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ABSTRACT

“Double-headed” ribs, which are known to occur in modern baleen whales, are reported from a middle Miocene cetothere. These “double-headed” ribs are actually the result of the fusion of an extra rib with the normal first rib. A comparison of the posterior cervical and anterior thoracic vertebrae indicates that this whale has only six cervical vertebrae. The extra pair of ribs is a result of the development of the seventh vertebra as a thoracic rather than a cervical. This type of development is consistent with genetic controls on segmented development observed in arthropods, and with the lowered constraints on skeletal development in mysticetes.

INTRODUCTION

So-called “double-headed” ribs have been noted in various mammalian species for over a century (Turner, 1871). They are particularly prominent in whales, occurring frequently in the living Sei whale (*Balaenoptera borealis*) (Tomilin, 1957) (Fig. 1), but are also found in other cetacean species, as well as in humans (Turner, 1871).

This structure, when present, usually occurs only on the first rib, and usually on both sides of the animal. Close examination of these specimens reveals that the extra head belongs to a separate rib, associated with the seventh cervical vertebrae. This rib typically fuses distally with the first thoracic rib, creating the appearance of a double-headed rib. While well documented in living cetaceans, cervical ribs have not previously been described in fossil specimens.

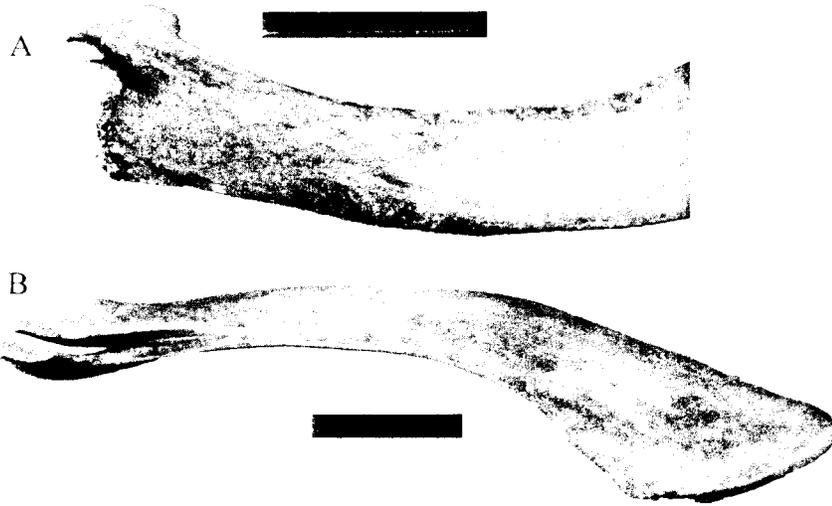


Figure 1. First right rib of *Balaenoptera borealis*, unnumbered specimen. A. Lateral view showing fused area. B. Internal view. Scales=10 cm.

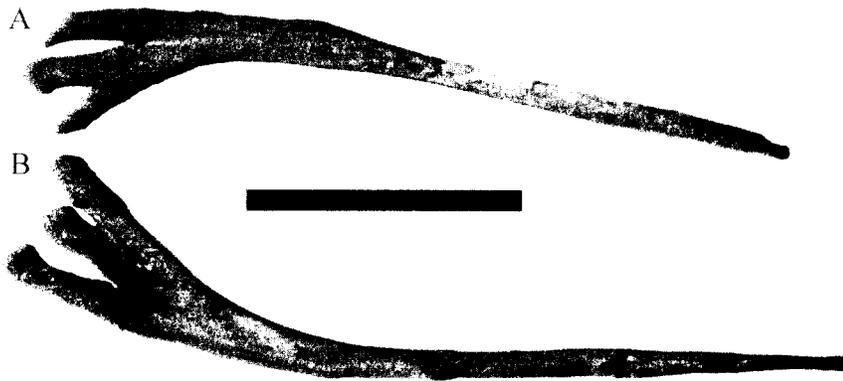


Figure 2. VMNH 1782, first ribs, anterior view. A. left. B. right. Scale=10 cm.

