COMPARISON OF EARLY DEVELOPMENT OF STERNUM AND CLAVICLE IN STRIPED DOLPHIN AND IN HUMPBACK WHALE

MILAN KLIMA

Institute of Anatomy, J. W. Goethe University, Frankfurt a.M., Germany

ABSTRACT

The morphogenesis of the sternum and the clavicle in whales was studied for the first time. The mode of development of these structures shows considerable differences between the toothed whales (Odontoceti) and the whalebone whales (Mysticeti). The toothed whales are, in this case, similar to all other mammals. Their sternum originates from three different embryonal elements. During development of the embryo a rudimentary clavicle is to be found in the shouldergirdle. The whalebone whales, on the other hand, differ from this mode of development. Their sternum originates from only two embryonal elements and there is no clavicle at all. The third sternum element cannot even be found as a rudimentary element, which is unique among mammals. The significance of these findings are discussed.

INTRODUCTION

The development of the sternum and shouldergirdle in man as well as in terrestrial mammals has been dealt with in quite a few papers (Ruge, 1880 ; Eggeling, 1904, 1906 ; Müller, 1906 ; Gladstone and Wakeley, 1932 ; Reiter, 1942 ; Chen, 1952, 1953 and others). According to the latest findings in this area (Klima, 1968, 1973, 1975) the sternum originates, during embryogenesis, from three different elements : 1. an unpaired ventrocranial element of the interclavicle, 2. a paired lateral element of the coracoid plates and 3. a paired lateral element of the sternal bands. These three elements always participate in the morphogenesis of the shouldergirdle and sternum in Monotremata as well as in Marsupialia and Placentalia. Apart from this these elements may behave rather different during the further course of ontogeny. They may be included in the interclavicle, the coracoid bones or the sternum. The sternum may be divided into the manubrium and sternebrae or not. In addition to this the breast-shoulder-apparatus may be large or small. But these three elements mentioned here represent a constant factor that is obviously determined genetically and has been found in the ontogeny of every mammal studied so far.

At present we know nothing about the morphogenesis of the sternum in whales. Although a few cetacean embryos have been studied (Eschricht 1849, Turner 1870, Kükenthal 1914, Schulte 1916, Slijper 1936), all of them, however, were too large to find out anything about the mode of the development of the sternum. Even the smallest of them, an embryo of *Balaena mysticetus* of about 10 cm length, studied by Eschricht and Reinhardt (1849), and an embryo of *Balaenoptera acutorostrata* of 10.5 cm studied by De Burlet (1917), had finished the morphogenesis of the sternum, that already had the typical form and location as is seen in adult animals. Besides, it would be of special significance to know the mode of development of the greatly reduced and transformed sternum of whalebone whales, whether it coincides with the pattern of all mammals, or whether it deviates from this scheme. In fact accurate examinations of the ossification process of the sternum in the whales are lacking so far. Some observations concerning this problem are being published at the moment (Krauss-Hoeft, 1978).

I had the opportunity to study two very favourable morphogenetic stages, one was a representative of the toothed whales (*Stenella coeruleoalba*), the other a representative of the whalebone whales (*Megaptera novaeangliae*). They allowed an exact observation of the mode of development of the sternum and of the clavicle in whales. The results can by all means be considered characteristic for both groups of whales, Odontoceti and Mysticeti, as the sternum of each group develops according to an uniform scheme. Considerable differences within the two suborders are not to be expected.

MATERIAL AND METHODS

The material of embryos examined belongs to the collections of the Department of Anatomy, Faculty of Medicine, University of Tokyo, Hongo, Tokyo. I was able to evaluate two important developmental stages out of several serial sections of the striped dolphin (*Stenella coeruleoalba*). More information about this material can be found in the paper by Kamiya and Pirlot (1974). From the serial sections of the humpback whale (*Megaptera novaeangliae*) two stages were also suitable for the purpose of my research. The material used is summarized in the following table:

	Body length:	Plane of section:
Stenella coeruleoalba	17 mm	longitudinal
Stenella coeruleoalba	35 mm	longitudinal
Megaptera novaeangliae	21 mm	transversal
Megaptera novaeangliae	37 mm	transversal

All of the embryos were made into celloidin slides in the customary histologic fashion, the sections being between 20 and 25 μ were stained with hematoxilin-eosin. I have made a graphic reconstruction of both a *Stenella* and a *Megaptera* embryo (Figs 2 and 7).

The osteological material of adult animals includes sterna of *Stenella coeruleoalba*, several further representatives of the family Delphinidae, and next to *Megaptera novaeangliae* further representatives of the family Balaenopteridae. This material came from the following collections: Institut voor Taxonomische Zoölogie, Amsterdam; Universitetets Zoologiske Museum, Kobenhavn; Rijksmuseum van Natuurlijke Historie, Leiden; British Museum (Natural History), London;

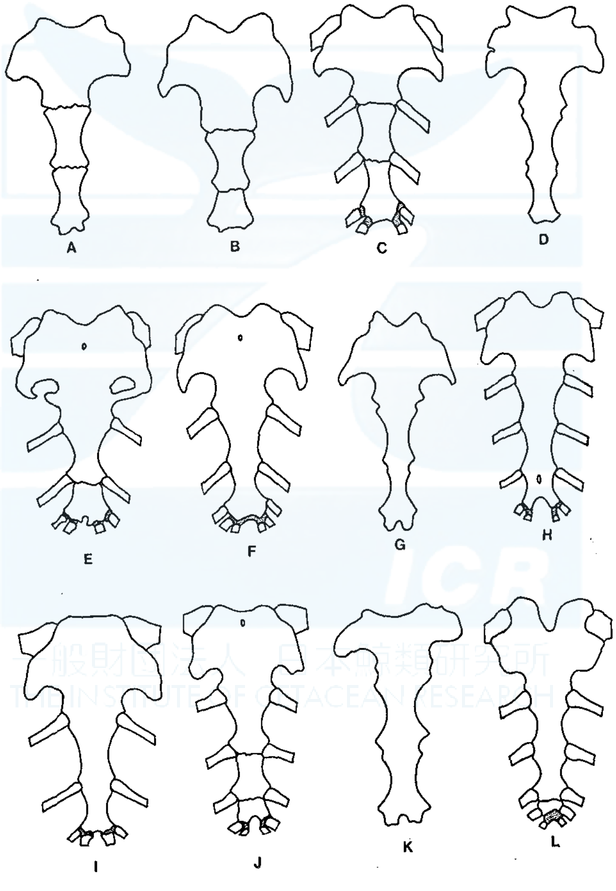
National Science Museum (Natural History Institute), Tokyo; Ocean Research Institute, University of Tokyo, Tokyo; The Whales Research Institute, Tokyo; Tokyo University of Fisheries, Tokyo; Museum National d'Histoire Naturelle, Paris.

