Studies on Dutch fossil Cetacea.

II. Form and structure of the whale vertebra.

A. Form.

F. J. M. Heshinga and Johanna Schut*

Cyrtodelphis. Van Deinse (1931) mentioned the relative rarity of this species in the Netherlands. According to Abel (1913) this species is common in the European Miocene. According to Van Deinse, few have been found in the Netherlands, "only 17 bullae." It is difficult to place it, for of the small loose bullae 17 could be found and no vertebrae or other skeletal parts. According to our understanding, the identification of the bullae is inaccurate, or the *Cyrtodelphis* vertebrae are identified as *Acrodelphis* sp. or something similar in the book.

Scaldicetus teeth. There are still found some typical whale teeth, which on the basis of older determinations always are called *Scaldicetus*. It is notable, as with *Cyrtodelphis*, that teeth are found but no other fragments. On the other hand there are many vertebrae of Odontoceti not nearer determined as such, but never the teeth belonging to them.

We limit ourselves to these two examples, from which we derive satisfying evidence, that proves the old name-giving and identification work system to be contradictory. This results from the fragmentary nature of many finds, also from Antwerp, and especially from the incomplete knowledge of earlier finds in Europe. As to names, the Austrian Cetacea have here received incomplete attention. The Danish and German material have gotten the same attention.

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In this situation of superficial knowledge, one classification of the fossil whale material is served by beginning with the vertebrae and vertebral fragments. Not alone because these fragments were found most frequently and also most complete, but also for the important function of the axial skeleton in Cetacea and the associated reduction of other skeletal parts, with [name] the shoulder- and pelvic girdles with the extremities belonging to them. We do well to realize, that when we study vertebrae, all further conclusions with relation to the whole vertebral column and the whole animal can be only indirect.

THE FORM AND STRUCTURE OF VERTEBRAL CENTRA

Vertebrae and vertebral centra can be contemplated from varying viewpoints:

1) The place of the vertebra in the column.

2) The size of the vertebra.

3) The morphological characteristics by which the vertebra can be identified, namely: round, oval, length, sharp or round keel, arterial grooves, piercing for blood vessels in transverse processes and vertebral centra, articular surfaces, grooves, processes, etc.

4) Characteristics associated with the structure of the first order: thin or thick compacta, structure of the spongiosa, relief of the epiphyses, etc.

5) The age of the individual whereon the vertebra belongs; judged by the condition of the epiphyses.

THE GENERAL FORM OF WHALE VERTEBRAE

All vertebrae have a vertebral centrum (with the exception of the atlas) from which various processes project. The place of the vertebra in the vertebral column determines the size of the vertebral centrum and the place, form, and size of the processes.

THE FIRST NECK VERTEBRA OR ATLAS

The atlas is a uniquely constructed typical vertebra consisting of two lateral blunt masses which are connected by a dorsal and ventral arch, thus forming a ring-shaped bone. The atlas does not have an obvious vertebral centrum. Of the ancestral vertebral centrum is apparent only the anterior half in the atlas (as ventral arch?) while the posterior half forms the odontoid process of the axis. In extinct Cetacea, this is not precisely known. The dorsal arch is similar to that of the other neck vertebrae; only the neural spine is little developed. From the lateral mass extend two transverse processes. Each transverse process has a dorsal and a ventral half. These halves meet on the end and are thus able to enclose a canal, the foramen transversum. We find the same structure back in the other neck vertebrae. In the atlas however is this canal not present.

Each lateral mass carries on the anterior border a concave articular surface for both occipital condyles. On the posterior surface are two flat articular surfaces for the anterior surface of the axis. Between these surfaces articulates the odontoid process of the axis over the ventral arch of tile atlas. In fossil atlases often are lacking the transverse and dorsal processes. Often only one half (i.e. one lateral mass) is recovered.

THE SECOND NECK VERTEBRA OR AXIS

The axis (epistropheus) is a flat vertebra and the heaviest of all neck vertebrae. The posterior side carries an epiphysis and is joined via an intervertebral disc with the third neck vertebra. The odontoid process bears a separate epiphysis, but of this we have in fossils never seen a trace.

