Thoracic–post-thoracic vertebrae. The specimen MUSM 2548 is represented by three thoracic and two thoracic–post-thoracic vertebrae (Fig. 3). Their precise position along the vertebral column cannot be identified in the absence of the complete series. Consequently, a relative position is given here in an anteroposterior sequence from A to E.

All thoracic and post-thoracic vertebrae possess a centrum transversely wider than dorsoventrally high (Table 2) and oval in shape. An exception to this pattern is the anterior epiphysis of vertebra A, which is dorsoventrally higher than transversely wide and more rectangular (Fig. 3a). Vertebrae A, B, and G are identified as thoracics because of the presence of a fovea for the rib tuberculum on the upper transverse process and a fovea for the rib capitulum along their centrum (Fig. 3a–b and 3d). In posterior view of vertebrae A, B, and G, the fovea for the rib capitulum is located along the doro-lateral surface of the centrum. The extent of this fovea suggests these to be posterior to the thoracic vertebra 1. Indeed, in all extant Ziphiidae examined, the fovea extends along the whole lateral surface of the centrum.
4.1.3 Sternum and ribs

Sternum. Two elements of the sternum are preserved in the specimen MUSM 2548: the complete manubrium and the left half of the sternebra 2 (Fig. 4). The two elements are unfused to each other. The manubrium is roughly H-shaped, its anterior margin being marked by a jugular notch. This bone is transversely wider (at least 220 mm) than antero-posteriorly long (193 mm). In anterior view, it is ventrally convex (Fig. 4b). Its lateral margin is concave, progressively narrowing posteriorly. A medial notch is present posteriorly, longer anteroposteriorly than transversely wide. The two posteriormost margins of the manubrium are less transversely widened than the anteriormost margins. An articular facet for the first rib is present anterolaterally. The shape of the preserved left element of sternebra 2 is similar to the left
Figure 4. Sternum of the specimen MUSM 2548, *Messapicetus gregarius*, in ventral view (a) and manubrium element in anterior view (b). Horizontal solid lines indicate major break. The dashed line represents a reconstruction of the second element of the sterna 2.

Humerus. The two humeri of the specimen MUSM 2542 are partially preserved. Since the left humerus lacks the humeral head and is less well preserved (Fig. 7a–d), only the right humerus is described here (Fig. 7a–d).

The shaft of the right humerus is broken at mid-length, slightly displacing dorsally the distal articulation with the radius and the ulna (Fig. 7a–d). The humeral head is hemispherical and separated from the great tuberosity by a neck visible in ulnar and radial view (Fig. 7c–d). In lateral view, the head of the humerus represents one-third of the total length of the humerus (Fig. 7b). In medial view, the surface of the great tuberosity is flattened, approximately reaching the same proximal level as the head of the humerus. In lateral view, a deltoid ridge is developed along the anterior margin of the humerus at approximately mid-length of the humerus.

In distal view, the articular facets for the radius and the ulna are separated by the distal crest. In lateral view, each articular facet occupies approximately half of the distal surface of the humerus.

Radius. The left radius of MUSM 2542 is complete (Fig. 7f–l). It curves proximodistally and slightly transversely. The facet for articulation of the humerus is oriented anteroproximally. Distally, the articulations for the scaphoid and the lunate can be differentiated based on their orientation (Fig. 7j–k). Each occupies approximately half of the distal anteroposterior width of the radius. The articulation for the scaphoid appears straight in lateral view, distally facing, while the articulation for the lunate is more oblique, postero-distally facing.

4.2 Muscle reconstruction of *M. gregarius* and comparisons with other ziphid species

4.2.1 Neck muscles

*M. longus colli*. In extant cetaceans, this muscle originates from the lower transverse process of C6 (Schulte, 1916; Uhen, 2004). It inserts into the ventral surface of the axis centrum. The M. longus colli flexes the neck. The origin of the M. longus colli could not be reconstructed here because of the uncertainty of the putative C5–C6 identification. In *Messapicetus gregarius*, right and left muscles inserted into the ventral excavations of the axis centrum separated by the hypapophysis (Fig. 8a).

The axis of *Ninozaphius platyrostris* displays ventral excavations for the M. longus colli similar to *M. gregarius*. Furthermore, de Muizon (1984) interpreted the presence of a ventral tubercle located on the atlas as another region of insertion for the M. longus colli. The M. longus colli most likely originated from the lower transverse process of C6 of *N. platyrostris*, even though we could not identify the precise area. Transversely, the preserved lower process of C6 in *N. platyrostris* measured 20 mm long. It was similar in size and shape to the lower transverse process of the putative C5–C6 of MUSM 2548.
Figure 5. Ribs of the specimen MUSM 2548, *Messapicetus gregarius*, in anterior view. Pair 1 (a) and (b); pair 2 (c) and (d); pair 3 (e) and (f); pair 4 (g) and (h); (i), (j), (k), and (l) cannot be precisely positioned.