A selection from this material is shown in the Figs 1 and 5 with a note of their origin. Two figures of the sternum of the blue whale (*Balaenoptera musculus*) were taken from the publications by White (1919) and Miller (1924).

RESULTS

Stenella coeruleoalba

The sternum of *Stenella* has the same basic shape as the sternum of all mem-



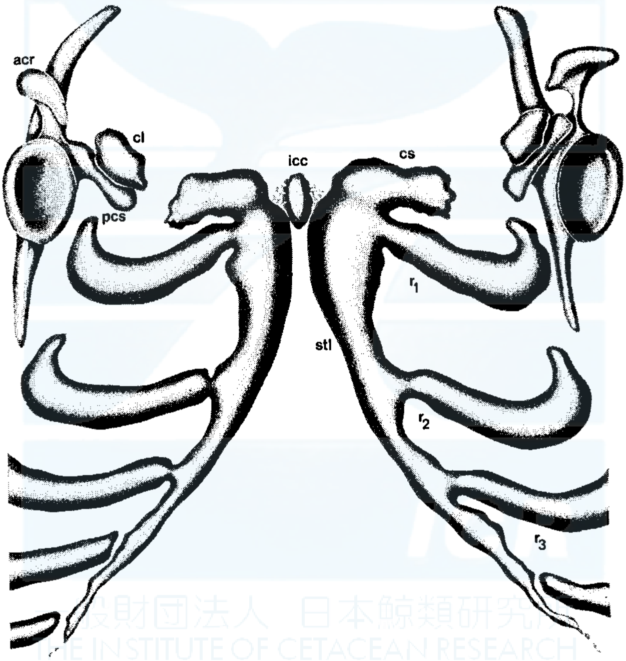
一般財団法人 日本鯨類研究所
THE INSTITUTE OF CETACEAN RESEARCH

Fig. 1. Ventral view of sternum in Odontoceti, Delphinidae: *Stenella coeruleoalba* (A, B), *Stenella attenuata* (C, D), *Stenella euphrosyne* (E), *Delphinus delphis* (F, G, H), *Grampus griseus* (I), *Tursiops truncatus* (J), *Lagenodelphis hosei* (K) and *Lagenorhynchus albirostris* (L). Collections: Inst. Taxonom. Zoöl., Amsterdam (C, E, F, H, J); Rijksmus. Nat. Hist., Leiden (B, I, L); British Mus. Nat. Hist., London (D, G); Ocean Res. Inst., Tokyo (A).

bers of the Delphinidae (Fig. 1). It is divided into a manubrium and two to three sternebrae.

The manubrium lies between the first and second pair of ribs. It is flattened dorsoventrally and rather broad laterally. It has a wide pointed projection on both sides towards the back. This projection can, in some cases, melt into a wide plate with the central part of the manubrium. Of the caudal margin of the plate there can be found closed window openings or half open notches (Fig. 1E). The wide cranial end of the manubrium is slightly dented in the middle. Near to the dent there may be one small hole. The thin caudal end has a slightly waved edge, that borders on the first sternebra.

The sternebrae are very flattened out dorsoventrally and their diaphysis is thinner than their epiphysis. The division into sternebrae is obviously only to be found in young animals. They develop out of bone cores, that are located between



財団法人 日本鯨類研究所
THE INSTITUTE OF CETACEAN RESEARCH

Fig. 2. *Stenella coeruleoalba*, embryo of 35 mm body length. Graphic reconstruction of the anlage of sternum and shouldergirdle in ventral view.

acr	Acromion
cl	Clavicle
cs	Paired lateral element of the coracoid plates (=Coracoidscapularplatte)
ht.........	Heart
icc	Unpaired ventrocranial element of the interclavicle (=Pars chondralis interclaviculae)
pcs	Processus coracoideus scapulae
$r_{1,2,3}$......	$\text{Ribs}_{1,2,3}$
stl.........	Paired lateral element of the sternal bands (=Sternalleiste)

successive rib connections (Krauss-Hoeft, 1978). Whith age they melt together, as the manubrium does, into a uniform and completely ossified sternum. The number of sternebrae varies between two and three ; in some exceptional cases there can even be four. This is coherent with the number of true ribs, that are incorporated into the sternum. Usually there are four to five, but there can be six or even seven pairs of true or vertebrosternal ribs. The connection of the last pairs of ribs to the sternum shows great inconsistency, probably the consequence of a regressive development, that one can see in the caudal region of the sternum in almost all mammals. In the Delphinidae, as, by the way, in all the Odontoceti, this regressive development has gone so far that the Processus xiphoideus has disappeared completely.

In contrast to most mammals there is no connection of the sternum with the shouldergirdle by means of the clavicle. The clavicle is completely reduced.

