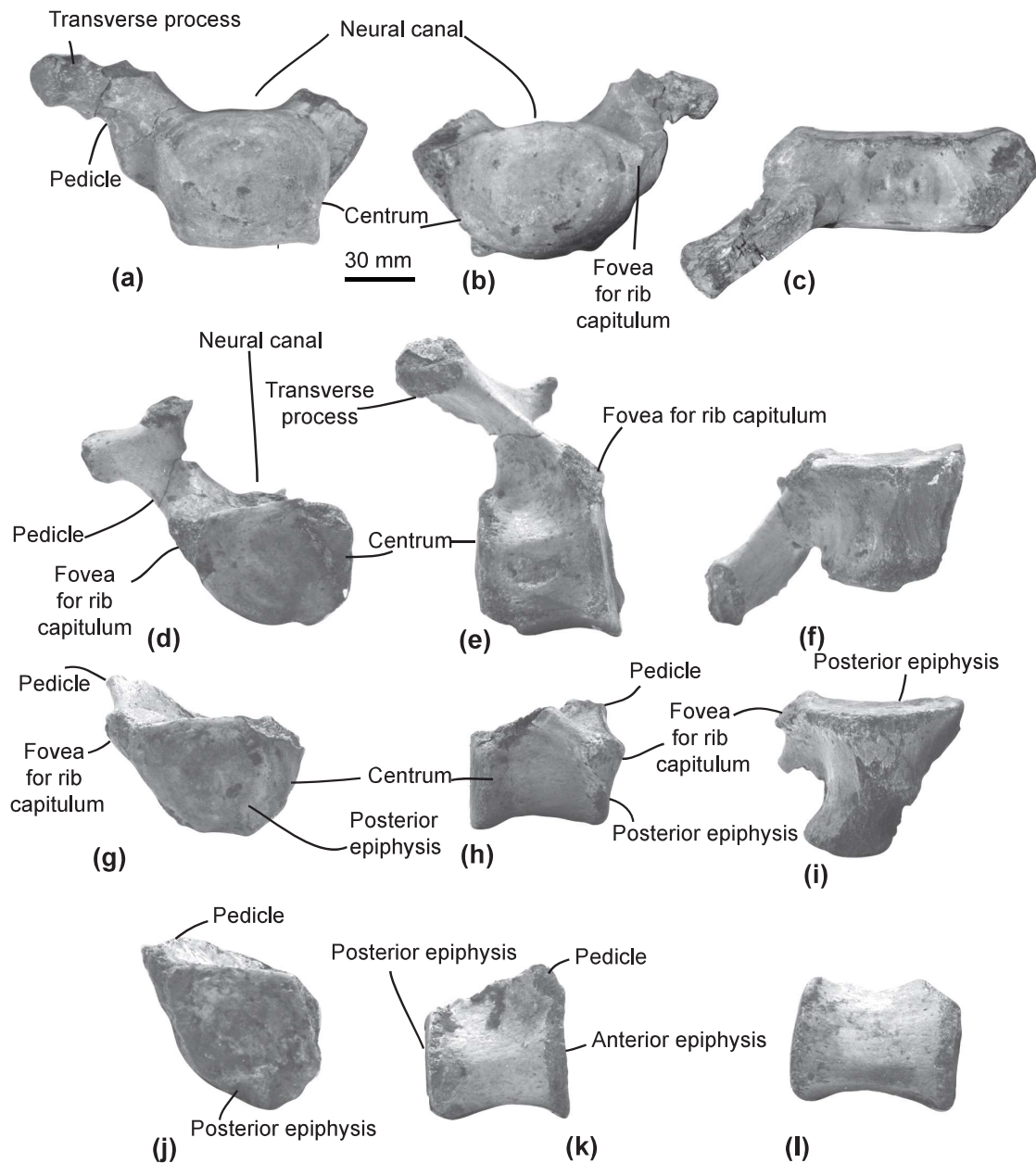


**Figure 2.** Cervical vertebrae of the specimen MUSM 2548, *Messapicetus gregarius*. Axis in anterior (a), posterior (b), and ventral view (c); C5–C6 in anterior (d), posterior (e), and dorsal view (f); C7 in anterior (g), posterior (h), and dorsal view (i).

*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 dorso-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.

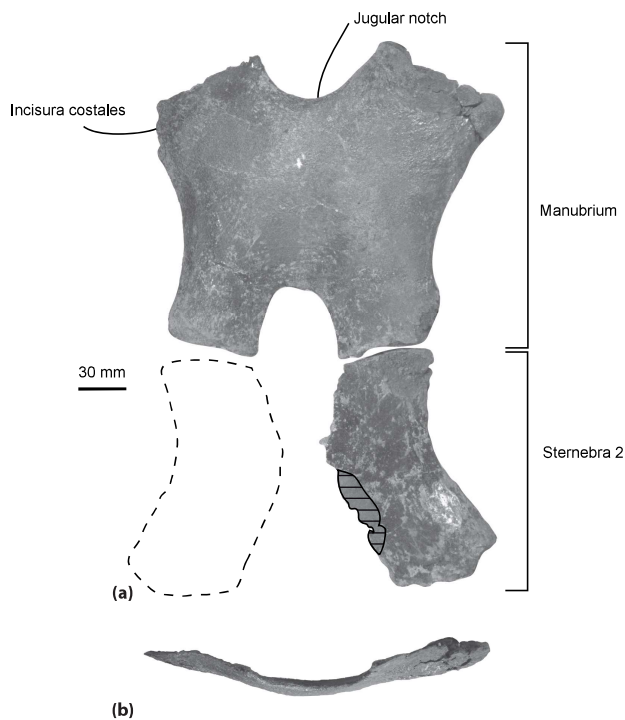


**Figure 3.** Thoracic and post-thoracic vertebrae of the specimen MUSM 2548, *Messapicetus gregarius*. Thoracic vertebra A in anterior (a), posterior (b), and dorsal view (c); thoracic B in posterior (d), left lateral (e), and ventral view (f); thoracic C in posterior (g), lateral (h), and ventral view (i); thoracic–post-thoracic D in posterior (j) and lateral view (k); thoracic–post-thoracic E in lateral view (l).

