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*On the zeuglodonts of Egypt and the relationship of archaeocetes to other cetaceans**

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On the zeuglodonts of Egypt and the relationship of archaeocetes to other cetaceans

By W. Dames

Berlin

The first report on the discovery in strata of similar time periods in North Africa of zeuglodonts common to the cetacean family of the Tertiary stratum of both hemispheres dates back nine years to the samples collected by Professor Schweinfurth on the western island of Birget-el-Qerün¹ in Fajum (Egypt) and donated to the Museum of Natural Science in Berlin. I described this find and the geological construction of the same island (the last part of Schweinfurth's discussion) in a proceedings report of the Royal Prussian Academy of Science in Berlin (1883, I, pp. 129 and following). Schweinfurth's samples comprised fragments of skulls, vertebrae, and ribs, which nonetheless were insufficient to answer the question as to whether zeuglodonts were related or unrelated to other, yet-undiscovered species. Nothing was presented regarding the presence of teeth, which is given deemed essential in the present work. The most interesting part was an especially well preserved axis, which is demonstrated to prevent head movement in living cetaceans. This will be described here and illustrated for the first time.

Schweinfurth's own reports of the discovery of additional remains have already been published.² Schweinfurth describes:

“Roughly over the bottom third of the geological horizon of the AAAß of the Mokattam site³ there emerges a violet-colored marl layer, which is distinguished by its wealth in animal vertebrae. Nonetheless, in Mokattam these are very scattered and separated. On the mountain where I dug, which was located

¹ Dr. Schweinfurth used the spelling Qerün is used by Dr. Scheinfurth (instead of Qurtün) in recent publications.

² *Zeitschrift der Gesellschaft für Erdkunde zu Berlin*, Bd. 21, 1886, p. 139.

³ For a description and discussion of the arrangement of the Mokattam Tertiary near Cairo, see Schweinfurth, “Ueber die geologische Schichtungslieferung des Mokattam bei Cairo (*Zeitschrift der Deutschen geol. Gesellschaft*, Bd. 25, 1883, p. 709).

12½ kilometers west of the old temple buildings (how can we best describe such sizes?), which constituted an isolated extension of the residue line of the third layer that could be comfortably approached from all sides, I made important bone finds.⁴ One involved a zeuglodont lower jaw with five teeth and the two jaws of another creature resembling a pig or a tapir, which in many aspects resembles Cuvier's *Choeropotamus*, but is of double the dimensions.”⁵

Together with this, there are two vertebrae from the eastern island of the Birket-el Qerün that are indistinguishable from those found on the ¶ mountain.

Through investigation of the vertebrates found together with the zeuglodonts (with the exception of the fish remains), I was, as indicated on page 153 of my above-referenced report, convinced that “the western islands of Birket-el-Qerün, by reason of their vertebrate remains, belong to the sub-Tertiary level.” It remains unclear, however, as to whether they can be deemed Eocene or Oligocene. A determination of the exact age would have to be made through consideration of the mollusks that had appeared with them. Mayer-Eymar's work to this effect, however, allows us to conclude only that these sub-Tertiary deposits are younger than Egypt's nummulites. This most likely indicates upper Eocene or Oligocene.⁶

In the following work, I will provide a description of the new find and several earlier ones and, as a supplement, I will deal with such double ribs from the zeuglodonts of Alabama. This will be followed by an assessment of the genus and species as well as a comparison with those of

⁴ Both the old temples mentioned in Obigum and the ¶ mountain appearing on the map of the depression area near Fajum appear on the map included in the article cited above.

⁵ The two above-mentioned fragments, which are related to a hoofed animal, proved through closer examination to be related to the *Zeuglodon* lower jaw fragments. They form the front part of the jaw that carries the incisor, canine, and premolar teeth.

⁶ K.A. Ziitel. Beiträge zur Geologie und Paläontologie der libyischen Wüste und der abgrenzenden gebiet von von Aegyptin. (*Palaeontographica*, Bd. 30 I 1993 pg. CXXVII); Mayer-Eymar, Die Versteinerungen der tertiären Schichten von des westlichen Insel im Birket-el-Qurün. See (Mittelägypten), ebenda p. 67, t. 23.

other regions, and finally a discussion regarding the systematic position of the zeuglodonts overall. which briefly draws upon the work of d'Arcy W. Thompson.⁷ As an appendix, there will be some remarks on fragments of skin covering found with the zeuglodonts.

I. Description of the fossil remains

Schweinfurth's zeuglodont findings in Fajum consist of fragments of premaxilla, a completely developed lower jaw, and a number of vertebrae.

As a point of comparison for my studies, I had at my disposition the zeuglodont collection that was used by J. Müller. Since my initial presentation, these have been moved following the dissolution of the last geological-palaeontological collection of the Royal Museum of Natural Science. Thus, all is now fully accessible to me, and the difficulties previously discussed have been eliminated. It was especially important for me to be able to compare some fragments mentioned by J. Müller, which are now in the Teyler Museum in Haarlem. Dr. T. C. Winkler was so kind as to give me extended access to these, and I express herein my gratitude. I am also grateful to Mr. Geheimrath, Dr. Mobius, and Dr. A. Nehring, who gave me access to cetacean and pinniped materials in the collections they curate in the Royal Museum of Natural Science.

1. Premaxilla fragments

One finds two very badly-preserved pieces of left and right premaxillae, which, due to their size probably belonged to one individual animal. Given the size, we can assume that this individual was the same animal whose lower jaws are described below. The left premaxilla bone

⁷ On the systematic position of the zeuglodont. (*Studies from the Museum of Zoology in University College, Dundee*, edited by d'Arcy W. Thompson, N. 9, Dundee, 1899.) The contexts were originally presented at the Congrès International de Zoologie in Paris 1899 under the title: "Faut-il associer les Zeuglodontes aux Cétacés?"

fragment has a length of 170 mm, and a height of approximately 35 mm, and a flat, curved surface. We find 3 alveoli of approximately 25 mm and gaps of equal size. In the front and rear alveoli, there are remnants of teeth, the middle being empty. The tooth of the front alveolus is laterally compressed to a length of 15 mm. The fragment of the rear tooth reveals an elliptical cross section, but is broken off beyond the alveolus. 15 mm of the tooth of the front alveolus have been preserved, and this is shown to be laterally compressed. The fragment of the rear tooth reveals an elliptical cross section, but it is broken off beyond the alveolus. Behind the alveolus are shallow holes where tips of teeth came to rest when the jaw was closed.

The premaxilla bone of the right side is only 120 mm long, and its surface was completely split and torn. It carries two empty alveoli, which are consistent with the second and third of the left side.

2. Lower jaw

A left ramus of the lower jaw is nearly intact and has most of the teeth, It represents the most intact part of the skeleton find. Missing are only about a third of the lower border, the rear border, the mandibular condyle and the extension of the crown. The rear part has been deformed through pressure over time, and thus appears narrower than it originally was. Moreover, the front end is broken off by a few millimeters, as is consistent with the state of the first alveolus.