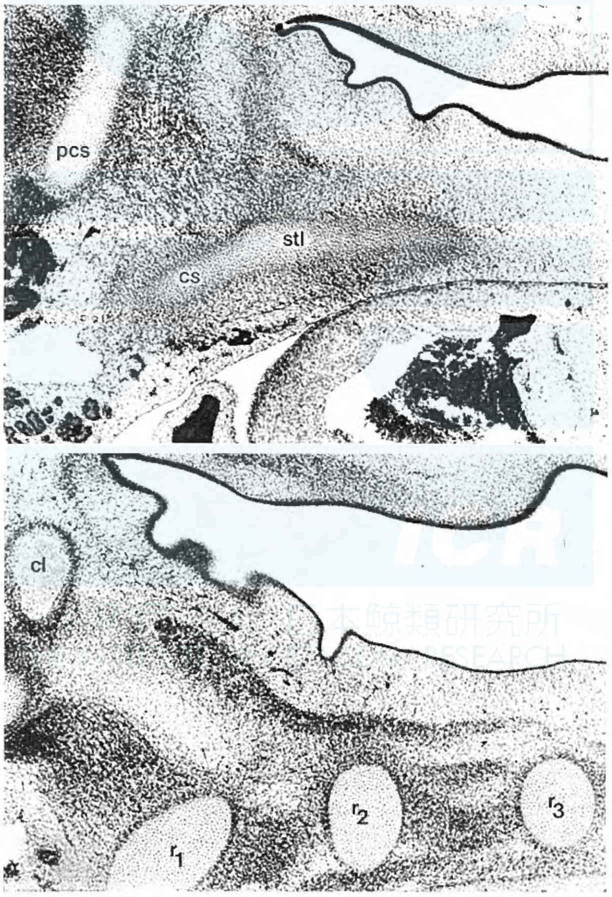


Fig. 3. *Stenella coeruleoalba*, embryo of 35 mm body length. Longitudinal section of the anlage of sternum (cs and stl) and clavicle (cl). For abbreviations see Fig. 2.

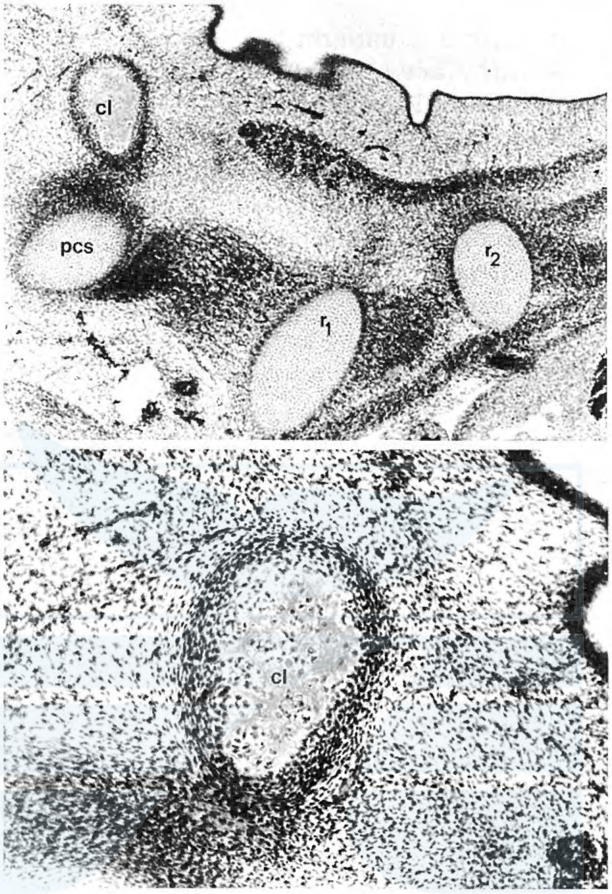


Fig. 4. *Stenella coeruleoalba*, embryo of 35 mm body length. Longitudinal section demonstrating the anlage of clavicle (cl). For abbreviations see Fig. 2.

The *Stenella* embryo of 17 mm has a thin strip of dense mesenchyme on each side of its body ventral of the rib ends. The dense mesenchyme extends from the first to the fourth pair of ribs. Both strips still lay far apart from each other, the cranial ends, however, come closer to the median line than the caudal ends. Details cannot be recognized. As far as the location is concerned these structures are unpaired lateral elements of sternal bands that can be seen in analogous stages of development in all other mammals.

In the *Stenella* embryo of 35 mm (Figs 2 and 3) the cranial ends of both of the sternal bands have moved closer to each other and are fusing in the median line. They extend from the first to the fifth pair of ribs. The cranial parts continue laterally each as an additional element. Both elements extend in the direction of the Processus coracoideus of the scapula but do not unite with it. They are paired craniolateral elements of coracoid plates such as one can see in the ontogeny of many other mammals. In the median line, in front and between the two sternal bands is located the third embryonal anlage, an unpaired ventrocranial element of interclavicle, or the so-called Pars chondralis interclaviculae of the Monotremata (Klima, 1973), an ancestral rudiment occurring in all mammals.

Between the sternum anlage and the Acromion scapulae there is on both sides an isolated desmal ossified element, that is equivalent to a rudimentary clavicle (Figs 2 and 4).

Megaptera novaeangliae

The sternum of the adult *Megaptera* is made of one piece. There is no division in manubrium and sternebrae in any phase of the ontogenesis. The sternum only comes in contact with the first pair of ribs; the other ones are floating ribs with free ends. These characteristics not only pertain to *Megaptera*, but to all members of the family Balaenopteridae and actually are peculiar to all Mysticeti.

The shape of the sternum of each species, however, is very different. It also varies a lot even within one species (Fig. 5). In *Megaptera* I have found sterna that one could call triangular, heart-shaped, trilobate or U-shaped. Each of these sterna, it makes no difference of which shape, pushes itself between the first pair of ribs with the thinner caudal end (Figs 5E, F, G). Thus the larger part of the sternum is located on the front margin of the ribs. This position is typical for the sterna of the Balaenopteridae. In many prepared skeletons, however, the sternum has subsequently been falsely placed in the middle between the first pair of ribs or even in back of it. Such an incorrect position of the sternum in *Megaptera* can be found for example in a paper by Rudolphi (1829, recently taken over by Arvy and Pilleri, 1977). Eschricht (1849) already pointed out many mistakes that have been made in this regard.