#### 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 sternebra 2.

half of the manubrium, except for the deeper excavation of its lateral margin.

**Ribs.** Among the 12 partial ribs recovered in specimen MUSM 2548 (Fig. 5), four pairs are tentatively positioned based on respective head shape (Fig. 5a–h) and by comparison with the identified ribs of *Ninoziphius platyrostris* (de Muizon, 1984). The first pair (Fig. 5a–b) is the shortest. Compared to the other ribs, it possesses the shortest neck, the widest and flattest body, and the thickest angle. The following pairs until pair 4 are progressively longer, thinner, and less flattened, with a longer neck and a shorter capitulum. At least the four first pairs are double-headed. The distal part of each rib is flattened and exhibits longitudinal striations, most likely where muscles inserted.

#### 4.1.4 Forelimb

**Scapula.** The fan-shaped partial right scapula of MUSM 2542 is marked by multiple fractures. Some pieces were displaced, thus slightly affecting its original shape (Fig. 6). In ventral view, the glenoid cavity is oval and more elongated anteroposteriorly than transversely wide. Posterodorsally to the glenoid fossa, the base of the coracoid process is too damaged to allow for a reconstruction. In lateral view, on the posterior surface of the scapula, a crest separating the infrapinnous fossa from the teres fossa is salient dorsoventrally.

**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. 7e–i), 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.

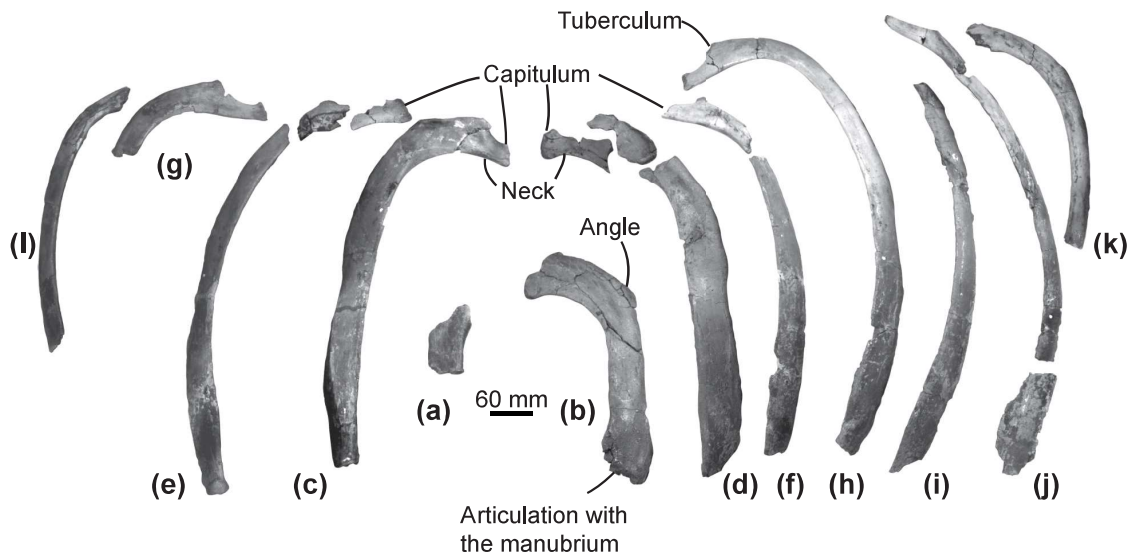
**Radius.** The left radius of MUSM 2542 is complete (Fig. 7j–l). It curves proximodistally and slightly transversely. The facet for articulation of the humerus is oriented anteroproximally. Distally, the articulations for the scaphoid and the lunate can be differentiated based on their orientation (Fig. 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, posterodistally facing.

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

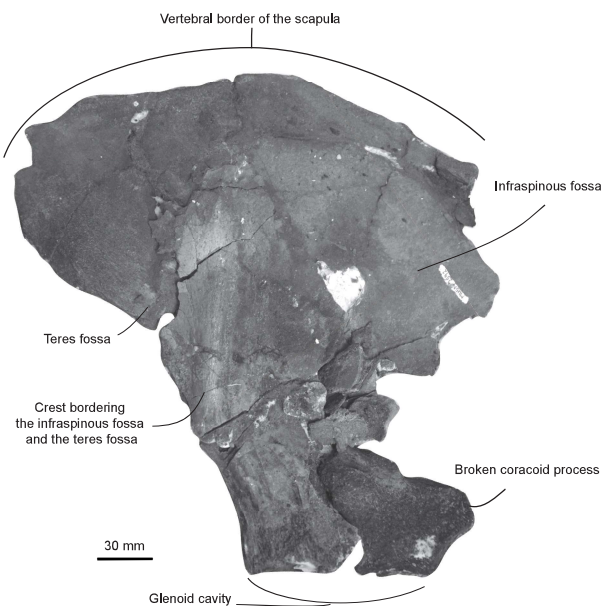
### 4.2.1 Neck muscles

***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 *Ninoziphius 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.

