

Z. Säugetierkunde 55 (1990) 202–212
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ISSN 0044-3468

Rudiments of the clavicle in the embryos of whales (Cetacea)

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Receipt of Ms. 28. 12. 1988

Acceptance of Ms. 10. 5. 1989

Abstract

Investigated the existence of a clavicle in 64 embryos and fetuses of seven species of Odontoceti and four species of Mysticeti. Among the Odontoceti, a regular appearance of the clavicle as a temporary rudiment during embryogenesis has been established for *Stenella coeruleoalba*, *Stenella attenuata*, *Delphinus delphis* and *Phocoena phocoena*. In *Physeter macrocephalus* a minute rudiment of the clavicle was found in one developmental stage only. The reduction of the clavicle in this species has progressed further than in other Odontoceti. In the Mysticeti the clavicle does not appear at all during embryogenesis. Its reduction is complete. The potential existence of a clavicle in adult Odontoceti is discussed. The histogenesis of the clavicle is accomplished by pure desmal ossification. The histogenetic process confirms that the mammalian clavicle represents a desmal element of the exoskeleton without contribution of the chondral elements of the endoskeleton.

Introduction

It is generally believed that the clavicle (clavicula; collar bone) is absent in the shoulder girdle of whales (Cetacea). For a long time there had been no indications in the literature that would have referred to the existence of a clavicle; neither in toothed whales (Odontoceti) nor in whalebone whales (Mysticeti). This included adults and embryos as well. Therefore, as recent as 1976, ARVY had to summarize her critical remarks on the subject of the cetacean "girdles" as follows: "The flippers are . . . joined to the antero-lateral wall of the thorax. They are non-articulated, except where they articulate with the shoulder blades. There is never any trace of a collar bone: clearly the 'scapular girdle' does not exist." In 1978 a positive result concerning the existence of a clavicle in Odontoceti, that is in one embryo of the striped dolphin *Stenella coeruleoalba*, was reported for the first time (KLIMA 1978). Four years later a clavicle was also detected in adult Odontoceti, namely in three specimen of the killer whale *Orcinus orca* (BEHRMANN 1982).

This paper reconsiders the question of the existence of a clavicle in whales. The results of the investigation of 64 embryos and fetuses of seven species of the Odontoceti and of four species of the Mysticeti are summarized.

Material and methods

The material used in this investigation has been provided by the following collections: Frankfurt (Institute of Anatomy, Johann-Wolfgang-Goethe-University, Frankfurt/M., FRG), Seattle (National Marine Fisheries Service, Mammal Laboratory, Seattle, WA, USA), Tokyo (Department of Anatomy, Faculty of Medicine, University of Tokyo, Hongo, Tokyo, Japan) and Utrecht (Hubrecht Laboratory, International Embryological Institute, Utrecht, The Netherlands).

The embryos were sectioned into series of microscopical slides following customary histological methods, except for the large fetuses which were examined by macroscopical dissection. All information concerning the material is summarized in Table 1. Embryos No. 4 and No. 9 (*Stenella coeruleoalba*) and No. 62 and No. 63 (*Megaptera novaeangliae*) have already been inspected earlier

Table 1. Material and results: Occurrence or absence of the clavicle in the examined embryos and fetuses

The size is given in millimeters for TL (total length from tip of snout to tip of tail) or for CR (crown-rump length). For details about the collection see text