In *Megaptera* as in all other Mysticeti the scapula is the only part of the shouldergirdle that is left. It is located relatively far away from the sternum, much further dorsolaterally than in the Odontoceti. A clavicle is not present.

In the *Megaptera* embryo of 21 mm, that can be compared with the 17 mm *Stenella* stage, the ribs are still far apart in the body wall on both sides of the pericardium (Fig. 6). Near to the ventral ends of the first ribs there is an indistinct dense mesenchyme zone. It is relatively small and confined to the area of the first pair of ribs only. The significance of this mesenchyme zone is uncertain. It could correspond to the later visible paired craniolateral elements of coracoid plates. The paired lateral elements of sternal bands as well as the clavicle are not developed.

In the *Megaptera* embryo of 37 mm (Figs 7 and 8), that can be compared with 35 mm *Stenella* stage, the ribs have already pushed themselves far ventrally. With them, they have taken the mesenchyme zones towards the median plane. These take up the space between and in front of the first pair of ribs, histologically already consisting of young cartilaginous tissue. They begin to fuse in the median plane. This tissue stays distinct from the rib anlage and spreads craniolaterally, analogous to the paired craniolateral elements of coracoid plates in *Stenella*. I think that these elements are identical, too. The paired lateral elements of sternal bands,

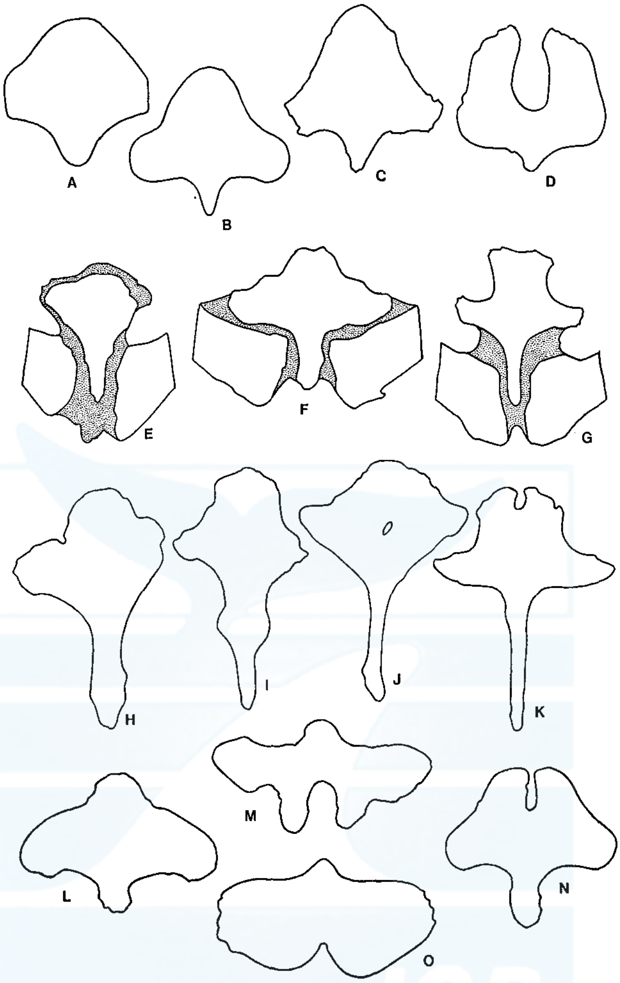


Fig. 5. Ventral view of sternum in Mysticeti, Balaenopteridae: *Megaptera novaeangliae* (A, B, C, D, F), *Balaenoptera acutorostrata* (E, G, H, I, J, K) and *Balaenoptera musculus* (L, M, N, O). Collections: Inst. Taxonom. Zoöl., Amsterdam (H, I); Univ. Zool. Mus., Kobenhavn (C, E, L); Rijksmus. Nat. Hist., Leiden (G); British Mus. Nat. Hist., London (A, B, O); Mus. National Hist. Nat., Paris (D); Nat. Sci. Mus., Tokyo (J); Whales Res. Inst., Tokyo (K); (M) after Waite, 1919; (N) after Miller, 1924.

out of which all other mammals as well as *Stenella* build up the largest part of the sternum, do not exist in *Megaptera*. On the other hand one can see between the cranial ends of the coracoid plates an unpaired ventrocranial element of interclavicle, histologically consisting of condensed mesenchyme, not very sharply delineated from the surrounding tissue.

In a similar case in the sternum of an embryo of *Balaenoptera acutorostrata* of

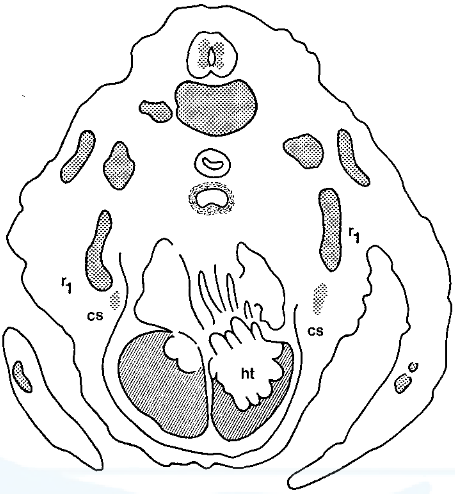


Fig. 6. *Megaptera novaeangliae*, embryo of 17 mm body length. Transversal section at the level of heart (ht). For abbreviations see Fig. 2.