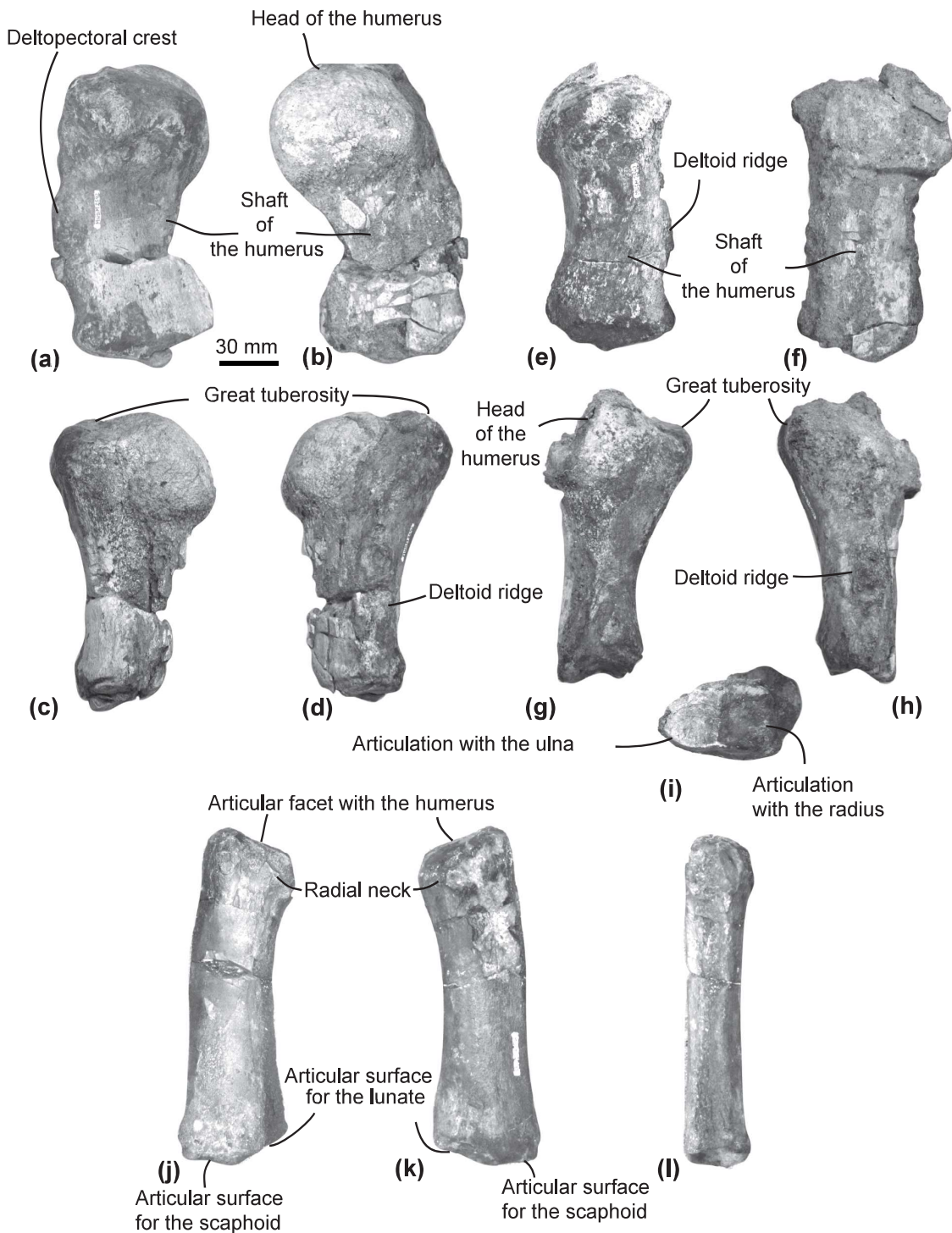
Heavily abraded posteroventrally, the partial atlas of the middle Miocene Berardiinae *Archaeoziphius microglenoideus* probably had a poorly developed (if any) ventral tubercle (Lambert and Louwye, 2006). This suggests a reduction of the *M. longus colli* insertion area as compared to *N. platyrostris*. The atlas of the late Miocene crown ziphiid *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 ziphiids 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 ziphiids, except in *Mesoplodon grayi* and *Berardius* spp. (Dataset 1, Ramassamy et al., 2018). In addition, the lower transverse process of C6 is more developed in *Mesoplodon bidens*, *M. densirostris*, and *M. grayi* than in *N. platyrostris* and other crown ziphiids observed (Fig. 9d–e). This feature indicates a relatively larger origin area for the *M. longus colli* in these three *Mesoplodon* 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, *Messapicetus 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, *Messapicetus gregarius*. Thoracic–post-thoracic vertebrae from A to E are ordered in relative position; e stands for estimated measurements, and “–” indicates missing measurements.