Plate I [XXX] depicts in actual size a lower jaw ramus. It demonstrates a steady increase in height from front to back, the first preserved tooth being 30 mm, the first double-rooted tooth measuring 45 mm, and finally the last tooth of the lower edge measuring 90 mm. The height of the crown extent could not be determined. On the exterior, the surface is slightly curved. The top margin is broad and thick in front and increasingly diminishes towards the rear, so that the last

teeth appear perched on a sharp ridge. On the inside, the surface quality reveals two distinct parts. A front section, which reaches from the tip to under the front edge of the first double-rooted tooth, has a rough surface and is broken by 3 indentations. A rear section with its flat curvature and smooth surface is similar to the outside. There is no doubt that the front, rough section shows the length of the symphysis in which the two lower jaw rami articulated and formed the last, smooth part of the free ramus. When we consider the above-described lower-jaw half and the place where the two parts meet, it is easy to recognize, by the ever-so-slight deviation from a straight line, that the animal had a remarkably narrow snout, which is also evidenced by the position of the alveoli.

On the upper jaw, one finds the alveoli for 11 teeth, of which 7 have been preserved. The teeth and their alveoli fall clearly into two groups, a front group with 5 single-rooted teeth and a rear group with 6 double-rooted teeth. The alveolus for the foremost tooth, which is clearly perceivable from the inside, is only 15 mm deep and slants from bottom to top. Their demarcation is such that they are, to a certain extent, cut away from the symphysis so that both front teeth hit directly on each other. After a 12 mm gap, one finds the second alveolus with an elliptical edge, whose longitudinal diameter measures 22 mm. It still holds its tooth, which has been laterally compressed and rounded in front, and whose cone is crumpled backward. Upon reconstruction of the tip that had been broken off, this would have had a length of 30 mm. This alveolus is somewhat separated from the symphysis border. More important are the next three alveoli, which appear at regular intervals on the outer side of the jaw. Measuring from the center of the inner edge of the alveoli to the symphysis border, one finds the following distances:

For the	second alveolus	5 mm
“	third	“ 9 mm

“ fourth “ 12 mm

“ fifth “ 16 mm

Thus, one finds an average increase in distance of 4 mm. The last alveoli for single-rooted teeth are empty; they all reveal the same elliptical cross-section. Also, all are of approximately the same size, namely a length of 25 mm and a diameter of 15 mm, so that the form and size of the teeth belonging to them were the same. Inasmuch as the alveolus of the second preserved tooth revealed the same form and size, one can assume the teeth from the three empty alveoli were of the same configuration. Between two alveoli, the jawbone is almost pressed into a semi-circle, so that the alveoli themselves seem to lie on ledges. This pressure would only have served to provide the teeth of the upper jaw room on the side of the lower when the jaws were closed. The teeth of the latter were reversed in similar indentations in the palatal region so that both rows stepped into alternate position.

The separation among the individual alveoli remained the same, namely 20 mm, and the same is the case of the distance between the last single-rooted tooth and the first double-rooted tooth.

The first double-rooted tooth is no longer on the side, rather on the upper ridge of the jaw ramus. At this point the symphysis begins and the branches start to diverge. This can be explained in that the teeth on the symphysis are leaving space for the tongue. At the location of the following teeth, any branching off to the side would be superfluous. The tooth has a long elliptical cross section of 35 mm in length; its crown, when taking into account the broken off part, consists of a 25-mm-high triangle, whose front side is constructed with a sharp brim, and where two small tips appear at the same interval. The longer rear side has four big, round tips, of which the lowest appears smaller than the others, which are of the same size. The jaw ridge

subsides behind the alveolus of this tooth into a recess which has been filled with rock and measures 10 mm. Thereafter begins the closed row of the last five teeth, which follow the rise of the jaw ridge, so that the last tooth is the highest.

The first tooth of this row is 45 mm long and 50 mm high⁸ On the front side, there are three denticles, which, although stronger than the teeth in front, appear weaker than the rear teeth. These get smaller as they go from top to bottom. Right next to this tooth there is the second tooth of this row of almost the same dimensions as the first. It is quite different, however, in that the tip of the front section reaches that of the back. In both front and back there are 3 denticles, even though the upper portion of the front side has been considerably eroded. It cannot be determined whether there was a fourth denticle here, which is likely. The third tooth of the row has weaker contours than the previous. The same is true of the remaining two teeth. A glance at Plate I [XXX], Fig 1 shows that, if one draws a line over the tips of the front and rear denticles, the front is at a more obtuse angle than the rear. The last remaining teeth show a greater distinction between the front and rear sides in which the front is more perpendicular and thus forms a right angle. The third-to-the-last tooth is 30 mm long and 25 mm high. Its front side is smooth and rounded; on the rear side there are 3 denticles, the first is broken off and is evidenced by a furrow on the surface of the tooth. The second is strongly developed and cut by deep incisions from top to bottom. The third, although just as strong, is smaller than the second one and lies so close to the front side of the next tooth that it reveals a longitudinal furrow.⁹ The second-to-the-last tooth is quite different than the third in that the front side is no longer like a ridge, but rather, seems to consist of a slope. From the tip there is slope to the inner corner of the

⁸ Here, as in the case of all teeth that follow, the length of the broken off, but easily reconstructable tips can be calculated.

⁹ The illustrations in Plate I [XXX] do not reveal the rear side of the third tooth, since this was uncovered following preparation of this Plate.

front side, and this is once again bordered by a ridge, which reaches only up to one half of the crown. On the almost-perpendicular and only slightly crooked front side, there are no denticles. Some 13 mm of the inner ridge, however, are somewhat dulled under the tip. On the rear side there are two sharp denticles divided by a deep indentation. Both are about ½ the size of the main cusp. The last tooth shows evidence of being truncated and is more developed than the second-to-the-last tooth. It is bordered by the following ridge up to the point at which its tip has been broken off. There is a small protuberance and a small break, which indicates a cingulum. The rear side has three powerful, sharp denticles of the same size, that are separated by the indentation. The dimensions of the last of the two teeth are almost the same, namely, 25–28 mm in length by 33 mm in height.

The teeth described above are the most complete set of the lower jaw of a zeuglodont ever discovered. It thus deserves special attention in that it fleshes out prior missing or incomplete information. We will now discuss the number of the teeth. The tooth formula of zeuglodonts has been described differently—Lydekker¹⁰ and Zittel¹¹ opted for 3.1.5/3.1.5 while Döderlen¹² has 3.1.5-8/3/1/5-8. The first tooth formula is only seen in the widely disseminated discussions of the skull of the small zeuglodont from Alabama, which has been thoroughly described and depicted by J. Müller¹³. This skull has 3.1.5 teeth. Whether the lower jaw had the same number has not been proven, although it is likely. This formula is hypothetical and only refers to the three forms identified by J. Müller—*Zeuglodon brachyspondylus* when it was of an early age. J Müller leaves it uncertain as to whether the number of teeth increased as the animal grew and reached that of the *Zeuglodon macrospondylus*, where there were at least 6 molars. Finally, in the

¹⁰ *Catalogue of the Fossil Mammalia in the British Museum (Natural History)*, V. p. 49.

¹¹ *Handbuch der Paläontologie*, IV, p. 367.

¹² *Elemente der Paläontologie*, p. 705.

¹³ Ueber die fossilen Reste der Zeuglodonten von Nordamerika mit Rücksicht auf die europäischen Reste aus dieser Familie, p. 31, t. 26.

smallest of the three types—*Zeuglodon pygmaeus*—there were eight double-rooted teeth above, and probably below. Dörderlin's formula for the zeuglodont species assumes that the lower jaw had 11 teeth. The above allows us to determine with certainty that the species *Dorudon* must be considered together with or included with the zeuglodonts. Neither of these, regardless of whether the number of their teeth is certain or is estimated, is the same as the others.