No.	Size (mm)		Labelling	Collection	Methods	Clavicle
	TL	CR				
Odontoceti						
Striped dolphin <i>Stenella coeruleoalba</i>						
1	7.0	—	—	Tokyo	slides	missing
2	11.0	—	—	Tokyo	slides	missing
3	12.0	—	—	Tokyo	slides	missing
4	17.0	—	—	Tokyo	slides	missing
5	25.0	—	2959.25	Seattle	slides	occurring
6	26.0	—	2959.26	Seattle	slides	occurring
7	26.0	—	2989.26	Seattle	slides	occurring
8	26.0	—	—	Tokyo	slides	missing
9	35.0	—	—	Tokyo	slides	occurring
10	35.0	—	2959.35	Seattle	slides	occurring
11	50.0	—	2989.50	Seattle	slides	occurring
Spotted dolphin <i>Stenella attenuata</i>						
12	21.0	7.5	K 13	Frankfurt	slides	missing
13	22.0	8.6	K 16	Frankfurt	slides	missing
14	25.0	9.2	K 12	Frankfurt	slides	missing
15	39.0	14.8	K 17	Frankfurt	slides	occurring
16	43.0	18.3	K 22	Frankfurt	slides	occurring
17	44.5	19.7	K 23	Frankfurt	slides	occurring
18	57.0	25.5	K 18	Frankfurt	slides	occurring
19	71.0	32.5	K 24	Frankfurt	slides	occurring
20	85.0	38.5	K 15	Frankfurt	slides	occurring
Common dolphin <i>Delphinus delphis</i>						
21	24.0	7.6	K 55	Frankfurt	slides	missing
22	39.5	13.0	K 56	Frankfurt	slides	missing
23	42.0	18.7	K 57	Frankfurt	slides	occurring
24	44.0	20.4	K 53	Frankfurt	slides	occurring
25	46.0	21.5	K 58	Frankfurt	slides	occurring
26	82.0	34.3	K 49	Frankfurt	slides	occurring
27	101.0	40.5	K 50	Frankfurt	slides	occurring
28	113.5	49.5	K 59	Frankfurt	slides	occurring
29	131.0	58.5	K 51	Frankfurt	slides	occurring
White-beaked dolphin <i>Lagenorhynchus albirostris</i>						
30	430.0	—	—	Frankfurt	dissection	missing
Common porpoise <i>Phocoena phocoena</i>						
31	(25.0)	10.0	MK 74	Frankfurt	slides	missing
32	(28.0)	11.0	MK 71	Frankfurt	slides	missing
33	39.0	14.0	MK 72	Frankfurt	slides	occurring
34	41.0	19.0	MK 73	Frankfurt	slides	occurring
35	42.0	18.0	MK 70	Frankfurt	slides	occurring
36	51.0	22.0	MK 67	Frankfurt	slides	occurring
37	60.0	24.0	MK 64	Frankfurt	slides	occurring
38	69.0	27.0	MK 75	Frankfurt	slides	occurring
39	70.0	29.0	MK 62	Frankfurt	slides	occurring
40	95.0	45.0	MK 61	Frankfurt	slides	occurring
41	107.0	46.0	MK 69	Frankfurt	slides	missing
42	125.0	55.0	MK 68	Frankfurt	slides	occurring
43	134.0	60.0	MK 76	Frankfurt	slides	missing
44	167.0	—	MK 48	Frankfurt	slides	missing
45	355.0	—	—	Frankfurt	dissection	missing

Table 1 (continued)

No.	Size (mm)		Labelling	Collection	Methods	Clavicle
	TL	CR				
Narwhal <i>Monodon monoceros</i>						
46	137.0	—	—	Utrecht	slides	missing
Sperm whale <i>Physeter macrocephalus</i>						
47	19.0	10.0	MK 58	Frankfurt	slides	missing
48	37.0	14.0	MK 51	Frankfurt	slides	missing
49	75.0	—	PC	Frankfurt	slides	missing
50	97.0	45.0	MK 62A	Frankfurt	slides	occurring
51	102.0	47.0	MK 66	Frankfurt	slides	missing
52	170.0	73.0	MK 53	Frankfurt	slides	missing
53	315.0	—	PH 4	Frankfurt	dissection	missing
54	435.0	—	PH 3	Frankfurt	dissection	missing
55	455.0	—	PH 2	Frankfurt	dissection	missing
56	565.0	—	PH 1	Frankfurt	dissection	missing
Mysticeti						
Gray whale <i>Eschrichtius robustus</i>						
57	—	15.0	2956 F4	Seattle	slides	missing
58	—	65.0	2956 F3	Seattle	slides	missing
Minke whale <i>Balaenoptera acutorostrata</i>						
59	455.0	—	3119	Frankfurt	dissection	missing
Fin whale <i>Balaenoptera physalus</i>						
60	156.0	—	—	Utrecht	slides	missing
61	400.0	—	MK 65	Frankfurt	dissection	missing
Humpback whale <i>Megaptera novaeangliae</i>						
62	21.0	—	—	Tokyo	slides	missing
63	37.0	—	—	Tokyo	slides	missing
64	107.0	—	—	Utrecht	slides	missing

with respect to the existence of a clavicle (KLIMA 1978). All the others were investigated for the first time.

The scientific, english and german names used in this paper as well as the zoological system of the whales closely follow the publications of FRASER (1976), NOWAK and PARADISO (1983) and GEWALT (1987). The terminology for the individual structures of the embryonic breast-shoulder apparatus is taken from KLIMA (1987).

Results

Appearance in Odontoceti

In the striped dolphin *Stenella coeruleoalba* the clavicle starts to develop in stages of about 25 mm TL and can still be recognized in stages of 50 mm TL. Later stages were not at disposal (Figs. 1 and 2).

In the spotted dolphin *Stenella attenuata* the first anlage of the clavicle appears in a 39 mm TL large stage and is conserved up to the largest stages of about 85 mm TL.

In the common dolphin *Delphinus delphis* the first anlage of a clavicle was detected in a 42 mm TL large stage and was observed continuously up to the largest of the available stages which measured 131 mm TL (Fig. 6).

No clavicle was detected in the only specimen of the white-beaked dolphin *Lagenorhynchus albirostris*, which had been investigated by us and measured 430 mm TL.