Feature	Axis	C5–C6	C7	A	B	C	D	E
Transverse width at the level of transverse processes	186e	–	–	162e	184e	–	–	–
Anterior transverse width centrum	–	73	75	69	70e	71	54e	–
anterior transverse height centrum	–	74	76	75	53	52	55	–
Posterior transverse height centrum	55	56	57	54	–	–	–	–
Posterior transverse width centrum	76	57	59	55	–	–	–	–
Anteroposterior thickness centrum	12	21	28	37	52	63	72	82
Transverse width neural canal	51	–	–	–	–	–	–	–

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

Species	Sample	Number of fused cervical vertebrae	Ventral tubercle on the atlas	Ventral excavations on the axis	Development of the lower transverse process of C6
<i>Messapicetus gregarius</i>	1	0	?	present	?
<i>Ninoziphius platyrostris</i>	1	2	present	present	reduced
<i>Archeoziphius microglenoideus</i>	1	?	absent	?	?
<i>Nazcacetus urbinai</i>	1	2	absent	absent	reduced
<i>Berardius</i> sp.	2	3	present	absent	reduced
<i>Hyperoodon ampullatus</i>	11	7	absent	absent	absent
<i>Mesoplodon bidens</i>	2	3	absent	absent	more developed than in the other cervicals
<i>Mesoplodon bowdoini</i>	1	3	absent	absent	reduced
<i>Mesoplodon densirostris</i>	2	3 to 5	absent	absent	more developed than in the other cervicals
<i>Mesoplodon grayi</i>	1	2	present	absent	more developed than in the other cervicals
<i>Tasmacetus shepherdi</i>	3	5 to 6	absent	absent	reduced
<i>Ziphius cavirostris</i>	4	4 to 5	absent	absent	reduced

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 *Nazcacetus urbinai* (Lambert et al., 2009), the lower transverse process of the axis is not as enlarged as in *M. gre-*

*garius* 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 ziphiids.

*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 ziphiid *N. platyrostris* and crown ziphiids 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 ziphiids, except *Hyperoodon ampullatus* (Fig. 9). The condition of the neural spine in extant ziphiids from our dataset confirms this statement, except in the case of *Tasmacetus shepherdii*, for which the proportionally longer neural spine was closer to *N. platyrostris* than to other extant Ziphiidae. In *Nazcacetus urbinai*, 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 Ziphiidae. Indeed, we observed an individualized great tuberosity in *Berardius* spp., *Hyperoodon* spp., *Indopacetus pacificus*, *Mesoplodon bidens*, *M. bowdoini*, *M. densirostris*, *M. grayi*, *Tasmacetus shepherdii*, and *Ziphius cavirostris*. A flattened great tuberosity was also present in the isolated humerus MNHN SAS 943, tentatively attributed to *Ninoziphius 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 *Ninoziphius platyrostris* and in all the extant ziphiids examined in this study.

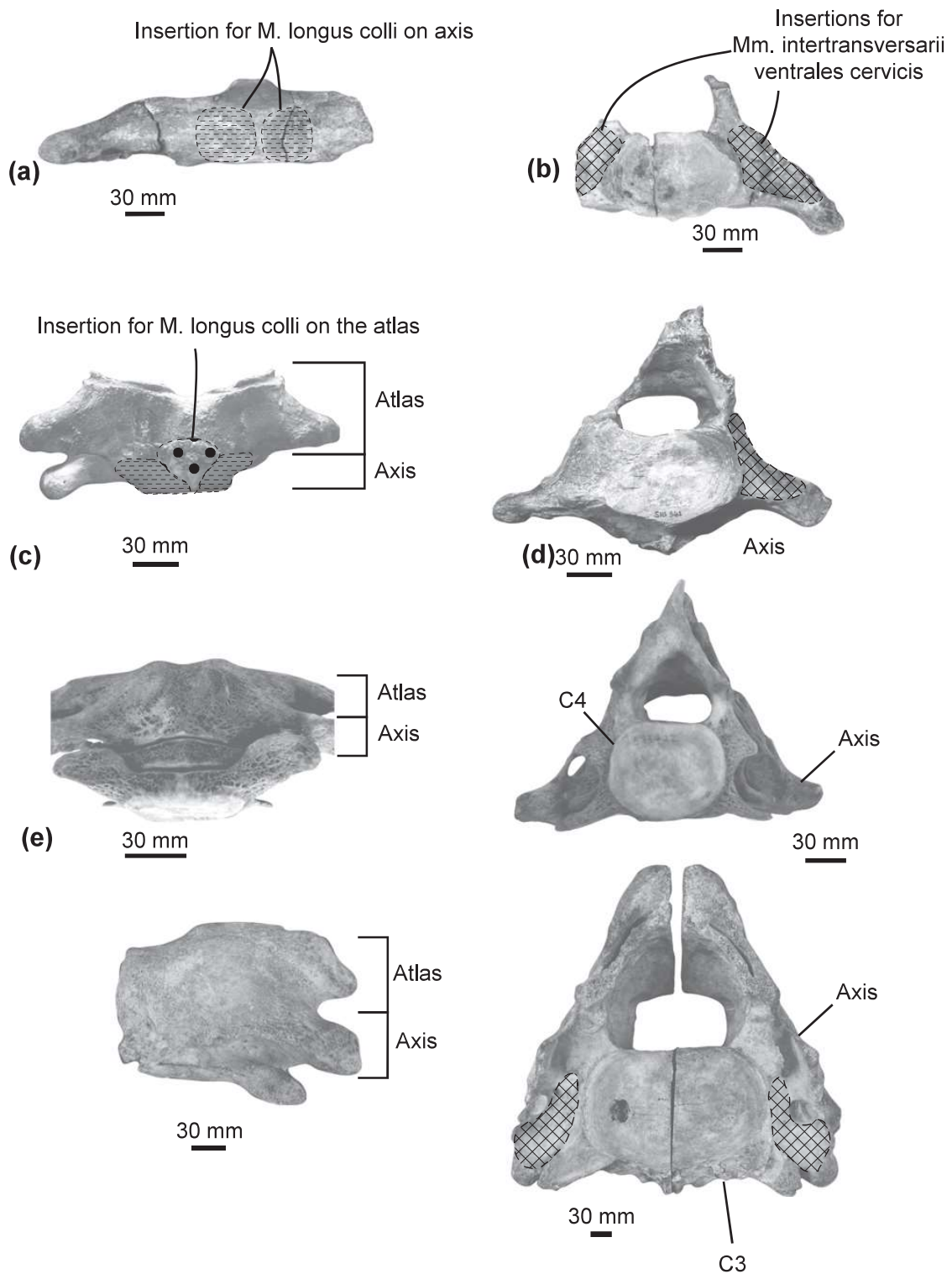
*M. infraspinatus*. The *M. infraspinatus* originates from the posterior surface of the scapula, posterior to the *M. deltoideus* (Benke, 1993; Marx et al., 2016). It inserts into a small fossa distal to the head of the humerus. This muscle acts as an extensor of the humerus and slightly participates 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 *Ninoziphius 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* spp., *Hyperoodon* spp., *Indopacetus pacificus*, *Mesoplodon bidens*, *M. bowdoini*, *M. densirostris*, *M. grayi*, *Tasmacetus shepherdii*, 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 ziphiids of the sample defines anteriorly the origin area of the *M. teres major*.