The same that can be said for the number of teeth applies to the proportion of teeth and their distribution among incisors, canines, and molars. The assumption that three incisors were present has only been proven by direct observation of the small skull of the *Zeuglodon brachyspondylus*. Whether this number also applies to the lower jaw has not been decisively determined. J. Müller's illustrations (*I.c.* vol. 26, p. 1) clearly show to the left of the snout the alveoli for four single-rooted and one double-rooted tooth in the lower jaw. It is impossible, however, to determine whether one was for the first incisor. There is no indication of the number of molars. The same can be seen in the incisors in the lower jaw, which also appeared in American zeuglodonts, as well as in the descriptions of J. Müller (*I.c.* vol. 22, pp. 5–6) of the front part of the lower jaw described by Emmons in *American Quarterly Journal of Agriculture and Science*, Vol. III, 1845. Here it is even more difficult to make a determination because, although the criteria as to which teeth were canine are present in the upper jaw behind the seam between the upper and middle jaws, they are lacking altogether in the lower jaw. We only know that the single-rooted teeth are all incisors and canines while the double-rooted are molars. For the Egyptian lower jaw, the concept of three incisors no longer applies. There are five single-rooted teeth, and if we assume the last to be a canine, that would leave four incisors. The most frontal of these, at the point of the snout, is placed on an oblique angle, moving outward from bottom to top. This would be an explanation of the set of teeth we are dealing with here; a second

explanation results from the acceptance that not all of the cheek teeth are double-rooted, the most frontal being single-rooted, as in the case with the higher number in *Squalodon*. Then the fourth single-rooted tooth would be a canine and the number of the incisors would be in accordance with what has been already described. A pair of teeth depicted by J. Müller (*l.c.* vol. 23, p. 4) appears to correspond to this. These teeth comprise a single-rooted and a double-rooted tooth next to each other in normal position. The front tooth has all the characteristics of an incisor or canine, but it is more conical than the last teeth and has a rudimentary denticle on the rear ridge. We can consider this to be an example of the general tendency towards simplification and towards the conversion of the cone formation of the recent odontocetes and the advancement of molars. However, this is of little consequence since, in the case of Fajum, the crowns of the analogous teeth are missing on the lower jaw. It is thus impossible to determine whether such a process is at play here. Moreover, such a case cannot refute the nature of the canines, since similar denticles are found in many carnivorous canine teeth.

It is so accepted that zeuglodonts necessarily existed and that the simplification of the front molars facilitated their conversion into early squalodonts. It is risky, however to classify a single-rooted tooth as a molar. Therefore, I posit for the first time that the Egyptian zeuglodont had four incisors. The tooth formula must thus be changed. The placement and direction of the first incisor allow us to state that it was very close to its neighbor on the other side, forming the tip of the snout. The upper, front incisors were somewhat further apart from each other. Thus, there were three incisors on each side of the top and four incisors on each side below.

Moreover, a glance at Plate I [XXX] shows how great a difference there is in the formation of the molars. We immediately see that the six molars fall into two groups of three teeth each, of which the frontal group is more isosceles in nature, the rear almost forming a right-angled

triangle. Both groups also differ considerably in their dimensions; the three front ones being notably larger.

Inside the front group there is a division into two parts, namely between the front one and the back ones. The front tooth is separated from the back ones by a short diastema and is smaller. Moreover, the rear ridge has clear denticles while the front ridge is smooth. The two rear teeth are notably bigger, touch each other directly, and have on both ridges fully developed denticles of the same size.

The second group consists of the three last teeth. They are all of approximately the same size, but are considerably smaller than the above-mentioned. They have no denticles on the front side, and are not tapered from top to bottom as is the first tooth of the first group. Rather, their lower portion is broader. Finally, the last tooth in this group has the above-mentioned protuberance and a weakly-formed cingulum on each side, which, although not well developed, is also found in the remaining two teeth.¹⁴

The sharp separation of the 6 molars into two groups of three teeth causes us to question whether there is not a division into molars and pre-molars. My belief in this assumption is based on the following grounds: The similarities in form of individual teeth of both groups contrasts with the sharp differences among them; there appears to be no gradual progression. The last three molars suggest that, for the most part, by reason of their widening at the front, their cingulum, and their protuberances, they are the closest of all zeuglodonts to land animals. If we consider zeuglodonts to be land animals, which will be argued below, it is essential that the molars were

¹⁴ There is a much narrower, but clearly detectable edge, which also envelops the enamel base of the teeth of the front group and can be deemed a rudimentary cingulum. I have discussed this below. I have examined the cheek teeth of the American zeuglodont and found, as can be expected, traces of the same. This is particularly clear in the right haft of the double-rooted teeth described by J Müller (*l.c.*, vol. 12, p. 2) at the point where there is an *a* next to the figure and following the hem from this point upward; and on another tooth, which was not depicted, the same occurs on both sides from the lowest denticle upward, as is the case with the last of the frontal protuberances of many carnivorous canine teeth are similar.

protected during the gradual process of simplification, which extended from front to rear. This will be dealt with at greater length. At this point, we can only suggest the likelihood that the difference between both groups of cheek teeth is most likely a separation into molars and premolars. J. Müller and Wortman have demonstrated that second dentitions are characteristic of zeuglodonts. We have not yet discovered rows of teeth which are completely intact which will allow us to arrive at a definitive conclusion. J. Müller did also not ignore the difference between the front and rear cheek teeth. Most parts of the pieces which reveal the greatest portion of the rows of teeth are mostly broken at the crown. Nonetheless, it is still clear that the differences reveal that the three rear teeth of the upper and lower jaw are much thicker than the front ones. J. Müller (*l.c.* p. 31) states: “The 3 rear cheek teeth lie closer behind each other...”¹⁵ –“Between the rear-most teeth of the upper jaw there are no breaks or impressions.” He believed that age differences were the explanation. On *l.c.* p. 15, he writes: “In general we can assume the likelihood that such positioning of the teeth vis-à-vis the jaw was characteristic of a not yet fully-grown animal, in cases in which the teeth touch each other.” A few lines down on the same page, he writes, “We can deem jaws in which the cheek teeth touch each other closely to be those of a non-fully-grown animal.” It is explained that in all previously-studied specimens in which the cheek teeth can be clearly observed, it is unclear as to whether the teeth would further separate from each other as the animal developed. The existence of pulp holes also suggests that these had existed for a long time and not that the animal found was not a child. I finally believe that one can make yet another claim from the Egyptian lower jaw, which also corresponds in dimension to the ribs found belonging to the same animal. There is no evidence that the animal was a juvenile. All previously-made observations have indicated that it was an adult.

¹⁵ This is not clear. See drawing (*l.c.* vol. 26, p.).

We are still hindered at arriving at a tooth formula for zeuglodont species, since the jaw fragments with teeth, including the one described above, are all fragments and suggest combinations that cannot be directly observed. Moreover, it has been seen that for each zeuglodont species there is a different formula. For *Zeuglodon macrospondylus*, we have 9-10:7-8/9-20; 7-8¹⁶, for *Zeuglodon brachyspondylus*, we have 3-1-5/3-1-5, for *Zeuglodon pygmaeus*, we have ?-?-8/?-?-8, and none of these fit the Egyptian lower jaw, which is characterized by ?/4-2-6. Or, if we assume the above division into premolars and molars, it will be expressed as ?/4-1-3-3-. How these differences can be best explained as well as what they suggest will be discussed as follows. No overarching formula for zeuglodonts has been found.