The largest sample of material that was at my disposal was from the common porpoise *Phocoena phocoena*. The first anlage of a clavicle was detected in a 39 mm TL large stage. It

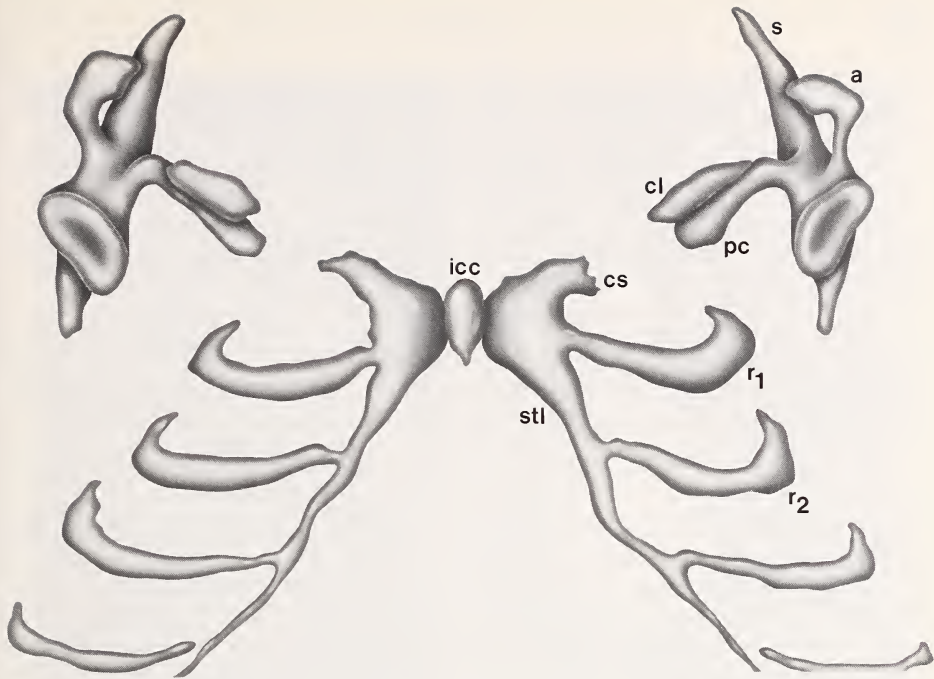


Fig. 1. *Stenella coeruleoalba*, embryo 25 mm TL (No. 5). Ventral view of the shoulder girdle and sternum. Abbreviations: a = acromion; cl = clavicle; cp = coracoid process; cs = coracoid-scapular plate; icc = unpaired sternal element; r1, r2 = ribs 1 and 2; s = scapula; stl = paired sternal band

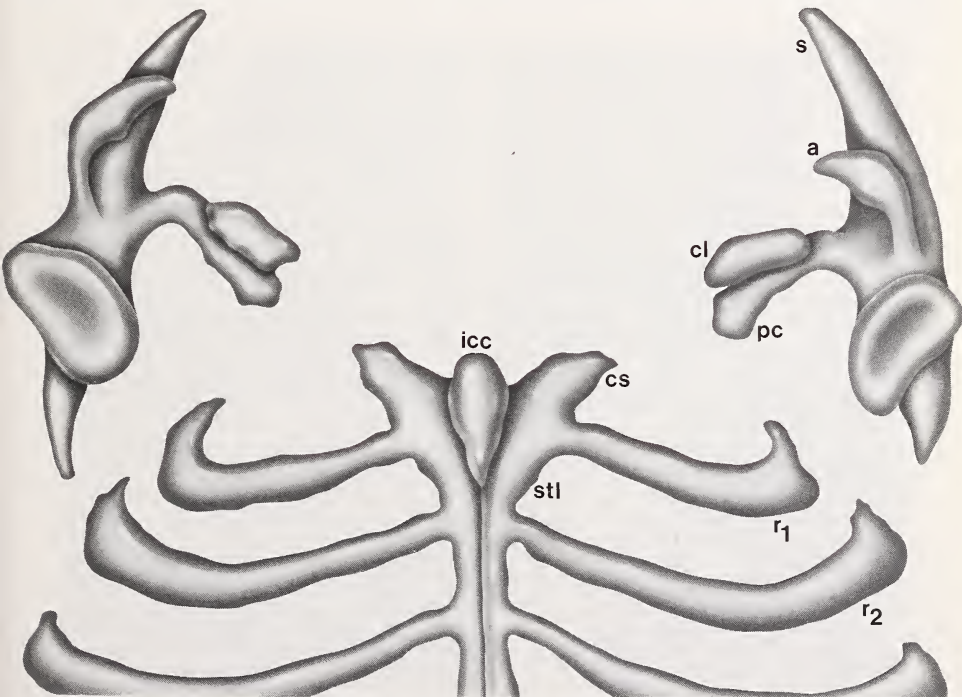


Fig. 2. *Stenella coeruleoalba*, embryo 35 mm TL (No. 10). Ventral view of the shoulder girdle and sternum. For abbreviations see Figure 1

is continuously present up to a stage of 95 mm TL. In one instance we found a very small clavicular rudiment in a 125 mm TL large stage. In stages of 134 mm TL to 355 mm TL a clavicle or clavicular rudiment is no longer detectable (Fig. 3).

