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Late Pliocene occurrence of *Hemisyntachelus* (Odontoceti, Delphinidae) in the southern North Sea

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Late Pliocene *Hemisyntachelus* is reported from the southern North Sea, marking the youngest and northernmost occurrence of the genus. The mandibular morphology of the North Sea fossils is compared to Pliocene *Hemisyntachelus* from Italy, the status and characteristics of the genus are discussed and arguments for the inclusion of Early Pliocene *Tursiops oligodon* from Peru in this genus are presented.

Keywords: Late Pliocene, *Hemisyntachelus*, *Tursiops oligodon*, Odontoceti, Delphinidae, North Sea

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INTRODUCTION

The fossil dolphin genus *Hemisyntachelus* BRANDT, 1873 is based on material from the Pliocene of Italy, with *Delphinus cortesii* FISCHER, 1829 designated as the type species. It was placed in the Delphinapteridae by Brandt (1873) without further explanation or systematic arguments. Previous to Brandt, Cuvier (1823) had already noted that some fossil *Tursiops*-like crania from Italy showed characters 'intermediate' between *Tursiops* and *Orcinus*.

The close resemblance of *Hemisyntachelus* and *Tursiops* caused controversy about the validity of the genus and the two have often been considered synonymous (cf. Capellini 1882, Portis 1885). Nevertheless, Slijper (1936) resurrected *Hemisyntachelus* and coined the family *Hemisyntachelidae* for it. Slijper's decision was based on morphological considerations, in particular the articulation of

ribs and thoracic vertebrae and the morphology of the lumbar vertebrae being different from those in *Tursiops*. Although Slijper was followed by some authors (e.g. Simpson 1945), others continued to disagree (e.g. Pilleri 1979) or expressed reservations and the need for further study (Barnes *et al.* 1985, Barnes 1990). Bianucci (1996) presented reasons to maintain *Hemisyntachelus* at the genus-level, such as a rostrum that is broader at the base, a more robust antorbital process, a smaller number of larger teeth, a shorter tooth row and a peculiar mandibular symphysis in comparison to *Tursiops*. He included *Hemisyntachelus* in the Delphinidae on the basis of two apomorphies: a wide mesethmoid in dorsal view and the reduction of the posterior ascendant branch of the premaxilla. Slijper (1936) and Bianucci (1996) thought *Hemisyntachelus* and *Tursiops* to be contemporaneous because they considered *Tursiops ossenae* SIMONELLI, 1911 from

the Pliocene of Italy to be a 'genuine' *Tursiops*. In an attempt to a phylogenetic analysis, Bianucci (1996) compared *Hemisyntrachelus* with *Tursiops*, while at the same time making remarks on features perceived 'intermediate' between *Hemisyntrachelus*, *Tursiops*, *Orcinus* and *Pseudorca*. He presented three hypotheses on the phylogenetic relationships of *Hemisyntrachelus*, of which the one considered most parsimonious by him shows *Hemisyntrachelus* as the sister taxon of *Pseudorca*, *Orcinus*, and 'other Globicephalinae'. However, a recent study based on full cytochrome b sequences (LeDuc *et al.* 1999) showed that *Tursiops* is paraphyletic, with *Tursiops aduncus* sharing a more recent common ancestor with *Delphinus* and some species of *Stenella* than with *Tursiops truncatus*. Moreover, LeDuc *et al.* (1999) found the Delphininae to be not closely related to *Orcinus* and *Pseudorca*, with *Orcinus* being outside the Globicephaline clade to which *Pseudorca* belongs. Clearly, further investigations are needed in order to resolve the phylogenetic position of *Hemisyntrachelus*.

Apart from *Delphinus cortesii*, other nominal taxa that have at times been included in *Hemisyntrachelus* are *Tursiops brochii* CAPELLINI, 1863; *Tursiops capellinii* DEL PRATO, 1897; *Tursiops astensis* SACCO, 1891; *Tursiops cortesii* var. *pedemontana* SACCO, 1891 and *Hemisyntrachelus pisanus* BIANUCCI, 1996, but - in his review of the genus - only *cortesii* and *pisanus* were considered valid by Bianucci (1996), who relegated *brochii*, *capellinii*, *astensis* and *pedemontana* to the synonymy of *cortesii*.

Pilleri (1979) speculated that taxa traditionally included in *Hemisyntrachelus* originated from an exclusively Italian radiation, but this view finds little support in the dubious taxonomic status of some of the nominal taxa and the controversial nature of the genus itself. Here, we present data on recently discovered specimens, assigned to *Hemisyntrachelus*, from the latest Pliocene of the southern North Sea, thereby considerably extending the known geographical and stratigraphical range of the

genus. The North Sea fossils are compared with Italian *Hemisyntrachelus* specimens, as well as with some Recent Delphinidae, to reconsider the validity of the genus and to establish distinctive characters for it. We also summarize the Late Pliocene marine mammal fauna of the southern North Sea of which *Hemisyntrachelus* was a member.

MATERIAL AND METHODS

All important fossils of *Hemisyntrachelus* in Italian collections were studied during the summer of 2003. Extant delphinids in the collections of KBIN, NNM and ZMA were used for comparison. For measurement methodology, see Fig. 1. Special attention was given to the following specimens:

Hemisyntrachelus cortesii, cast of holotype (MP);

Hemisyntrachelus pisanus, holotype (MB 1coc14);

Tursiops oligodon, holotype (SMNK pal. 3841);

Tursiops ossenae, holotype (MB 8561);

Orcinus citoniensis, holotype (MB 1coc11);

Tursiops capellinii (= *Hemisyntrachelus cortesii*) (MPP 48-48);

Hemisyntrachelus sp. (NMR 9991-01756, NMR 9991-01757, Y-1409, A-3231).

Collection acronyms

A - private collection of mr L. Anthonis of Bouwel, Belgium

IFG - Museo di Geologia e Paleontologia dell'Università di Firenze, Florence, Italy

KBIN - Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium

MB - Museo Giovanni Cappellini dell'Università di Bologna, Italy

MP - Museo di Storia Naturale e del Territorio Certosa di Calci dell'Università di Pisa, Calci, Italy

