SMNK	State Museum of Natural History, Karlsruhe, Germany
ZMA	Zoological Museum Amsterdam; now part of Naturalis Biodiversity Center, Leiden, The Netherlands.

Material and methods

NMR 999100016974 (hereafter mentioned as NMR 16974): rostrum with parts of maxilla, premaxilla, palatine and presphenoid.

Referred specimens – NMR 999100008080 (hereafter NMR 8080): anterior fragment of right half of rostrum; NMR 999100008081 (hereafter NMR 8081): anterior fragment of left half of rostrum.

Casts of the holotypes of *Hemisyntrachelus cortesi* (NMR 999100008180) and *H. pisanus* (NMR 999100008159) and skulls of extant delphinids in the collections B, NMR and RMNH were used for comparison.

Dimensions of the rostrum and referred specimens were noted as per Perrin (1975). Morphological terminology of the odontocete skull follows Ichishima (2016) and Mead & Fordyce (2009).

Systematics

Order Cetacea Brisson, 1762
Suborder Odontoceti Flower, 1867
Superfamily Delphinoidea Gray, 1821
Family Delphinidae Gray, 1821
Genus *Hemisyntrachelus* Brandt, 1873
Hemisyntrachelus sp.

Referred specimens

NMR 16974 (Fig. 1, Tables 1 & 2)

General – Rostrum with parts of maxillae, premaxillae, palatine, presphenoid and vomer. In lateral view the apex of the rostrum curves downward.
Based on the size and robustness of the rostral bones, the degree of suture fusion, and the well-developed posterior (maxillary) alveoli, NMR 16974 is the rostrum of a fully adult dolphin. Small dorsal maxillary vascular sulci near the alveoli suggest initial bone resorption and may be considered a token of full mature or even old age.

Premaxilla – A small (40 mm) but prominent, upheaved flange is located at the most anterior tips of the premaxilla. For most of its length the massive and wide premaxilla towers above the maxilla. In dorsal view it continues at roughly the same width until it reaches the concave premaxillary sac fossa. Both premaxillae are separated for most of the length by the open mesorostral groove. The groove is relatively wide and deep. Posteriorly the mesorostral groove