In a specimen of the narwhal *Monodon monoceros* with a size of 137 mm TL no anlage of the clavicle was detected.

All in all, ten stages of the sperm whale *Physeter macrocephalus* measuring 19 mm TL to 565 mm TL had been at disposal. The clavicle was seen as a minute rudiment in a stage of 97 mm TL only (Figs. 4 and 5).

Appearance in Mysticeti

In the investigated Mysticeti, the gray whale *Eschrichtius robustus*, minke whale *Balaenoptera acutorostrata*, fin whale *Balaenoptera physalus* and humpback whale *Megaptera novaeangliae* none of the available stages showed any anlage of the clavicle.

Morphogenesis

In mammals that have a completely developed clavicle as adults as well it connects the cranio-lateral rim of the sternum with the acromion of the scapula. It attaches "joint-like" to both skeletal elements and, together with the sternum, forms the sterno-clavicular joint, with the scapula the acromio-clavicular joint, respectively. The lateral end of the clavicle comes close to the coracoid process of the scapula. With this skeletal element, however, it shares only a loose connection established by ligaments of the ligamentum coraco-claviculare.

A similar topographical position is displayed by the clavicular rudiments of whale embryos, whenever such rudiments are present at all. They are located precisely at the

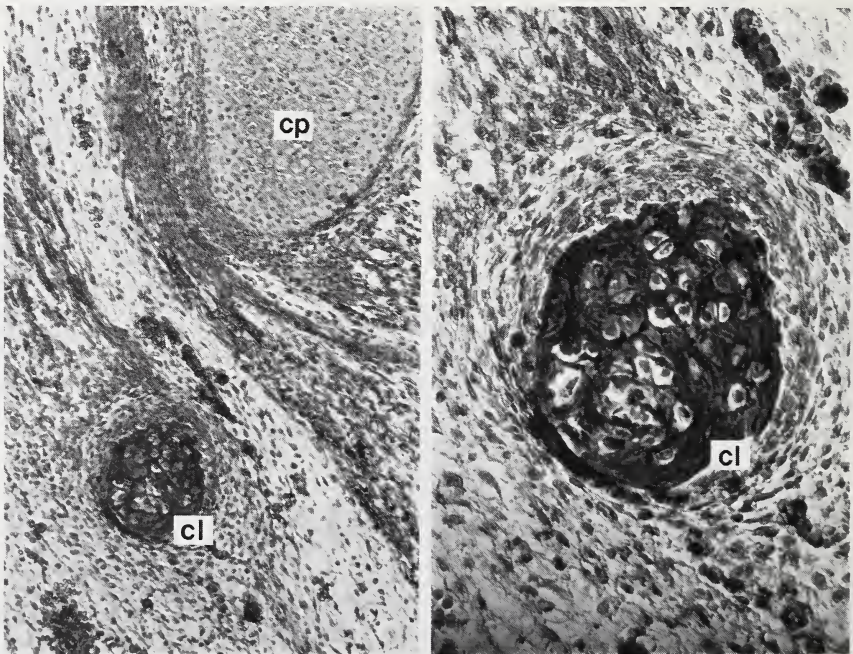


Fig. 3. *Phocoena phocoena*, embryo 70 mm TL (No. 39). A section of the clavicle (cl) and coracoid process (cp). Left: overall view; right: detail. For orientation see Figure 4