MPP - Museo di Paleontologia dell'Università di Parma, Italy

NMR - Natuurhistorisch Museum Rotterdam, the Netherlands

NNM - Nationaal Natuurhistorisch Museum Naturalis, Leiden, the Netherlands

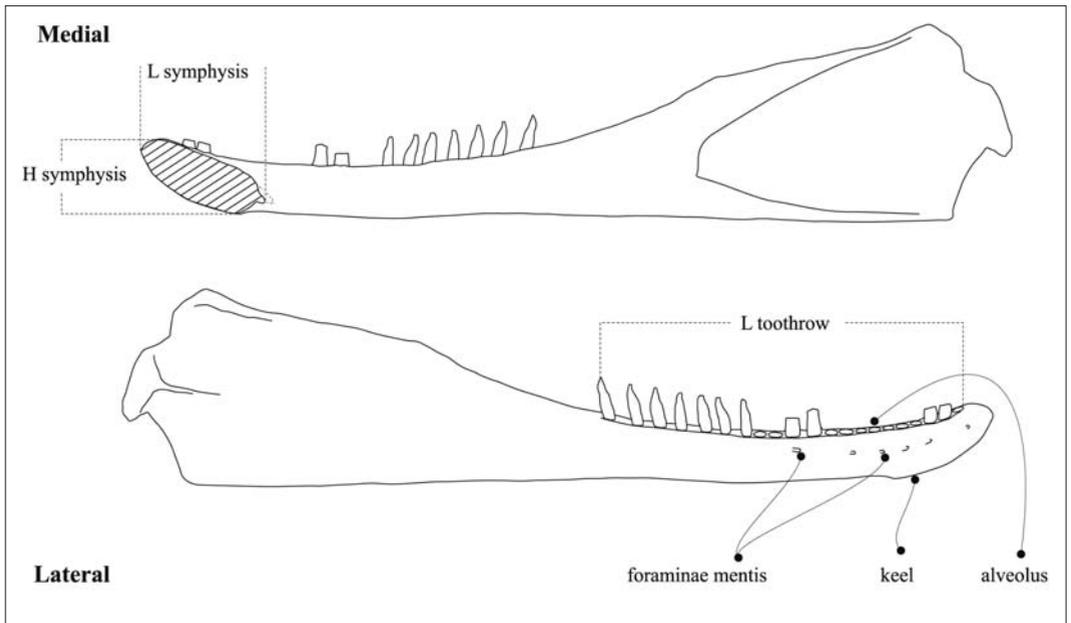


Figure 1 Measurements taken on delphinid mandibula in this study.

NWHCH - Norfolk Museums and Archaeology Service, Norwich, UK
 SMNK - Staatliches Museum für Naturkunde, Karlsruhe, Germany
 Y - private collection of mr C. van Hooydonk of Rucphen, the Netherlands
 ZMA - Zoölogisch Museum, Universiteit van Amsterdam, the Netherlands

CHARACTERISTICS OF HEMISYNTRACHELUS

Slijper (1936) stated that *Hemisyntachelus* differs from other delphinid genera (such as *Tursiops* and *Orcinus*) by the shape of the lumbar vertebrae and the articulation of the ribs. In his emended diagnosis of the genus Bianucci (1996, 1997) compared *Hemisyntachelus* to *Tursiops* and listed the following distinctive characters: sturdy vertebrae, atlas with a dorso-ventrally compressed neural arch and pointed transverse processes, broad base of a long rostrum, not narrowing premaxilla on the apical portion of the rostrum, deep and narrow antorbital notch, square-shaped neurocranium in dorsal view, anterior location of the robust

antorbital process of the frontal, periotic with robust anterior process and low pars cochlearis with wide external auditory window, broad tympanic - in ventral view - with a narrow medial lobe, short dental rows with 14-16 robust teeth and short mandibular symphysis. Moreover Bianucci (1997) considers the robust anterior process of the periotic as distinctive for the genus. Most of the postcranial and cranial characters cannot be recognized unambiguously in fragmented fossils, but mandibular characters in *Hemisyntachelus* are remarkably constant and easy to quantify, as well as well-differentiated from other delphinid genera (Fig. 2), to the extent that even fragments of mandibulae can be identified unambiguously.

The mandibula of *Hemisyntachelus* differs from all other Delphinidae by the combination of the following characters (see Table 1):

- low length/height ratio of the symphysis (< 1.6);
- presence of a prominent ventral keel on the symphysis;
- few labial foramina mentis (< 4);

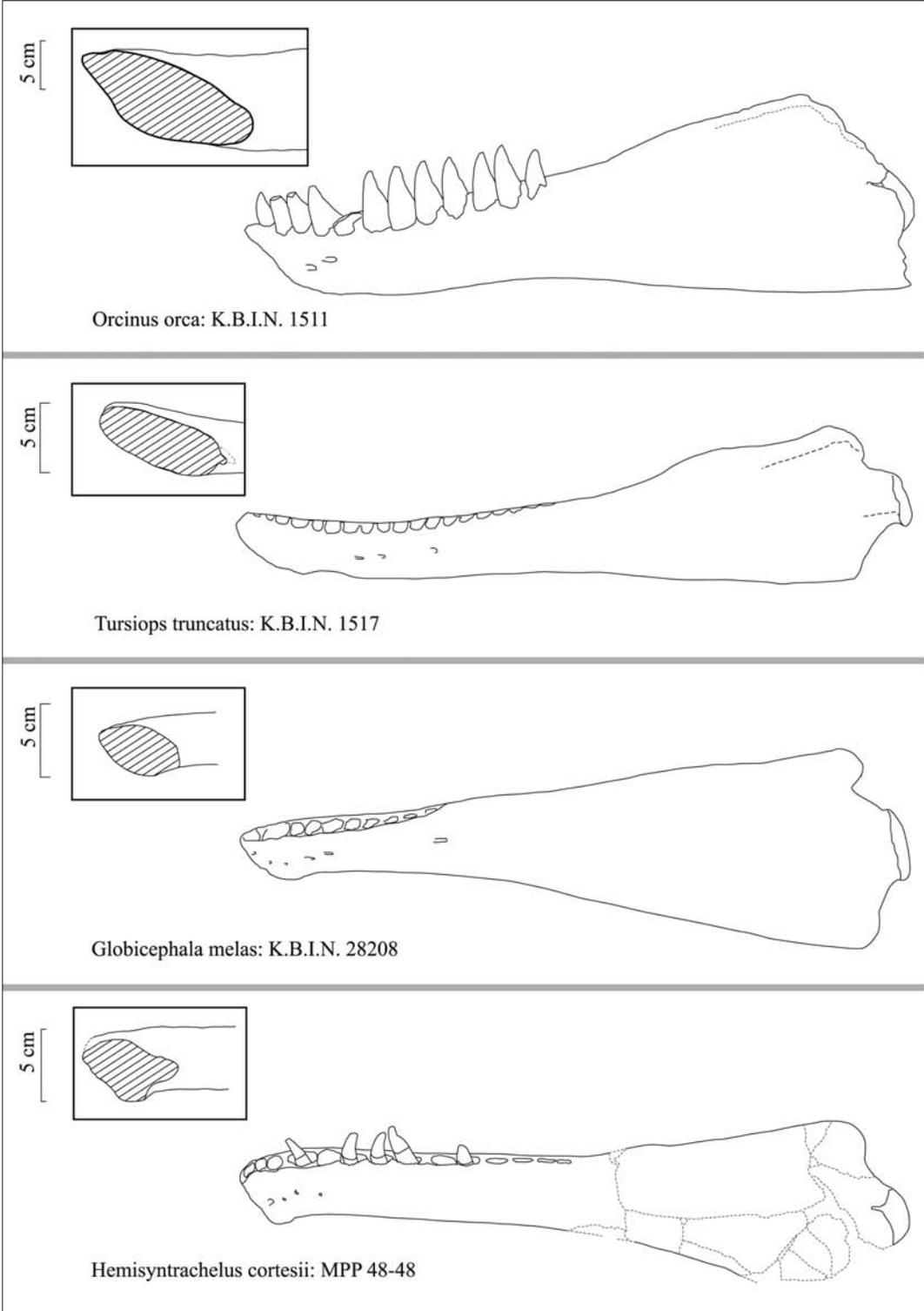


Figure 2 Mandibular characters of *Hemisyntrachelus* (bottom) compared with those of other delphinid genera.