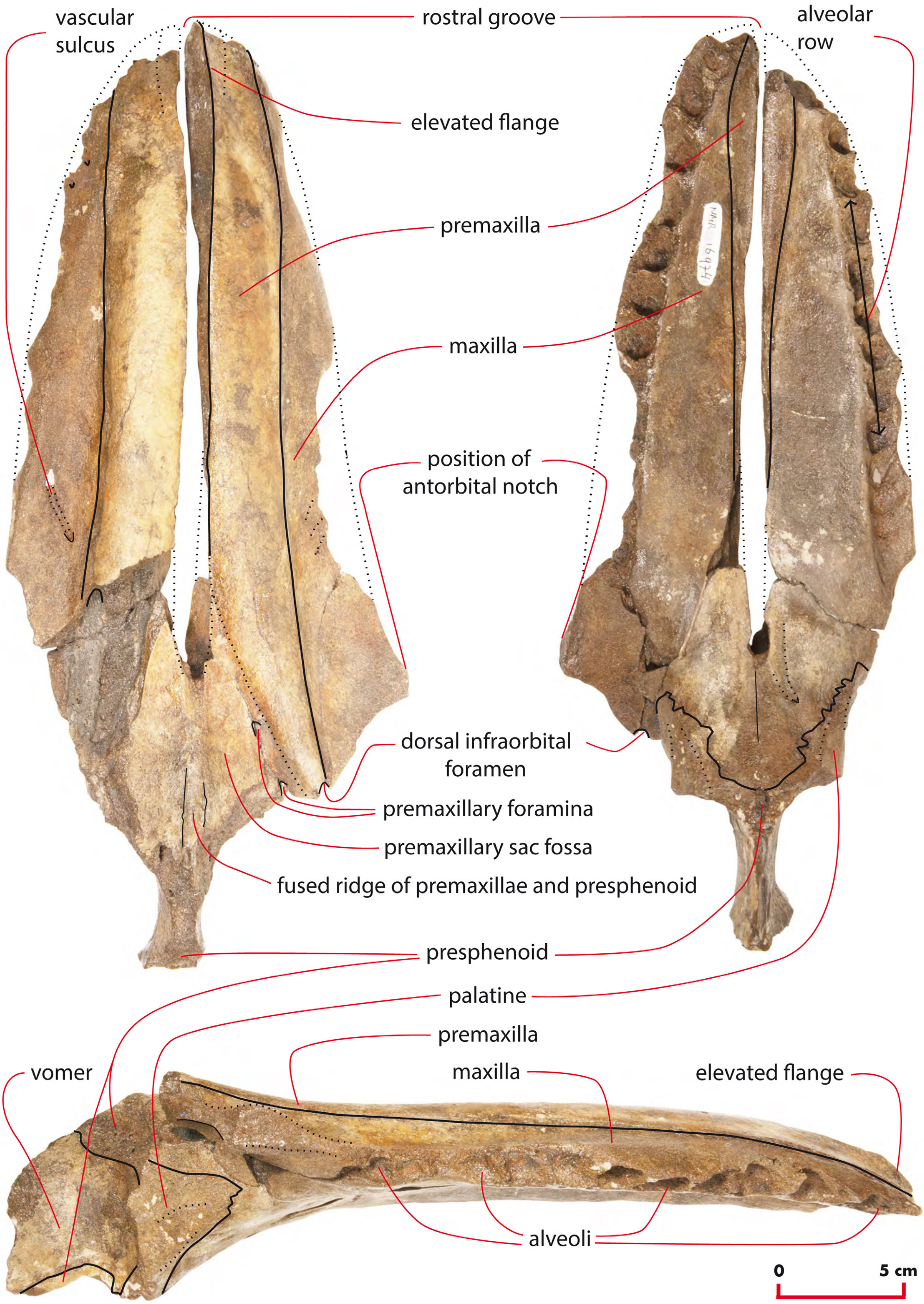

Figure 1. *Hemisyntrachelus* sp., NMR 999100016974 in dorsal, ventral and right lateral view.

	NMR 16974		**NMR 8080**	**NMR 8081**	**NMR 8180** ***H. cortesi***		**NMR 8159** ***H. pisanus***	
alveoli	**Diameter left**	**Diameter right**	**Diameter right**	**Diameter left**	**Diameter left**	**Diameter right**	**Diameter left**	**Diameter right**
1	X	X	X	0.4	0.7	0.4	0.2	0.2
2	X	0.3	0.6	0.6	0.8	0.6	0.5	0.5
3	X	1.2	1.0	1.1	0.9	0.6	0.5	0.6
4	1.2	1.6	1.3	1.5	0.9	1.1	0.6	0.7
5	1.5	1.9	1.4	1.4	1.0	1.0	0.6	0.8
6	1.2	1.8	1.5	1.5	1.0	1.1	0.7	0.8
7	1.6	1.7	1.5	1.4	0.8	1.0	0.9	0.9
8	1.4	1.7		1.4	1.0	1.0	0.8	0.8
9	1.4	X		1.2	1.1	1.0	0.8	0.8
10	1.5	X		1.2	1.1	0.7	0.9	0.8
11	1.6	X		1.1	1.0	0.8	0.6	0.9
12	1.3	X			1.0	0.8	0.9	0.9
13	1.0	0.6			0.9	0.7	0.9	0.9
14	0.7	X			0.9	0.8	0.8	0.8
15							0.9	0.8
16							X	0.7
17							X	0.6
18							X	0.5
Length of tooth row	26.1	26.5	X	X	25.4	26.5	32.0	35.5

Table 1. Comparison of alveoli diameters measured in centimetres and taken from posterior to anterior margin. The X indicates that no measurements could be taken.

	NMR 16974	**NMR 8080**	**NMR 8081**	**NMR 8180** ***H. cortesi***	**NMR 8159** ***H. pisanus***
Rostrum length	32.2	X	X	35.0	42.2
Width at base	20.2 E	X	X	17.4	20.6
Width at tooth nr. 7	13.4 E	Total right 5.7	Total left 6.2	9.1	9.6
	Rost. gape 0.6	Rost. gape X	Rost. gape X	Rost. gape 0.3	Rost. gape 0.2
	Premax 3.3	Premax 3.3	Premax 3.2	Premax 2.8	Premax 3.0
	Max 3.1	Max 2.2	Max 2.9	Max 2.6	Max 3.1
Width at tooth nr. 11	13.8 E	Total X	Total left 6.6	11.8	14.2
	Rost. gape 1.0	Rost. gape X	Rost. gape X	Rost. gape 0.6	Rost. gape 0.2
	Premax 3.0	Premax X	Premax 2.7	Premax 3.0	Premax 3.6
	Max 3.4	Max X	Max 3.7	Max 2.6	Max 3.4
Apex to vomer	34.8	X	X	36.0	43.5
Palatine width	7.7	X	X	6.4	7.2
Palatine height	8.9	X	X	10.1	X
Ventral premaxillae exposure	12.0	15±	16.5	7.0	9.0

Table 2. Comparison of rostral dimensions measures in centimetres. X indicates no measurements could be taken. Estimated measurements are indicated with E. ± is used were precise measurements were impossible.

ends because both premaxillae fuse solidly with the small elevated tip of the presphenoid. This structure forms an upheaved massive ridge which limits the midline of the premaxillary sac fossa. The fusion is solid but some remains of a suture can be noted. In the right premaxillary fossa at least two premaxillary foramina are present. They are slightly oval with no sign of sulci in their proximity and located on the medial side of the ascending process of the premaxillae. The premaxillary fossae are somewhat asymmetric, the right one being a little transversely wider and deeper than the left one. Ventrally the premaxilla is exposed for *ca.* 180 mm until being covered by the maxilla.