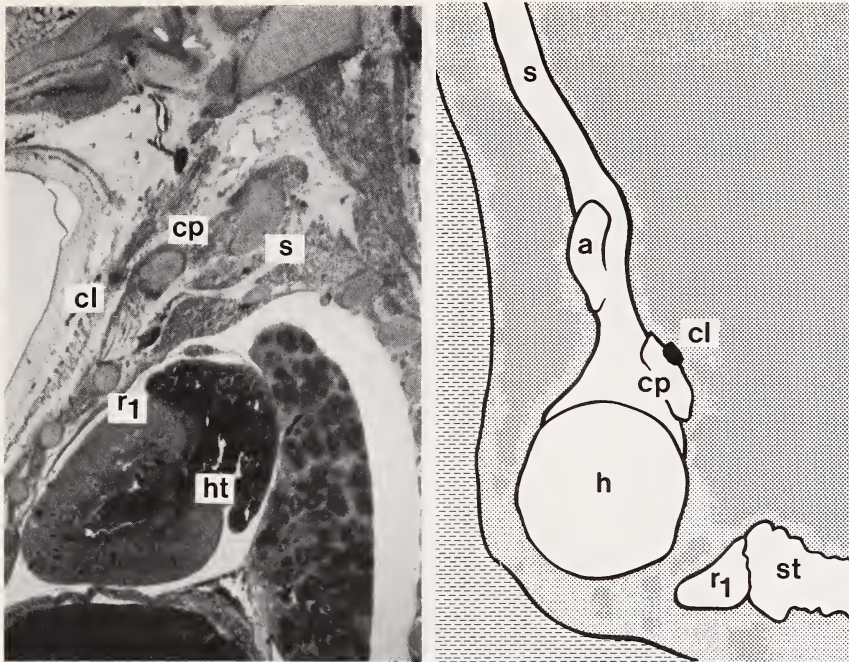


Fig. 4. Left: Position of the clavicle in embryos of *Phocoena phocoena*, 70 mm TL. Photograph of a longitudinal section of the thorax. Right: Position of the clavicle in embryo of *Physeter macrocephalus*, 97 mm TL. Diagrammatic drawing of the right shoulder viewed from the front. Abbreviations: a = acromion; cl = clavicle; cp = coracoid process; h = humerus; ht = heart; r1 = rib 1; s = scapula; st = sternum

interconnecting line between the anterior rim of the sternum and the tip of the acromion. However, they are very small in all phases of their development and therefore not able to bridge the relatively large distance between sternum and acromion. Consequently they remain at a substantial distance from both structures. Their closest position to any other skeletal element is towards the coracoid process. However, a direct connection between both structures does not exist.

The morphogenesis of the clavicle starts at a developmental stage when the paired anlagen of the breast-shoulder apparatus are still far apart in the lateral breast wall. Two processes are recognizable in the scapula anlage, the acromion and the coracoid process. The sternal anlage is visible in a small gap extending from the coracoid process towards ventromedial. It is composed of a part of the paired coracoid-scapular plates, the paired sternal bands and of an unpaired sternal element. In the course of further development all mentioned anlagen shift towards ventromedial and approach each other. The sternal anlagen fuse into a uniform piece of skeleton in the median plane. (For details see KLIMA 1978, 1987.)

During all these morphogenetic processes the clavicle's anlage remains in its position. It shows a close relation to the coracoid process. It is located, somewhat cranially shifted, ventromedially of the coracoid process, without establishing a direct connection with this element. Its longitudinal axis runs parallel with the coracoid processes' longitudinal axis. As the coracoid process shifts towards ventromedial the anlage of the clavicle displays the same movement. This topographic position as well as the mutual morphogenetic activities are recognizable from the depiction of two developmental stages of the shoulder girdle and sternal apparatus of *Stenella coeruleoalba* (Figs. 1 and 2).

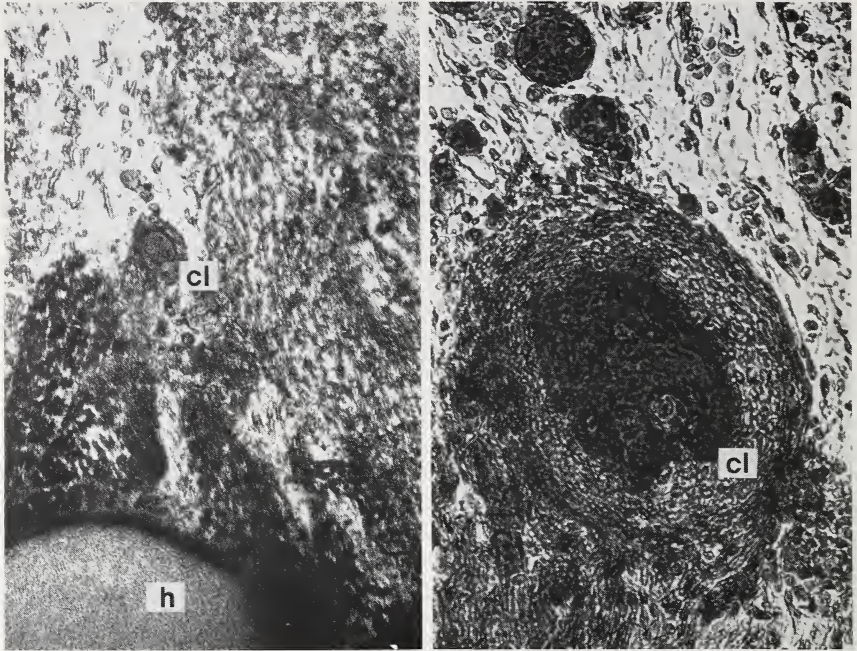


Fig. 5. *Physeter macrocephalus*, embryo 97 mm TL (No. 50). A section of the clavicle (cl) and humerus (h). Left: overall view; right: detail. For orientation see Figure 4