- downward sloping mandibular tip;
- less than 17 teeth per tooth row;
- teeth robust, round and pointed
(\varnothing of alveolae > 8 mm)

The *Hemisyntrachelus* specimens from the southern North Sea show all the diagnostic characters of the genus and can be distinguished from the known species of the genus by the following characters (see Table 1):

- extremely short symphysis (length/height ratio < 1.3);
- a single large mental foramen within the symphyseal border;
- symphyseal border posterior to the third alveolus;

- size of teeth (\varnothing of alveolae > 12 mm);
- estimated tooth count of 12.

Unfortunately, so far no complete mandibula has been found in the southern North Sea, but based on the diameter of the teeth versus the length of the ramus it is likely that the North Sea *Hemisyntrachelus* had 12 (certainly < 14) teeth in the dental row. This assumption is perhaps corroborated by a single left maxilla [NWHCH 15.76(2)] from the Late Pliocene Norwich Crag of Britain illustrated by Newton (1891: 79), which shows 12 alveoles. However, based on a maxillary fragment, *Hemisyntrachelus* (and many other delphinids) cannot be identified unambiguously.

Table 1 Mandibular characters of several Delphinid taxa compared with *Hemisyntrachelus* specimens from Italy (IFG 1547) and the southern North Sea.

	1 Lsy/Hsy	2 Nr.teeth	3 Tip	4 Esy teeth	5 No/for	6 S/for	7 Keel	8 D/Alv.
T. truncatus	2.0	18-26	U	5-6	3-12	S	W	6-10
T. ossenae	1.9	20	S	5	>5	S	W	+/- 10
O. orca	1.9	10-14	S	6	3-7	S	W	> 30
O. citoniensis	1.5	14	S	5	2	S	S	15
G. melaena	1.7	7-13	D	5	3-7	S	W	10-13
H. cortesii	1.3-1.5	14-16	D	4-5	1-4	S-L	S	12-14
H. pisanus	1.5	16	D	5	1-2	L	S	14
H. oligodon	1.5	12	D	4	4	S	S	15
IGF 1547	1.2	12?	D	3-4	1-2	L	S	17
Y-1409	0.95	12?	D	3-4	1	L	S	17
A- 3231	1.25	12?	D	3-4	1	L	S	18
NMR 9991-01756	1.0	12?	D	3	1	L	S	17
NMR 9991-01757	1.0	12?	D	3-4	1	L	S	17

1 = Length symphysis: high mid-symphysis
 2 = Number of teeth
 3 = Shape of mandible-tip. U=up, S= straight, D = down
 4 = Number of alveoli/teeth on symphysis

5 = Number of mental foramina
 6 = Size of foramina. S = small, L = large
 7 = Keel. S= strong, W=weak
 8 = Length of first alveolus after symphysis (mm.)

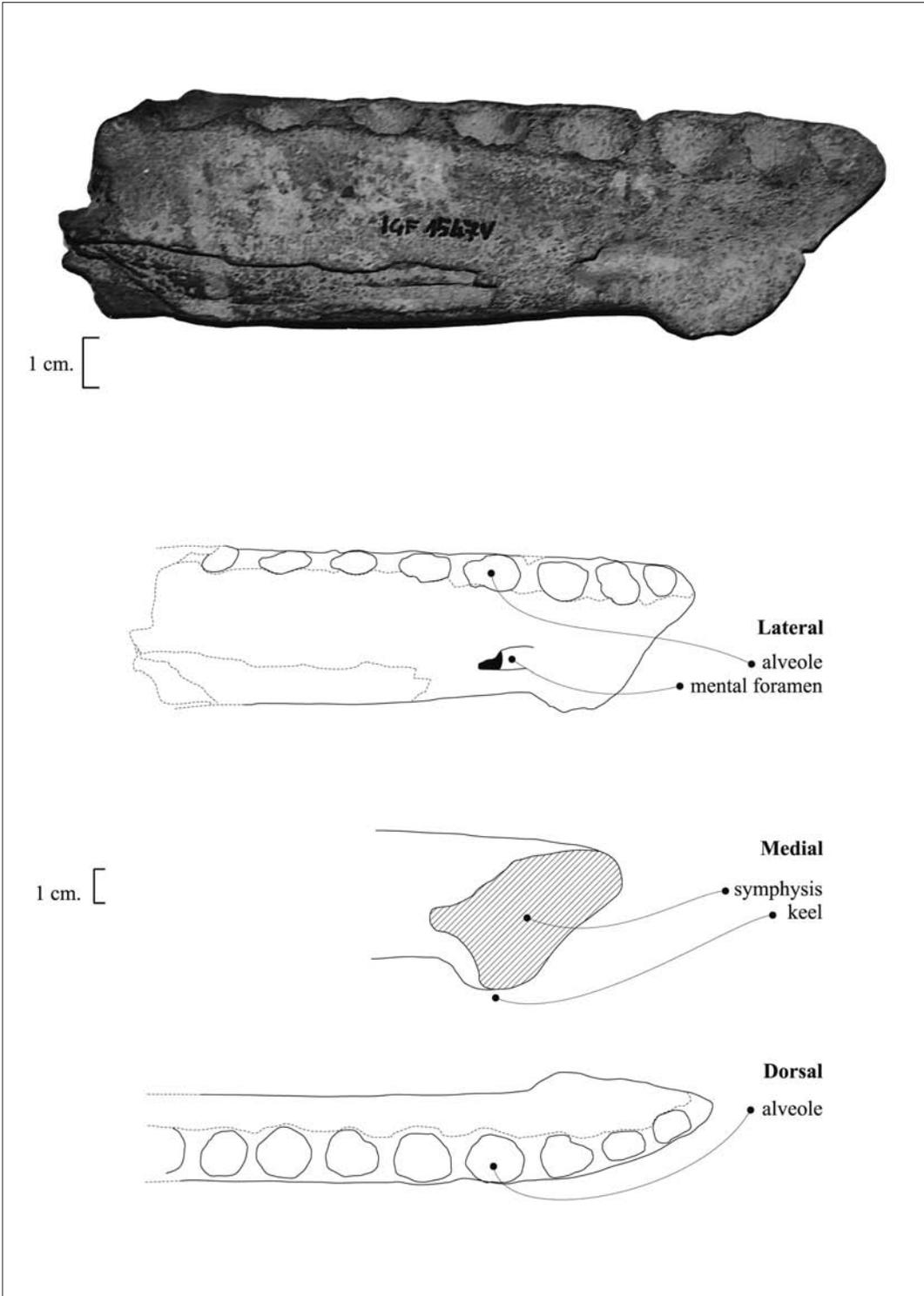


Figure 3 Mandible fragment IFG 1547, an Italian specimen matching the characters of *Hemisyntrachelus* from the southern North Sea.

