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SHORT COMMUNICATION

Juvenile morphology: A clue to the origins of the most mysterious of mysticetes?

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Abstract The origin of the pygmy right whale (*Caperea marginata*) has long been one of the most vexing conundrums of marine mammal evolution. The extremely disparate skeletal structure of *Caperea* and a patchy fossil record have left morphology and molecules at odds: whereas most morphological analyses ally *Caperea* with right whales (Balaenidae), most molecular studies instead suggest a close relationship with rorquals (Balaenopteridae) and grey whales (Eschrichtiidae). The morphological evidence supporting a *Caperea*-balaenid clade consists of several shared features of the skull and mandible, as traditionally observed in adult individuals. Here, we show that at least two of these features, the ascending process of the maxilla and the coronoid process, arise from substantially different precursors early during ontogeny and therefore likely do not represent genuine synapomorphies. Both of these juvenile morphologies have adult counterparts in the fossil record, thus indicating that the ontogenetic variation in the living species may be a genuine reflection of differing ancestral states. This new evidence contradicts previous morphological hypotheses on the origins of *Caperea* and may help to reconcile morphological and molecular evidence.

Keywords Cetacea · Mysticeti · Baleen whale · *Caperea* · Pygmy right whale · Evolution

Introduction

The pygmy right whale *Caperea marginata*, the only member of the subfamily Neobalaeninae (sensu Fordyce and Marx 2012), is the most disparate and least known of the living baleen whales (Mysticeti) (Kemper 2009). Its singular morphology poses a distinct obstacle to meaningful comparisons with other taxa and has so far largely thwarted attempts to put the species into a broader taxonomic and evolutionary context. This issue is further compounded by the virtual absence of any fossil record (Graf et al. 2011; Bisconti 2012; Fitzgerald 2012), despite apparently ancient origins of the lineage as early as 20–25 million years ago (McGowen et al. 2009; Steeman et al. 2009). Cladistic analyses of morphological data have generally allied *Caperea* with balaenids (Ekdale et al. 2011; Bisconti 2012; Churchill et al. 2012; but see Marx 2011 and Fordyce and Marx 2012). By contrast, molecular and combined evidence analyses mostly support a close relationship with balaenopterids and eschrichtiids (Deméré et al. 2008; McGowen et al. 2009; Steeman et al. 2009; Geisler et al. 2011). Adults of *Caperea* and balaenids resemble each other in several morphological features, such as an arched rostrum, an anteriorly projected supraoccipital, and the reduction or virtual absence of both the ascending process of the maxilla and the coronoid process of the mandible (Fig. 1). Here, we show that at least two of these features, the virtual absence of the ascending process of the maxilla and the coronoid process, arise from substantially different structures present in neonates and juveniles of *Eubalaena* and *Caperea*. We furthermore show that

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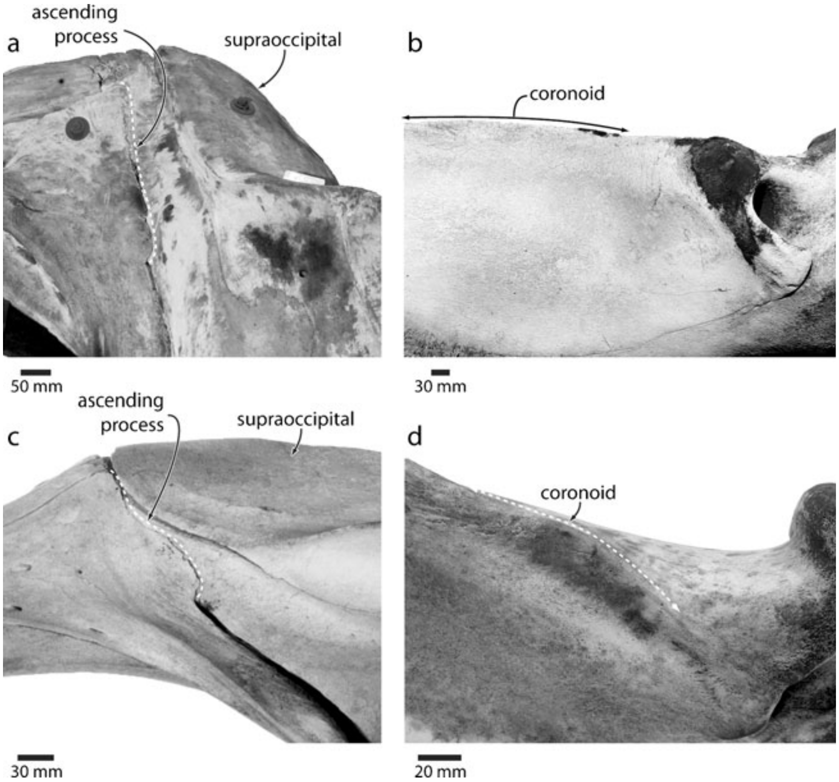