Maxillae – Due to *post-mortem* damage the lateral margin of the rostrum is mostly incomplete: the right margin is well preserved only at the position of the 7th alveolus and around the base of the rostrum, and the left margin at the position of the 11th alveolus. The right border of the maxilla is laterally damaged for a long tract anterior to the antorbital notch. Roughly at the level of the antorbital notch (not preserved) the transverse width of the right half of the rostrum is 92 mm. Therefore, by doubling the width of the half rostrum, the width of the base of the rostrum can be estimated to have been a minimum of 184 mm. Medially, on the right of the posteriorly damaged surface, just below the maxilla-premaxilla suture, a large infraorbital foramen was originally present. On the right maxilla at *ca.* 110 mm anterior from the base of the rostrum 1-3 very tiny foramina are located. On the other side (on the left maxilla) at a more anterior position, one larger dorsal infraorbital foramen is present as a 24 mm long shallow gully. More towards the apex of the rostrum, at the position of the 4th-5th alveoli, four small openings are present in the left maxilla. Their origin and/or purpose are unknown, but are not the result of trauma or inflammation (*pers. comm.* E.J.O. Kompanje).

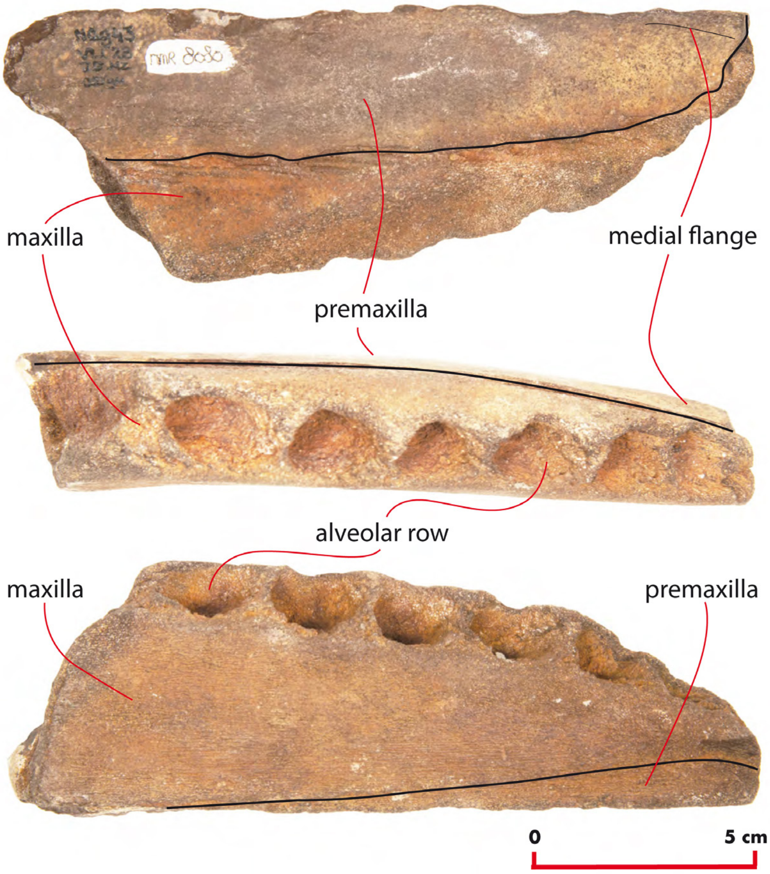

Figure 2. *Hemisyntrachelus* sp.*,* NMR 999100008080 in dorsal, lateral and ventral view.

In ventral view, on both sides a wide, prominent and slightly medially concave tooth row consisting of thirteen large and deep alveoli can be seen. The largest alveoli are located in the middle of the tooth row. Minor damage at the apex might hide the presence of a small 14th alveolus. At a distance of 180 mm from the apex of the rostrum, the premaxillae are no longer visible, but the maxillae are still medially separated by a groove of *ca.* 10 mm. Posteriorly the maxillae fuse medially over a length of *ca.* 75 mm, the suture not being well defined. More posteriorly the maxillae are covered by the palatines.

Palatine – Laterally and ventrally the anterior tip of the palatine is visible as a bone plate covering the maxilla. The outline broadens towards the base of the rostrum. Posteriorly the palatine reaches the bony nares.

Presphenoid – The presphenoid is present as a massive septum separating the bony nares. Posteriorly its broken surface forms the most caudal point of the fossil. Anteriorly it is dorsally exposed as a small upheaved narrow ridge between the premaxillae, which is completely fused with both premaxillae. Based on the architecture and morphology of the nasal septum of the presphenoid, wide and large bony nares must have been present.

Vomer – Thin strips of vomer are present on the posterior lateral left and right walls of the presphenoid.

NMR 8080 (Fig. 2, Tables 1 & 2)

NMR 8080 is a well-preserved part of the right anterior half of a rostrum. In lateral view a downwards pointing apex is noticed, but to a lesser degree than in NMR 16974. Medially, the anterior tip of the premaxilla shows a constriction and a slight upheaval which results in a flange. Dorsally the premaxilla is wide and medially it is slightly upheaved. It covers the maxilla over the entire length of the fossil. The suture with the maxilla is clearly visible. Laterally the surface seems slightly eroded. Ventrally the premaxilla forms the anterior most tip of the rostrum and is visible for more than 150 mm. The tooth row is partly preserved and seven large, deep and semi-circular alveoli are present, which held robust teeth.