Histogenesis

As a part of the exoskeleton, the clavicle stems histogenetically from desmal ossification. First of all, the embryonic mesenchyme condenses at the location where the anlage of the clavicle comes into being (Fig. 6a). Singular mesenchyme cells become bone-forming osteoblasts and start with the secretion of the first osseous ground substance. In the further course of ossification (Fig. 6b) the peripheral zone appears more distinct. It is becoming bone-forming periost. In its inner layer numerous osteoblasts differentiate out of mesenchyme cells. Then the ground substance, the osteoid, is massively secreted into the inner portion and nearly fills the complete anlage (Fig. 3 *Phocoena phocoena*). Immured bone cells, the osteocytes, are located in its inside. Soon however, the bone substance is loosened up (Fig. 6c). Openings are penetrating from the outside and step by step the channel system of the primary bone marrow develops. In the further course of development decomposition processes are gradually taking over (Fig. 6d). They are initiated by an ever increasing number of osteoclasts. These giant multinuclear cells attack the inner wall of the bone from the primary marrow cavity and gradually dissolve it. Finally, the osteoclasts dissolve the last remnants of the bone and the anlage of the clavicle is completely decomposed.

Discussion

The whales (Cetacea) of both suborders, Odontoceti and Mysticeti, belong to mammalian forms that have reduced the clavicle completely (SLIJPER 1936; BOURDELLE and GRASSÉ 1955; ARVY 1976). There is no direct connection between the skeleton of the forelimb and