As a conclusion to the description of the lower jaw find in Fajum, we must emphasize the presence of the giant mandibular foramen, which is explained by damage to the lower jaw. From behind, compression has made the lower jaw thinner than it really was. The front remains as it was. We find that the preserved part of the crown appendix and the part bearing teeth are solid. Everything else is filled by a red gypsum and rock-salt substance. Up through the third double-rooted tooth, the alveoli foramen can be directly observed. And through its circumference, it can be assumed that it must have continued until under the first double-rooted tooth. In this respect, it is completely connected to the American type.

3. Vertebrae

a) Cervical vertebrae

In Schweinfurth's second discussions, there was nothing regarding the cervical vertebrae of the zeuglodont. Thus, the axis I mentioned earlier remains the only existing find of this kind. I have not appended my earlier description. I am repeating it word by word. I am supplementing it

¹⁶ This was not observed by J. Müller but instead was estimated. It is too high.

with the illustration in Plate II (XXXI) and am comparing it with a description of an American axis, which J. Müller (*l.c.* p. 33) briefly mentioned.

My earlier description (*l.c.* p. 132) claimed, “The greatest interest in the axis, comes from the fact that, with the exception of one fragment mentioned by J. Müller (*l.c.* p. 33), it is the first recognized as belonging to zeuglodonts and provides information regarding the construction of the neck region of this animal. The same coincides in size with that of Müller (*l.c.* Plate XIII, Fig. 1 and 2), particularly with regards to the oblique oval of the surface of the joint, which is well preserved on the right side. The body of the vertebra is short and compressed: from the tip of the odontoid process to the rear ridge of the surface of the joint and is, in the case of the third cervical vertebra, 95 mm long. The odontoid process is short and blunt, 49 mm long and has a long oval recess on either side of the tip, as is the case with a number of carnivores. Underneath this extension there is a narrow, smooth elevation which rises like an embankment or a quill, which connects the right and the left atlas joints. The transverse process, as well as the upper curve, are broken off and, regarding the first, we can recognize from the place of breakage, that it stood vertically and was narrow on top and wider on the bottom. At the spot where the atlas joint of the transverse process diverts from the center of the vertebra, there is a 5-mm-wide indentation, which slants inward at a diagonal, and which widens and touches from behind the joint of the third cervical vertebra, but still rises as a transverse process, widening by 9 mm. The rear joint is smooth and concave, ca. 75 mm high and 80 mm wide (about the same dimensions as what Müller found, especially in the lower half—with cushion-like edges, which are separated by a pointed, and relatively deep incision.) The surface of the joint stands on a vertical axis with its upper part forward, and its lower part towards the back.”

From the sloping placement of the joint surfaces, it can be deemed that zeuglodonts could lift and lower their head and were thus distinct from cetaceans, I believed that these characteristics together with the form of the teeth suggested a closer relationship with seals. I abandoned this idea, as discussed below, after I had the opportunity to further study my material and to compare it more completely with pinnipeds.

J. Müller only was able to be familiar with a fragment of the axis, which was described in the supplement to his work and was sent to Europe with Koch's collection. Regarding this, he stated that the width of the somewhat conical rear surface of the vertebra body must have measured 3" and that the transverse process was not at the base, but rather, on the side and that it had no recesses. The front surface had an especially low odontoid process dropped behind the side surface of the joint. This description can only be based on a fragment that I have studied in the Teyler Museum. Aside from this fragment there is a second one in the local collection where one also finds the third cervical vertebra. J. Müller does not deal with these two vertebrae at all, although they are especially important for an understanding of the cervical vertebrae. Only upon receipt of the specimens could one determine whether they were first found in mineral and subsequently prepared or whether they were acquired separately. As a supplement to J. Müller's discussion and as a comparison with the axis from Fajum described above, I have depicted the American fragment [Plate III, XXXII], figs. 1 a and b, Plate IV [XXXIII], Fig. 2) and explained these depictions through peculiarities that distinguish them from the first one mentioned.

The odontoid process is significantly shorter and wider; even if the piece is also rather worn down with the extension of the same appearing narrower than it originally was, there still remains a noteworthy difference in size. The sharp tip of the front side of the tooth extension is almost even. The joint surfaces for the atlas, in contrast, are similar in formation and are of

relatively the same size. The same is true of the transverse processes, which extend at the same height, and as best as can be determined, are of the same size. The size of the foramen, particularly of the Egyptian axis, which has a front diameter of 5 mm, is strikingly different from the American one, which is 55 mm.¹⁷ Moreover, this foramen gradually developed from an early canal form to a later conical depression on the backside. Thus, the foramen here only shows a thin border. The rear joint surfaces are alike in size, form and the slanted placement on the vertical axis and differ only in that *Zeuglodon brachyspondylus* has a more pronounced cushion-like thickening and the median incision is deeper. The backside view in Plate III [XXXII], Fig. 1 does not show this incision since the lower border is damaged. Thus, we would still doubt as to whether American zeuglodonts even had such an incision at all if the size did not correspond to the axis of the Teyler Museum¹⁸. The preserved axis of the lower portion of the right half of the spike extension is compressed from front to back; it bends backward directly after the truss.

b) Lumbar vertebrae

Through Schweinfurth's new collection of 1886, we have been able to add two lumbar vertebrae and two caudal vertebrae to the earlier material of breast and lumbar vertebrae that I have reported on (*l.c.* p. 131). The former two and one of the latter are depicted in the Plates of this appendix.

The vertebrae depicted in Plate V [XXXIV], figs. 1a and b apparently belong to the rear lumbar region, which is determined by their shortness and the positioning of the branches of the upper curves. The fact that these belong to a fully-grown animal is evidenced through the solid development of the epiphysis centering on the frontal side. Also, the rear side reveals fragments

¹⁷ One can state without a doubt that the only broken-off fragment from which J. Müller determined that the transverse process had no holes is inadequately preserved.

¹⁸ Also, a second axis fragment from the same museum clearly shows the median incision.

of the epiphysis on the lower and right-side borders, while the remaining portion reveals the radial, rough furrows and ridges of the surface of the epiphysis-like cetacean vertebra. The front and hind sides have almost circular borders (height = 120 mm, width = 125 mm) and are also almost even. They are only slightly depressed in the middle. On the upper side, the placement of the neural spine is clearly preserved. The length of the vertebra, including the front epiphysis, measures some 90 mm. These clearly are on the front border and end at a distance of 30 mm from the rear border of the center, without touching the epiphysis. Their width at the base is 15 mm; between them, there is a space of 45 mm, which goes up to a convex longitudinal border, next to which there is an oval recession, which is neither strictly symmetrical nor consistent in size. The lower side is concave at an angle and reveals in the middle two asymmetrical holes of unequal size. While the right recession is bigger here, on the lower side, the left recession is bigger. There is a third small equally oval recession in the median. The broken-off transverse process, however, lies directly against the lower border. We see that they are slightly turned forwards and backwards, and that they occupy almost all of the length of the centrum of the vertebra, without taking into account the epiphysis and are of a regularly elliptical cross section. (Length 46 mm, diameter 25 mm).