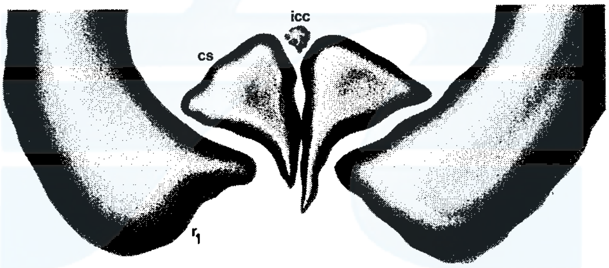


Fig. 7. *Megaptera novaeangliae*, embryo of 37 mm body length. Graphic reconstruction of the anlage of sternum in ventral view. For abbreviations see Fig. 2.

10.5 cm length, shown by De Burlet (1917), the elements mentioned had already fused. There still are to be distinguished one rounded central process between two rounded lateral processes. This central process develops, without doubt, from the unpaired element of the interclavicle. Should the element of the interclavicle not be present, the result would probably be an U-shaped sternum, as I was able to establish in the specimen of *Megaptera* out of the Paris collection (the later sternum was presented earlier in the following papers of Gervais, 1871 ; Lessertisseur and Saban, 1967 ; Arvy and Pilleri, 1977).

DISCUSSION

General considerations

Even the comparison of the sternum and shouldergirdle in adult animals

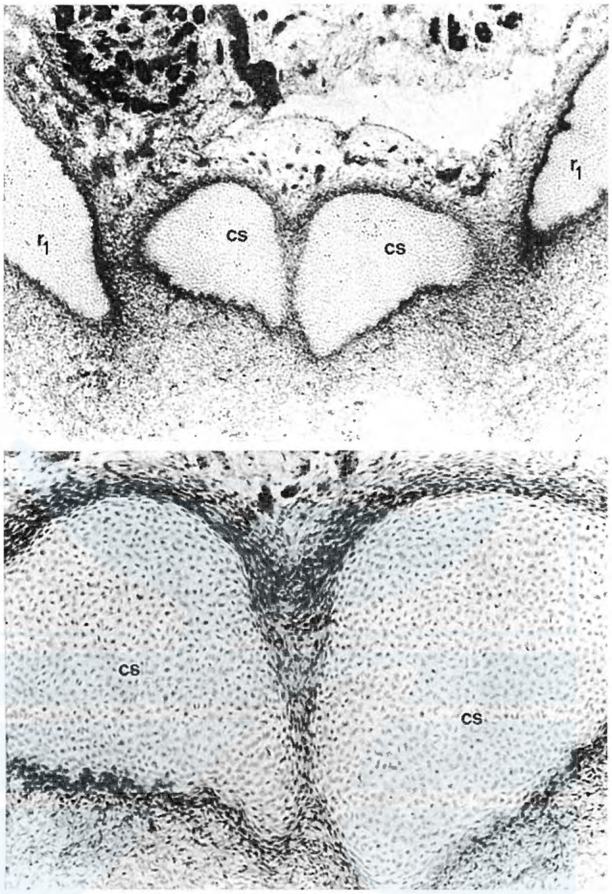


Fig. 8. *Megaptera novaeangliae*, embryo of 37 mm body length. Transversal section of the anlage of sternum (cs). For abbreviations see Fig. 2.

shows considerable differences between both suborders of Cetacea, the Odontoceti and the Mysticeti. These differences become even more apparent when the early development is examined. The morphogenesis of the sternal complex of the Odontoceti is similar to that of all other placental mammals, while the morphogenesis of the Mysticeti, on the other hand differs greatly from this pattern. Herein both groups obviously have been submitted to completely different evolutionary trends. The Mysticeti have reduced the sternal complex to a very great extent. In this regard the Mysticeti are a unique group within the mammalia.

The shape of the sternum

The sternum of adult Odontoceti shows many typical characteristics of sterna of terrestrial mammals. It is divided into a manubrium and several sternebrae that usually melt into a compact piece in old age. Normally the sternum is longer than wide and closes off the ventral portion of the chest. The number of true

THE INSTITUTE OF CETACEAN RESEARCH

ribs varies to a great extent. Most Odontoceti have four to five pairs of true ribs, some species have only three, but some are known to have seven or eight pairs of true ribs. These numbers usually vary within one and the same species. These circumstances also occur in most terrestrial mammals. In Odontoceti the caudal end of the sternum is a bit more reduced. The Processus xiphoideus is completely absent.

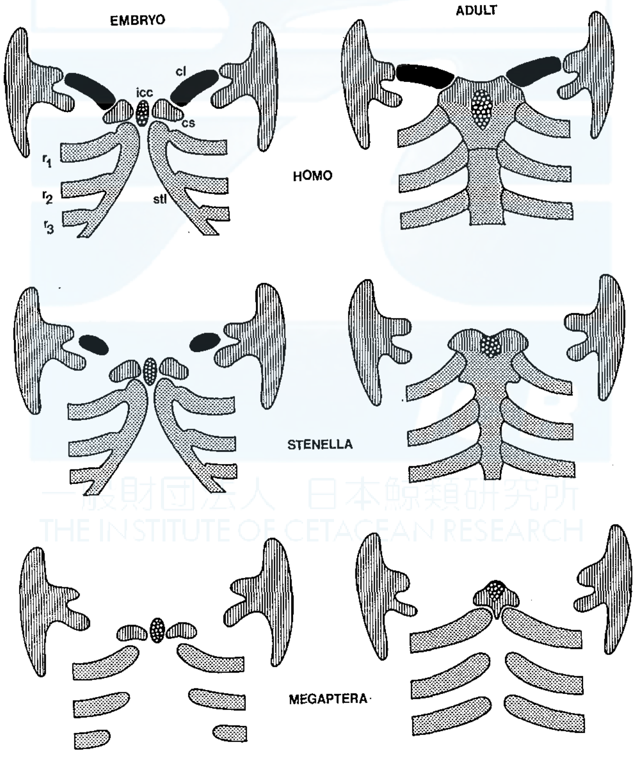
The sternum of adult Mysticeti consists of one single piece of bone that is located in front and between the first pair of ribs and has a relatively loose connective tissue link. All of the remaining ribs have completely loose ends on the ventral side of the thorax. A division of the sternum in manubrium und sternebrae is not to be seen. The sternum is usually wider than long and it is often triangular, heart-shaped, cross-shaped or U-shaped. Although the different species of Mysticeti show the same shape of the sternum, its morphological variability is so great that it can hardly be used as a criterion for the separation of species. This was recognized by Omura and published in numerous papers (Omura 1957, 1972, 1975). Contrary to some authors, who for instance thought that the sternum of *Balaenoptera* was of taxonomic importance, Omura (1957) writes: " . . . the sternum is to be regarded as a rudimentary organ and subject to individual variation largely, it is thought to have less taxonomic value ". This statement is, without doubt, valid for all Mysticeti.