Fig. 1 Comparison of the ascending process of the maxilla (**a**, **c**) and the coronoid process (**b**, **d**) of adult individuals of *E. australis* (**a** USNM 267612, **b** CNPMAMM 741) and *C. marginata* (**c** OM VT227, **d** NMNZ MM002235). **a**, **c** In lateral view; **b**, **d** in medial view

both of these juvenile morphologies have adult counterparts in the fossil record, corroborating that the ontogenetic variation in the living species genuinely reflects ancestral states. Together, these observations suggest that at least some of the shared features potentially uniting *Caperea* and balaenids into a clade represent superficial convergences, as opposed to true synapomorphies, thus potentially helping to reconcile morphological and molecular evidence.

Material and methods

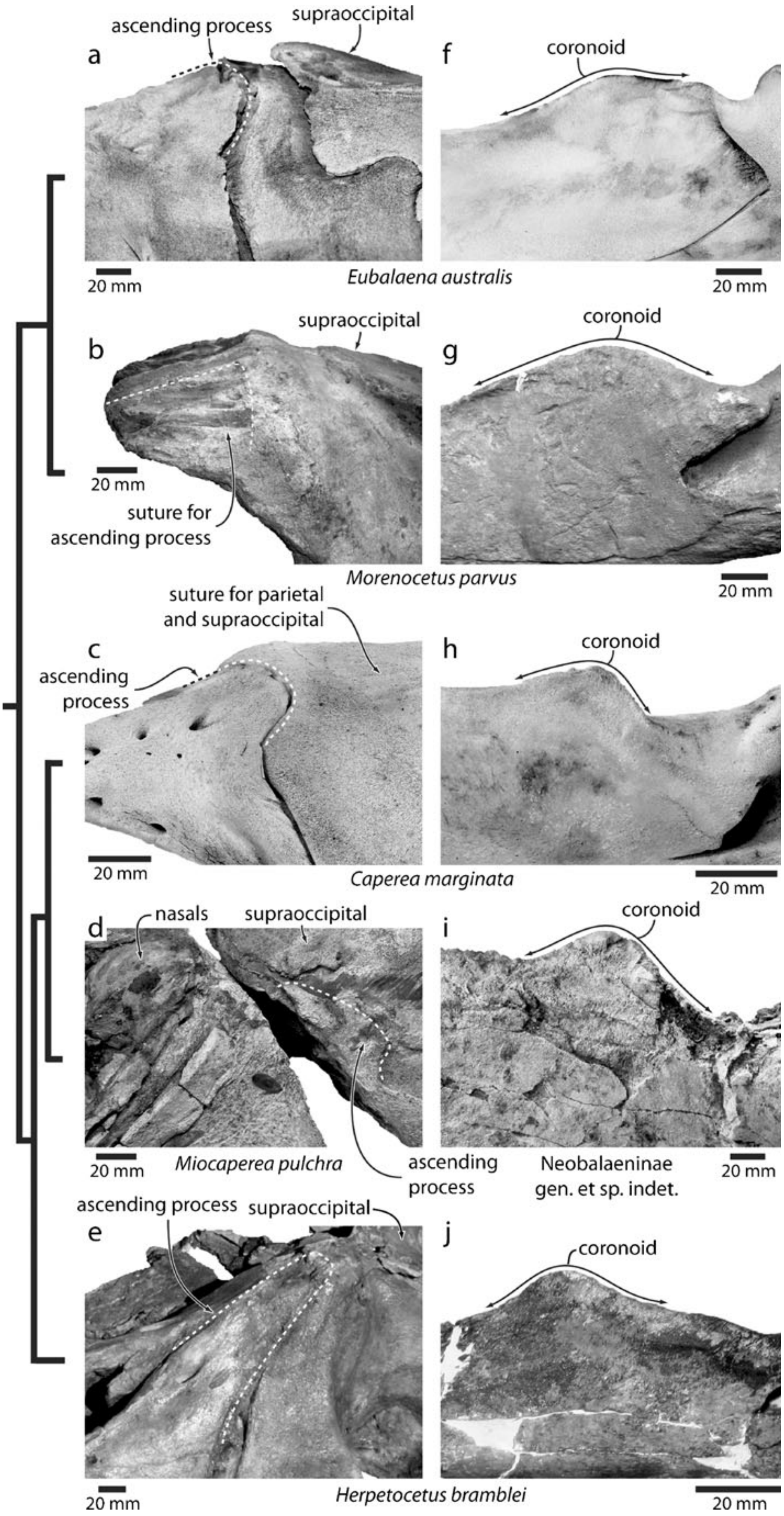
Our main observations are based on neonate and juvenile specimens of *Eubalaena australis* housed at the Laboratorio de Mamíferos Marinos, Centro Nacional Patagónico, Puerto Madryn, Argentina (CNPMAMM) (neonates, specimens 746 and 748; juvenile, specimen 747) and a neonate *Eubalaena glacialis* housed at the Natural History Museum of Los Angeles County, Los Angeles, USA (LACM 54763), as well as corresponding specimens of *C. marginata* held at the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ) (neonates, MM002262 and MM002898; juveniles, MM002254 and TMP011345). A juvenile specimen of *Balaena mysticetus* was not available to the authors. CNPMAMM 748 was dissected by MRB, and NMNZ TMP011345, by REF, FGM, MRB, and colleagues. A complete list of material examined for this study is provided in the Supplementary Material. Additional institutional abbreviations are as follows: Museo de Ciencias Naturales de La Plata (MLP), Buenos Aires, Argentina; Museo Paleontológico "Egidio Feruglio" (MPEF), Trelew, Argentina; Otago Museum (OM), Dunedin, New Zealand; Staatliches Museum für Naturkunde, Stuttgart (SMNS), Germany; University of California Museum of Paleontology (UCMP), Berkeley, USA; and United States National Museum of Natural History (USNM), Washington DC, USA.