A study of mandibular characters of Italian specimens revealed two distinct groupings within the two *Hemisynttrachelus* species (see Table 1):

- the typical *cortesii* group. The majority of Italian specimens are characterized by a relatively long symphysis (length/height ratio > 1.3 , < 1.6), two or - less often - more mental foramina, and 14-16 relatively slender teeth (alveolar \varnothing 10-14 mm). Both the holotypes of *cortesii* and *pisanus* fall within this grouping.
- a single specimen (IFG 1547; Fig. 3), which matches the characters of *Hemisynttrachelus* from the southern North Sea (see below), with a symphyseal length/height ratio < 1.3 , large, robust and almost round alveoli with a mean alveolar diameter of 15 mm, and a single, large and pronounced mental foramen.

DESCRIPTION OF NORTH SEA MATERIAL

All specimens were collected from stockpiles of a shell reworking factory at Yerseke, province of Zeeland, the Netherlands.

Y-1409 (Fig. 4) - A well-preserved distal part of a left mandibula, collected in 2000 by mr. C. van Hooydonk of Rucphen, the Netherlands and stored in his private collection. On the medial side, the 138 mm long ramus shows a short and weak mandibular symphysis, characteristic for the genus. Seven deep and cylindrical alveoles, that clearly held robust teeth, are situated on the dorsal side of the mandibula, the ramus being broken at the eighth alveole. A single large, deep and funnel-shaped foramen is positioned on the lateral side at about 14 mm below the fourth alveole and about 58 mm posterior to the anterior edge of the mandibula; the lower part of this edge forms a sharp and prominent keel.

A-3231 (Fig. 5) - A well-preserved distal part of a left mandibula, collected during November 2000 by mr L. Anthonis, Bouwel, Belgium and stored in his private collection. On the medial side, the 114 mm long ramus shows a short

and not very prominent mandibular symphysis in the shape characteristic for the genus. Five deep cylindrical alveoles for robust teeth are seen on the dorsal side of the mandibula, the ramus being broken at the sixth alveole. A large, deep and funnel-shaped foramen is present on the lateral side of the ramus at about 18 mm below the position of the fourth alveole and about 61 mm from the anterior edge of the mandibula. The ventral edge of the symphysis forms a prominent keel.

NMR 9991-01756 (Fig. 6) - A well-preserved distal part of a left mandibula, collected during April 2000 by mr L. Anthonis. On the medial side, the 92 mm long ramus shows a short and not very prominent mandibular symphysis, characteristic for *Hemisynttrachelus*. Five deep, cylindrical alveoles for robust teeth are present on the dorsal side of the mandibula, the ramus being broken just after the fifth alveole. A large, deep and funnel-shaped foramen is present on the lateral side of the ramus, about 19 mm below the position of the fourth alveole and 61 mm posterior to the anterior edge of the mandibula. Two very small foramina are present on the mandibular edge, with the ventral part of this edge forming a prominent keel.

NMR 9991-01757 (Fig. 7) - A well-preserved distal part of a right mandibula, collected in 2000 by mr T. Lambrechts. On the medial side, the 114 mm long ramus shows a short and not very prominent mandibular symphysis, characteristic for the genus. Seven deep, cylindrical alveoles are located on the dorsal side of the mandibula, the ramus being broken at the position of the eighth alveole. A large, deep and funnel-shaped foramen is present on the lateral side of the ramus about 22 mm below the position of the fourth alveole and about 66 mm posterior to the anterior edge of the mandibula. The ventral part of this edge is eroded, but shows signs of a prominent keel having been present.

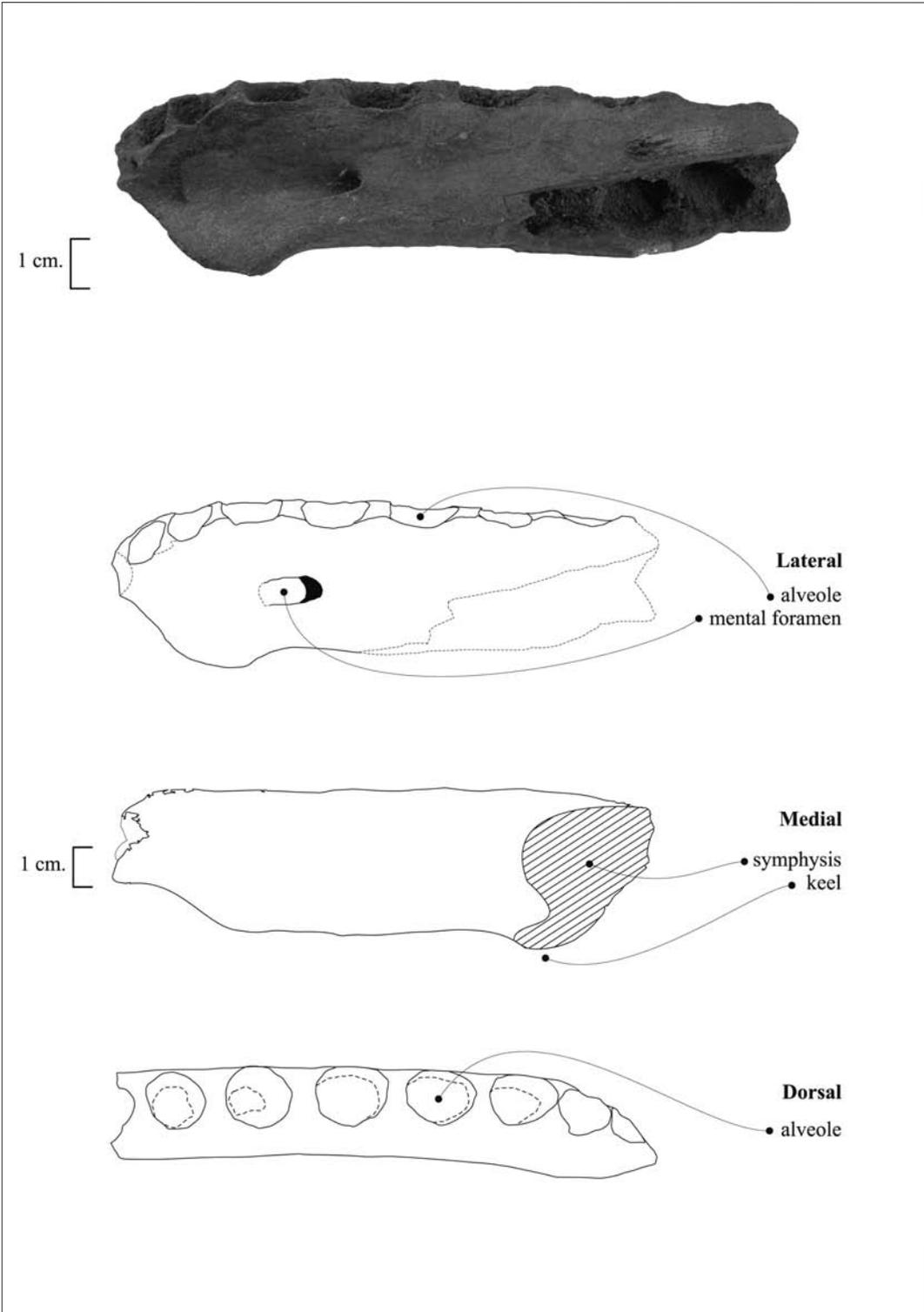


Figure 4 Y-I409, a well-preserved distal part of a left mandibula of *Hemisyntrachelus* from the southern North Sea.