The size of the sternum

There is not only a considerable difference in the shape but also in the size of the sternum of Odontoceti and Mysticeti. It stands to reason that not the absolute but rather the relative size of the sternum must be considered. Arvy and Pilleri (1977) are correct, when they write: " . . . the adjective ' small ' can hardly be applied to sternums of . . . 41×36 cm (*Eubalaena glacialis*) . . . 49×67.5 cm (*Balaenoptera acutorostrata*) or 47×60 cm (*Balaenoptera musculus*) ". But this " truth " is in no reasonable relation to the actual circumstances. In spite of its enormous size, the sternum of the Mysticeti is actually, when compared with the rest of the skeleton, the smallest that can be found in mammals. I have started some measurements on these grounds (the studies are not yet completed) and have been able to find the following relationships: the relative size of the sternum or the length of the sternum in percent (%) of the length of the whole skeleton is usually between 7 and 14% in most Odontoceti, the genera *Platanista* and *Inia* are closer to the lower percentage, whereas the genera *Berardius* and *Ziphius* are near to the higher percentage. For *Stenella* I found a percentage of 10.1. *Physeter* obviously differs from all the other Odontoceti; with a percentage of 4.8. It is closer to the relative size of the Mysticeti sternum that is between 1.4 and 3.5%. *Balaenoptera* is towards the lower percentage whereas *Eubalaena* is closer to 3.5%. For *Megaptera* I found 2.2% relative sternum length.

The early development of the sternum and the clavicle

The reduction of the sternal complex of the Mysticeti takes place in an early period of embryogenesis. In this case it does not manifest itself as a secondary differentiation of an existing structure. Rather we have to do with a reduction that goes as far as a complete absence of an embryonal element. As written in detail in the introduction, the sternum of terrestrial mammals originates from three different elements. This is also the case in the Odontoceti. On the other hand the Mysticeti do not even have an anlage of the paired sternal bands. The reduction of this element has obviously moved below the threshold of morphogenesis. It is astonishing that this is just the element that is most important for the development of the sternum of all other mammals, not only for the caudal half of the manubrium but also for all of the sternebrae or the whole corpus, respectively. It is also the largest element. Phylogenetically it is the youngest and most " modern " element that still plays a small role in the development of the sternal complex in Monotremata but increasingly determines the development of the sternum of Marsupialia and Placentalia. In these cases it substitutes the two older, ancestral or " primitive " elements, the interclavicle and the coracoid plates. It is remarkable that just these two ancestral elements mentioned above remain in the Mysticeti, as if they were established firmer and more " conservative " in



一般財団法人 日本鯨類研究所
THE INSTITUTE OF CETACEAN RESEARCH

Fig. 9. Comparison of the development of sternum and shouldergirdle in terrestrial mammals (*Homo*), in toothed whales (*Stenella*) and in whalebone whales (*Megaptera*). For abbreviations see Fig. 2.

the genetic code as the " modern " element of sternal bands. The sternum that develops from these elements is only a rudimentary structure without any greater functional significance. The further trend in the development of the Mysticeti is probably towards a complete reduction of the sternum. According to its location the sternum of recent Mysticeti corresponds to the anterior resp. cranial part of the manubrium, in the development of which take part laterally the elements of the coracoid plates, and medially the element of the interclavicle.

The members of the Odontoceti as well as of the Mysticeti do not have a clavicle as adult. This is also the case in some terrestrial mammals. However, they have a clavicle at least temporarily during the genesis of the embryo. A rudimentary clavicle is also obvious in the Odontoceti during the embryogenesis, as has been proved in this paper for *Stenella*. No rudimentary clavicle can be found in *Megaptera*, which, as I think, can be considered a rule for all Mysticeti. This total reduction is in complete correspondence with the extensive reduction of the sternum.

Monophyly or Polyphyly ?

The question of monophyly or polyphyly of the Cetacea is a theme that has often been discussed vehemently. Final evidence for one or the other hypothesis cannot be found at present.

The Cetacea have to be derived from terrestrial mammals. As common ancestors ancient insectivora come into account from which not only the Ungulata, but also the +Creodonta have evolved. Among the +Creodonta it were probably the +Mesonychidae from which the +Archaeoceti originated as the first ancestors of the whales that were adapted to aquatic life. This happened at the end of the Cretaceous period, in other words about 70 million years ago.

As to the hypothesis of a monophyletic derivation, the Odontoceti as well as the Mysticeti would originate from the +Archaeoceti. This hypothesis is supported by the development of the very specialized auditory ossicles, that is supposed to be almost identical in the three cetacean suborders (Van Valen, 1968) as well as the correspondence in the karyotype and the structure of the chromosomes in Odontoceti and Mysticeti (Arnason, 1969, 1974 and Kulu, 1972). The striking differences are, according to this hypothesis, secondary and brought about by different dietary specialization.