As in the atlas there are on either side two processes, enclosing a canal. As a rule these are broken in fossil remains. On the anterior side are, next to the odontoid process, two indistinct limited articular surfaces for the posterior side of the atlas. The inconspicuous odontoid process of Cetacea rests on the ventral arch of the atlas. The whole structure of the articulation between atlas and axis allows only a small degree of motion. The spongy structures, noteworthy in this area, to which we will return later, give great strength to these vertebrae. As well of atlases as of axes is an appropriate number present in Dutch collections.

N.B. As well in the atlas as in the axis the foramen transversum breaks in the transverse process in most species of Cetacea. This is then suggested (also in *Eurhinodelphis*) by a hollowing out.

THE THIRD TO THE SEVENTH (OR LAST) NECK VERTEBRA

In figure 7 and 8 the neck vertebra is illustrated; missing divide is thereby marked. In general there remains only the vertebral centrum with the beginning of the four processes pointing backward. The vertebrae are always very short. They have thin epiphyses which grow together relatively early with the vertebral centrum, so that neck vertebrae without or with attached epiphyses are rare. Ours are only a few examples known. Short disc-shaped, round, oval or rectangular vertebral contra with four processes are thus always neck vertebrae.

The neural canal is always very broad. When the origin of the process is strongly eroded, one can mistake the highest for the first two thoracic vertebrae, whereof the first especially is still very short.

THE THORACIC VERTEBRAE

As thoracic vertebrae we define vertebrae which bear a rib. There are diverse types of thoracic vertebrae. Dependent on the articulation of the rib there are vertebrae which bear a one-headed rib and those which bear a two-headed rib. Dependent on the transverse process on which the rib articulates: this transverse process can rise out of the neural arch or out of the vertebral centrum. Between them are transitional forms. The neural arches arise in the thoracic vertebrae always clearly from the anterior half of the vertebral centrum; see figure 24 and 25. In the Physeteridae comes still another type clearly to the front, whereby the transverse processes of the thoracic vertebrae backwards become smaller and thinner while besides another transverse process arises from the vertebral centrum at the place of the head of the rib. The two-headed ribs then become one-headed. This process thus replaces the capitulum of the rib and in the transitional vertebra (± tenth thoracic vertebra in *Physeter macrocephalus*) are both present which then surround a canal. This appears to be important for the classification of fossils. This phenomenon was by Abel (1931) also discovered in *Eurhinodelphis*. One consults Flower (1885) for further details and illustrations.

Only in thoracic vertebrae will the vertebral centra generally be found [in contact] with the origin of the neural arch. The typical thoracic vertebral centrum is roughly as high as it is long. The anterior ones are shorter, the posterior ones can be much longer. The neural canal is broad and becomes posteriorly in the thoracic column gradually somewhat smaller. A typical vertebral

centrum is round or oval; in the anterior thoracic vertebrae the outline can especially be transformed through the insertion of the neural arch. As these are large in proportion to the vertebral centrum, the outline can be a triangle with rounded angles.

THE LUMBAR VERTEBRAE

Lumbar vertebrae are vertebrae with a robustly built oblong vertebral centrum with two transverse processes. The neural canal is narrow and high except for the anterior lumbar vertebrae where the transition to the broader canal of the thoracic vertebrae is accomplished near the high narrow lumbar vertebral outline. Both anteriorly and posteriorly, lumbar vertebrae have a round or practically round outline; in the middle the form is otherwise, through the origin of the transverse processes and the eventual keel.

THE CAUDAL VERTEBRAE

The first caudal vertebrae resemble in all ways the last lumbar vertebrae; as a rule they are somewhat larger. They are distinguished from the lumbar vertebrae in that all caudal vertebrae (with the exception of the very last one) bear articular surfaces for the chevron bones on the under side. The chevron bones are situated opposite the intervertebral discs and thus form a sort of ventral intervertebral arch. They articulate as a rule with both vertebrae, sometimes also only with the anterior or posterior vertebra. As far as we know, no fossil chevron bones have been found in the Netherlands.

The articular surfaces for chevron bones on the vertebrae are often closed [obscure?] but mostly easily distinguished. Anteriorly on the tail the neural canal becomes quickly narrower, lower and rounded. The processus spinosus (neural spine) becomes shorter and disappears, the

metapophyses come to lie lower and control finally the form of the neural arch. This is among our fossils still well preserved. Also the metapophyses disappear and the vertebral canal finally becomes an open sometimes diamond-shaped groove. See figures 16-23. The transverse processes rapidly becomes smaller posteriorly and finally disappear entirely; the vertebrae become barrel-shaped (round or oval in cross section); on the end of the tail sometimes they are box-shaped, with a rectangular profile.