Figure 6. Right scapula of the specimen MUSM 2542, *Messapicetus gregarius*, in dorsal view.

Heavily abraded posteroventrally, the partial atlas of the middle Miocene Berardiinae *Archaeoziphus microglenoides* probably had a poorly developed (if any) ventral tubercle (Lambert and Louwye, 2006). This suggests a reduction of the M. longus colli insertion area as compared to *N. platyrostris*. The atlas of the late Miocene crown ziphid *Nazcacetus urbinai* lacks a ventral tubercle (Lambert et al., 2009); the absence of ventral excavations in the axis of the latter further indicates reduced insertions for the M. longus colli as compared to *M. gregarius* and *N. platyrostris*. Furthermore, the lower transverse process of C6 in the holotype of *N. urbinai* is as long transversely as the process of other posterior cervicals, thus indicating a reduced origin area for the M. longus colli. Osteological markers for insertion areas of the M. longus colli into the atlas and the axis were generally more reduced in the observed extant ziphids as compared to *M. gregarius* and *N. platyrostris* (Table 2); the axis consistently lacks deep ventral excavations for the M. longus colli in contrast to *M. gregarius* and *N. platyrostris* (Fig. 8).

A ventral tubercle is rarely present on the atlas of extant ziphids, except in *Mesoploodon grayi* and Berardiinae spp. (Dataset 1, Ramassamy et al., 2018). In addition, the lower transverse process of C6 is more developed in *Mesoploodon bidens*, *M. densirostris*, and *M. grayi* than in *N. platyrostris* and other crown ziphids observed (Fig. 9d–e). This feature indicates a relatively larger origin area for the M. longus colli in these three *Mesoploodon* species.

*Mm. intertransversarii ventrales cervicis*. This muscle also originates from the lower transverse process of C6 (de Muizon, 1984; Schulte, 1916; Uhen, 2004). It bears multiple insertions into the posterior side of the transverse processes of the atlas, axis, C3, and C4. It participates in the lateral flexion of the neck. On the posterior side of the unfused axis of *Messapicetus gregarius* MUSM 2548, the presence of a large depression along the lower transverse process suggests a large area of insertion for the Mm. intertransversarii ventrales cervicis (Fig. 8b).

Similar insertion areas are observed in *N. platyrostris* (Fig. 8d). As for the M. longus colli, the Mm. intertransver-
Figure 7. Humeri and left radius of MUSM 2542, *Mesaspicetus gregarius*. Right humerus in medial (a), lateral (b), ulnar (c), and radial view (d); left humerus in medial (e), lateral (f), ulnar (g), radial (h), and posterior view (i); left radius in lateral (j), medial (k), and ulnar view (l).
Table 2. Measurements of the vertebrae from specimen MUSM 2548, *Mesapicetus gregarius*. Thoracic–post-thoracic vertebrae from A to E are ordered in relative position; e stands for estimated measurements, and "-" indicates missing measurements.

