The genus *Tusciziphius* is represented by a single species, which was previously only known from the holotype skull from the Early Pliocene of Tuscany, Italy. This article reports the second specimen of this species from Miocene/Pliocene strata of South Carolina (USA, east coast), kept in the Natuurhistorisch Museum Rotterdam. The specimen provides information on features not preserved on the holotype skull and reveals that the species was not endemic to the Mediterranean but must also have roamed the North Atlantic realm.

Correspondence: Klaas Post (corresponding author), Natuurhistorisch Museum Rotterdam, P.O. Box 23452, 3001 KL Rotterdam, the Netherlands, e-mail klaas@fiskano.nl; Olivier Lambert, Institut royal des Sciences naturelles de Belgique, Département de Paléontologie, Rue Vautier, 29, B-1000 Brussels, Belgium; e-mail Olivier.Lambert@naturalsciences.be; Giovanni Bianucci, Dipartimento di Scienze della Terra, Università di Pisa, Via S. Maria, 53, I-56126 Pisa, Italy; e-mail bianucci@dst.unipi.it

**Keywords:** *Tusciziphius crispus*, Cetacea, Ziphiidae, Neogene, USA

**INTRODUCTION**

In his revision of the fossil beaked whales of the Italian Pliocene, Bianucci (1997) realised the unique features of a fossil neurocranium in the collection of the University of Florence and redescribed it as a new genus and species named *Tusciziphius crispus*. The holotype cranium had already been found during the 19th century and was identified by Capellini (1885) as *Choneziphius planirostris* (Cuvier, 1823). Since 1885, neither in Italy nor in the rest of the world, another fossil of *Tusciziphius* was found or recognised. In 2002 a fossil ziphiid skull from South Carolina was publicly sold by the relatives of an American collector. The first author realised the importance of the specimen and could arrange that the fossil was donated to the Natuurhistorisch Museum Rotterdam, thus saving it from oblivion. The cranium is described here, assigned to *Tusciziphius crispus*, and compared to other Neogene ziphiids.

**METHODS**

**Terminology and measurements**

Anatomical terms are taken from Heyning (1989) and Bianucci *et al.* (2007). Measurements were taken following directions of Ross (1984), Bianucci (1997), Lambert (2005) and Bianucci *et al.* (2007).

**Institutional abbreviations**

IGF: Museo di Geologia e Paleontologia dell’Università di Firenze, Florence, Italy. NMB: Natuurhistorisch Museum Boekenberg, Antwerp, Belgium. NMR: Natuurhistorisch
Figure 1  Skull of Tusciziphius crispus (NMR 9991-3020): A  dorsal view; B  corresponding line drawing.

SYSTEMATIC PALAEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Cetacea Brisson, 1762
Suborder Odontoceti Flower, 1867
Family Ziphiidae Gray, 1865
Genus Tusciziphius BIANUCCI, 1997

Type and only included species Tusciziphius crispus BIANUCCI, 1997

Holotype IGF-1594 V, incomplete cranium from Val di Pugna, Tuscany, Italy.

Referred specimen NMR 9991-3020, from South Carolina, USA; incomplete cranium with rostrum, vertex and facial structures, but without basicranium, supraoccipital and mandible (Figs. 1-4).

Emended diagnosis Skull equal in size to extant Ziphius cavirostris. Rostrum very dense and relatively short as in Choneziphius planirostris. Premaxillae on rostrum elevated, forming a dome near the rostral base and completely fused medially, closing the mesorostral groove. Broad and massive base of rostrum. Palatine extended anterior to the mid-length of the rostrum. Premaxillary crests and sac fossae very asymmetrical (right side largest). Ascending process of the premaxilla anteriorly curved near the vertex, causing the vertex to overhang the bony nares (in dorsal view). Vertex elevated as in Choneziphius but less than in Ziphius. Extreme ossification and fusion of vertex elements. Premaxillary crests, especially the right one, extremely transversally expanded, but not posteriorly curved as in Mesoplodon and Hyperoodon. Nasals large, antero-posteriorly elongated and laterally shifted to the left side of the skull. Nasals not protruding anteriorly past the premaxillary crests. Frontal hardly exposed on the vertex. Supraoccipital, posterior to the vertex, moderately constricted between the two maxillae. Large temporal fossa and relatively elevated lambdoidal crest.

DESCRIPTION AND COMPARISON

While the holotype (Fig. 5) is a fairly complete neurocranium without rostrum, NMR 9991-3020 includes the rostrum, but misses most of the basicranium. At first sight NMR 9991-3020 seems smaller and less robust than the holotype but observations and measurements (Table 1) confirm that this impression is only caused by the lack of the massive basicranium.