NMR 8081 (Fig. 3, Tables 1 & 2)

NMR 8081 is a well preserved left anterior part of the rostrum. The apex is downwards pointing (markedly visible in lateral view) in more or less the same manner as in NMR 16974. The anterior tip of the premaxilla shows the medial flange (as prominent as in NMR 16974). The premaxilla is dorsally wide and posteriorly more upheaved from the maxilla than in NMR 8080 (and more prominent than in NMR 16974). The suture with the maxilla is dorsally visible but damaged for most of the length of the fossil, leaving part of the originally covered maxillary surface bare. The opening on the dorsal surface of the

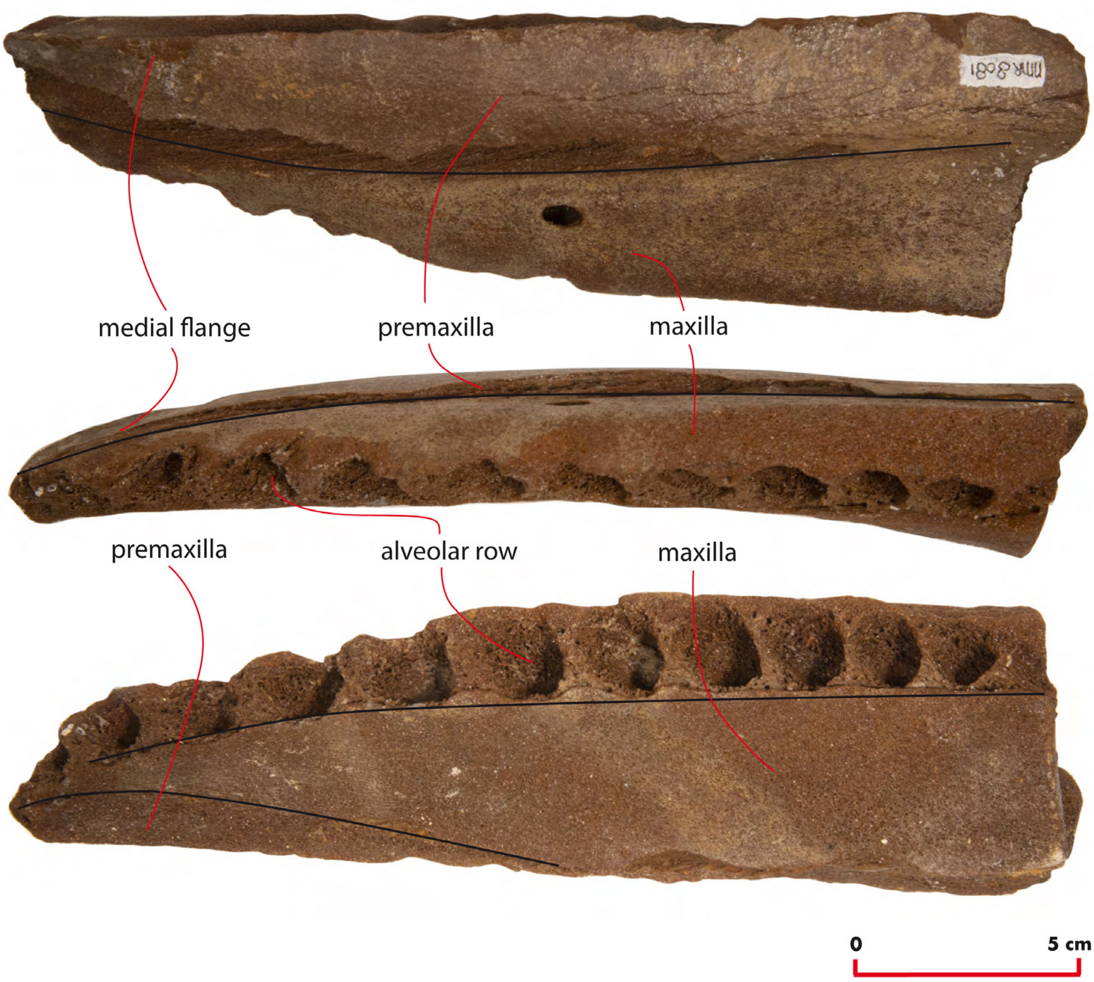

Figure 3. *Hemisyntrachelus* sp., NMR 999100008081 in dorsal, lateral and ventral view.

maxilla is probably caused by post mortem damage. In ventral view the premaxilla forms the anterior most tip of the rostrum and is visible for 165 mm. The tooth row is partly present and 11 large circular and deep maxillary alveoli for robust teeth are present.

Comparison and discussion

Bianucci (1996) described *Hemisyntrachelus* as a stocky dolphin with aspects intermediate between *Orcinus*, *Pseudorca* and *Tursiops*. Different from all Delphinidae (and especially *Tursiops*) in the combination of the following characters: (1) broad rostrum at the base, (2) anteriorly located robust and rounded antorbital process, (3) posteriorly shortened tooth row with less, but significantly larger teeth in comparison to *Tursiops*, (4) short and unusual mandibular symphysis compared to *Tursiops*, (5) narrow medial lobe of tympanic bulla, and (6) in dorsal view square shaped neurocranium. Post & Bosselaers (2005) doubted – based on fossils of the mandibula - the validity of *H. pisanus*, but their conclusion was wrong because the cranium of the holotype shows many valid characters that differ from *H. cortesii*, amongst others: longer rostrum (422 mm versus *ca*. 340 mm), higher tooth count (16 versus 14), and smaller alveoli. *Hemisyntrachelus oligodon* differs from *H. cortesii* and *H. pisanus* in – amongst others – tooth count (11), and presphenoid dorsally present at rostrum entering the mesorostral canal to a level anterior to the base of the rostrum.