<table>
<thead>
<tr>
<th>Feature</th>
<th>Axis</th>
<th>C5–C6</th>
<th>C7</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transverse width at the level of transverse processes</td>
<td>186e</td>
<td>–</td>
<td>–</td>
<td>162e</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Anterior transverse width centrum</td>
<td>–</td>
<td>73</td>
<td>75</td>
<td>69</td>
<td>70e</td>
<td>71</td>
<td>54e</td>
<td>–</td>
</tr>
<tr>
<td>anterior transverse height centrum</td>
<td>–</td>
<td>74</td>
<td>76</td>
<td>75</td>
<td>53</td>
<td>52</td>
<td>55</td>
<td>–</td>
</tr>
<tr>
<td>Posterior transverse height centrum</td>
<td>55</td>
<td>56</td>
<td>57</td>
<td>54</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Posterior transverse width centrum</td>
<td>76</td>
<td>57</td>
<td>59</td>
<td>55</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Anteroposterior thickness centrum</td>
<td>12</td>
<td>21</td>
<td>28</td>
<td>37</td>
<td>52</td>
<td>63</td>
<td>72</td>
<td>82</td>
</tr>
<tr>
<td>Transverse width neural canal</td>
<td>51</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Table 3. Summary of the main features relative to neck musculature in extant and fossil Ziphiidae. All specimens were directly consulted.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample</th>
<th>Number of fused cervical vertebrae</th>
<th>Ventral tubercle on the atlas</th>
<th>Ventral excavations on the axis</th>
<th>Development of the lower transverse process of C6</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Mesapicetus gregarius</em></td>
<td>1</td>
<td>0</td>
<td>?</td>
<td>present</td>
<td>?</td>
</tr>
<tr>
<td><em>Ninoziphius platyrostris</em></td>
<td>1</td>
<td>2</td>
<td>present</td>
<td>present</td>
<td>reduced</td>
</tr>
<tr>
<td><em>Archeziphius microglenoideus</em></td>
<td>1</td>
<td>?</td>
<td>absent</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td><em>Nazzacetus urbinaei</em></td>
<td>1</td>
<td>2</td>
<td>absent</td>
<td>absent</td>
<td>reduced</td>
</tr>
<tr>
<td><em>Berardius sp.</em></td>
<td>2</td>
<td>3</td>
<td>present</td>
<td>absent</td>
<td>reduced</td>
</tr>
<tr>
<td><em>Hyperoodon ampullatus</em></td>
<td>11</td>
<td>7</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td><em>Mesoplodon bidens</em></td>
<td>2</td>
<td>3</td>
<td>absent</td>
<td>absent</td>
<td>more developed than in the other cervicals</td>
</tr>
<tr>
<td><em>Mesoplodon bowdoini</em></td>
<td>1</td>
<td>3</td>
<td>absent</td>
<td>absent</td>
<td>reduced</td>
</tr>
<tr>
<td><em>Mesoplodon dentirostris</em></td>
<td>2</td>
<td>3 to 5</td>
<td>absent</td>
<td>absent</td>
<td>more developed than in the other cervicals</td>
</tr>
<tr>
<td><em>Mesoplodon grayi</em></td>
<td>1</td>
<td>2</td>
<td>present</td>
<td>absent</td>
<td>more developed than in the other cervicals</td>
</tr>
<tr>
<td><em>Tasmacetus shepherdi</em></td>
<td>3</td>
<td>5 to 6</td>
<td>absent</td>
<td>absent</td>
<td>reduced</td>
</tr>
<tr>
<td><em>Ziphius cavirostris</em></td>
<td>4</td>
<td>4 to 5</td>
<td>absent</td>
<td>absent</td>
<td>reduced</td>
</tr>
</tbody>
</table>

sarii ventrales cervicis likely originated from the lower transverse process of C6, even though the precise areas cannot be identified. Unlike *M. gregarius*, the atlas and axis were fused in *N. platyrostris*, considerably reducing lateral flexibility in the anterior neck region.

In *Nazzacetus urbinaei* (Lambert et al., 2009), the lower transverse process of the axis is not as enlarged as in *M. gregarius* MUSM 2548, and the cervical vertebrae 3 to 7 are free, while the atlas and axis are fused.

Conversely, many extant Ziphiidae display extensive fusion of the neck vertebrae; none of the species with data available bear a free axis at the adult stage (Lambert et al., 2015). For example, in *Hyperoodon ampullatus* all cervical vertebrae are consistently fused in both males and females (Fig. 9c). With regard to the lower transverse process of C6,
as for the *M. longus colli*, an accurate origin of the *Mm. intertransversarii cervicis* could not be identified in extant ziphuids.

*M. rectus capitis dorsalis major*. This muscle originates from the neural spine of the axis and inserts into the nuchal crest of the supraoccipital bone (Schulte, 1916; Uhen, 2004). It extends and stabilizes the head.

Even though the neural spine of the axis is not preserved in *M. gregarius* MUSM 2548, a comparison between the stem ziphid *N. platyrostris* and crown ziphuids is relevant. The subcomplete neural spine of the holotype of *N. platyrostris* was assessed by de Muizon (1984) to be longer and thinner than in extant ziphuids, except *Hyperoodon ampullatus* (Fig. 9). The condition of the neural spine in extant ziphuids from our dataset confirms this statement, except in the case of *Tasmacetus shepherdi*, for which the proportionally longer neural spine was closer to *N. platyrostris* than to other extant Ziphidae. In *Nazzacetus arkinai*, the neural spine of the axis is strongly reduced compared to *N. platyrostris*, suggesting a smaller origin area for the *M. rectus capitis dorsalis major*.

### 4.2.2 Forelimb muscles

*M. supraspinatus*. The *M. supraspinatus* originates from the scapula, in the supraspinous fossa, and along the medial side of the acromion (Benke, 1993; Marx et al., 2016). It inserts into the great tuberosity of the humerus. The main action of the *M. supraspinatus* is to abduct the humerus.