The supporters of diphyletic or polyphyletic derivation of Cetacea have the opinion that the living Odontoceti and Mysticeti do not stem from one and the same root, or that the +Archaeoceti represent a completely independent group, respectively. All correspondences in morphology would be, as far as this hypothesis is concerned, convergent functional adaptations to aquatic life (Slijper, 1962; Yablokov, 1964 and others). Summarizing accounts on the problem of monophyly and polyphyly of Cetacea recently can be found in Gaskin (1976) and Oelschläger (1978).

The results in this paper on the early development of the sternal complex can give us some ideas as to the question of monophyly and polyphyly of Cetacea.

一般財団法人 日本鯨類研究所
THE INSTITUTE OF CETACEAN RESEARCH

However, it cannot give any final answer. At first glance the great difference between Odontoceti and Mysticeti in the mode of development seems to point to polyphyly. How far these differences reach back into the phylogenetic past can hardly be determined. For such a determination one would need to know the possible speed of the regressive development of the single sternal elements. As we do not know this speed we have to compare the situation in Cetacea with analogous cases in other mammals. For instance different groups of mammals have completely lost their teeth. The best known example of a reduction of skeletal elements is that of the regressive development of the clavicle. The sternum is, however, neither to be compared with dentin structures nor with desmal bone. It originates from a chondral base and for this reason can only be compared with a chondral element of the skeleton. A genuine analogy for the reduction of the sternum in Cetacea is for instance the reduction of the finger bones in Ungulata, or the complete reduction of the hind limbs as well as of the pelvis of Odontoceti and Mysticeti. The reduction of the structures just mentioned took place in a comparable, if not shorter period of time than the 70 million years that were necessary to bring forth the recent Cetacea. It could be quite possible, that the reduction of the sternum of the Mysticeti also took place in this period of time. For this reason a monophyletic development of the Cetacea cannot be excluded.

Still there are several unsolved problems in this field. All structures mentioned above are not reduced completely. They appear, at least for a short span of time during embryogenesis, as relics of tissue. This is not true for the sternal bands in Mysticeti. In all of the examples mentioned we are able to give a functional explanation for the reduction of the organ concerned. We consider the loss of teeth an extreme dietary specialization, the reduction of the clavicle to be caused by a change in the mode of locomotion of the front extremities, the diminution of finger bones as an adaptation to faster running. The loss of the hind limbs as well as of the pelvic girdle has to be considered a consequence of the transition from a terrestrial to an aquatic habitat and, in correlation with this, of the takeover of the locomotory function by the trunk-tail-apparatus. There is no plausible explanation for the reduction of sternal apparatus in Mysticeti or for its persistence in the Odontoceti. Neither the mode of locomotion nor the breathing mechanism, the size of the body, the depth of diving or any other imaginable factors show any correlation that could give a plausible answer.

一般財団法人 日本鯨類研究所
THE INSTITUTE OF CETACEAN RESEARCH

CONCLUSION

The sternum as well as the shouldergirdle of whales are reduced to a great extent. Compared with terrestrial, four-legged mammals the reduction of this apparatus is, however, advanced not to the same extent in the toothed whales (for example *Stenella*) as in the whalebone whales (for example *Megaptera*). The toothed whales conform in general with terrestrial mammals, which also manifests itself in the development of the embryo. All of the three embryonal elements, which are typical for terrestrial mammals and out of which the sternum originates, also occur in toothed whales. They are 1. an unpaired ventrocranial element of interclavicle, 2. paired craniolateral elements of coracoid plates, and 3. paired lateral elements of sternal bands. The complete sternum anlage of the embryo extends from the first to the fifth pair of ribs. A rudimentary clavicle is obvious. In whalebone whales on the other hand the sternum originates from only two primordial elements. Even at an early stage their extension is very small; the whole anlage fills only the small cleft between the first pair of ribs. The paired lateral elements of sternal bands are completely missing. Thus the embryonal element, that plays the largest role in the development of the sternum in all Marsupialia and Placentalia, and that phylogenetically is the youngest and most " modern " of all, is absent. On the other hand the oldest and most " primitive " elements, the interclavicle and the coracoid plates are present. Not even a rudimentary clavicle is to be found. No constructive connections, that would explain the different modes of development of whalebone whales and the toothed whales as a functional adaptation could be found. With regard to the embryogenesis of the sternum and the shouldergirdle, the toothed whales and the whalebone whales have obviously evolved in separate directions. Monophyly of both groups is nevertheless not to be excluded.

ACKNOWLEDGMENTS

I am most grateful to the Deutsche Forschungsgemeinschaft for financial support of this study. My sincere thanks are due to Dr H.P.J. van Bree, Institut voor Taxonomische Zoölogie, Amsterdam, Dr T. Kamiya, Department of Anatomy, Faculty of Medicine, University of Tokyo and Dr H. Omura, director of the Whales Research Institute of Tokyo for their generous supply with material for examination and for kind help in many other ways. Thanks are also due to Mr H. Schneeberger for drawing the two models of sternum, Mrs U. Bremer and Ms I. Giesendorf for technical preparation of the manuscript. I also express my gratitude to Dr H. A. Oelschläger for reading the manuscript and giving me constructive comments.

REFERENCES

Arnason, U., 1969. The karyotype of the fin whale. *Hereditas*, 62: 273–284.

Arnason, U., 1974. Comparative chromosome studies in Cetacea. *Hereditas* 77: 1–36.

Arvy, L. and G. Pilleri, 1977. The Sternum in Cetacea. pp. 123–148. *In*: G. Pilleri (ed.) *Investigations on Cetacea*, VIII, Berne, pp. 383.

Burlet, H. M. de 1917. Beitrag zur Entwicklungsgeschichte der Wirbelsäule der Cetaceen. *Morph. Jb.*, 50: 373–402.

Chen, J. M., 1952. Studies on the morphogenesis of the mouse sternum. I. Normal embryonic development. *J. Anat.* (Lond.) 86: 373–386.