Besides more or less equal dimensions, NMR 16974 shows the characteristic features of the rostrum of the holotype of *H. cortesii*: *i.e.* the massive construction, broad base, large and deep circular alveoli, and - most probably - the same number of teeth (14). Moreover, we noted that in lateral view both NMR 16974 and the holotype show the typical downwards oriented apex of the rostrum (also present in *Delphinapterus leucas* (Pallas, 1776)). Both also have a lateromedially elevated premaxilla which towards (and at) the apex of the rostrum forms a sort of upheaved sharp ridge in the middle (to a reduced degree this is sometimes observed in *O. orca*, large specimens of *Tursiops,* and taxa within the Globicephalinae). These observations allow NMR 16974 to be referred to *Hemisyntrachelus*. NMR 8080 and 8081 - being mirror prints of the relevant parts of NMR 16974 - should therefore be identified as *Hemisyntrachelus* as well.

NMR 16974 differs from *H. cortesii* and *H. pisanus* in: 1) the clearly concave premaxillary sac fossa, 2) the more prominent upheaved constriction on the rostrum-tip, 3) the complete dorsal fusion of the posterior parts of the premaxillae with the presphenoid, 4) the broader base of the rostrum, 5) the from the apex more posteriorly exposed ventral parts of the premaxilla, and 6) the significantly bigger alveoli being located more closely to each other (Fig. 4).

The most striking feature of NMR 16974 is the condition of the presphenoid. Filling the mesorostral canal towards a location more anterior than the base of the rostrum, dorsally wigged between the medial borders of the premaxillae, higher elevated than the dorsal surface of the premaxilla, and completely fused with the premaxillae, it becomes a solid part of the base of the rostrum. This is clearly not the result of a pathological condition or inflammation (*pers. comm*. E.J.O. Kompanje, January 2020). The phenomenon is not noticed in any of the Italian specimens of *Hemisyntrachelus* (*pers. comm*. Bianucci, June 2019), but seems present (albeit to a lesser extent) in *H. oligodon* (Fig. 5). Until now the peculiar fusion of presphenoid with premaxillae has never been reported in fossil Cetacea. In extant Cetacea this feature is only present (to a more or lesser extent) in adult specimens of *Peponocephala electra* Gray, 1846 and – to a much lesser extend – in some specimens of *Globicephala* (Figure 6 and Table 3). Strikingly all genera showing this feature are Globicephalinae.

Beside the similarities in the presphenoid-premaxillary fusion, NMR 16974 differs significantly from *P. electra* in the following characters: 1) dorsoventrally more upheaved and robust premaxillae located on top of the maxillae versus the very flat premaxillae of *P. electra* almost completely embedded in the maxillae, 2) in lateral view convex rostrum with ventrally curved apex, versus a very straight and flat rostrum in *P. electra*, 3) NMR 16974 is considerably larger (estimated rostrum width of 184 mm versus 123 to 133 mm in *P. electra* and has fewer teeth (14 versus 21 to 23 in *P. electra*).

The anterior parts of the mandibles of *Hemisyntrachelus* sp. described by Post & Bosselaers (2005) (Fig. 7) are very much alike *H. cortesii*, *H. pisanus* and *H. oligodon* but also show details that differ. The mandibular symphysis is shorter, has a much more pronounced chin-like keel, and shows a single mental foramen which is large and located very anteriorly. Obviously one cannot prove that these fragmentary mandibular fossils and NMR 16974 belong to one and the same taxon, but the fact that the mandibular fragments and the three described rostral fossils originate from the same sites and belong without doubt to the same genus, motivates the hypothesis that NMR 16974 and the mandible fossils (and dozens of postcrania) might belong to one and the same taxon.

The mandibles of the Globicephalinae have some characteristic features in common. Besides a convex lateral general outline *Hemisyntrachelus*, *Peponocephala* and *Globicephala* have a very short medially and ventrally directed symphysis of the mandible which is combined with an outward and laterally bending of the alveolar row (and therefore laterally directed teeth) towards the apex of the mandible (Fig. 8).