Even though the bad preservation of the region around the supraspinatus fossa and the acromion in *M. gregarius* MUSM 2542 precludes a reconstruction of the origin of this muscle, the flattened and individualized great tuberosity of the humerus observed in MUSM 2542 suggests this muscle to be as developed as in extant Ziphidae. Indeed, we observed an individualized great tuberosity in *Berardius ssp.*, *Hyperoodon ssp.*, *Indopacificus pacificus*, *Mesoplodon bidens*, *M. bowdoini*, *M. densirostris*, *M. grayi*, *Tasmacetus shepherdi*, and *Ziphius cavirostris*. A flattened great tuberosity was also present in the isolated humerus MNHN SAS 943, tentatively attributed to *Ninoxiphius platyrostris* by de Muizon (1984).

*M. deltoideus*. The *M. deltoideus* originates from the infraspinous fossa, the spine of the scapula, and part of the acromion. It inserts into the lateral side of the anterior edge of the deltoid ridge of the humerus. Its main action is to extend the humerus, while the acromial fibres are involved in the abduction of the latter (Marx et al., 2016; Benke, 1993). We could not accurately assess the origin area of the *M. deltoideus* based on the partial scapula of *M. gregarius* MUSM 2542. Nevertheless, the presence of a deltoid ridge along the anterior surface of the humerus indicates a moderate development of this muscle as compared to Physeteroidea that display a deltoid ridge more developed proximodistally (Benke, 1993). A developed deltoid ridge is also present in MNHN SAS 943 *Ninoxiphius platyrostris* and in all the extant ziphuids examined in this study.

*M. infraspinatus*. The *M. infraspinatus* originates from the posterior surface of the scapula, posterior to the *M. deltoideus* (Benke, 1993; Marx et al., 2016). It inserts into a small fossa distal to the head of the humerus. This muscle acts as an extensor of the humerus and slightly participates in its adduction (Benke, 1993). The posterior crest along the lateral surface of the scapula of *Messapicetus gregarius* MUSM 2542 defines posteriorly the origin of the *M. infraspinatus*. This crest is similarly developed as in a fragmentary scapula of MSNUP 115760 partial skeleton of *Messapicetus longirostris* described by Bianucci et al. (2016a). However, the eroded surface of the two humeri of *M. gregarius* MUSM 2542 precluded us from assessing its insertion area. In the isolated humerus MNHN SAS 943, tentatively associated with *Ninoxiphius platyrostris* by de Muizon (1984), we note the presence of a fossa distal to the head of the humerus where the *M. infraspinatus* most likely inserted. We observe a similar fossa in *Berardius ssp.*, *Hyperoodon ssp.*, *Indopacificus pacificus*, *Mesoplodon bidens*, *M. bowdoini*, *M. densirostris*, *M. grayi*, *Tasmacetus shepherdi*, and *Ziphius cavirostris*.

*M. teres major*. The *M. teres major* originates from the posterior region of the scapula in the teres fossa (Benke, 1993; Marx et al., 2016). It inserts into the posteroproximal part of the humerus. This muscle adducts the humerus and allows its inward rotation. The posterior crest in the scapula of *Messapicetus gregarius* MUSM 2542, *M. longirostris* MSNUP 115670, and all extant ziphuids of the sample defines anteriorly the origin area of the *M. teres major*.