As in the holotype, the vertex is anteriorly curved and covers - in dorsal view - the bony nares. Premaxillary crests, nasals and the preserved parts of the frontals of NMR 9991-3020 show the same general morphology as the holotype but are completely fused (even more so than the holotype) to the extent that sutures are hardly or not visible. This extent of complete co-ossifying is not seen in other Ziphiidae and might represent an autapomorphy of the genus. The vertex is moderately elevated, somewhat lesser than in fossil Caviziphius BIANUCCI & POST, 2005 and Choneziphius, and by no means as elevated as in extant Ziphius. The premaxillary crests are very robust, the left crest is smaller than the right one. The right premaxillary crest shows a large, semi-circular, partly flat, dorsal surface with a highest point towards the right nasal. The left premaxillary crest shows a long wavy-like dorsal surface. The extremely long and slender nasals are somewhat oriented to the left (antero-posteriorly) and laterally bordered by the premaxillary crests along their entire length, as in the holotype. In lateral view the nasals are not extending in front of the premaxillae. In fact the nasals seem reduced and depressed at their anterior midpoint (a condition seen in Hyperoodon, Mesoplodon and their fossil relatives), but it is difficult to confirm this observation on the holotype because of a crack. The frontals are preserved on the vertex and morphology and size are as in the holotype. The vertex is most constricted (in dorsal view)
Figure 2: Skull of Tusciaziophius crispus (NMR 9991-3020): A (left) lateral view; B corresponding line drawing; C (right) lateral view.
at the point where nasals and frontals meet. In anterior view the degree of asymmetry of the vertex of *Tusciziphius* is striking and expressed by the very wide, high and robust right pre-maxillary crest. The premaxillary sac fossae show the same architecture and asymmetry as in the fossil genera *Caviziphius* and *Choneziphius*, however the right fossa of *Tusciziphius* is not excavated in a similar way as in these last two genera (and especially in *Caviziphius*) but posteriorly excavated as well as anteriorly and anteromedially thickened and elevated. Contrary to *Beneziphius* LAMBERT, 2005, *Messapicetus* BIANucci, LANDINI & VAROLA, 1992 and *Ziphirostrum* DU BUS, 1868, no prenarial basin is present in front of the premaxillary sac fossa. Even a shallow basin, as in *Choneziphius*, is absent. The premaxillary foramina are difficult to observe, the left foramen seems retained in the anterior corner of the deep premaxillary sac fossa, while the right foramen is absent (as seems the case in *Eboroziphius* LEIDY, 1876). The premaxillae are completed fused immediately anterior to the premaxillary sac fossae. This condition is also noted in *Caviziphius*, *Eboroziphius*, unnamed Belgian specimens and in *Pelycorhamphus*COPE, 1895 (Lambert 2005). The fusion of the premaxillae extends over the entire length of the rostrum till just a few centimetres in front of the apex and a medial suture between the premaxillae is not visible. Creation of a mesorostral tunnel by the joined and fused premaxillae is also noted in *Caviziphius* and *Choneziphius*, but in the last genus a suture remains visible.

The antorbital notch area is not well preserved (as in the holotype). Six maxillary foramina are present posteriorly to the rostrum base and are surrounded by ridge-like structures. These excrescences are also visible on other parts of the dorsal surface of NMR 9991-3020, mostly on the median premaxillary dome and the anterior margin of each premaxillary sac fossa, and seem of the same nature as is often noticed at or near the base of the rostrum of *Beneziphius* and *Choneziphius*. These surface structures may have served as attachment for facial muscles (Lambert 2005), or might have been caused by blood vessels. A remarkable asymmetry is shown by the positions of the two anterior most foramina. The right foramen is located just 11 mm from the medial maxillary foramen near the border of the right premaxillary sac fossa, while the left-one is located at a c. 40 mm more anterior position near the rostrum base. Maxillary and premaxillary foramina cannot be observed on the holotype due to bad preservation. On the supraoccipital process, marked maxillary crests towards the base of the rostrum - such as seen in *Choneziphius* and *Ziphius* - are not present.