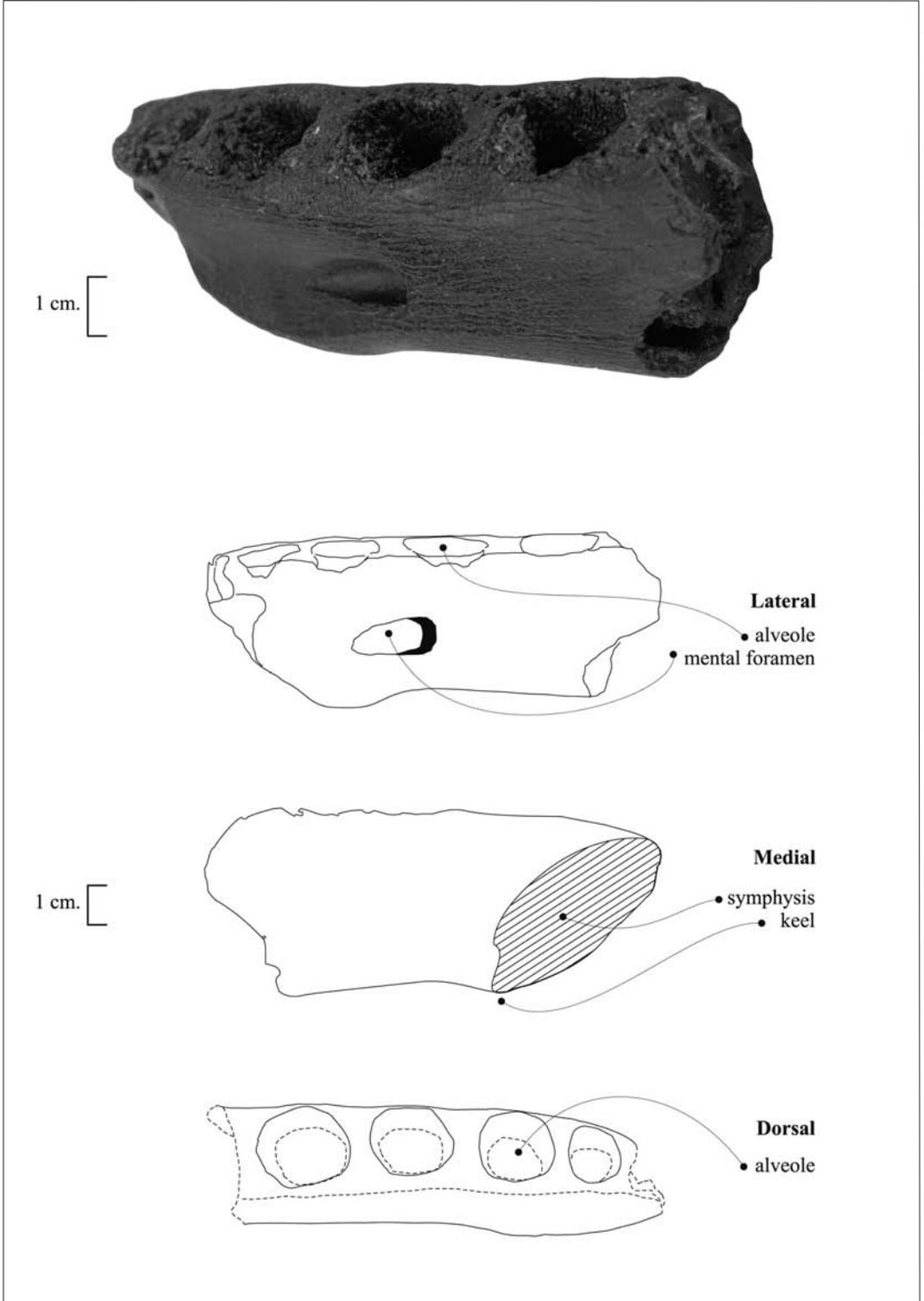


Figure 5 A-3231, a well-preserved distal part of a left mandibula of *Hemisyntrachelus* from the southern North Sea.

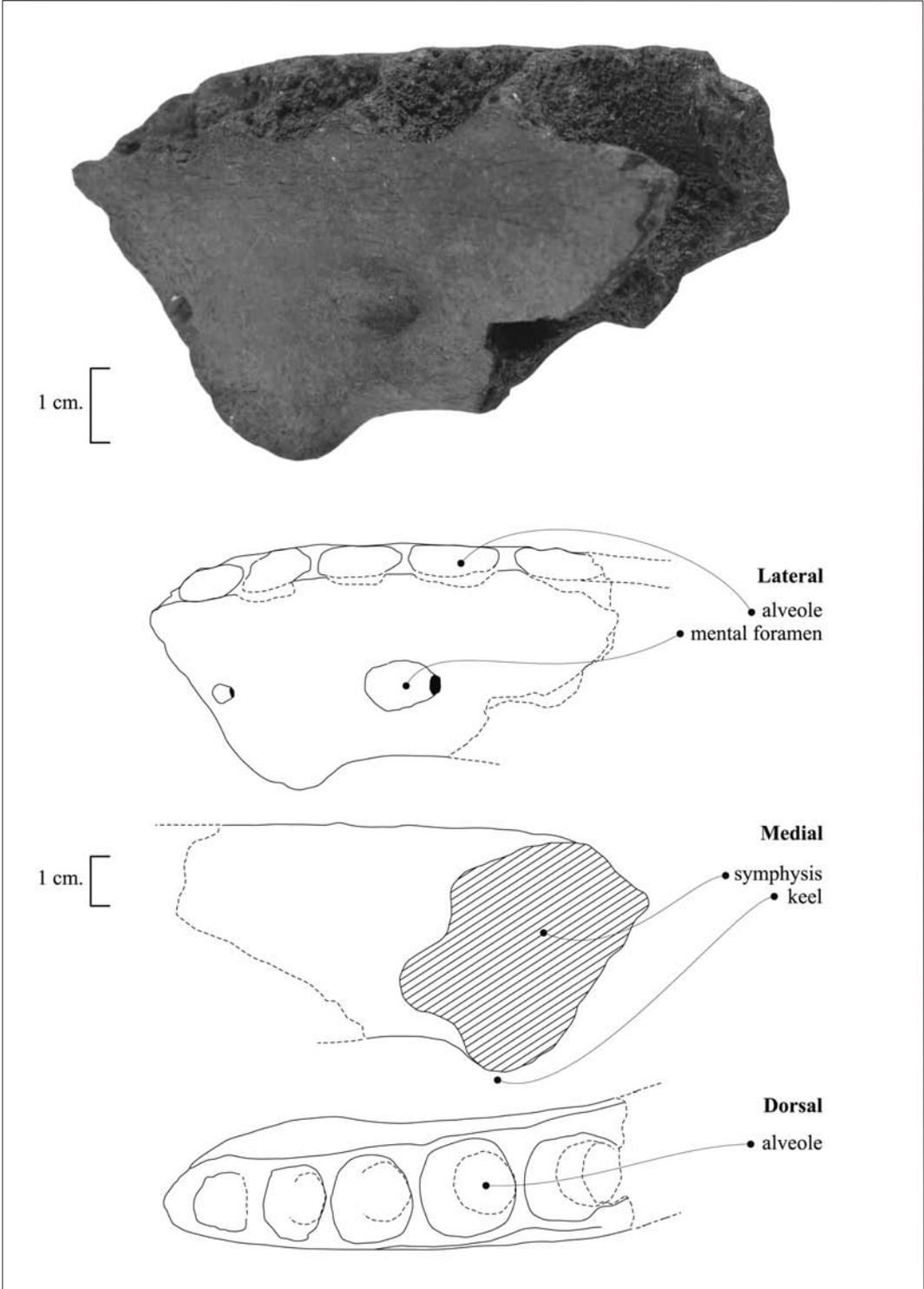


Figure 6. NMR 9991-01756, a well-preserved distal part of a left mandibula of *Hemisyntrachelus* from the southern North Sea.