### 4.3 Statistical results

#### 4.3.1 Hamular fossa of the pterygoid sinus

The relationship between HF proportions and deep-diving abilities was revealed as significant with and without phylogenetic correction (with phylogenetic correction: $F$ ratio = 12.504; $p$ value = 0.001; without phylogenetic correction: $F$ ratio = 18.078; $p$ value = $2.82 \times 10^{-5}$). The four linear measurements taken were sufficient to distinguish ziphid species from other odontocetes of the sample, particularly when the principal components (PCs) 1 and 2 were combined (Fig. 11). All ziphuids were characterized by an enlarged HF both anteroposteriorly and dorsoventrally as compared to other odontocetes (Fig. 11). The deep-diving species *Grampus griseus* and *Physeter macrocephalus* showed the same tendency as observed in ziphid species. The species *Glisicelpha melas*, *Monodon monoceros*, and *Pseudorca crassidens* also possessed an anteroposteriorly and dorsoventrally enlarged HF, but could be distinguished from Ziphidae based on their anteriorly wider HF. *Messapicetus gregarius* exhibited an enlarged HF similar to other Ziphidae. However, *M. gregarius* could be differentiated from other ziphuids
Figure 8. Comparison of muscular insertions along the atlas and axis in *Messapicetus gregarius* MUSM 2548 in ventral view (a) and posterior view (b); in *Ninocetus platyrostris* MNHN SAS 941 in ventral view (c) and posterior view (d); in *Mesoplodon densirostris* USNM 593522 in ventral view (e) and posterior view (f); in *Berardius* sp. MNHN 1885-278.
Figure 9. Comparative reconstructions of the cervical complex in several cetaceans with neck muscle origins discussed in this paper. The reconstructions concerned M. rexavicus gregarius (MUSM 2548) (a), Ninoziopoides platyrostris (MNHN SAS 941) (b), Hyperoodon ampullatus (SNM CN11x) (c), Mesoplodon bidens (MNHN A14519) (d), Inia geoffrensis (SNM CN11x) (e), and Xiphias cristatus (IRSNB 3240-M 361) (f). Dotted lines correspond to broken parts.
based on its IIF being posteriorly wider and dorsoventrally enlarged.

4.3.2 Forelimb

The relationship between forelimb measurements after log-
shape ratio transformation and deep-diving abilities was re-
vealed as not significant with and without phylogenetic cor-
rection (with phylogenetic correction: \( F_{\text{ratio}} = 0.90638 \); \( p \) 
value = 0.5595). Ziphidiidae, including *Messapicetus gregari-
us*, were most efficiently discriminated when PC1 (25.60 %) 
and PC2 (19.99 %) were combined (Fig. 12). All ziphidiids ex-
hibited a relatively elongated humerus and radius, a distally 
narrow humerus and radius, a shortened scapula, and a more 
developed deltoid tuberosity as compared to other odonto-
cetes (Fig. 10). A similar tendency was also observed in *Phy-
seter macrocephalus* (Fig. 12). The basilosaurid *Dorudon atrox*
exhibited an even longer humerus and radius and a more 
developed deltoid tuberosity than extant Ziphidiidae. On the 
other hand, the deep-diving species *Delphinaepteras leu-
cas*, *Globicephala melas*, *Grampus griseus*, and *Pseudorca crassidens* displayed the opposite tendency, with humerus 
and radius distally widened and a shortened humerus.

5 Discussion

5.1 Neck flexibility in stem Ziphidiidae

Our reconstruction of neck muscles in the stem ziphidiids *Mes-
sapicetus gregarius* and *Ninozipphus platyrostris* indicate a 
higher lateral and dorsoventral flexibility of the neck in both 
species as compared to other ziphidiids of the sample. These 
stem ziphidiids had extended insertion areas for the *M. longus*
collis and the *Mm. intertransversarii ventrales cervicis* as 
compared to extant ziphidiids (Fig. 9) and the late Miocene 
crown ziphid *Nasocetus urbani*.

In addition, the proportionally longer cervical vertebrae of 
long-snouted stem ziphidiids compared to crown beaked 
whales allowed for wider lateral and dorsoventral move-
ments.

We also interpret the low degree of fusion of the cervi-
cal vertebrae in *M. gregarius* and *N. platyrostris* as an 
argument in favour of a more flexible neck. Even though ex-
tant cetaceans may display intraspecific variation regarding
the degree of fusion of their cervical vertebrae (Buchholz,
2001), we argue that the low degree of fusion of the cer-
vical vertebrae in stem ziphidiids is consistent for three 
reasons. First, we assessed the ontogenetic stages of the studied 
specimen of *Messapicetus gregarius* as being an adult, al-
though the degree of fusion generally increases with age in 
cetaceans (Buchholz, 2001). Second, extant ziphidiids gen-
erally possess at least three fused cervical vertebrae at adult 
age, thus contrasting with the condition in the analysed stem 
ziphidiids (Lambert et al., 2015). Finally, the axis of *M. gre-
garius* MUSM 2548 displays an anterior articular facet for 
the atlas, including the odontoid process. In the dog, the ab-
scence of the odontoid process results in tilting or dorsal dis-
placement of the axis into the vertebral canal, leading to the 
compression of the spinal cord (Evans and Lahunta, 2013). 
Therefore, the presence of this articular facet in *M. gregari-
us* would contribute to maintaining a correct articulation be-
tween the atlas and the axis in the absence of fusion between 
these two elements.