The rostrum base is fairly wide (Table 1) and shows, at the lateral borders, a slight constriction (obviously a remnant of the antorbital notch - see Figure 1). The dorsal maxillary surface at the rostrum base is slightly convex and highest at the border. At this level the joined premaxillae are elevated to a bulbous 35 mm high and 70 mm long dome, which is showing the rough surface as described earlier. This condition seems also present in *Eboroziphius*. A similar but non-homologous feature (of the ossified vomer) is present in *Mesoplodon timidirostris* (Miyazaki & Hasegawa 1992) and is observed in undescribed *Mesoplodon*-like fossil rostra from the South African coast (pers. obs.). More anteriorly the dorsal surface of the maxilla becomes flat to, near the apex, concave. The fused premaxillae keep their elevated ridge-like shape towards the apex and are firmly pachyostosed, a condition also present in *Caviziphius* and *Choneziphius*. In lateral view the rostrum shows a blunt outline (again reminding the general shape of *Choneziphius* rostra), while the sharp border at the rostrum base gradually eases out into a ridge towards the apex. Remnants of a non-functional and shallow alveolar groove run below this line towards the apex. It seems that the apex is slightly restored by the use of some sort of consolidate. The eventual original damage, however, must have been marginal because the restoration surface is minor. The incomplete apex shows - in anterior view - the large circular opening of the
mesorostral tunnel, and - ventrally - two small foramina. Whether or not the dorsal fusion of both premaxillae might have continued till the original apex, or might have stopped just before, is not clear.

The ventral part of the rostrum base is damaged and important observations cannot be noted. However, laterally the anterior border of the palatine was extended to at least 130 mm anterior from the rostrum base. The sutures of the pterygoid attachment are not clearly detectable, but leave the possibility open that pterygoid (and palatine) covered the ventral walls of the rostrum to a more anterior position than in Caviziphius and Choneziphius.

**STRATIGRAPHIC ASSIGNMENT**

The skull was found by the late Vito Bertucci during 1999 in the Morgan River, Beaufort County, South Carolina, USA, at a location between 32°26′50″N, 80°35′57″W and 32°27′09″N, 80°28′44″W. These coordinates and the phosphatised condition of the fossil seem to hint to the ‘locally abundant Phosphate Beds’ which were mentioned in ancient literature and considered to be of Late Miocene origin (Leidy 1877). Recent studies note sub-cropping of a small patch of the Early-Middle Pliocene Goose Creek Limestone at the indicated coordinates, surrounded by Early Miocene and Oligocene strata (Weems & Lewis 2002). The Goose Creek Limestone consists of quartzose and phosphatic calcarenite with a base often marked by a lag of phosphate pebbles (Weems *et al.* 1982).

The Morgan River, which runs between the mentioned coordinates, is also a rich source of fossils, collected by divers. The Charleston Museum collections contain a rostrum of Euhinodelphinidae and teeth of *Carcharodon megalodon* collected from the bottom of this river, indicating either sub cropping of Middle- and/or Late Miocene strata, or the presence of reworked Miocene strata in the area (pers.com. A. E. Sanders). Sanders (2002) reported Goose Creek Limestone adherent to the holotype of *Ceterhinops longifrons* (one of the nominal odontocete taxa from South Carolina described by Leidy in 1877).

Taking into account the absence of a more exact locality of the described cranium, the
presence of Miocene and Pliocene strata in the area, and the fact that advanced ziphiids are only known from the Late Miocene onward, it seems prudent to assume a Late Miocene / Middle Pliocene background for NMR 9991-3020. The holotype (IGF-1594 V) originates from Early Pliocene strata (Bianucci et al. 2001).

**DISCUSSION AND PHYLOGENETIC OBSERVATIONS**

*Tusciziphius crispus* is closely related to the North Atlantic fossil ziphiid species *Caviziphius altirostris* and *Choneziphius planirostris* by several characters such as the short and blunt rostrum, the rostral fusion of the premaxillae (closing dorsally the mesorostral groove), the extreme rostral pachyostosis without mesorostral ossification of vomer and/or mesethmoid, the architecture and extreme asymmetry of the premaxillary sac fossae, and the moderately high vertex. Some features of *Caviziphius* and *Tusciziphius* such as extreme lateral development of the premaxillary crests, complete fusion of the vertex, elevation of the anterior margin of the premaxillary sac fossa, and complete fusion of premaxillae on dorsal surface of the rostrum, seem more derived than in *Choneziphius*.

*Tusciziphius* and *Caviziphius* also share an anteriorly projecting vertex overhanging the bony nares, which is also noted in extant Ziphius but lacks in *Choneziphius*.

Moreover extreme development of the right premaxillary crest is seen in the first two genera, but lacks in *Choneziphius* and *Ziphius*.

Extant *Ziphius* - on the other hand - shows essential differences from the three fossil forms in the architecture of the rostrum (ossified vomer as in several *Mesoplodon* species), the more elevated vertex, and a vertical and rectilinear outline of the lateral margins of the ascending processes of the premaxilla in anterior view (the premaxillary crest is not distinctly wider than the ascending processes of the premaxilla).