Chen, J. M., 1953. Studies on the morphogenesis of the mouse sternum. III. Experiments of the closure and segmentation of the sternal bands. *J. Anat.* (Lond.) 87: 130–149.

Eggeling, H., 1904. Zur Morphologie des Manubrium sterni. *Denkschr. med.-naturw. Ges., Jena, Festschr. f. Haeckel*, 11: 59–114.

Eggeling, H., 1906. Clavicula, Praeclavium, Halsrippen und Manubrium sterni. Berichtigung und Zusammenfassung. *Anat. Anz.*, 29: 99–110.

Eschricht, D. F., 1849. Zoologisch-anatomilch-physiologische Untersuchungen über die nordischen Wallthiere. Leipzig.

Eschricht, D. F. and J. Reinhardt, 1866. On the greenland rightwhale (*Balaena mysticetus* LINN.). *Roy Soc. Transl.*, 1–150.

Gaskin, D. E., 1976. The evolution, zoogeography and ecology of cetacea. *Oceanogr. Mar. Biol. Ann. Rev.*, 14: 247–346.

Gervais, P., 1871. Remarques sur lánatomie des Cétacés. *Nouv. Arch. Mus.*, 7: 65–146.

Gladstone, R. J. and C.P.G. Wakeley, 1932. The morphology of the sternum and its relation to the ribs. *J. Anat. Phys.*, 66: 508–564.

Kamiya, T. and P. Pirlot, 1974. Brain Morphogenesis in *Stenella coeruleoalba*. *Sci. Rep. Whales Res. Inst.* 26: 245–253.

Klima, M., 1968. Early development of the human sternum and the problem of homogloization of the so-called suprasternal structures. *Acta anat.* (Basel), 69: 473–484.

Klima, M., 1968. Das Vorkommen einer rudimentären Crista sterni in der Embryogenese der Säugetiere. *Anat. Anz.*, 123: 190–212.

Klima, M., 1973. Die Frühentwicklung des Schultergürtels und des Brustbeins bei den Monotremen (Mammalia: Prototheria). *Adv. Anat. Embryol. Cell. Biol.* (Berlin, Heidelberg, New York), 47: (2), 1–80.

Klima, M., 1975. Ancestrale Rudimente in der Morphogenese des Manubrium sterni beim Menschen. *Verh. Anat. Ges.* 69: 793–797.

Krauss-Hoeft, C., 1978. Morphogenese und Ossifikation des Sternum bei den Cetacea. *Inaug. Diss.*, Frankfurt a.M.

Kükenthal, W., 1914. Untersuchungen an Walen (zweiter Teil). *Jena. Z.f. Naturw.*, 51: 1–122, Taf. 1–3 c.

Kulu, D. D., 1972. Evolution and cytogenetics. pp. 503–527. *In*: S. H. Ridgway, (ed.) *Mammals of the sea*, Springfield.

Miller, G. S. Jr., 1924. Some hitherto unpublished photographs and measurements of the blue whale. *Proc. U.S. Nat. Mus.*, Vol. 66: Art. 7, pp. 1–4.

Müller, Ch., 1906. Zur Entwicklung des menschlichen Brustkorbes. *Gegenbaurs Morph. Jb.*, 35: 591–696.

Oehngren, S., 1919. Über die sog. Episternalbildungen bei den Säugetieren. *Anat. Anz.*, 52: 161–187.

Oelschläger, H. A., 1978. Erforschungsgeschichte, Morphologie und Evolution der Cetacea. *Natur u. Museum, Frankfurt a.M.*, 108: 317–324.

Omura, H., 1957. Osteological study of the little piked whale from the coast of Japan. *Sci. Rep. Whales Res. Inst.*, 12: 1–21.

Omura, H., 1972. An osteological study of the Cuvier's beaked whale, *Ziphius cavirostris*, in then orthwest Pacific. *Sci. Rep. Whales Res. Inst.*, 24: 1–34.

Omura, H., 1975. Osteological study of the minke whale from the Antarctic. *Sci. Rep. Whales Res. Inst.*, 27: 1–36.

Reiter, A., 1942. Die Frühentwicklung des Brustkorbes und des Brustbeins beim Menschen. *Z. Anat. Entwickl.-Gesch.*, 111: 676–722.

Rudolphi, K. A., 1829. Über Balaena longimana. *Mem. Acad. Sci. Berlin*, 1–12, 5 pl.

Ruge, G., 1880. Untersuchungen über Entwicklungsvorgänge am Brustbein und an der Sternoclavicularverbindung des Menschen. *Gegenbaurs Morph. Jb.*, 6: 362–414.

Schulte, W., 1916. The sei whale (*Balaenoptera borealis* LESSON). 2. Anatomy of a foetus of *Balaenoptera borealis*. *Mem. Amer. Mus. Nat. Hist.*, New Ser. 1 (6): 389–502.

Slijper, E. J., 1936. Die Cetaceen, vergleichend-anatomisch und systematisch. *Martinus Nijhoff, s'-Gravenhage.*,

Slijper, E. J., 1962. *Whales.*, Hutchinson, London, 474 pp.

Turner, P., 1870. On the sternum and ossa innominata of the longniddry whale (*Balaenoptera sibbaldii*). *J. Anat.*, 4, 2nd. ser., 3: 271–281.

一般財団法人 日本鯨類研究所

Valen, L. van, 1968. Monophyly or diphyly in the origin of whales. *Evolution*, Kansas, 22: 37–41.

Waite, E. R., 1919. Two Australasian blue whales with special reference to the Corvisart Bay whale. *Records South Austral. Mus.* 1 (2): 157–168 (pl. 11–16).

Yablokov, A. V., 1964. Convergence or parallelism in the evolution of cetaceans. *Paleont. Zhur.*, 97–106 (In Russian; translated in *Int. Geol. Rev.* 7: (1965): 1461–1468.

ICR
一般財団法人 日本鯨類研究所
THE INSTITUTE OF CETACEAN RESEARCH