Results

The ascending process of the maxilla of neonates of both *E. australis* (CNPMAMM 746 and 748) and *E. glacialis* (LACM

Fig. 2 Comparison of the ascending process of the maxilla (**a**–**e**) and the coronoid process of the mandible (**f**–**j**) of *E. australis* (**a** CNPMAMM 746, **f** CNPMAMM 748; both neonates), *M. parvus* (**b** MLP 5–11, **g** MLP 5–21), *C. marginata* (**c** NMNZ MM002898, **h** NMNZ MM002262; both neonates), *M. pulchra* (**d** SMNS 46978), Neobalaeninae gen. et sp. indet. (**i** MPEF PV2572), and *H. bramblei* (**e** UCMP 219111, **j** UCMP 219112). **a**–**c** In lateral view; **d**, **e** in oblique dorsolateral view; **f**–**j** in medial view

▶


ascending process
supraoccipital
a
f
coronoid
20 mm
Eubalaena australis
20 mm
supraoccipital
b
coronoid
g
20 mm
suture for
ascending process
Morenocetus parvus
20 mm
suture for parietal
and supraoccipital
c
ascending
process
h
coronoid
20 mm
Caperea marginata
20 mm
d
nasals
supraoccipital
i
coronoid
20 mm
Miocaperea pulchra
ascending
process
Neobalaeninae
gen. et sp. indet.
20 mm
ascending process
supraoccipital
e
j
coronoid
20 mm
Herpetocetus bramblei
20 mm

54763) is bluntly triangular, short anteroposteriorly, and nearly confluent with the posterior margin of the maxilla (Fig. 2a). A similar morphology can be inferred for the archaic extinct balaenid *Morenocetus parvus*, known from a subadult specimen (MLP 5–11) from the Early Miocene (ca. 20 Ma) of Argentina (Cabrera 1926). Although the maxilla is missing in the latter, a well-developed sutural contact surface on the frontal indicates a similar, blunt shape for the ascending process (Fig. 2b). In contrast to *Eubalaena* spp., the ascending process of neonate *Caperea* (NMNZ MM002262 and MM002898) is parallel sided (as opposed to triangular), quite distinct, and clearly offset from the posterolateral portion of the maxilla by a distinct 90° angle (Fig. 2c) (see also Fordyce and Marx 2012, Fig. S1). In juveniles (NMNZ MM002254), the ascending process widens transversely and shortens anteroposteriorly, becoming less distinct, but the rectangular outline and the angle offsetting the process from the rest of the maxilla remain clearly marked. The same holds true for the fossil neobalaenine *Miocaperea pulchra* (SMNS 46978), which is intermediate between neonate and adult *Caperea* in having an anteroposteriorly short, but relatively well-developed and rectangular ascending process (Fig. 2d). In neonates of *Eubalaena* spp., *Morenocetus*, and neonates of *Caperea*, the ascending process is well separated from the anterior border of the supraoccipital (Fig. 2a–c), which makes it unlikely that the shape of the former is dictated by the position of the latter. This differs from the situation in the adults of both *Eubalaena* (*E. australis*, MLP 1508; USNM 267612; *E. glacialis*, USNM A23077) and *Caperea* spp. (NMNZ MM002900; OM VT227), in which the anterior telescoping of the supraoccipital results in the anteroposterior compression of the vertex, and thus the anteroposterior shortening and virtual disappearance of the ascending process. The same likely holds true for *M. pulchra*.