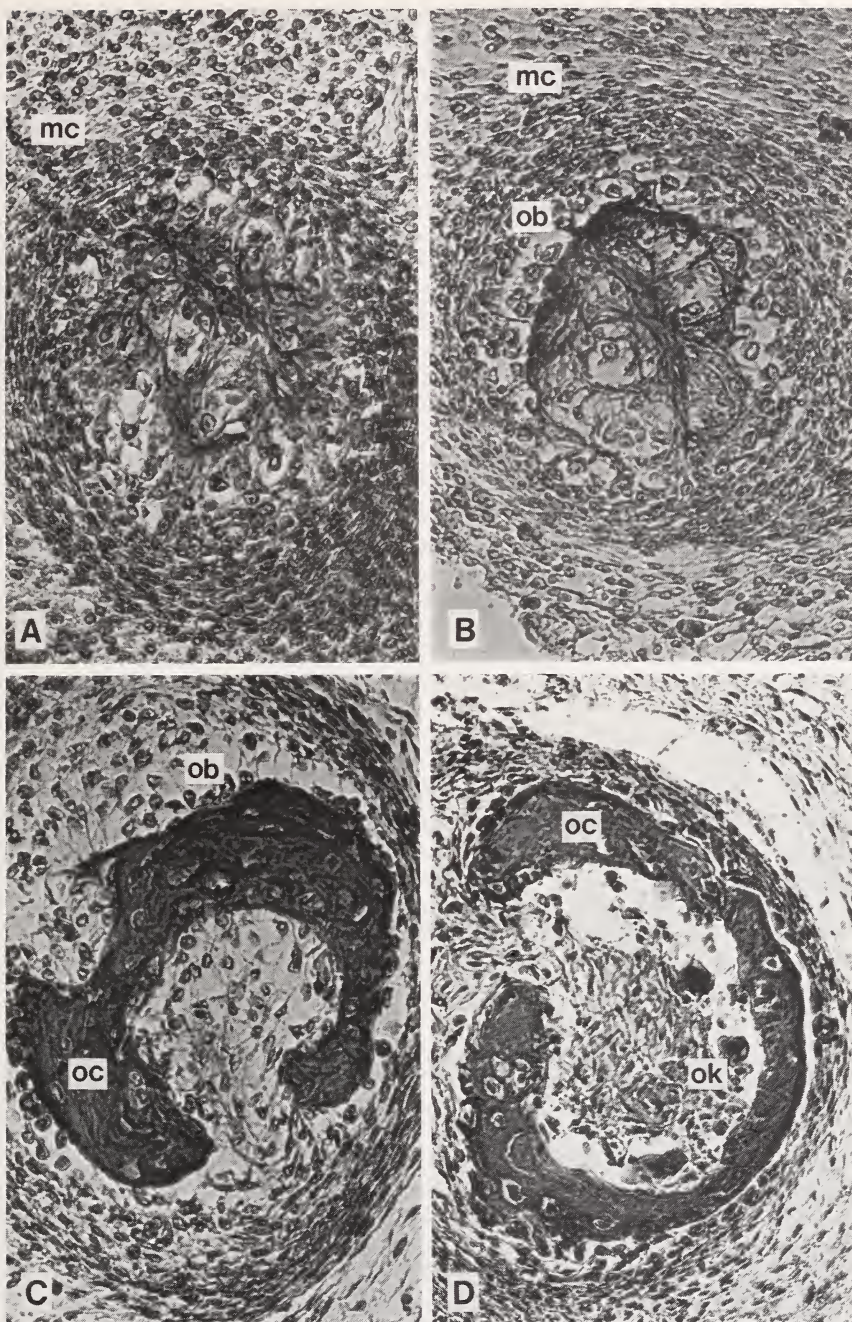


Fig. 6. Some selected stages of the ossification of the clavicle in *Delphinus delphis*. A = embryo 42 mm TL (No. 23); B = embryo 44 mm TL (No. 24); C = embryo 113 mm TL (No. 28); D = embryo 131 mm TL (No. 29). Abbreviations: mc = mesenchyme cells; ob = osteoblast; oc = osteocyte; ok = osteoclast. For details see text about histogenesis

the rump, except in the amazon dolphin (*Inia geoffrensis*) where the humerus supports itself to the sternum via a secondary joint (KLIMA et al. 1980).

The first positive result concerning a rudiment of the clavicle in whales (KLIMA 1978) leads to the following statement: "A rudimentary clavicle is also obvious in the Odontoceti during embryogenesis, as has been proved for *Stenella*. No rudimentary clavicle can be found in *Megaptera*, which, as I think, can be considered as a rule for all Mysticeti. This total reduction is in complete correspondence with the extensive reduction of the sternum." This opinion has generally been confirmed by the present investigation.

The investigations demonstrate a well developed rudimentary clavicle during embryogenesis in the following Odontoceti: striped dolphin *Stenella coeruleoalba*, spotted dolphin *Stenella attenuata*, common dolphin *Delphinus delphis* and common porpoise *Phocoena phocoena*. The clavicle starts to form in stages around 30 mm TL and is completely decomposed in stages measuring around 130 mm TL. During morphogenesis it is especially well developed at a time when the paired anlagen of the breast-shoulder apparatus interconnect in the median plane. The clavicle is located close to the coracoid process. It maintains a long distance to acromion and sternum. Histogenetically, the clavicle shows a typical desmal ossification.

Two additional representatives of the Odontoceti, the white-beaked dolphin *Lagenorhynchus albirostris* and the narwhal *Monodon monoceros* were investigated. However, in these cases I had only singular stages different from the above mentioned size-ranges. No rudiment of the clavicle was detected here.

The sperm whale *Physeter macrocephalus* takes a special position amongst the investigated Odontoceti with respect to the development of its clavicle. Despite the fact that extensive material in suitable size-ranges and developmental stages was at disposal, we found a minute rudiment of the clavicle only in one individual measuring 97 mm TL. Obviously, the reduction of the clavicle in the sperm whale, who displays many other special adaptations as well, has progressed further than in other Odontoceti.

No rudiment of the clavicle was detected in any representative of the investigated Mysticeti i.e. in the gray whale *Eschrichtius robustus*, minke whale *Balaenoptera acutorostrata*, fin whale *Balaenoptera physalus* and humpback whale *Megaptera novaeangliae*. The result supports the assumption that the reduction of the clavicle has progressed further in Mysticeti than in Odontoceti.

I consider it possible that a rudimentary clavicle may occasionally appear in adult Odontoceti. The necessary prerequisites are given by the regular appearance of the clavicle during embryogenesis. Exactly this requirement is not met in Mysticeti and therefore I trust that an occasional appearance of a rudimentary clavicle will never be demonstrated in Mysticeti.

In this sense I regard the reported existence of a clavicle in the adult killer whale *Orcinus orca* (BEHRMANN 1982) as a rare, occasional appearance. Apparently the clavicle may appear now and then in a few adult Odontoceti just as, for example the variable ossa suprasternalia (ASHLEY 1955; KLIMA 1968) or surplus cervical ribs (HAYEK 1928; TÖNDURY 1958) may sometimes come to existence in humans. A regular appearance seems to be unlikely. The opinion of BEHRMANN (1982) that the clavicles of the killer whale like those of the sea lion serve the function to support the animal on lands is incorrect. Sea lions like all Pinnipedia do not possess any clavicle at all.