### 4.3 Statistical results

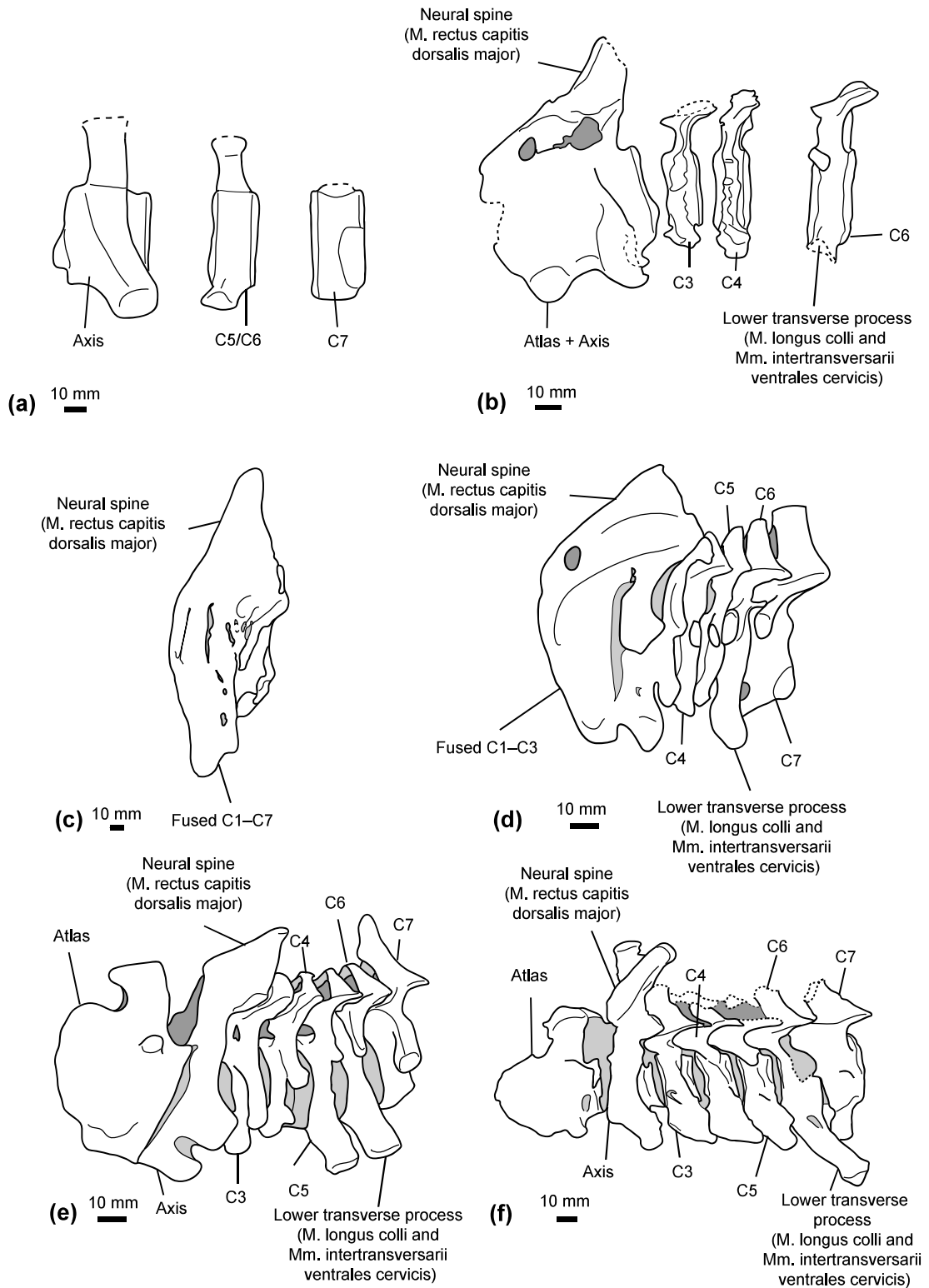
#### 4.3.1 Hamular fossa of the pterygoid sinus