NMR 9991-3020 is - at present - the best preserved fossil ziphiid specimen from the East Coast of North America. The many nominal ziphiid species from South Carolina described by E.D. Cope in 1869 (Cope 1869a,b) and J. Leidy in 1877 (Leidy 1877), are based on fragmentary specimens and do not resemble, or cannot be compared to *Tusciziphius*. However *Eboroziphius coelops* LEIDY, 1877 and *Pelycorhamphus pertortus* COPE, 1895 deserve special attention. Both species are only known by their holotype: the former is a rostral fragment known from the Phosphate Beds of South Carolina and the latter is a very fragmented specimen from the Miocene of the Chesapeake Group (East Coast USA). The preserved parts of these rostral fragments clearly show similarities with *Caviziphius* and *Tusciziphius* at the level of the premaxillary sac fossae and fused premaxillae lacking a prenarial basin.
However the deep right premaxillary sac fossa observed in these specimens link them to *Caviziphius* rather than to *Tusciziphius*. Unfortunately, more in-depth observations are hindered by the fact that *Eboroziphius coelops* and *Pelycorhamphus pertortus* are based on too fragmentary specimens with few diagnostic features, and - in fact - must be considered nomina nuda.

Based on dimensions and morphology of the rostrum, the unnamed isolated rostrum NMB 002 from the North Sea - which was compared to *Eboroziphius* by Lambert (2005) - might be congeneric with *Caviziphius*.

All observations do confirm a close relationship between *Caviziphius* and *Tusciziphius*. A detailed phylogenetic analysis of above-mentioned partly (or seemingly) contradicting observations and a comparison of characters of the known fossil and extant ziphiids is beyond the aim and reach of this article. The study on eight newly described beaked whale genera from South Africa (Bianucci et al. 2007), and future works on newly discovered, well-preserved ziphiids from Peru by same the same authors, will review the present status of fossil ziphiids in general, and might unravel the complicated phylogeny of this diversified toothed whale family.

**CONCLUSIONS**

- *Tusciziphius crispus* is a Late Miocene-Middle Pliocene beaked whale and its distribution is noted on both sides of the North Atlantic realm (the Mediterranean and the east coast of the USA). *Tusciziphius* shares this transatlantic distribution with *Choneziphius* (Lambert 2005) and *Messapicetus* (Fuller & Godfrey 2005, 2007).
- NMR 9991-3020 adds new data to the mor-

---

### Table 1  Measurements (in mm) of the two known fossil skulls of *Tusciziphius crispus*: IGF 1594 V (holotype) and NMR 9991-3020; e = estimation

<table>
<thead>
<tr>
<th>measured unit</th>
<th>IGF 1594 V</th>
<th>NMR 9991-3020</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greatest postorbital width</td>
<td>415</td>
<td>&gt;372</td>
</tr>
<tr>
<td>Width of premaxillae at base of rostrum</td>
<td>-</td>
<td>86</td>
</tr>
<tr>
<td>Greatest width between zygomatic processes of squamosals</td>
<td>450</td>
<td>-</td>
</tr>
<tr>
<td>Distance from base of rostrum to anterior tip of palatine</td>
<td>-</td>
<td>e130</td>
</tr>
<tr>
<td>Height of skull between pterygoids and vertex</td>
<td>339</td>
<td>-</td>
</tr>
<tr>
<td>Length of temporal fossa</td>
<td>159</td>
<td>-</td>
</tr>
<tr>
<td>Height of temporal fossa</td>
<td>88</td>
<td>-</td>
</tr>
<tr>
<td>Width of cranium between posterior borders of temporal fossa</td>
<td>214</td>
<td>-</td>
</tr>
<tr>
<td>Width of condyles</td>
<td>128</td>
<td>-</td>
</tr>
<tr>
<td>Width of foramen magnum</td>
<td>46</td>
<td>-</td>
</tr>
<tr>
<td>Height of right condyle</td>
<td>69</td>
<td>-</td>
</tr>
<tr>
<td>Width of right condyle</td>
<td>46</td>
<td>-</td>
</tr>
<tr>
<td>Minimal posterior distance between maxillae on the vertex</td>
<td>-</td>
<td>84</td>
</tr>
<tr>
<td>Transverse width of premaxillary crests</td>
<td>192</td>
<td>e184</td>
</tr>
<tr>
<td>Minimal distance between premaxillary crests</td>
<td>52</td>
<td>e39</td>
</tr>
<tr>
<td>Width of bony nares</td>
<td>-</td>
<td>69</td>
</tr>
<tr>
<td>Width of premaxillary sac fossae</td>
<td>-</td>
<td>173</td>
</tr>
<tr>
<td>Width of right premaxillary sac fossa</td>
<td>-</td>
<td>108</td>
</tr>
<tr>
<td>Width of left premaxillary sac fossa</td>
<td>-</td>
<td>51</td>
</tr>
<tr>
<td>Length of medial suture between nasals</td>
<td>70</td>
<td>68</td>
</tr>
<tr>
<td>Greatest width of nasals</td>
<td>64</td>
<td>-</td>
</tr>
<tr>
<td>Greatest width of right nasal</td>
<td>-</td>
<td>e27</td>
</tr>
<tr>
<td>Length of right nasal</td>
<td>90</td>
<td>82</td>
</tr>
<tr>
<td>Width of right premaxillary crest</td>
<td>-</td>
<td>&gt;101</td>
</tr>
<tr>
<td>Width of left premaxillary crest</td>
<td>-</td>
<td>51</td>
</tr>
<tr>
<td>Minimal width of right premaxillary dorsal to the premaxillary sac fossa</td>
<td>-</td>
<td>68</td>
</tr>
</tbody>
</table>
phology of the genus: size and architecture of the rostrum, median fusion of the premaxillae, median fusion and elevation of the premaxillae, extension of the palatine to the ventral side of the rostrum, position of the maxillary foramina, ossification and fusion of the vertex elements.