Furthermore, I consider the position of the clavicle on the mounted skeleton of the killer whale (BEHRMANN 1979, 1982) to be incorrect. The sternal end should be positioned in front of the first rib's connection and the scapular end should run alongside the coracoid process towards the acromion. Afterwards however, the exact topographic positions can not easily be reconstructed. A direct connection to the acromion would not be essential as the presented results concerning embryos of Odontoceti clearly show. This absolutely reflects a statement made by NAUCK (1938): "As a well developed acromion exists in nearly

all Cetacea despite a missing clavicle, acromion and clavicle are not causally dependent from each other . . . ”

According to the histogenesis of the clavicle it should again be stressed that all our investigations revealed a pure desmal ossification. This finding is important because it contributes to the debate concerning the origin of the clavicle in mammals. There is an ongoing controversy whether the clavicle originates as a desmal or chondral or as a mixed element (FUCHS 1912; FAWCETT 1913; HANSON 1920; BRANDT 1935; NAUCK 1938; ZAWISCH 1953; KOCH 1960; LESSERTISSEUR and SABAN 1967; OLÁH and LUDWIG 1971; STARCK 1979 and others). My results definitely confirm the opinion of STARCK (1979) that the clavicle of mammals is a pure dermal skeletal element (membrane bone) independent from the special histogenetic mode of osteogenesis.

In many mammals chondral tissue additionally appears at both ends of the desmal anlage of the clavicle. The cartilage borders at the neighboring skeletal elements of the chondral breast-shoulder apparatus, that is medially at the sternum and laterally at the acromion but, it never joins them to form a singular unit. Some authors assume that the chondral parts of the clavicle represent certain elements of the chondral shoulder girdle. Thus, the medial chondral part is assumed to correspond to the original procoracoid which does not exist in placentals any more. However, more recent investigations of monotremes, marsupials and placentals (KLIMA 1973, 1987) have shown that the embryonic material of the procoracoid is either integrated into the manubrium sterni or forms the independent praeclavium. The same developmental mode is demonstrated in this investigation which has been conducted with the embryos of Odontoceti (see also KLIMA 1978). The anlage of the procoracoid becomes a part of the sternum. It becomes visible at the sternum at the same time when the isolated anlage of the clavicle which is located far away, develops as a pure desmal element (Figs. 1 and 2). Thus, the chondral parts cannot belong to the initial developmental pattern of the clavicle.

Acknowledgements

My sincere thanks go to all individuals and institutions who helped in the accumulation of material for this research, especially to Dr. G. C. BANGMA, Utrecht, Mrs. P. DEIMER, Hamburg, Dr. A. JONSGARD, Oslo, Prof. T. KAMIYA, Tokyo, Dr. W. M. MARQUETTE, Seattle and Dr. W. P. PERRIN, La Jolla. I am grateful to Mrs. R. GUNTRUM, Mrs. G. LEIBE and Mrs. U. TRAUTMANN, Frankfurt, for their technical assistance, to Mr. H. L. SCHNEEBERGER, Frankfurt, for preparing the drawings and to Mr. P. GERMROTH, Frankfurt, for translating the manuscript.

Zusammenfassung

Rudimente des Schlüsselbeins bei den Embryonen von Wältieren (Cetacea)

Es wurde nach dem Vorkommen von Schlüsselbein (Clavicula) bei 64 Embryonen und Feten von sieben Arten von Zahnwalen (Odontoceti) und vier Arten von Bartenwalen (Mysticeti) gesucht. Unter den Odontoceti ist ein regelmäßiges Auftreten der Clavicula während der Embryogenese als ein vorübergehendes Rudiment bei Streifendelphin *Stenella coerulescens*, Fleckendelphin *Stenella attenuata*, Gewöhnlichem Delphin *Delphinus delphis* und Kleintümmler *Phocoena phocoena* nachgewiesen worden. Die untersuchten Stadien von Weißschnauzendelphin *Lagenorhynchus albirostris* und Narwal *Monodon monoceros* waren zu groß, um bei ihnen die Anlage einer Clavicula ebenfalls nachzuweisen. Bei Pottwal *Physeter macrocephalus* ist nur bei einem einzigen Stadium ein winziger Rest der Clavicula festgestellt worden. Ihre Rückbildung der Clavicula ist bei dieser Art weiter fortgeschritten als bei anderen Odontoceti. Von den Mysticeti sind folgende Arten untersucht worden: Grauwal *Eschrichtius robustus*, Zwergwal *Balaenoptera acutorostrata*, Finnwal *Balaenoptera physalus* und Buckelwal *Megaptera novaeangliae*. Bei den Mysticeti erscheint die Clavicula während der Embryogenese überhaupt nicht mehr. Ihre Rückbildung ist vollständig.

Das eventuelle Auftreten der Clavicula bei erwachsenen Odontoceti (Befund bei Schwertwal *Orcinus orca* von BEHRMANN 1982) wird diskutiert.

Die Histogenese der Clavicula erfolgt durch eine rein desmale Ossifikation. Dadurch wird bestätigt, daß die Clavicula der Säugetiere ein rein desmales Element des Exoskelettes darstellt, ohne Beteiligung der knorpeligen Elemente des Endoskelettes.

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Zeitschrift/Journal: [Mammalian Biology \(früher Zeitschrift für Säugetierkunde\)](#)

Jahr/Year: 1990

Band/Volume: [55](#)

Autor(en)/Author(s): Klima Milan

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