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 =  $2.82 \times 10^{-6}$ ). The four linear measurements taken were sufficient to distinguish ziphiid species from other odontocetes of the sample, particularly when the principal components (PCs) 1 and 2 were combined (Fig. 11). All ziphiids 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 ziphiid species. The species *Globicephala melas*, *Monodon monoceros*, and *Pseudorca crassidens* also possessed an anteroposteriorly and dorsoventrally enlarged HF, but could be distinguished from Ziphiidae based on their anteriorly wider HF. *Messapicetus gregarius* exhibited an enlarged HF similar to other Ziphiidae. However, *M. gregarius* could be differentiated from other ziphiids



**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 *Ninoziphius 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 *Messapicetus gregarius* (MUSM 2548) (a), *Ninoziphius platyrostris* (MNHN SAS 941) (b), *Hyperoodon ampullatus* (SNM CN1x) (c), *Mesoplodon bidens* (MNHN A14519) (d), *Inia geoffrensis* (SNM CN1x) (e), and *Xiphiacetus cristatus* (IRSNB 3240-M.361) (f). Dotted lines correspond to broken parts.

based on its HF 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 revealed as not significant with and without phylogenetic correction (with phylogenetic correction:  $F$  ratio = 0.90638;  $p$  value = 0.5595). Ziphiidae, including *Messapicetus gregarius*, were most efficiently discriminated when PC1 (25.60 %) and PC2 (19.99 %) were combined (Fig. 12). All ziphiids exhibited 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 odontocetes (Fig. 10). A similar tendency was also observed in *Physeter macrocephalus* (Fig. 12). The basilosaurid *Dorudon atrox* exhibited an even longer humerus and radius and a more developed deltoid tuberosity than extant Ziphiidae. On the other hand, the deep-diving species *Delphinapterus leucas*, *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 Ziphiidae

Our reconstruction of neck muscles in the stem ziphiids *Messapicetus gregarius* and *Ninziphius platyrostris* indicate a higher lateral and dorsoventral flexibility of the neck in both species as compared to other ziphiids of the sample. These stem ziphiids had extended insertion areas for the *M. longus colli* and the *Mm. intertransversarii ventrales cervicis* as compared to extant ziphiids (Fig. 9) and the late Miocene crown ziphiid *Nazcacetus urbinai*.

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

We also interpret the low degree of fusion of the cervical vertebrae in *M. gregarius* and *N. platyrostris* as an argument in favour of a more flexible neck. Even though extant cetaceans may display intraspecific variation regarding the degree of fusion of their cervical vertebrae (Buchholtz, 2001), we argue that the low degree of fusion of the cervical vertebrae in stem ziphiids is consistent for three reasons. First, we assessed the ontogenetic stages of the studied specimen of *Messapicetus gregarius* as being an adult, although the degree of fusion generally increases with age in cetaceans (Buchholtz, 2001). Second, extant ziphiids generally possess at least three fused cervical vertebrae at adult age, thus contrasting with the condition in the analysed stem ziphiids (Lambert et al., 2015). Finally, the axis of *M. gregarius* MUSM 2548 displays an anterior articular facet for

the atlas, including the odontoid process. In the dog, the absence of the odontoid process results in tilting or dorsal displacement 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. gregarius* would contribute to maintaining a correct articulation between the atlas and the axis in the absence of fusion between these two elements.

The more extensive fusion of the cervical vertebrae in the extant ziphiids *Hyperoodon* spp., *Indopacetus pacificus*, *Tasmacetus shepherdi*, and *Ziphius cavirostris* likely impacted lateral movements of the neck. In those species, the lower transverse process of C6 was also reduced, indicating a reduction of the areas of origin for both *M. longus colli* and *Mm. intertransversarii cervicis*. Conversely, *M. bidens*, *M. densirostris*, and *M. grayi* possess developed C6 processes, suggesting some degree of neck flexibility among crown ziphiids.