The vertebra described is very similar to the one in Plate VI (XXXV), figs. 1a- c, which through the deeper placement of the transverse process, shows smaller size and length somewhat further behind in the row of vertebrae. It is possible that this belonged to a not-yet-fully-grown animal, since there is no longer a trace of the epiphysis. The age difference between the two individuals, whose vertebrae are depicted in Plates V (XXXIV) and VI (XXXV) is not so great, as evidenced by size. Also, the lack of an epiphysis, which appears at different times in different

individuals, is not enough reason to draw this conclusion. A complete description is superfluous, given that the size of the vertebra is enough to determine difference.

c) Caudal vertebrae

G. Schweinfurth collected the two caudal vertebrae described below together with the above-mentioned lumbar vertebrae in his layer B of Birket-el-Qerün, which is called El Kenissa on the map of the lengthy report. They correspond in size to the lumbar vertebrae found at the same site. Thus, they most likely belong to the same individual. It would be of particular interest to prove this, since it would shed light on how different in a single individual the joining of the epiphysis with the center can be; there is, as expected, no trace of this on the lumbar vertebrae; on the caudal vertebrae, the entire length of the epiphysis is fused to the center. Even if the lumbar vertebrae did not belong to the same individual as the caudal vertebrae, the three vertebrae show that the joining process does not happen at the same time in individuals of the same size. Although different, they doubtless belonged to two animals of the same size.

The stone containing the three vertebrae is the same red, solid tone with shell fragments, which are also to be found on the island of Birket-el Qerün referred to on the above-mentioned map as Gesiret-el Qern. G. Schweinfurth identifies them on the labels of the collection as stemming from the middle (B) of the three layers, in which the above-described cetacean remains were found.

The caudal vertebra depicted in Plate VII (XXXVII), Figs. 1a–c is slightly smaller than the above-mentioned lumbar vertebra (height 75 mm, width between the transverse processes 90 mm, length 65 mm, the positioning between the two branches of the of the neural spine, measured in the center, 20 mm.) From the measurements, it is evident that the vertebra was

somewhat wider than it was high. In contrast it was nearly as long as tall. The transverse processes emerge from somewhat above the lower border. They have a pear-shaped cross-section with the thicker portion at the bottom, and have a vertical furrow of 6 mm in diameter, which is characteristic of caudal vertebrae. The center is slightly concave between the upper curves and the transverse processes. The middle of the lower side is bordered by two slight elevations, between which there are two perforations of unequal size, separated by a narrow barrier. The side portions are between the elevations and the transverse processes, and are just as concave as the side portions of the former. The stumps of the branches of the neural spine take up almost the whole length of the center. At the rear, they do not entirely reach the border. Between them and somewhat in back of the middle, there is an undivided indentation of 7 mm length and 4 mm diameter. The rear side is even. The front side is badly damaged, but it has nonetheless certainly had the same form.

Since the pedicles of the neural arch have a somewhat larger interval than the second vertebra described below, it must have lain before it in the spinal column.

The other caudal vertebra is so similar to the first that it is only necessary to point out certain differences. The dimensions vary only slightly (height 80 mm, width between the transverse processes 75 mm, length 65 mm, intervals of both pedicles of the neural arch—measured in the middle of the center—16 mm). The difference mainly lies in the somewhat increased height and smaller intervals of the branches of the upper curve. From this, we can see that the transverse process emerges slightly higher from the side. The size of the upper and lower indentations is also somewhat different. Both are oval and of approximately 14 mm in length and 10 mm in diameter.

It is impossible to determine the exact nature of the furrow of the transverse processes, since these are broken off. Of equal importance are the narrowness of the medullar canal, the placement of the transverse processes, and the concave lower side which belongs to the front portion of the row of caudal ribs. This front side has arches. The rear portion has neither arches nor transverse processes.

II. Comparison of Egyptian zeuglodont remains with those from other places

In my earlier publication about the presence of zeuglodonts in the African Tertiary, I was forced, due to the unusual nature of the material, to consider whether this was a totally new species or whether it could be identified as belonging to something that had already been described. I had divided the first finds into a larger and smaller species, but had mentioned that they were similar to other types in the same way that Gaudry had done for *Zeuglodon macrospondylus* and *Zeuglodon brachyspondylus*. I have further discussed the new finds above, and have found that there are no pieces that could possibly belong to the "species major," since the vertebrae belong to fully-grown animals, yet which are similar in size to *Zeuglodon brachyspondylus*. I studied the vertebrae described in *l.c.* p. 131 again. I also studied the twelfth lumbar vertebra from the skeleton taken by J. Müller so that it could be determined whether this vertebrae belonged to the others, between which it had been laid, which I now doubt, given that larger lumbar vertebrae have been found which correspond to the large dorsal vertebrae. This cannot be exactly determined until one finds a complete skeleton. We can determine, however, that the largest remains of Egyptian zeuglodonts do not reach the dimensions of the American ones.

The division of zeuglodonts into numerous types is so insufficiently proven that one must take special care in categorizing these types. What is of interest is their existence and their spread to older Tertiary times.¹⁹

Obviously, one must first consider the well-known zeuglodonts of America. A considerable amount has been written regarding diverse forms there, yet there has been nothing conclusive. While J. Müller divided them into two types (*Zeuglodon macrospondylus* and *Zeuglodon brachyspondylus*), there may have been as well a third type that could even have been smaller. Gaudry and I have argued that there is possibly a third and smaller size, and that diverse sizes could be due to sexual differences. Thus, it can be suggested that both in Alabama and Fajum there could coexist both a smaller and larger form. Leidy²⁰ is of another opinion and, with reservation, classifies the type with small vertebrae such as J. Müller's *Zeuglodon brachyspondylus* within the species *Dorudon serratus*.²¹ I am not in agreement here. The two forms from Alabama can be two types or two subtypes in any case. The formation of their teeth suggest that they are different from *Dorudon serratus*. In the local collection we have the gypsum casting of those described by Gibbes and J Müller (*l.c.* vol. 21, pp. 2–4). The determination is unclear. The main cusp is, in all actuality, at least 4 mm higher and also considerably more pointed. Moreover, the illustration shows the teeth to be curvier than they actually were. The height of the main cusp was also significant enough to distinguish the crown of *Dorudon serratus* teeth from the Alabama zeuglodonts. The same is true of the vertebrae. The branches of the latter are almost parallel, while branches of *Dorudon* diverge at an 80° angle. If

¹⁹ Lydeker has recently published a complete overview of all zeuglodont types. "On zeuglodont and other cetacean remains from the Tertiary of the Caucasus." (*Proceedings of the Zoological Society of London* for 1892. London, 1893, p. 561) in the comparison of the numerous types of zeuglodonts.

²⁰ The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. Philadelphia, 1869.

²¹ The species *Dorudon*, as seen from its name, was determined by the size of the teeth and not the vertebrae. See v. Zittel *(*Handbuch der Paläontologie*, IV. Pag. 168.

these teeth belonged to the skull variety, that Tuomey depicted and J. Müller (*l.c.* vol. 23, p. 1) subsequently copied, then one would have to consider the curvy forehead of *Dorudon serratus*, and the smooth forehead of *Zeuglodon brachyspondylus*. It remains to be seen if *Dorudon* and *Zeuglodon* are two separate species or if *Dorudon serratus* is a special type of zeuglodont. I would lean towards the first interpretation, recognizing that the skull studied by Tuomey and *Dorudon* teeth are of the same kind, since the high number of cheek teeth supports this hypothesis.

The Egyptian type of zeuglodont is connected to the typical zeuglodont type from Alabama; the same difference as between the tooth formation of *Zeuglodon* and *Dorudon* also applies to the first. Any eventual differences between *Zeuglodon brachyspondylus* and the Egyptian zeuglodont remain to be determined. Because of its size, *Zeuglodon macrospondylus* is not under consideration. None of the big vertebrae that I described in *l.c.* pg. 131) as belonging to the zeuglodont species are to be found in the later Scheinfurth collection.

Upon comparison of the two forms, two differences become evident; one concerns the tooth formula and the other the shape of the axis.