- *Tusciziphius* seems closely related to two other Late Miocene-Early Pliocene ziphiids from the North Atlantic (*Choneziphius* and especially *Caviziphius*), and is - in some characters - more derived than both of them. However their essential phylogenetic relation and the relationships to other ziphiids (fossil and extant) are still not clear.

- The species is known from two fossils only; new fossils might provide additional information on essential morphological features (apex of rostrum, prominential-antorbital notch, petro-tympanic complex, post-crania) and geographic distribution.

**ACKNOWLEDGEMENTS**

Henry van der Es (NMR) and John de Vos (NNM) are thanked for access to fossils stored under their care. Jonathan H. Geisler (Georgia Southern Museum) and Albert E. Sanders (Charleston Museum) kindly provided literature and comments on the geology of Tertiary deposits from South Carolina. Michelangelo Bisconti (Natural History Museum of Livorno) assisted in many ways and Mark Broch helped in textual matters.

**REFERENCES**

Bianucci, G., 1997 - The odontoceti (Mammalia Cetacea) from Italian Pliocene. The Ziphiidae - Palaeontographia Italica 83: 163-192


Bianucci, G. & Post, K., 2005 - *Caviziphius altirostris*, a new beaked whale from the Miocene southern North Sea basin - Deinsea 11: 1-6


Cope, E.D., 1869a - On two extinct Mammalia from the United States - Proceedings of the American Philosophical Society 11(82): 188-190


Cuvier, G., 1823 - Recherches sur les ossements fossiles, 5 (1ère partie) - G. Dufour et E. D'Ocagne, Paris, pp 405-444


Fuller, A.J. & Godfrey, S.J., 2005 - Miocene ziphiids (Cetacea: Odontoceti) from the Chesapeake Group of Calvert Cliffs, Maryland, USA - Evolution of aquatic tetrapods. Fourth Triannual Convention Abstracts 1: 26


Heyning, J.E., 1989 - Comparative facial anatomy of beaked whales (Ziphiidae) and a systematic revision among the families of extant Odontoceti - Contributions in Science, Nat. Mus. LA County 405: 1-63

Lambert, O., 2005 - Systematics and phylogeny of the fossil beaked whales *Zhiphirostrum* du Bus, 1868 and *Choneziphius* Duvernoy, 1851 (Cetacea, Odontoceti), from the Neogene of Antwerp (North of Belgium) - Geodiversitas 27(3): 443-497

Leidy, J., 1876 - Remarks on fossils from the Ashley Phosphate Beds - Proceedings of the Academy of Natural Sciences of Philadelphia 1876: 80-81, 86-87
Leidy, J., 1877 - Description of vertebrate remains, chiefly from the Phosphate Beds of South Carolina. Journal of the Academy of Natural Sciences of Philadelphia 2:(8): 209-261


Ross, G.J.B., 1984 - The smaller cetaceans of the south east coast of southern Africa - Annals of the Cape Provincial Museums of Natural History 15:(2) 173-410


Received 2 June 2007
Accepted 3 September 2007