The more extensive fusion of the cervical vertebrae in the 
extent ziphidiids *Hyperoodon spp.*, *Indopacetus pacificus*, *Tas-
macetus shepherdi*, and *Ziphus cavirostris* likely impacted 
lateral movements of the neck. In those species, the lower 
transverse process of C6 was also reduced, indicating a re-
duction of the areas of origin for both *M. longus* collis and 
*Mm. intertransversarii cervicis*. Conversely, *M. bidens*, *M. 
densirostris*, and *M. grayi* possess developed C6 processes, 
suggesting some degree of neck flexibility among crown 
ziphidiids.

The cervical vertebra of the specimen MUSM 2548 iden-
tified as C5–C6 bears a small lower process similar in shape 
and development to C6 of *N. platyrostris* (de Muizon, 1984).
This condition differs from the eurinodelphinid *Ziphice-
tus cristasus*, the platanistoid *Okeiakeia marplesi*, and the 
basilosaurid *Dorudon atrox*, in which the strong and 
thickened lower transverse process indicate a developed origin 
for the *M. longus* collis (Fig. 9e; Lambert, 2005; Tanaka and 
Fordyce, 2014; Uhen, 2004). The lack of a developed lower 
process in C6 may suggest a less flexible neck in *N. platyro-
stris* and possibly *M. gregarius* compared to the aforemen-
tioned species. Yet, both *M. gregarius* and *N. platyrostris* 
display large insertions for the *M. longus* collis and the *Mm.
intertransversarii ventrales cervicis* that are more developed 
than in any extant ziphid.

While the spinous process of the axis was not preserved for 
*M. gregarius*, *N. platyrostris* displays a weaker spinous pro-
cess compared to other extant Ziphidiidae. However, a strong 
spinous process is present in *Inia geoffrensis*, an odontocete 
with a highly flexible neck. In *H. ampullatus*, de Muizon 
(1984) noted a particularly strong spinous process of the axis, 
most likely supporting the head.

Neck rigidity might be related to deep-diving specializa-
tion in Ziphidiidae. However, differences in the degree of flexi-
bility observed among extant ziphidiids advocate for a more 
complex functional interpretation. Data on potential differ-
ences in swimming and feeding strategies between extent 
ziphidiid species are currently insufficient to explain the con-
trasted neck morphologies observed.

5.2 Forelimb morphology and its relation to deep 
diving

Our reconstruction of the forelimb muscles of *M. gregarius* 
suggest no important differences with extant ziphidiids. Mul-
tivariate analyses confirm this close relation, showing that 
*M. gregarius* and other extant ziphidiid possess a relatively
similar forelimb morphology. In particular, the morphology of the radius was uniform among ziphids, lacking the distal widening seen in many odontocetes. Elongation of the humerus in *M. gregarius* does not appear as obvious as we previously suggested, this feature being present in all ziphids compared to other odontocetes. This suggests the flipper of *M. gregarius* to be relatively similar in shape to extant Ziphiidae. The latter display flippers that are longer than the wide, the elongated state described by Sanchez and Berta (2010).

Results of the D-PGLS indicate that the morphology of the forelimb is not associated with deep-diving abilities, suggesting that forelimb proportions cannot be used to assess deep-diving specialization in odontocetes.

Functional aspects of the flipper of ziphids remain poorly known, but we suspect the flipper shape of *M. gregarius* to be associated with aspects of locomotion other than deep diving, like prey capture. Several cetaceans with a broad flipper, such as the killer whale *Orcinus orca* or the humpback whale *Megaptera novaeangliae*, are able to perform quick manoeuvres, helping them to catch mobile prey in the epipelagic domain (Benke, 1993; Woodward et al., 2006). With their small and elongated flipper type, extant ziphids would probably not be as manoeuvrable, privileging speed and possibly optimizing their hydrodynamic profile instead.

### 5.3 Variation in the HF and its relation to deep diving

Our measurements of the HF were sufficient to discriminate ziphids from other odontocetes. Furthermore, the variation in HF measurements is correlated with deep-diving specialization, thus suggesting that enlargement of the HF is a good proxy to assess deep-diving abilities. The increase in size of the HF in deep divers happens in two different ways: either by the anteroposterior and dorsoventral enlargement of the HF as in ziphids, *Grampus griseus*, and *Physeter macrocephalus*, or by the anterior enlargement of the HF as in *Globicephala melas*, *Monodon monoceros*, and *Pseudorca crassidens*. *Mesapicetus gregarius* exhibits differences in the proportions of the pterygoid sinus fossae when compared to other Ziphiidae (Fig. 11). Although less anteriorly elongated than in extant ziphids, the HF of *M. gregarius* is also wider posteriorly, more enlarged dorsoventrally, and narrower anteriorly.
Although it remains unclear if *Messapicetus gregarius* was able to perform regular dives beyond 1000 m, this species was most likely capable of hearing beyond 700 m. This new finding seemingly falsifies our former hypothesis that several long-snouted stem ziphiiids were not deep divers (Lambert et al., 2015). However, several scenarios can explain this apparently contradictory result.