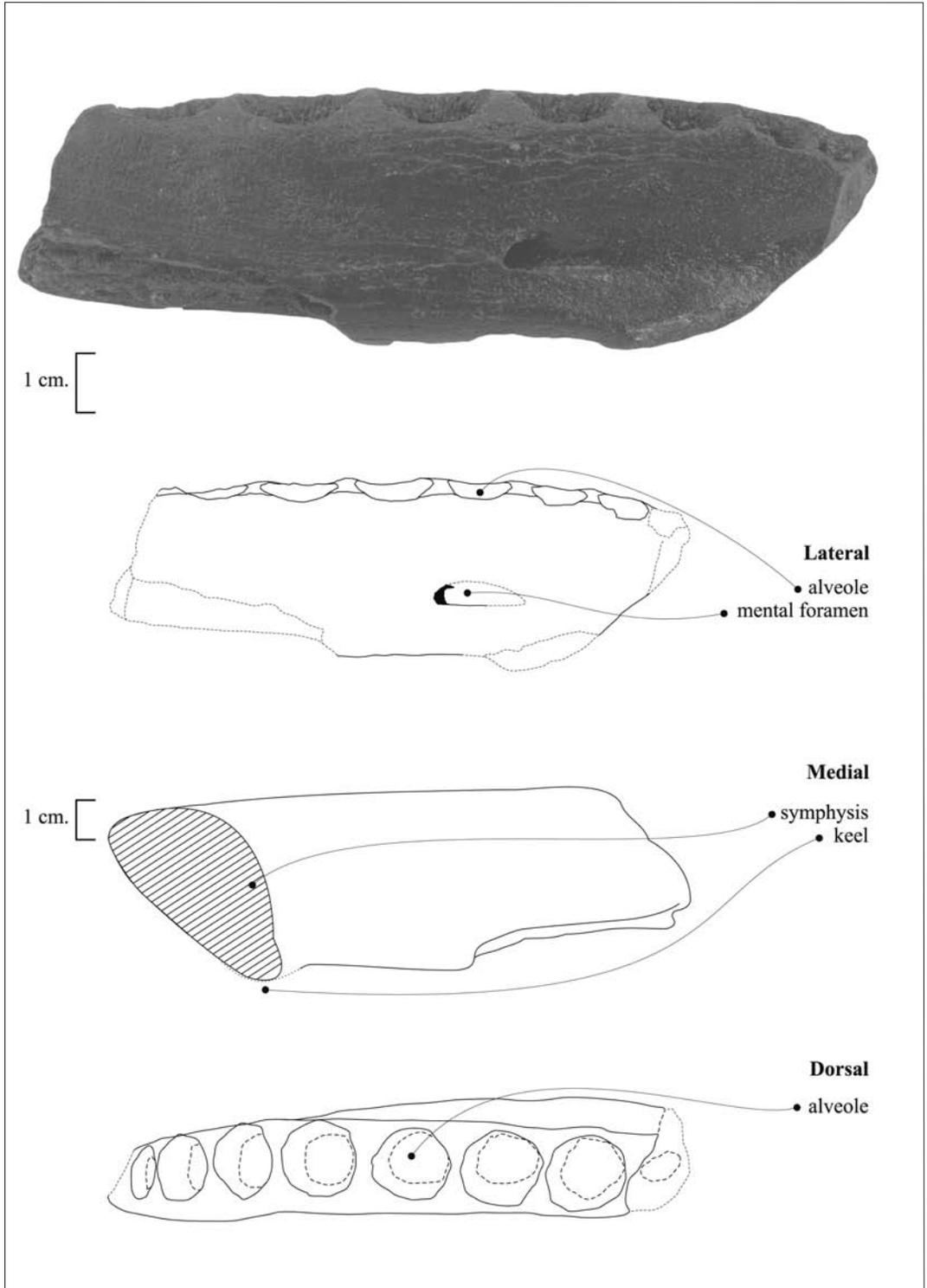


Figure 7 NMR 9991-01757, a well-preserved distal part of a right mandibula of *Hemisynttrachelus* from the southern North Sea.

STRATIGRAPHY

The shells stockpiled at the shell reworking factory at Yerseke are dredged from the Roompot area, at the outlet of the former Oosterschelde estuary (Fig. 8). At this location, the Early Pleistocene 'IJmuiden Ground Formation' and the Late Pliocene 'Westkapelle Ground Formation' are sub-cropping at or just below the sea floor (Ebbing *et al.*, 1992). The somewhat older Late Pliocene 'Brielle Formation' is located well below the sea floor and, therefore, a surface mixture of older Pliocene elements can be safely excluded. Marine mammal fossils from the Roompot area are of a dull black colour and are completely mineralised.

The 'IJmuiden Ground Formation' is a pro-delta sediment of Tiglian to Eburorian age,

whereas the 'Westkapelle Ground Formation' consists of early Tiglian marine sediments. Here, the typical marine mammal fauna is always found together with fossils from a well-documented Tiglian TC3 land fauna typified by *Anancus arvernensis*, *Mammuthus meridionalis*, *Stephanorhinus etruscus* and *Eucladoceros ctenoides* (de Vos *et al.*, 1998). The marine mammal fauna probably originates from the 'Westkapelle Ground Formation', while it is likely that the warmer land mammal fauna comes from the 'IJmuiden Ground Formation'. Therefore, we conclude that *Hemisyntrachelus* fossils from this locality have to be dated as Late Pliocene (2-1.8 Ma, not younger than Tiglian TC3), allowing for the possibility - and, indeed, the probability - that at least parts of the marine mammal fauna may also be present