MATERIAL AND AGE

Within the collections of the Virginia Museum of Natural History is a skeleton of a primitive baleen whale (VMNH 1782). The specimen consists of a partial skull, right mandible, and the first 28 vertebrae, with portions of at least 18 ribs, including 11 from the right side. The skeleton was found in the bank of Mill Pond Creek, near Gravitt's Millpond, in Hanover Co., Virginia, from the Calvert Formation, Calvert Beach Member, Bed 14, giving an approximate age of 14 Mya (Ward, 1992). The specimen was collected by Al Myrick and L. W. Ward for the National Museum of Natural History in 1969. It remained stored until 1990, when it was transferred to VMNH and prepared for exhibit.

VMNH 1782 is most likely referable to the same taxon as two specimens stored at the United States National Museum (USNM 21308, USNM 18389), which are labeled *Mesocetus* sp. The genus *Mesocetus* is currently assigned to the mysticete family Cetotheriidae, a polyphyletic group of baleen whales that are common in the middle Miocene and are morphologically more primitive than any living mysticete taxon. Among the typical cetothere-grade characters observed in VMNH 1782 are relatively long cervical vertebrae, prominent rib-vertebrae articulations even on the posterior ribs, and the retention of two articulations on the anterior ribs. *Mesocetus* is a European genus, and the establishment of this genus in North America was based on limited material, so the assignment of any North American specimen to *Mesocetus* is questionable.

During preparation of the skeleton in 1990, the unusual structure of the first rib on each side became apparent (Figure 2). These ribs, instead of having the two articulations found on the second rib, appeared to have an additional capitulum. Upon further preparation, it became apparent that the extra capitulum and shaft represented a small rib fused to the anterior margin of the first thoracic rib (Figure 3).

DISCUSSION

The presence of an additional rib articulation is of no taxonomic significance. However, in older literature new varieties, species, or even genera (for example, *Sibbaldius* Gray) were occasionally proposed based on

this feature alone (Turner, 1871; Tomilin, 1957). The feature appears to occur at random in cetacean populations, with no obvious relationship to ancestry or geography. As mentioned above, it is especially common in the Sei whale, *Balaenoptera borealis*.

The presence of an additional rib has several possible explanations. First, the rib could be a late ontogenetic ossification of cartilaginous structures. Cetaceans show a great deal of ontogenetic variation in the ossification of some structures, most notably the mesethmoid cartilage. However, Turner (1871) documented extra ribs in fetuses of various whale species, indicating that ontogenetic variation is not a factor in this case.

Second, it is possible that the rib could be a holdover from the reptilian ancestors of all mammals, which possessed cervical ribs. This postulates a gene that codes specifically for cervical ribs, that has been repressed without being altered significantly since the Jurassic, some 180 million years. Such a gene would be remarkably stable to survive for so long without being expressed.

A third, developmental explanation seems more probable. It appears that vertebrates may develop in a sequential series analogous to that seen in arthropods. In arthropods, the activation of genes at the appropriate place and time determines the type of segment which will develop in the growing larva (e.g. Lewis, 1978). (For a summary of this type of phenomenon, see Gould, 1983.)

In this scenario, all vertebrae grow under the control of a single gene or group of genes. The activation of a second gene at a particular time changes the growth of the affected vertebrae from a cervical to a thoracic, along with their associated ribs. This implies that the additional rib that occasionally appears is not, in fact, a cervical rib. The animal has actually only developed six cervical vertebrae, with the seventh forming instead as the first thoracic.

Examination of the vertebrae of VMNH 1782 supports this explanation. The seventh vertebra is quite different in appearance from the sixth cervical vertebra, but is instead very similar to the eighth vertebrae, particularly in the shape of the centrum in dorsal view, and in the shape of the transverse process, especially distally (Figures 4 and 5). Although no other skeletons of *Mesocetus?* are available for study, in other Miocene cetaceans the seventh cervical vertebra tends to be unique, and does not strongly resemble the sixth cervical or the first thoracic.