First, *Messapicetus gregarius* may have fed both in epipelagic and deeper benthopelagic grounds. While extant ziphiiids are very specialized, other deep divers are more opportunistic. For example, *Pseudorca crassidens* and *Delphinapterus leucas* feed on a wide variety of prey at different depths from 100 up to 700 m in the case of *P. crassidens* and 900 m for *D. leucas* (Martin et al., 1998; O’Corry-Crowe,
A more flexible feeding behaviour may have occurred in stem ziphids like *M. gregarius*. Different individuals in the species may also have different preferences. In *Megaptera novaeangliae*, maternal females favour shallower waters with their calves, perhaps to protect them from sexually active males or to avoid turbulent offshore sea conditions and/or predators (Smulkea, 1994). In the case of *Messapicetus gregarius*, males and females have been identified at Cerro Colorado based on secondary sexual characters (i.e., intraspecific variation in tusk development and surrounding structures; Lambert et al., 2010a). The co-occurrence of male and female mature specimens and a calf at the same location suggests that *M. gregarius* did not follow the same strategy as *M. novaeangliae*, but does not discard a seasonal use of this basin as a potential nursery ground.

A second plausible explanation for the enlarged HF of *M. gregarius* is predation avoidance. Three potential predators for *M. gregarius* were present at Cerro Colorado during the late Miocene: the sperm whale *Libyan melvillei* and the giant sharks *Cosmopolitodus spp.* and *Carbonaroches megalodon*, the latter being believed to have fed on small-sized baleen whales and pinnipeds (Collareta et al., 2017; Lambert et al., 2010b; Landini et al., 2017a). *M. gregarius* may have performed deep dives to avoid these two predators. This strategy is already suspected in extant beaked whales based on several mass strandings of *Mesoplodon densirostris* and *Ziphius cavirostris* directly related to naval exercises involving mid-frequency active sonars (Amico et al., 2009; Cox et al., 2006; Filadello et al., 2009). It is generally accepted that the sound exposure forces beaked whales to alter their own diving behaviour, causing a decompression syndrome (Cox et al., 2006; Tyack et al., 2007). Zimmer and Tyack (2007) noticed the resemblance between the tonal mid-frequencies used and the calls of killer whales (*Orcinus Orca*), suggesting that ziphids try to avoid the latter. Furthermore, two studies were able to trigger this avoidance behaviour in *Mesoplodon densirostris* by exposing the animals to killer whale calls. A few cases of active predation have also been reported, suggesting that this avoidance strategy is not perfect (Wellard et al., 2016). One flaw of this hypothesis is that depth estimates for the PI sequence of the Pisco Formation at Cerro Colorado do not exceed some tens of metres, thus limiting the diving possibilities of the specimens living in the area (Claudio Di Celma, personal communication, 2017; see also depth estimates in Landini et al., 2017a, b). Therefore, this scenario is only possible if *M. gregarius* did not limit itself to the epipelagic grounds where it is currently found.

A last explanation for the enlargement of the HF in *M. gregarius* is a reversion to an epipelagic habitat in this species. This scenario implies the specialization for deep diving to be more ancestral among ziphids, with a secondary change in habitat for *M. gregarius*. Enlargement of the HF in this species would therefore be explained because of phylogenetic inertia. Our former hypothesis proposed a unique acquisition of the deep-diving behaviour in Ziphiidae between long-snouted stem ziphids and crown ziphids (Lambert et al., 2015). However, a recent phylogenetic analysis suggested that the ecological shift to deep diving occurred twice in the family with the inclusion of deep-diving forms in the *Messapicetus* clade (Bianucci et al., 2016c). Using this new phylogeny, our former hypothesis stated in Lambert et al. (2015) is no longer the most parsimonious, further reducing the amount of indirect evidence in favour of *Messapicetus* as an exclusively epipelagic form, although several other lines of evidence indicate that a shallow coastal environment represented an important part of its home range.

A combination of these features is also possible. Currently, we are unable to favour one hypothesis or the other.

### 6 Conclusions

Ziphid postcrania are rare in the fossil record (Bianucci et al., 2016a; de Muizon, 1984; Ramassamy, 2016). As a result, the description of cervical vertebrae and forelimb elements of the stem ziphid *Messapicetus gregarius* from the late Miocene of Peru yields new information about the anatomy and ecology of extinct Ziphiidae.