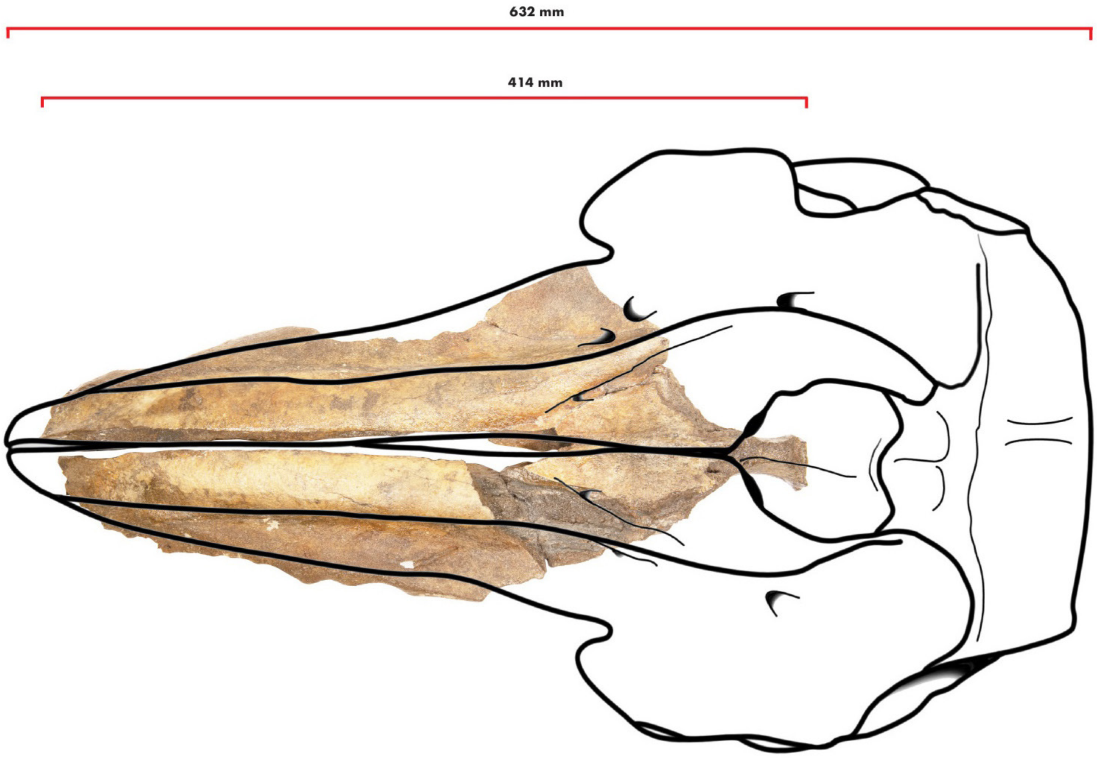

Figure 4. Dorsal comparison of NMR 999100016974 with line drawing of *Hemisyntrachelus cortesii* (redrawn from Bianucci, 1997, fig 4).

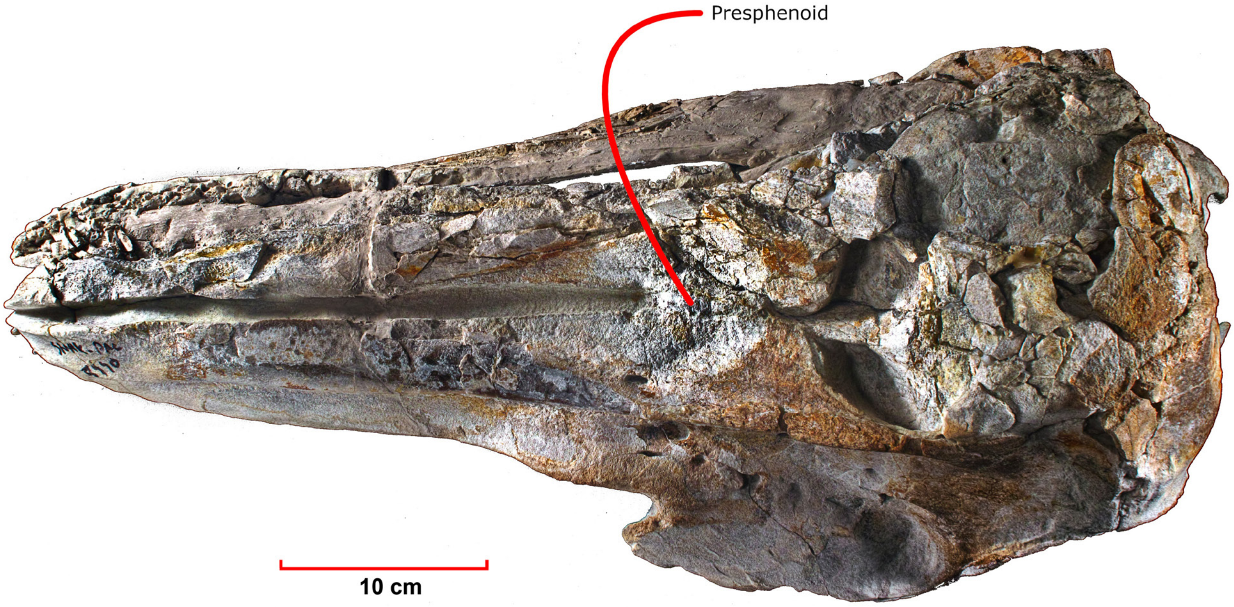

Figure 5. Dorsal view of *Hemisyntrachelus oligodon* (Pilleri & Siber, 1989), SMNK-PAL 3841 (Photo: Volker Griener of the State Museum of Natural History Karlsruhe, Germany).