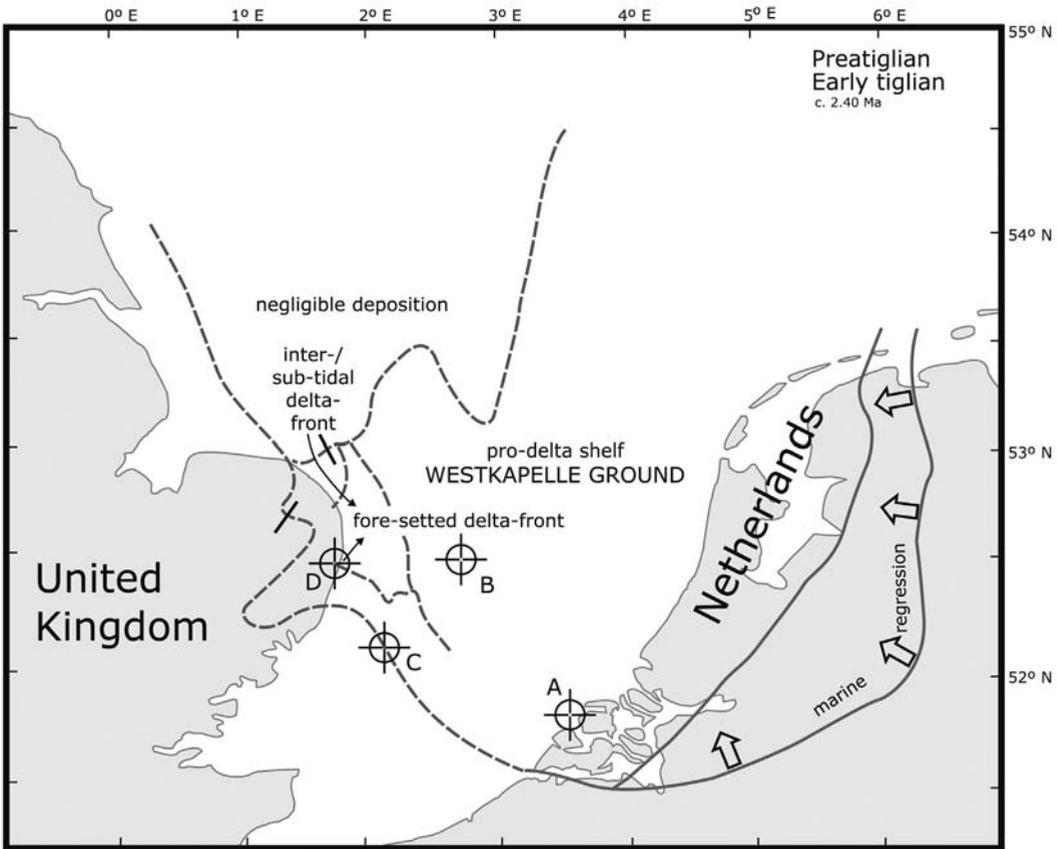


Figure 8 Coastal configuration and components of the North Sea delta during Praetiglian - Early Tiglian, c. 2.4 Ma (after Funnell 1996). **A** Roompot; **B** Noordhinder; **C** Outer Gabbard; **D** Easton Bavents.

in older Pliocene sediments. However, there are reasons to restrict *Hemisyntrachelus* to the latest Pliocene, as unambiguous *Hemisyntrachelus* fossils have neither been found in earlier Late Pliocene sediments, such as the Belgian ‘Kruisschans Sands’ and ‘Merksem Sands’, nor in the well-studied Early and Middle Pliocene sediments of Belgium.

Large numbers of postcranial fossils of *Hemisyntrachelus* and the contemporary marine mammal fauna have been collected in other parts of the North Sea (e.g. Noordhinder, 52°30’N-02°40’E, and Outer Gabbard, 52°10’N - 02°10’E; Fig. 8) and are stored in Naturalis and in several private collections in The Netherlands. These postcrania are morphologically similar to the Italian postcrania and it seems beyond reasonable doubt to link the postcrania and the mandibulae to one and the same genus. A problematic fact is that this

hypothesis is difficult to prove because none of these fossils is collected in situ and therefore we limit ourselves to the study of the mandibulae only. At both locations, the ‘Westkapelle Ground Formation’ (or its lateral component, the ‘Smits Knoll Formation’) sub-crops at the sea bottom, but the slightly older ‘Red Crag Formation’ and ‘Brielle Formation’ are also present near the sea floor (Cameron *et al.*, 1984).

The marine mammal fauna typically associated with *Hemisyntrachelus* is also found *in situ* at Easton Bavents along the British east coast (Fig. 8). Although the stratigraphy of this site has been a source of debate since the 19th century, recent finds of the Pliocene walrus *Alachtherium* and other marine mammals at this locality are unambiguously of latest Pliocene age (Funnell & West 1962, A.J. Stuart & N. Larkin in litt.). It appears that

Table 2 The Late Pliocene marine mammal association of the southern North Sea.

Cetacea		
	Mysticeti	
	Balaenidae Balaenopteridae	Eubalaena cf. belgica Balaenoptera sp.1 Balaenoptera sp.2
	Odontoceti	
	Ziphiidae Physeteridae Monodontidae Delphinidae	Mesoplodon sp. Physeter sp. Dophinapterus sp. Orcinus sp. Orcinus cf. citoniensis Globicephala sp. Hemisyntrachelus sp. Tursiops sp. Stenella/Delphinus sp.1 Stenella/Delphinus sp.2
Pinnipedia		
	Odobenidae Phocidae	Alachtherium cretsii cf. Pagophilus sp. cf. Pusa sp.

during the Late Pliocene, a peculiar marine mammal fauna occurred in the North Sea, with *Hemisyntachelus* probably being present during a limited time frame only.

MARINE MAMMAL ASSOCIATION

Fossil material of a multitude of marine mammals, listed in Table 2, have been collected from the Late Pliocene of the North Sea locations Roompot, Noordhinder, Outer Gabbard and Easton Bavents. Except for *Hemisyntachelus* and *Alachtherium*, this largely unstudied faunal association consists of extant genera. At the species level, at least *Physeter* sp., *Orcinus* sp., *Globicephala* sp., *Delphinapterus* sp., and probably two phocids, appear to represent as yet undescribed taxa.

DISCUSSION

Several cranial and hundreds of post-cranial fossils confirm the Late Pliocene presence of *Hemisyntachelus* in the southern North Sea. This delphinid was a member of a temperate to cold marine mammal fauna, mainly consisting of extant genera. Some of the members of this fauna were already present in the area during the Middle and Late Pliocene (e.g. *Eubalaena*, *Delphinapterus*, *Alachtherium*), while others, such as *Hemisyntachelus*, may have been restricted to the latest Pliocene. In Italy, *Hemisyntachelus* occurred throughout the entire Pliocene (Bianucci 1996, 1997, in litt.).

Pilleri & Siber (1989) described *Tursiops oligodon* from the Early Pliocene Pisco Formation of Peru and remarked on its resemblance to Italian *Tursiops* (= *Hemisyntachelus*) *cortesii*. Based on the massive structure of the cranium, the long and broad rostrum, the anterior location of the orbit, the deep antorbital notch, the morphology of bulla and periotic, and particularly the characters of the mandibula (downward sloping tip, short symphysis with a length/height ratio of 1.5, pronounced keel on the ventral part of the symphysis, and the 12 almost round, robust teeth), we conclude that *Tursiops oligodon* shows all of the characteristics of *Hemisyntachelus*. The presence of Early

Pliocene *Hemisyntachelus* in Peru demonstrates that the genus is neither endemic to the Mediterranean (cf. Pilleri 1987, Bianucci 1997) nor restricted to the Mediterranean and the North Atlantic, but had a much wider distribution and a temporal occurrence spanning at least the Early to Late Pliocene, implying that future finds of *Hemisyntachelus* elsewhere in the Pacific are to be expected.