The tooth formula of the lower jaw of *Zeuglodon brachyspondylus* has not yet been ascertained. If we assume—as demonstrated by observation of the impressions of the tooth tips, that the number of teeth of the upper jaw and the premaxilla was the same as that of the lower jaw, then *Zeuglodon brachyspondylus* had /3.1.5 teeth, and the Egyptian one /4.1.6, thus one incisor and one molar more. Considering all four jaw halves, this gives for the first type a total of 36 and for the last type 44 teeth. There is a percentage relationship of 4:5. One can now ask what systematic importance this difference holds. The case of land mammals for which a tooth formula can be determined per genus and species, suggests that the above difference implies two

genera and two species. I thus believe that the difference in tooth count reflects more a difference in genus than in species. It is well known that in the case of marine mammals, odontocetes as well as pinnipeds, the number of teeth differ, and this increases with the tendency toward polydonty. As Flower has determined²², there are, for instance, 20 to 25 lower jaw teeth on each side in the case of *Physeter*, 9 to 12 lower jaw teeth for *Kogia*, “about” 30 for *Platanista*, 26-30 for *Inia*, 50-60 for *Pontoporia*. This is enough proof that there is not only deviation among individuals of the same genus, but also among closely related species of the same family (*Inia* and *Pontoporia* together with *Platanista* constitute the family Platanistidae). That is also the case with pinnipeds. Within notably narrower parameters, *Otaria* shows 3.1.6.1 or 2/2/1/4/1, thus 34 or 26 teeth. For *Halichoerus grypus* Nehring has found that on the top there are sometimes 5 and sometimes 6 molars.²³

From this we can determine that marine mammals are not as strictly bound to a specific tooth formula per genus or species as are land mammals. Whether zeugolodons are considered odontocetes or pinnipeds, differences in number of teeth among species is of secondary importance. Nonetheless, in the case of the species compared, it is so noticeable that it must be taken under consideration. Unfortunately, there is no comparison in the shape of the teeth, since

we have come across only incisors or roots, and no complete molars with a crown. As much as can be seen from the broken-off teeth, they did not have the above-described thickening of the front part on the rear teeth, and if the two teeth depicted by J. Müller (*I.c.*, vol. 23, pp. 4a, b) are the canine and molar, there is a very striking contrast with the casting of the front border, which here has very strong denticles, while the Egyptian type, as described, has only rudimentary denticles.

²² *Encyclopaedia Britannica*, Vol. XV, pg. 396.

²³ *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin*, 1883, pp. 107. Here there are also reports on *Callorhinus*, *Eumetopias*, and *Trichechus*, *Paläont. Abh.* N.F. I. (der ganzen Reihe V) Bd. Heft 5.

More important and decisive for the uniqueness of the Egyptian zeuglodont is the shape of the axis. As mentioned, its overall shape corresponds to that found by J. Müller in the American specimens. Nonetheless, it is quite different for reason of 1) a considerably more strongly developed odontoid process, and 2) a narrower measurement of the foramen transversarium. While the first characteristic assumes a freer head movement, the second implies a thinner vertebral artery. Thus, they are osteologically as well as anatomically different from the American type, which at least suggests a separation. Indeed, one could ask whether there are grounds to consider this a separate species based upon the characteristics of the axis. The last section will attempt to show that zeuglodonts of this type were mammals. I believe, without hesitation, that the zeuglodont of Fajum is its own species and is distinguishable from other varieties, and I name this species in honor of its homeland

Zeuglodon osiris

III. Placement of zeuglodonts in the mammalian system

Notwithstanding the time when the mammal nature of zeuglodonts was not yet recognized—which has been demonstrated by R. Owen and J. Müller—there has only been debate among zoologists and paleontologists as to whether pinnipeds and cetaceans were mammals. In v. Zittel's *Handbook of Paleontology*²⁴, the above-mentioned authors gave their opinions to this question, a discussion thereof would be unnecessary here. The majority of these points of view were only hypothesized and based upon one or another noteworthy characteristic. In recent years, however, zeuglodonts have taken their place among cetaceans in all handbooks or similar works in which cetacean fossils are discussed, as well as in special treatises devoted to

²⁴ l. c. IV, p. 184.

zeuglodonts. There remains no doubt as to their cetacean nature. When I began this study, I never thought I would have to include an entire section to this effect. However, this has become necessary due to a recently published work by d'Arcy W. Thompson²⁵, who has firmly argued for the pinniped nature of zeuglodonts for reason of their osteological and odontological characteristics. This needs to be proven or refuted, as I will attempt below.

As a first indication for the pinniped nature of the zeuglodonts, we must consider the number of teeth, which corresponds to that of *Otaria*, as well as the shape of the teeth. I have noted the fact that the number changes and is in fact larger. If d'Arcy W. Thompson deems the shape of the teeth to be only superficially similar to the *Squalodon*, this only an assumption since he had no material to work with. Under the circumstances, it is hard to tell from individual teeth whether they belonged to a zeuglodont or a squalodont. It is generally assumed in the case of the latter that the front has weak teeth while the rear has strong teeth. Such is also the case of the first double-rooted teeth of *Zeuglodon osiris*. On the other hand, the squalodont teeth of Malta, described by Scilla, as well as *Squalodon vocontiorum* of Delfortrie are equally strong in front and back (compare J. Müller's copy of the first *l.c.* vol. 23., p. 6) and these are so similar to *Zeuglodon caucasicus* of Lydeker that we could be convinced they belonged to a squalodont if this were not contradicted by the height of the lower jaw ramus. D'Arcy W. Thompson is unconvinced that cetaceans such as squalodonts definitely had teeth like zeuglodonts, and he therefore refutes such similarity. On the other hand, the similarity to pinniped teeth is not so great as one could believe. The difference between the teeth of zeuglodonts and that of pinnipeds is especially great. In the case of the latter, the canines falling between the incisors and the

²⁵ On the systematic position of *Zeuglodon*. *Studies from the Museum of Zoology in the University College of Dundee*, 1890.

molars²⁶ are more like those of a beast of prey and are sharp. The incisors remain, likewise, like those of a land carnivore; the molars reveal from front to back, as in the case of diverse species of seals, different forms. Zeuglodonts, on the other hand, just like odontocetes have incisors and canines of the same size and shape and are separated by diastemata. This is precisely the opposite of pinnipeds. The cheek teeth as well, as shown above, fall into two separate groups in one and the same jaw ramus. The only relationship which is present is the compression on the side and the multi-cusped crown of the molars of some but not all pinnipeds. Upon closer comparison, the similarity is thus not as great. Specifically, the relationship between the length and the thickness of the teeth is quite different. The case of *Phoca vitulina*, concerning the shape of the teeth, is closest to zeuglodonts. In *Otaria*, the secondary cusps have disappeared and there remain only small protuberances in front and in back of the cingulum; the teeth are relatively thick, the cingulum is strongly developed, and the denticles are only clear in the back. On the other hand, zeuglodont teeth are long, narrow, and mostly have denticles in front and in back, and the cingulum has become nothing more than rudimentary. The similarity that we find here and there in shape is a weak and inconclusive explanation for the occurrence of convergence, since they are phylogenetically insignificant.