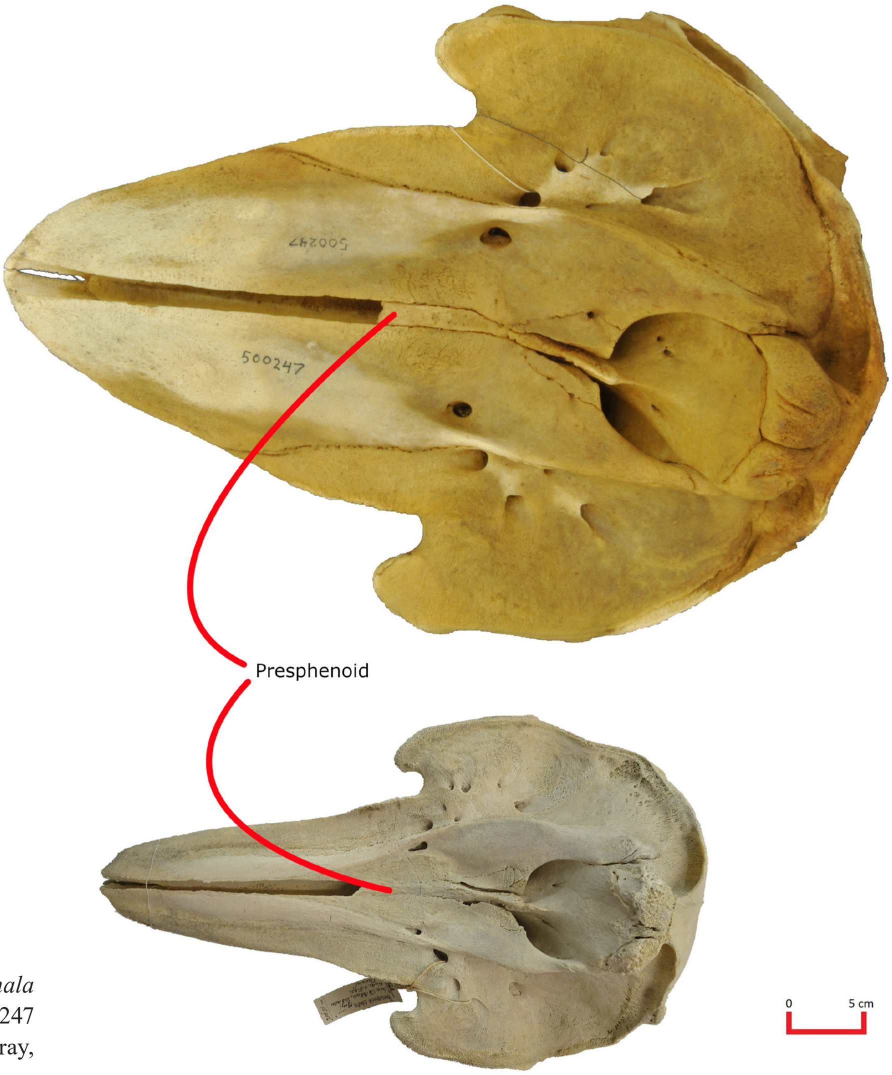

Figure 6. Dorsal view of *Globicephala melas* Traill, 1809, USNM 500247 and *Pepenocephala electra* Gray, 1846, ZMA 15956.

Pepenocephala electra status presphenoid

Collection number	**Position in (filling) mesorostral grove**	**Fusion with premaxillae**	**Dorsal surface**	**Ontogenetic stage**	**Origin**
RMNH 38434	At rostrum base	Not fused	Concave	Adult or subadult	Bitung, Indonesia
RMNH 38435	Up to 36 mm anterior of rostrum base	Completely fused	Convex	Adult	Bitung, Indonesia
RMNH 38436	Up to 21 mm anterior of rostrum base	Fused	Slightly convex	Adult	Bitung, Indonesia
RMNH 38437	Up to 43 mm anterior of rostrum base	Completely fused	Concave	Adult	Bitung, Indonesia
RMNH 38438	Up to 20 mm anterior of rostrum base	Partially fused	Convex	Adult	Bitung, Indonesia
RMNH 38439	Up to 19 mm anterior of rostrum base	Fused	Convex	Adult	Bitung, Indonesia
ZMA 8025	At rostrum base	Not fused	Concave	Adult	Lamakera, Indonesia
ZMA 15956	Up to 37 mm anterior of rostrum base	Fused	Convex	Adult	Malakula, Vanuatu
ZMA 15958	Up to 10 mm anterior of rostrum base	Fused	Convex	Adult	Malakula, Vanuatu
ZMA 15959	Up to 5 mm anterior of rostrum base	Fused	Concave	Adult	Malakula, Vanuatu
ZMA 15960	At rostrum base	Fused	Convex	Adult	Malakula, Vanuatu
ZMA 22254	Present 22 mm posterior of rostrum base not filling the mesorostral grove	Not fused	Concave	Juvenile	Playa Grandi, Curaçao

Globicephala melas status presphenoid

Collection number	**Position in (filling) mesorostral grove**	**Fusion with premaxillae**	**Dorsal surface**	**Ontogenetic stage**	**Origin**
B2 1717	At rostrum base	Fused	Convex	Adult	North Sea
B2 377	At rostrum base	Fused	Concave	Adult	North Sea
Unknown	Up to 10 mm anterior of rostrum base	Not fused	Convex	Adult	North Sea
Unknown	Up to c. 20 mm anterior of rostrum base	Fused	Damaged	Adult	North Sea
NMR 999000003005	At rostrum base	Not fused	Concave	Adult	North Sea
NMR 999000001380	At rostrum base	Not fused	Flat	Adult	North Sea
NMR 999000003006	At rostrum base	Not fused	Concave	Adult	North Sea

Globicephala macrorhynchus status presphenoid

Collection number	**Position in (filling) mesorostral grove**	**Fusion with premaxillae**	**Dorsal surface**	**Ontogenetic stage**	**Origin**
NMR 999000001443	At rostrum base	Not fused	Concave	Adult	Falkland Islands
NMR 999000001381	At rostrum base	Not fused	Flat	Adult	Western Australia

Table 3. Presphenoid morphology of *Pepenocephala electra*, *Globicephala melas* and *Globicephala macrorhynchus* Gray, 1846.