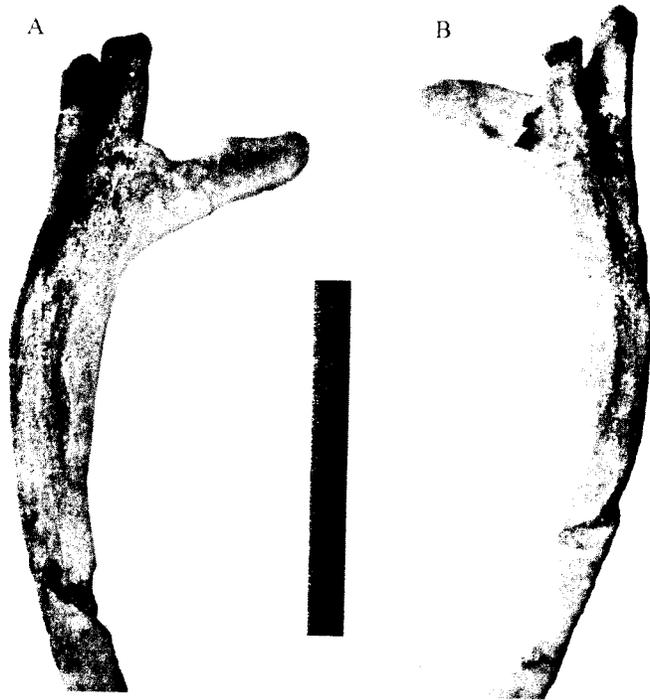


Figure 3. VMNH 1782, first ribs, anterior view. A. right. B. left. Note the fusion of the small anterior rib on each side. Scale=10 cm.

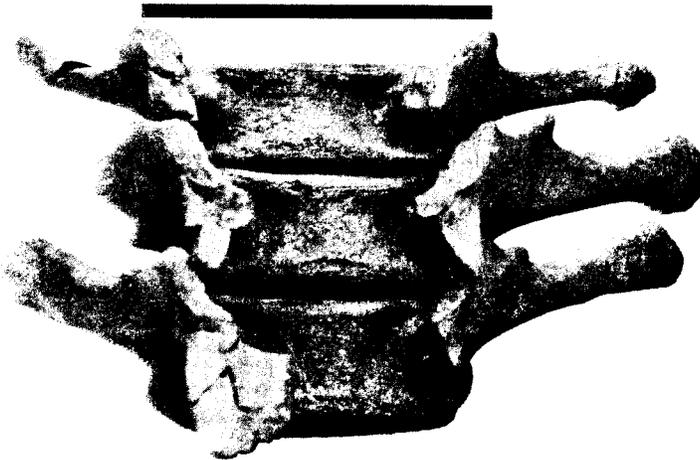


Figure 4. VMNH 1782, sixth, seventh, and eighth vertebrae, dorsal view, anterior at top. Scale=10 cm.

It is possible that this mechanism could influence other unusual structures in cetaceans. Modern mysticetes will occasionally possess the remnants of external hind limbs, complete with bones and non-functional musculature. This could be due to the development of sacral vertebrae which are normally absent in cetaceans. In this case, however, development is somewhat different, since it has been observed that whales very commonly develop a remnant pelvis without any hindlimb development or vertebral modification. This would suggest a separate genetic origin for the vertebrae and the hindlimbs.