The shape of the skull is another argument that d'Arcy W. Thompson puts forth to argue for the pinniped nature of zeuglodonts. He discusses the shape and placement of the nasals, the frontals and the parietals, which are reduced and lacking overlaying in the case of cetaceans. This difference is stressed too often. It is, however, clarified below that the noticeably sideways propagation of the frontals is arbitrarily likened to the apophysis that has been found in the frontal bone of *Otaria*. If the rear view of the zeuglodont skull is shown to be exactly the same as

²⁶ Lower molars are here, as follows, where nothing special is noticed, all the molars, premolars and molars thus, understood.

the frontal bone of *Otaria*, then it is doubtful as to whether it has actually been compared to an *Otaria* skull. At least it has been impossible for me to find more similarity between the sharp-edged, triangle-peaked back of the zeuglodont and the marked forward bend, which is separated from the rest of the skull by a furrow and almost semicircular in nature of *Otaria* than between any other mammal skulls. If Thompson further assumes that the occipital condyles of *Otaria* and bears are more separated than in the case of *Zeuglodon*, then this is also unfounded. One of the *Otaria ursina* skulls that I have found, which measures 19 cm in length, has a space between the occipital condyles of 2 mm. In this respect, there is more of a difference than a similarity between the two. J. Müller (*l.c.* p. 32), has recognized that the occiput of *Zeuglodon* has nothing to do with pinnipeds, but rather, can only be compared to odontocetes. Müller states, “the rear view of the *Zeuglodon* skull corresponds exactly to that of the *Delphinus (Platanista) gangeticus*—I will return later to the characteristics of the pterygoids and the cochlea. If the information provided by d’Arcy W. Thompson neither speaks to his opinion nor to its opposite, the same is true of the skull characteristics he mentions. Above all, there is the lengthening of the skull in a rostrum, which is foreign to all pinnipeds, but is quite developed in all odontocetes. Moreover, the placement of the nostrils must be observed. In *Zeuglodon*, these are in middle of the skull, bent backward, and are separated from the tip of the snout and divided by long through long, pointed parts of the premaxilla. On the other hand, in the case of pinnipeds, these lie at the front of the skull and point forward. It is especially important for an author who wants to argue for the pinniped nature of *Zeuglodon* to pay attention to two skull characteristics similar to cetaceans: the fossa on the lower side border of the occiput and the auditory bulla. The fossa was correctly depicted by d’Arcy W. Thompson in his second illustration to Müller (*l.c.* vol. 27, p. 1), but he fails to mention it at all. J Müller states (*l.c.* p. 38, Illustration, “fossa like a dolphin.”

And later in the text (*l.c.* p. 31.) We already recognize the lateral wing of the occipital, which is on the rear side of the temporal. and has the form of the jugular process like that of a dolphin.” More problematical to the objectivity of this discussion is the omission of the existence of a true cetacean kettledrum leg [*Paukenbeins*]. Certainly no skull characteristic is as typical of the cetaceans as its marine auditory bulla. Its presence in this typical, fully developed form is significant for the and rules out *a priori* a pinniped nature.

In light of these tests for the genus and species, on which d’Arcy W. Thompson formed his opinion, mention of the following points seems superfluous. Nevertheless, mention thereof may well assist in countering such a position regarding the placement of *Zeuglodon* with regard to other cetaceans, which will be developed in the following portion of this section. These tests will provide evidence that can at once introduce and simplify our discussion. They will also be of service to other fields of paleontology, particularly when a researcher chooses to distort or withhold evidence to prove a preconceived idea.

We must note that d’Arcy W. Thompson worked from a Koch copy²⁷ instead of from the lower jaw that J. Müller²⁸ and V Carus²⁹ described. This copy is constructed, artificial, and inaccurate, yet clearly is that of a *Zeuglodon osiris*. There are only three pinniped traits: the long, low form, which many researchers would have deemed cetacean had it reached the development of that of a dolphin. If this is also applicable to *Delphinus*, then the writer would have easily found other odontocete forms that are similar to *Zeuglodon*, namely, the similarity in length and height (the gradual increase in height towards the rear, in the length of the symphysis and in the

²⁷ Das Skelet des *Zeuglodon macropondylus* (*Naturwissenschaftlicher Abhandlungen*, gesammelt und durch Subskription herausgegeben von Wilhelm Haidinger Bd. 4, 1851 t. 7 f. 3).

²⁸ L.c.t.11.f.1-7, t. 22 f 5,6

²⁹ Das Kopfskelet des *Zeuglodon hydrarchos*. Zum Erstenmale nach einem vollständigen Exemplar beschrieben und abgebildet. (*Nova Acta Academiae Caesareae Leopoldinae Carolinae Naturae Curisorum*, Vol. XXII, P. II, t. 39^a, f. 3)

sharp angle of divergence of the branches, as demonstrated by the lower jaw of *Physeter*, while these have no similarities to the lower jaw of pinnipeds, which are similar to land beasts of prey. Moreover, the thin, long, low crown extensions, that gradually heighten towards have not been determined by any osteologists other than d'Arcy W. Thompson as being closer to pinnipeds than cetaceans. Even more significant is the assertion that the alveoli holes are big, but not as big as a dolphins'. Even if this assertion were true, it would suggest nothing as to the pinniped nature since a somewhat smaller size is, in sharp contrast, found in the alveoli holes of the seal and its relatives. What can we say about the mandibular foramen in the zeuglodont lower jaw? J. Müller states *l.c.*: "It is concave, like a dolphin's. Only the front-most part, the mandibular foramen, and the extensions are solid. The indentations are filled with stone, which was pressed in due to the especially large entrance of these holes. We see the openings to the large mandibular foramen in the beautiful fragment on Plate XI, fig. 7. In this respect, *Zeuglodon* is close to dolphins." And nonetheless, d'Arcy W. Thompson, despite what Müller has shown, has tried to claim that the alveoli hole is narrower than that of a dolphin. If we needed further proof for the incorrectness of this opinion, we could look at Plate 1 [XXX], we see that the circumference of the foramen lower jaw of *Zeuglodon osiris* is like that of the American variety. I note that, as also mentioned by J. Müller (*l.c.* vol. 26, p. 1), in the case of the lower jaw which was sent to me from Haarlem, the giant mandibular foramen and the large indentations are clearly visible.—Regarding the angular process which is missing in the *Zeuglodon* lower jaw, d'Arcy W. Thompson states that we must look at the seal in order to find a parallel case. Here the opposite is true. No dolphin—in fact, no odontocete at all—has a discernable angular process in the lower jaw. The same is true of *Zeuglodon*. In contrast, all pinnipeds without exception have them, in especially developed form. Thanks to the generosity of Dr. Nehring, I was able to examine the lower jaws of *Phoca*

vitulina, *Phoca groenlandica*, *Phoca barbata*, *Halichoerus grypus*, *Otaria ursina*, and *Cystophorua oristata*. All of these have a angular process, which is weakest in *Phoca vitulina*, but which is present under the coronoid process. The angular process is more developed in *Phoca groenlandica* and *Phoca barbata*. It is visible as a sharp, short notch on the lower rim, directly uinder the cylinder close to it, in *Halichoerus grypus*. *Cystophora* is similar to *Phoca*, whereas *Otaria ursina* is notably stronger and is like that of a cat. In truth, it is obvious that d'Arcy w. Thompson use a characteristics present in pinnipeds but absent in all odontocetes and *Zeuglodon*, as proof that the latter belonged to the pinnipeds. Together with this problem, there is the failure to mention another important, decisive difference between the lower jaw of a pinniped and a zeuglodont, namely, the joint cylinder. There can be no more greatly imaginable difference in form and placement between the two. In pinnipeds, it is completely at a diagonal on the long axis, with a semi-circular surface, and, as in the case of terrestrial carnivores, faces upward. In the case of dolphins, it is the head of the joint almost even and vertical, virtually circular in nature and is a rather long, elliptical border. The latter is consistent with what Carus (*l.c.* p. 381, pl. 39a, fig. 3) has thoroughly described as the joint head of the zeuglodont. This author states as follows: "The new findings of Koch allow us to clearly see what the lower jaw had. Dolphins are very similar in that their long branches are shovel shaped and curve outward. They widen more in the rear and have a simple joint protuberance that is oriented more backward than forward."