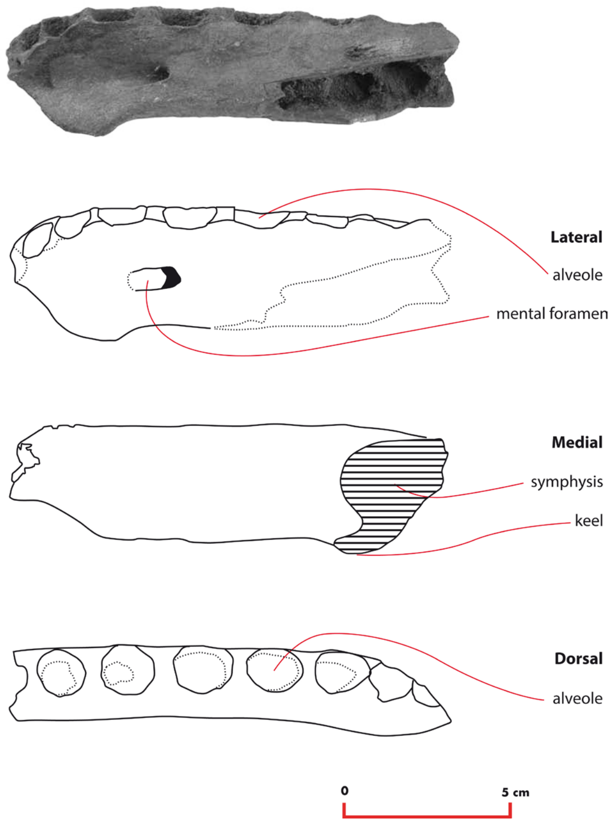

Figure 7. Mandible fragment Y-1409 of *Hemisyntrachelus* sp. (based on Post & Bosselaers, 2005, fig. 4).

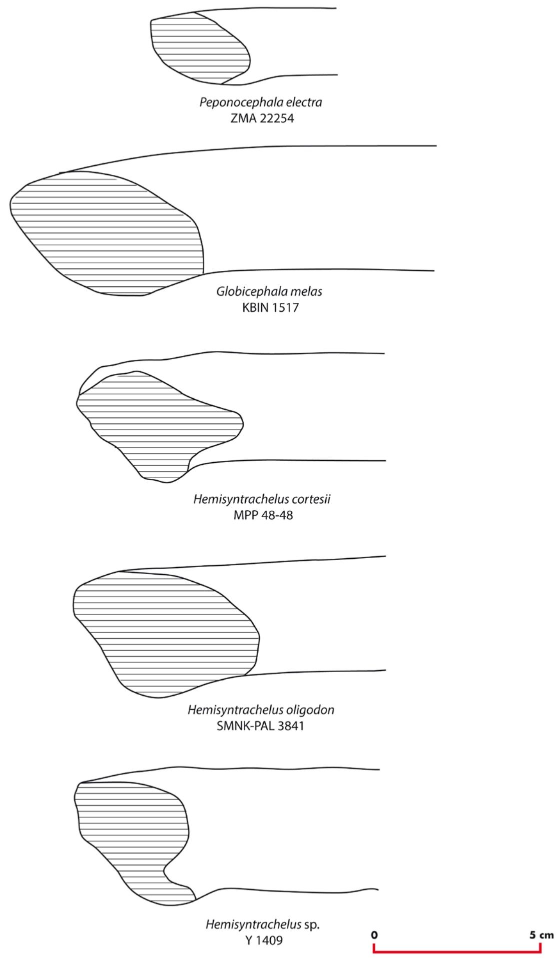

Figure 8. Mandibles of different species of Globicephalinae.

The Italian specimens originate from formations varying in age from 5.3 Ma until 3 Ma and indicate an early to late Pliocene age for the genus (Freschi *et al.*, 2019). The holotype of the Peruvian *H. oligodon* from the Sud-Sacaco locality of the Pisco Formation has a presumed ago of *ca.* 5 Ma (Lambert & De Muizon, 2013). With their late Pliocene to early Pleistocene dating, the North Sea specimens present the latest occurrence of the genus.

Conclusion

NMR 16976 reconfirms the presence of the genus *Hemisyntrachelus* in the North Sea. It differs in some aspects from the known species of the genus and therefore represents a new unnamed species of the genus. We refrain from naming the species until more complete fossils are found. An enlarged presphenoid and occasional fusion of the presphenoid with parts of the premaxillae seems to occur only within the lineage of the Globicephalinae and might be restricted to that lineage. NMR 16976 and adult specimens of *P. electra* are extreme examples of this ‘character’.

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