Till date, two species of *Hemisyntachelus* (*H. cortesii* and *H. pisanus*) have been described, both from Italy. *H. pisanus* differs from *H. cortesii* by its larger dimensions, aspects of the periotic, and especially in the straight ventral line of the mandibula compared to the more inclined shape of the mandibula in *H. cortesii* (Bianucci 1996). In our study, we were unable to identify significant mandibular differences between the two species (cf. Table 1). Scrutinizing the mandibles of the holotype of *H. pisanus* revealed that the jaws were carefully but extensively restored. We are of the opinion that the typical shape of the ventral border of the mandibula might have been caused by restoration. Since delphinid periotics do not allow for unambiguous identification at the species level (Bianucci 1996), we must consider the possibility that *H. pisanus* is a large sized *H. cortesii* and that the differences in size are the result of sexual dimorphism, a hypothesis corroborated by recent finds of very large specimens of *H. cortesii* (Bianucci 1997).

The fact that one specimen (IFG 1547), amongst a multitude of Italian *Hemisyntachelus* fossils, shows characteristics similar to those of the North Sea fossils seems striking, but this may just as well prove that our knowledge of the Late Pliocene marine mammal fauna of Europe is only limited. This is illustrated by *Orcinus citoniensis*, an orca from the same Italian fauna that produced *Hemisyntachelus*, which - despite 120 years of paleontological exploration - is known from a single skeleton only.

Bianucci (1997) made a remark on globicephaline features in *Hemisyntachelus*, such as the broad rostrum, the small medial lobe on the bulla, and the margin of the premaxilla.

Although phylogenetic conclusions are beyond the scope of the present paper, we might point out that Bianucci's observation is corroborated by the lack of variation in mandibular characters among the nominal taxa included in *Hemisyntachelus* at present, which is in marked contrast to most delphinids, and by the characteristically downward sloping tip of the mandibula of *Hemisyntachelus*.

In conclusion, the following observa-

tions can be made. *Hemisyntachelus* is a delphinid that can be distinguished from *Tursiops*, *Globicephala* and *Orcinus* and other Delphinidae by its mandibular characteristics. It was present in the Mediterranean during the Pliocene, in the northeastern Atlantic during the Late Pliocene and in the southeastern Pacific during the Early Pliocene and was part of a temperate to cold marine mammal fauna. Based on the present study, *H. pisanus* from

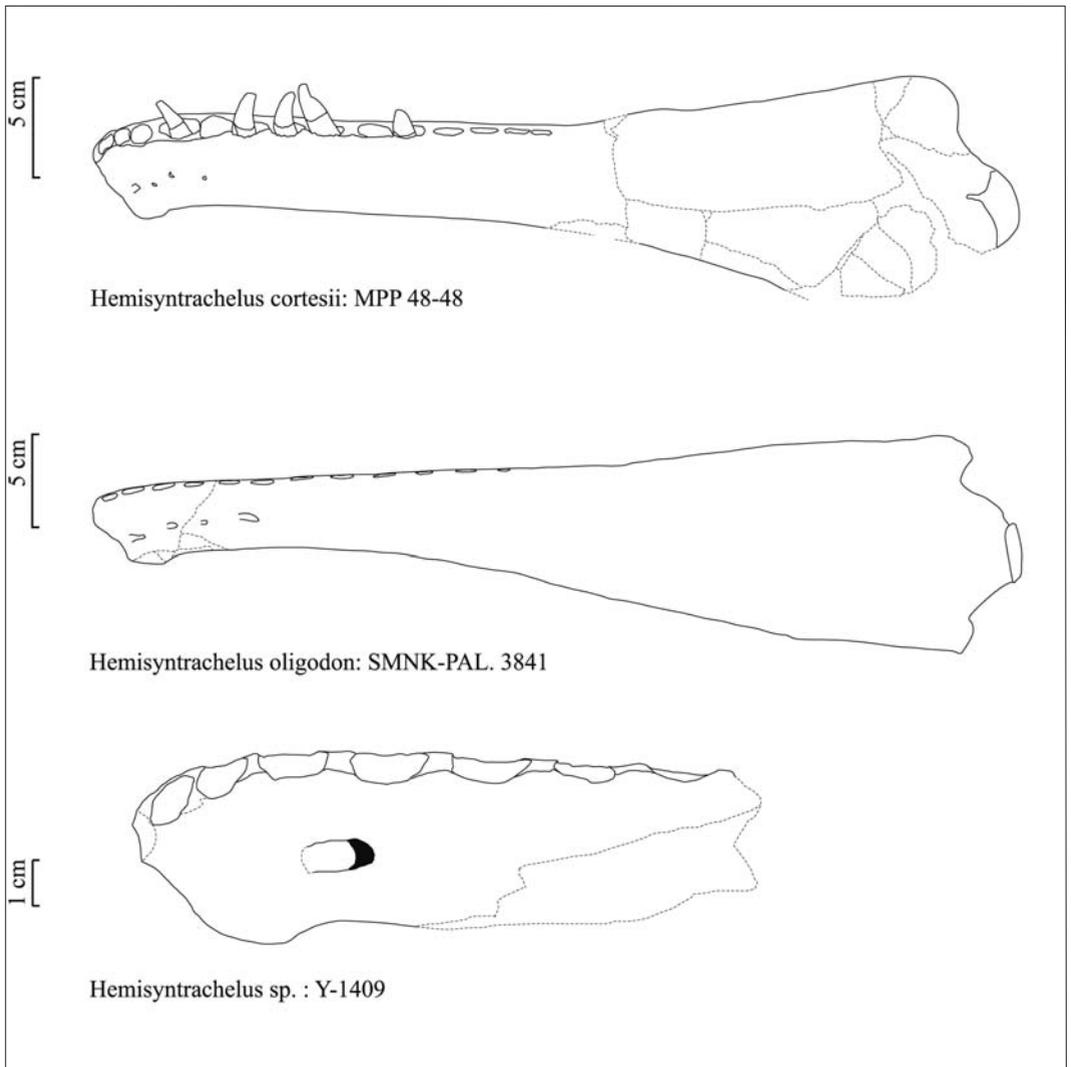


Figure 9 MPP 48-48 *Hemisyntachelus cortesii* of the Pliocene of Italy; SMNK-PAL. 3841 *Hemisyntachelus oligodon* of the Early Pliocene of Peru; and (bottom) Y-1409, a mandible fragment possibly of an as yet unnamed species from the Pliocene of Italy and the Late Pliocene of the southern North Sea.

Italy should be considered conspecific with *H. cortesii*, while *Tursiops oligodon* from Peru should be included in *Hemisyntachelus*. This study also indicates that the fossils from the southern North Sea and a single Italian specimen might represent a new species. However, because of the fragmentary nature of the material it seems prudent to refrain from formally naming a new species until more complete fossils become available. Therefore, *Hemisyntachelus* presently includes two and perhaps three species, viz. *Hemisyntachelus cortesii* (FISCHER, 1829) of the Pliocene of Italy, *Hemisyntachelus oligodon* (PILLERI & SIBER, 1989) of the Early Pliocene of Peru, and possibly an as yet unnamed species from the Pliocene of Italy and the Late Pliocene of the southern North Sea (Fig. 9).

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