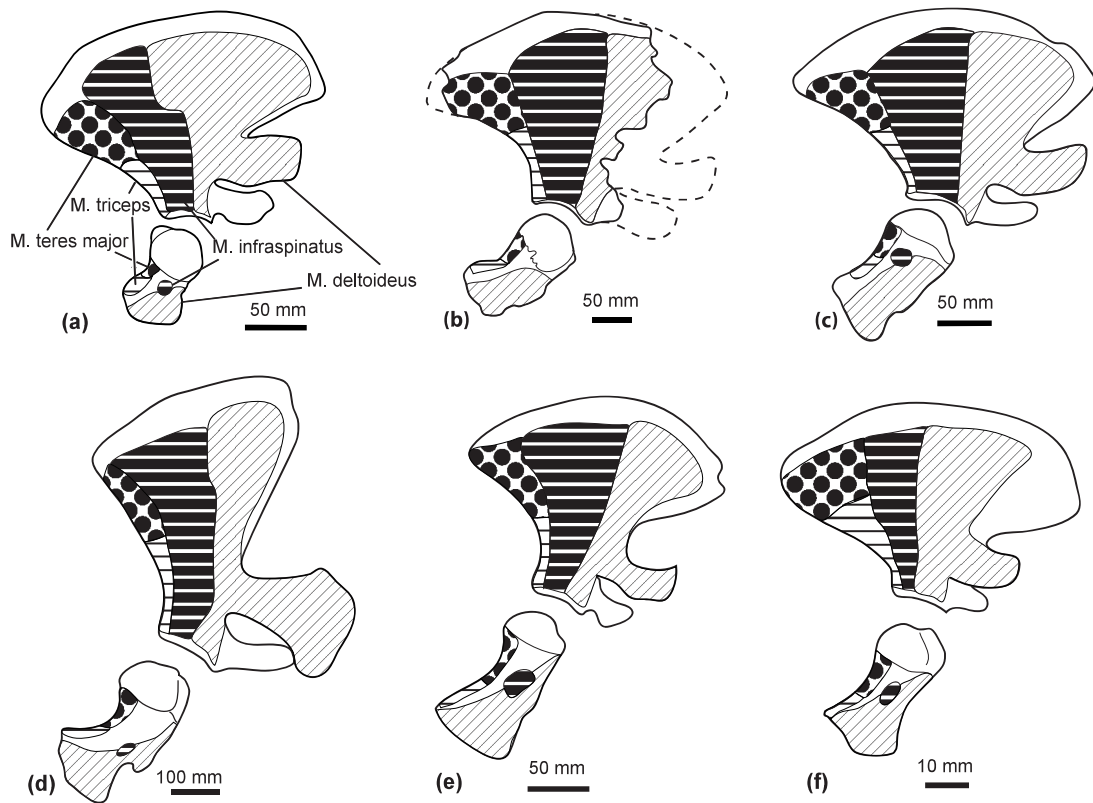
The cervical vertebra of the specimen MUSM 2548 identified as C5–C6 bears a small lower process similar in shape and development to C6 of *N. platyrostris* (de Muizon, 1984). This condition differs from the eurhinodelphinid *Xiphiacetus cristatus*, the platanistoid *Otekaikea marplei*, and the basilosaurid *Dorudon atrox*, in which the strong and thickened lower transverse process indicate a developed origin for the *M. longus colli* (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. platyrostris* and possibly *M. gregarius* compared to the aforementioned species. Yet, both *M. gregarius* and *N. platyrostris* display large insertions for the *M. longus colli* and the *Mm. intertransversarii ventrales cervicis* that are more developed than in any extant ziphiid.

While the spinous process of the axis was not preserved for *M. gregarius*, *N. platyrostris* displays a weaker spinous process compared to other extant Ziphiidae. 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 specialization in Ziphiidae. However, differences in the degree of flexibility observed among extant ziphiids advocate for a more complex functional interpretation. Data on potential differences in swimming and feeding strategies between extant ziphiid species are currently insufficient to explain the contrasted 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 ziphiids. Multivariate analyses confirm this close relation, showing that *M. gregarius* and other extant ziphiids possess a relatively



**Figure 10.** Comparison of the muscle origins and insertions of the scapula and humerus in lateral view in *Tursiops truncatus* (SNM CN2x) (a); a reconstruction of the scapula of *Messapicetus gregarius* (MUSM 2548) (b); *Mesoplodon bidens* (SNM CN4x) (c); *Physeter macrocephalus* (SNM CN1x) (d); *Inia geoffrensis* (NRS A608415) (e); *Pontoporia blainvillei* (SNM CN1x) (f). Insertion of the *M. infraspinatus* could not be assessed in *M. gregarius*. Scale = 50 mm. Dotted lines correspond to the reconstructed parts.

similar forelimb morphology. In particular, the morphology of the radius was uniform among ziphiids, 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 ziphiids 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).

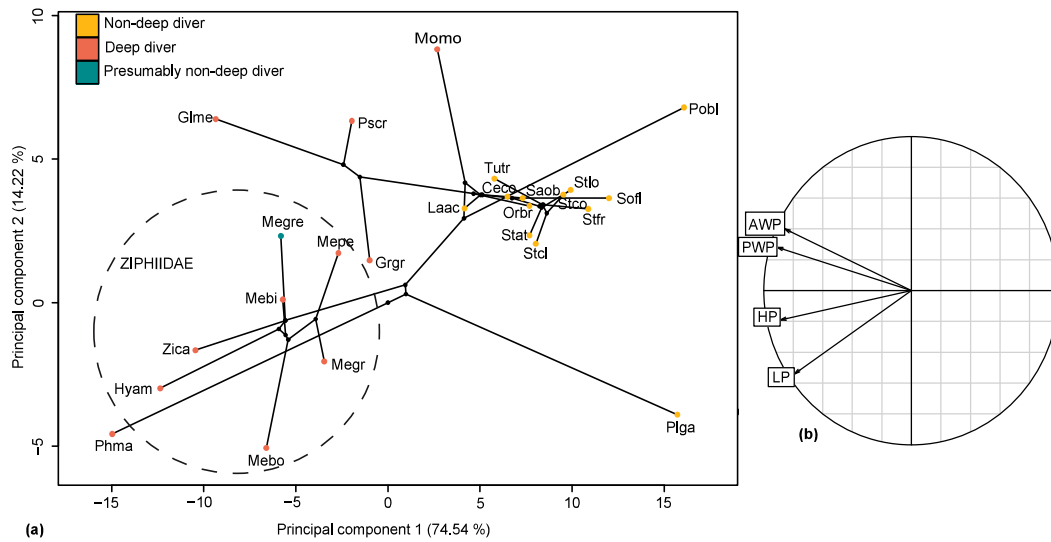
Results of the D-PGLS indicate that the morphology of the forelimb is not associated with deep-diving abilities, suggesting that forelimb proportions cannot be used to assess deep-diving specialization in odontocetes.