In the lumbar vertebrae and sometimes in the posterior thoracic vertebrae (*Acrodelphis* species) a groove can be seen in the vertebral centrum in which the segmental artery ran – to compare with the intercostal artery. In the caudal vertebrae this groove is usually easily seen. According to Slijper (1936) these grooves in odontocetes run in the lumbar vertebrae and in the anterior caudal vertebrae along behind the transverse process. After that they go through the transverse process. In the primitive whales and the baleen whales they run in the lumbar vertebrae also posterior to the transverse process; in the first caudal vertebrae however it goes in front of and later through the transverse process. Now this simple pattern must always occur in the fossil whales. In both types in each case the artery is picked up by the vertebral centrum with the disappearance of the transverse process; which causes the typical foramen of the side angles of the caudal vertebra.

As from the figures appearing above, the processus is practically always missing in the fossil vertebral remains. Only the posterior caudal vertebrae are always well preserved because there was nothing to break off. Although this consequently is always true of most specimens, they will never serve for identification. They should be assigned to "primitive and similar forms" as a specific characteristic. It is important, that just these vertebrae were found isolated by preference. Of the fossil whale tails one knows little.

THE VERTEBRAL CENTRA

Concerning the idea of definition we direct this description of a vertebra from the middle of the column, consequently posterior thoracic vertebra or an anterior lumbar vertebra. The more typical forms anterior and posterior on the column we leave out of consideration.

A typical whale vertebral tantrum is properly composed of three bone pieces, namely the vertebral centrum, in sensu stricto and the two epiphyses. These last are attached to the anterior and posterior surfaces of the vertebral centrum as flat round bone discs. Between the vertebral centrum and the epiphysis lies in the living individual a layer of cartilage which provides for the lengthening growth of the bone. At a later age after the cessation of lengthening growth, the epiphyses fuse to the vertebral centrum, the anterior ones first. The term vertebral centrum is thus used in general in two senses: the vertebral centrum with or without epiphyses or with one epiphysis can be meant. Sometimes this arrangement can be especially confusing in fossil material where the epiphyses are missing. Further we consider the vertebral centrum still the beginning of the transverse processes and/or the beginning of the neural arch. This is summarized in figure 24 and 25.

If we see a vertebral centrum from above, then we see the bottom of the neural canal. In the middle of this a crista (crest) can be poorly or more clearly visible. Next to the crista two depressions are usually situated. In many vertebrae the crista is missing, however. Next there are two vascular openings lying in the middle of the vertebra at the foot of the neural arch. Sometimes one of the two is more strongly developed than the other, often there are in front of and behind the middle yet more openings to be seen. This is true, however, of the former. From these openings run two vascular canals which form the beginning of a relatively small vascular

system, typical of whales, which in whales so far known to us has not yet been described. These vascular canal openings, as shown in figure 27, run out into a cavity precisely in the middle of the vertebral centrum. We have named this cavity the sinus centralis.

Often and especially in caudal vertebrae, one or two vascular canals run out of the sinus centralis near the ventral side of the vertebra. Further we see, in vertebrae which are broken in the right direction, still more small vascular canals running in all directions from the sinus centralis. We have the impression, that this system plays a greater role in young vertebrae than in older where often they are obliterated. Possibly this is a modification of the transvertebral venous system as described by Breschet (1827) and Vonwiller (1923). See figure 28.

Near the posterior the neural canal is always smaller. The outlets of the vascular canals become progressively always closer to one another to lie in the angle between the two vascular canals, which is progressively smaller. Mostly in the posterior lumbar vertebrae, one of the canals is much smaller than the other. Again further near posterior is there still only one canal with an outlet in the middle. At the same time in the caudal vertebrae, consequently - something striking can happen. The vascular canals anterior and posterior to the central canal become prominent; the central vascular canal itself can disappear and there arise a new V-shaped vascular system on the V further to the front. See figure 29.

In some types of vertebrae, both vascular canals also originate in front of the vertebral column directly next to the crista, thus close to the median line. This concerns then mostly vertebrae with a relatively small vertebral centrum with broad robust neural arches. See figure 31. In figure 32 finally we see the vascular canal openings in the neural canal of a caudal vertebra.