Our reconstruction of the neck muscles of *M. gregarius* and *Ninozipeus platyrrostris* suggests that these stem ziphids had a flexible neck able to make stronger dorsoventral and lateral movements than most extant ziphids. The absence of fusion of the neck vertebrae in one specimen of *M. gregarius* is interpreted as a typical characteristic of the species because of (1) the adult ontogenetic stage of the specimen, (2) the presence of an odontoid process allowing for a precise articulation between the axis and the atlas, and (3) the fusion of the cervical vertebrae being present in all other ziphid species examined. The presence of larger transverse processes of C6 in some species of *Mesoplodon* and the interspecific variation in the degree of fusion of the cervical vertebrae of extant ziphids indicate various degrees of flexibility in the neck in the latter.

The proportions of the forelimb bones of *M. gregarius* are similar to those of extant ziphids. We estimate the flipper shape of *M. gregarius* to resemble the shape in extant ziphids. Changes in the forelimb morphology in Ziphiidae are not related to deep-diving abilities when phylogenetic context is taken into account and suggest that other proxies should be used to infer diving abilities in odontocetes.

Finally, our measurements of the hamular fossa of the pterygoid sinuses are sufficient to evaluate deep-diving abilities in odontocetes with and without phylogenetic correction. The enlargement of the hamular fossa is also present in *Messapicetus gregarius*, implying that this species was able to hear at least beyond 700 m. We propose several explanations to rectify this result with other evidence suggesting that *M. gregarius* was an epipelagic predator: (1) this species was perhaps more opportunistic than extant ziphids and fed at
different depths; (2) it performed deep dives to avoid potential predators; (3) or the enlarged HF in *M. gregarius* corresponds to an ancestral adaptation not matching the epipelagic habitat of this species (3). A combination of any of these different scenarios is also plausible.

**Data availability.** Dataset 1: R script used for the analysis.
Dataset 2: complete set of linear measurements used in the present study.
Dataset 3: list of supplementary references for the maximum depth records.
All data information can be found at https://doi.org/10.6084/m9.figshare.5259517.v2.

**Author contributions.** All authors took part in the fieldwork and collected field data. OL, GB, MU, and BR identified and interpreted the ziphodont remains. Measurements were taken by AC, GB, OL, and BR. Photos were taken by BR, AC, and GB. BR wrote the paper and performed the analyses. All authors commented on the paper at all stages.

**Competing interests.** The authors declare that they have no conflict of interest.

**Special issue statement.** This article is part of the special issue “Secondary adaptation of tetrapods to life in water – Proceedings of the 8th International Meeting, Berlin 2017”. It is a result of the 8th International Meeting on the Secondary Adaptation of Tetrapods to Life in Water, Berlin, Germany, 3–8 April 2017.

**Acknowledgements.** We thank the following colleagues for kindly allowing us to access some of the comparative material we used in this study: Morten T. Olsen and Daniel K. Johansson for access to the SNM collection, S. Bruaas for the IRSNB collection, Christian de Muizon and Christine LeFèvre for the MNHN collections, Chiara Sorbini for the MSNUP collections, and Charles Potter for the USNM collections. We are indebted to Klaas Post for his help in the field to collect and identify the specimens.

We thank Walter Aguirre, who collected the specimens, and Walter Aguirre, Rodolfo Salas-Gismondi, and Rafael Varas-Malca, who prepared the specimens and provided assistance during our stay at the MUSM.

BR also wishes to thank his supervisors Mette E. Steeman and Thomas Pape for the advice they provided on the paper, which is part of his PhD thesis. He also thanks Andrew Steward from the Te Papa Tongarewa Museum of New Zealand for the photographs of *Taurosaurus shepherdii* he kindly provided. Finally, he thanks Pavel Gol’din, Thomas Guillerme, and Nina M. Jakobsen for the help they provided for the statistical analyses.

We thank the reviewers, Annalisa Berta and Mark D. Uhen, and the Chief Editor Florian Witzmann, who provided relevant comments and improved the quality of the paper.

The research was partially supported by a grant from the Dansk Slots- og Kulturstyrelsen (FORM.2016-0021) to B. Ramassamy, a grant from the Italian Ministero dell’Istruzione dell’Università e della Ricerca (PRIN project 2012Y3BMK), and by a National Geographic Society Committee for Research Exploration grant (9410-13), both to G. Bianucci.

Edited by: Florian Witzmann
Reviewed by: Annalisa Berta and Mark D. Uhen

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