Functional aspects of the flipper of ziphiids 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

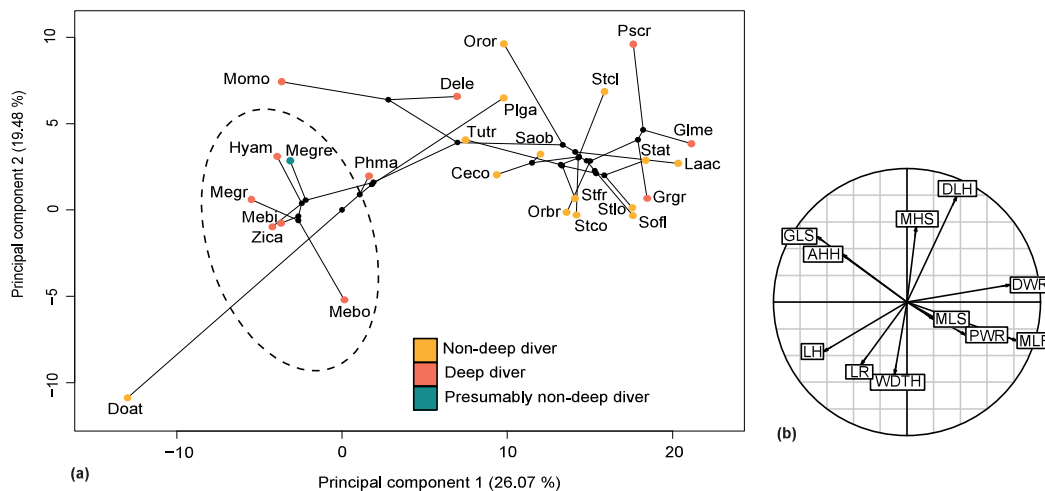
and elongated flipper type, extant ziphiids would probably not be as manoeuvrable, privileging speed and possibly optimizing their hydrodynamic profile instead.

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

Our measurements of the HF were sufficient to discriminate ziphiids 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 ziphiids, *Grampus griseus*, and *Physeter macrocephalus*, or by the anterior enlargement of the HF as in *Globicephala melas*, *Monodon monoceros*, and *Pseudorca crassidens*. *Messapicetus 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 ziphiids, the HF of *M. gregarius* is also wider posteriorly, more enlarged dorsoventrally, and narrower anteriorly.



**Figure 11.** Phylomorphospace of the principal components 1 and 2 for the hamular fossa of the pterygoid sinus (a) and its correlation circle (b). The dotted circle delimits the Ziphiidae family. The branches represent the phylogenetic relationships between the different species. Abbreviations: Ceco: *Cephalorhynchus commersonii*; Glme: *Globicephala melas*; Grgr: *Grampus griseus*; Hyam: *Hyperoodon ampullatus*; Laac: *Lagenorhynchus acutus*; Mebi: *Mesoplodon bidens*; Megr: *Mesoplodon grayi*; Megre: *Messapicetus gregarius*; Mepe: *Mesoplodon peruvianus*; Momo: *Monodon monoceros*; Orbr: *Orcaella brevirostris*; Phma: *Physeter macrocephalus*; Pobl: *Pontoporia blainvillei*; Plga: *Platanista gangetica*; Pscr: *Pseudorca crassidens*; Saob: *Sagmatias obscurus*; Sofl: *Sotalia fluviatilis*; Stat: *Stenella attenuata*; Stcl: *Stenella clymene*; Stfr: *Stenella frontalis*; Tutr: *Tursiops truncatus*; Zica: *Ziphius cavirostris*.



**Figure 12.** Phylomorphospace of the principal components 1 and 2 for the forelimb (a) and its correlation circle (b). The dotted circle delimits the Ziphiidae family. The branches represent the phylogenetic relationships between the different species. The abbreviations are the same as in Fig. 11 except for the following: Dele: *Delphinapterus leucas*; Doat: *Dorudon atrox*; Mebo: *Mesoplodon bowdoini*; Oror: *Orcinus orca*; Stco: *Stenella commersonii*.

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 ziphiids 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 bathypelagic grounds. While extant ziphiids 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,

2009; Oleson et al., 2010; Richard et al., 2001). A more flexible feeding behaviour may have occurred in stem ziphiids 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 (Smultea, 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 *Livyatan melvillei* and the giant sharks *Cosmopolitodus* spp. and *Carcharocles 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; Filadelfo 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., 2011). Zimmer and Tyack (2007) noticed the resemblance between the tonal mid-frequencies used and the calls of killer whales (*Orcinus orca*), suggesting that ziphiids 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 P1 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 ziphiids, 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 ac-

quisition of the deep-diving behaviour in Ziphiidae between long-snouted stem ziphiids and crown ziphiids (Lambert et al., 2015). However, a recent phylogenetic analysis suggested that the ecological shift to deep diving occurred two times 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

Ziphiid postcranial elements 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 ziphiid *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 *Ninoziphius platyrostris* suggests that these stem ziphiids had a flexible neck able to make stronger dorsoventral and lateral movements than most extant ziphiids. 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 cervicals being present in all other ziphiid 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 ziphiids 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 ziphiids. We estimate the flipper shape of *M. gregarius* to resemble the shape in extant ziphiids. 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 sinus 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 ziphiids 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.5259157.v2>.

*Author contributions.* All authors took part in the fieldwork and collected field data. OL, GB, MU, and BR identified and interpreted the ziphiid 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.

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