The coronoid process of neonates and juveniles of both *E. australis* (CNPMAMM 747 and 748) and *E. glacialis* (LACM 54763) is anteroposteriorly long, dorsoventrally low, and plate-like; the lateral outline of the coronoid is broadly triangular, but poorly defined, with the anterior border of the process being confluent with the dorsal margin of the horizontal ramus (Fig. 2f). The same morphology occurs in slightly better developed form in *Morenocetus* (MLP 5–21), with the relatively greater height of the coronoid in this taxon accentuating its plate-like nature (Fig. 2g). In neonates and juveniles of *Caperea* (NMNZ MM002262, MM002898, and TMP011345), the coronoid process is developed as a low, but well-defined triangular structure, clearly offset from the dorsal margin of the mandibular body (Fig. 2h) (see also Fordyce and Marx 2012, Fig. S14). An almost identically shaped coronoid is preserved in a large, isolated fossil mandible from the Late Miocene (ca. 10 Ma) of Argentina (MPEF PV2572), likely referable to Neobalaeninae (Fig. 2i) (Buono et al. 2012).

Discussion

Juvenile individuals of both *Caperea* and *Eubalaena* spp. clearly diverge in the morphology of the ascending process of the maxilla and coronoid process. It is possible that these differences might reflect varying developmental rates, rather than fundamentally different morphologies. Thus, for example, heterochrony might have caused the development of the ascending process in *Eubalaena* to be delayed relative to *Caperea*, even though the ancestral morphologies of these two taxa may well have resembled each other. However, the occurrence in the fossil record of closely related taxa with adult morphologies virtually identical to or, in the case of *M. pulchra*, at least resembling those of *Caperea* and *Eubalaena* juveniles, implies that the latter preserve genuinely different ancestral features. The near absence of the ascending process and coronoid in the modern taxa thus fails the test of primary homology (de Pinna 1991; Rieppel and Kearney 2002), and at least some of the resemblance of adults of both species should thus likely be interpreted as a result of convergent evolution, which may have biased morphological analyses towards recovering a monophyletic *Caperea-balaenid clade.*

Given the potential problems associated with the use of ontogenetic evidence in a phylogenetic framework, the question arises whether and how these features can be reliably compared and coded in cladistic analyses. The marked ontogenetic variation of the ascending process and the coronoid in balaenids and neobalaenines contrasts with the situation in other living mysticetes, such as *Balaenoptera acutorostrata*, in which the adult morphology of these structures is already fully developed in neonates (Supplementary Material). Most fossil species are currently known from too few specimens to determine which pattern—ontogenetic variability vs. relative stasis—is more common among baleen whales. However, a well-developed coronoid process is present in most fossil mysticetes, many of which also possess ascending processes broadly resembling either that of neonate *Caperea* (e.g., *Archaebalaenoptera castriarquati*, *Balaenoptera siberi*, *Herpetocetus bramblei*, and *Piscobalaena nana*) or neonate *Eubalaena* (e.g., *Diorocetus hiatus*, *Isanacetus laticephalus*, and *Parietobalaena palmeri*). This suggests that the reduction and, hence, the marked ontogenetic variation of these structures in *Caperea* and modern balaenids may be the exception, rather than the norm. If so, comparisons of the juvenile morphologies of balaenids and *Caperea* with adults of other living and fossil mysticetes within a phylogenetic framework should be relatively unproblematic.

It is interesting to note that an anteroposteriorly long, plate-like coronoid process as seen in balaenids is also present in archaeocetes, such as *Zygorhiza kochii*, and many of the most archaic families of mysticetes, such as mammalodontids (e.g., *Mammalodon colliveri*) and eomysticetids (e.g., *Eomysticetus whitmorei*), although it needs to be stressed that the coronoid of balaenids clearly differs from that of all of these taxa in its low dorsoventral height and lateral outline. By contrast, a well-defined triangular process as seen in juvenile *Caperea* and MPEF PV2572 is characteristic of balaenopterids (e.g., *Balaenoptera* spp.), cetotheres (e.g., *P. nana*), and several Oligocene and Miocene taxa of uncertain affinity (e.g., *D. hiatus*, *Mauicetus parki*, and *P. palmeri*), with cetotheriids such as *H. bramblei* in particular being characterized by a relatively low and bluntly triangular coronoid process (Fig. 2j; see also Boessenecker 2011, Figs. 12–18). Equally, a short and bluntly triangular ascending process of the maxilla as seen in balaenids also occurs in many extinct Miocene taxa (e.g., *Diorocetus* and *Parietobalaena*), whereas the parallel-sided ascending process characteristic of neobalaenines more closely resembles that of cetotheres (e.g., *H. bramblei*, Fig. 2e) and balaenopterids (e.g., *Archaebalaenoptera* and *Balaenoptera* spp.). Together, these observations and interpretations support the hypothesis that neobalaenines might be more closely related to balaenopterids and cetotheres than to balaenids (e.g., Fordyce and Marx 2012), thus reconciling molecular and morphological evidence.

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