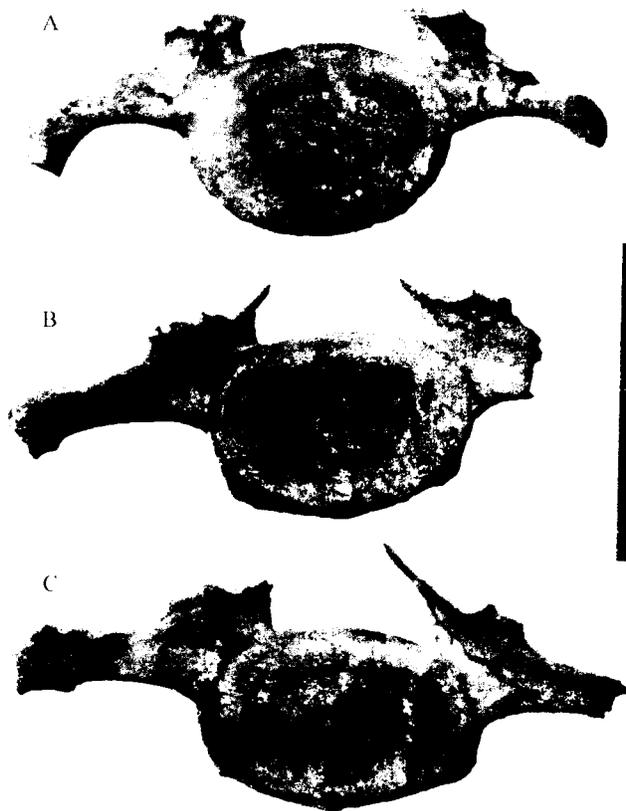


Figure 5. VMNH 1782, sixth, seventh, and eighth vertebrae, anterior view. A. sixth vertebra, B. seventh vertebra, C. eighth vertebra. Note the similarity of the seventh and eighth vertebrae when compared to the sixth. Scale=10 cm.

“Double-headed” ribs seem to occur in mysticetes more commonly than in any other group. This may reflect the relatively low structural importance of the postcranial skeleton in mysticetes. Many aspects of the mysticete skeleton are greatly reduced or are highly variable. For example, the mandibular articulation is almost absent, and there is no mandibular symphysis, the mandibles being held together by ligaments only. The cervical vertebrae are dramatically shortened, and the ribs are reduced. In extant species, the anterior ribs usually have only a single articulation, while the posterior ribs do not articulate with the vertebrae at all. The sternum is greatly reduced, and highly variable in shape between individuals of the same species. The rib count is often different between the left and right sides of the same animal, and within a species the vertebral count can vary by as many as five vertebrae. Moreover, such vertebral variation is known to occur in the thoracic, lumbar, and caudal regions, so it is perhaps not surprising that it should occur within the cervical series too. It seems that the reduction and decreased importance of the skeleton in mysticetes has led to a relaxation of developmental constraints, allowing developmental variation to flourish which would be detrimental in typical terrestrial species.

This type of development may provide an explanation for other cervical anomalies observed in some mammalian species. As mentioned above, odontocete whales and humans both occasionally show the same six-cervical pattern observed in mysticetes. The modern sloth genera *Bradypus* and *Choleopus* both show anomalous cervical patterns. *Bradypus* has eight or nine cervicals, while *Choleopus* has five to eight (Carroll, 1988). The modern manatee, *Trichechus*, has only six cervicals (Romer, 1966). Like cetaceans, manatees have forelimbs modified into flippers, functionally very different from a typical quadrupedal mammal. The three terrestrial mammals mentioned (*Homo*, *Bradypus*, and *Choleopus*) also have highly modified shoulders and forelimbs relative to their quadrupedal ancestors. Perhaps in quadrupedal mammals the position of the first rib is tightly constrained, whereas the modifications to the forelimbs in humans and tree sloths relax these constraints and render the exact position of the first rib insignificant, within certain limits.

Other parts of the mammalian vertebral column show large variations in vertebral count. It is likely that the variation seen in the cervical series of these genera, and in fact all of the variation in vertebral counts observed in

mammals, is a result of the same developmental factors that are observed in cetaceans.

ACKNOWLEDGMENTS

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