The fact that the rami of the lower jaw were not connected by synostoses as d'Arcy W. Thompson maintained, can be seen through our first Plate. This is not the case in seals.

The author then discusses vertebrae. The underdevelopment of the cervical vertebrae in *Inia* and *Platanista* is deemed to be unimportant. He must thus use the shape of the vertebrae to support his opinion. But here he only mentions the elements that support his argument. He first

undertakes a comparison of the cervical vertebrae of *Zeuglodon*, which J. Müller (*I.c.* vol. 26, fig. 2) has depicted as the underside of the tip of the snout of the famous *Zeuglodon* skull. Unfortunately, he refers neither to a gypsum cast nor to an original of this vertebra. I have not seen an original either. Thus, I cannot say whether the depiction corresponds completely to the original or whether it was somewhat schematic, given the complete lack of gradation. Be it as it may, the long, downwards bent diagonal extension is unknown in living cetaceans. Any similarity to *Phoca vitulina* is missing; the latter's are oriented outwards and only slightly downwards. On the front border, there is a cusp, which is missing in *Zeuglodon*. Moreover, *Phoca*'s cervical vertebrae have strong zygapophyses in the front and the back, no trace of which can be seen on the above-mentioned figure. I have, through examination of originals and depictions of the vertebrae which he could have compared, found that the fifth cervical vertebra of *Pontoporia* (*Stenodelphis blainvillei*, see Bruhl³⁰) coincides with the illustration. In all essential points, such as the relative size of the neural canal and the transverse foramina in the center and upper arc, which in the case of *Pontoporia* is open above, as well as the direction of the diagonal extension, coincide more closely. Only *Zeuglodon*'s are considerably longer. In any case, the relationship to *Pontoporia* contradicts the comparison with *Phoca vitulina*.

It is obvious, that, in what concerns the atlas, it is closer to the seal because of a perforation in the diagonal wing, which is absent in dolphins. But this characteristic, as well as the wide diagonal extension, the half-moon shape of the space for the odontoid process, and the form of shape of the surface of the joint, is shared with many land mammals and not just with seals. In any case, it is so much more defined, as is the case with *Phocaena*'s fully developed rear median peg, that J. Müller stresses its coincidence in form with *Balaenoptera rostrata* and Dr. Nehring, to whom I gave Müller's originals (J. Müller (*I.c.* vol. 13, pp. 1, 2) and requested

³⁰ *Zootomie für Lernende. Osteologie* r. 118 f. 143.

an expert opinion, deemed to belong undisputedly to the cetaceans, although, as had been expected, unrelated to a living species. It is obvious that the author used the axis to support his opinion. The strong projection of the teeth is mostly absent in cetaceans and it is only slightly evidenced in the seal-like nature of *Zeuglodon*. It is also a characteristic of all other mammals and can also be attributed to insects and micropods. Secondly, the above-mentioned description shows that the size of the tooth projection oscillates and in *Zeuglodon brachyspondylus* can be of limited dimension as is the case of *Balaenoptera*. On the other hand, in the case of definite odontocetes, the tooth projection of the same size, can be evidenced in *Zeuglodon osiris*. Leidy and Cope³¹ have depicted the axis of *Priscodelphinus gradaevus*. Moreover, the oval indentations in both sides of the tooth projection were once used as an indication of a *Phoca* nature. Had d'Arcy W. Thompson compared these to carnivores, he would have seen that such cavities are more or less pronounced in land mammals. The similarities, which he believed to have found in the surface of the joint of the third cervical vertebra, were based on my initial description, which had no illustration. If he had looked at Plate II [XXXI], he would have seen a complete depiction of this joint, as it is now found only in *Zeuglodon*.

The characteristics of the dorsal vertebrae—short diagonal extension and clear rear zygapophyses, in which he found a similarity to pinnipeds, are also as faulty as the above. They extend from seals to other land mammals. Similar is the lengthening of the vertebra centra of *Zeuglodon*. Neither cetaceans nor seals approach zeuglodonts in this respect, but both have a similar, but less-pronounced lengthening. This characteristic supports neither opinion. Regarding the lumbar vertebrae, the illustrations of the *Phoca vitulina* are incorrect. The zygapophyses in all actuality are clearly developed and the diagonal extensions are thinner. In fig. 7, the author gives a copy of a lumbar vertebra of a *Zeuglodon* “after J. Müller.” In vain, I looked for the

³¹ The Cetacea (*American Naturalist*, 1890, p. 605, fig. 2)

Mark D. Uhen User 6/10/09 3:06 PM

Comment: Something's not right in here, and there is a missing footnote number 2 from page 208.

original for this copy in J. Müller's work. Perhaps, *I.c.* vol. 16.2 or vol. 20 no. 6 or 7 might come into play. But in all three of these illustrations, J. Müller clearly shows the break-away point of the diagonal extension, and the stumps are decidedly straight and pointing outward, while those in d'Arcy W. Thompson's illustrations are clearly crumpled backward.

Regarding vertebrae in general, we can say that d'Arcy W. Thompson has, for the dorsal as well as the lumbar vertebrae, used atypical examples, namely ribs of the small variety of *Zeuglodon brachyspondylus*, which J. Müller also felt belonged to juveniles. Many characteristics, which appear to contradict a cetacean nature, speak to juvenile terrestrial ancestors, and are more developed in adult animals. The rudiments of the neural arches and the thick diagonal extensions disappear here. Vertebrae such as the ones described here in Plate V [VVVIV] are true cetacean vertebrae, and have nothing to do with pinnipeds. Why has d'Arcy W. Thompson neglected so much of J. Müller's work? If we consider our above-mentioned figure of the neural arc and the diagonal extension looking at the outline of the place of breakage, we could arrive at d'Arcy W. Thompson's findings (p. 9). But why did he not even mention that all centers of the dorsal vertebrae of zeuglodonts lack the facets on the capitulum of the ribs? It is well known enough, that, of all mammals, only cetaceans have the connection of the ribs on the upper arc on the one side and the connection of the upper arcs and centrum on the other side. But the centrum itself never reaches down, so that the ribs on the rear vertebrae are only connected by the diagonal extensions. I further question as to why he has failed to mention that the caudal vertebrae, which are similar to the odontocetes, bear no similarity to the pinnipeds?

The author finds similarities in the scapula to the pinnipeds in what concerns a clear spine, a long, crumpled acromion and in the lack of a coracoid process. His consideration of the only scapula found and described by J. Müller (*I.c.* vol. 27, p. 2) is based on a figure that is in part

unclear and in part reconstructed. The spine was described and depicted as much stronger than it actually was. The acromion, moreover, is depicted with a sharp ridge that is not to be found on the highly-damaged original. In any case, the low spine and the acromion, which is bent to the side, have more relationship to cetaceans than the depiction suggests. Similarly, in the case of the coracoid process, it is hard to determine the spot from which it diverted from the scapula. This is also damaged.

Nothing more needs to be said regarding the ribs and the phalanges. The phalanges of zeuglodonts are not unknown. These have been evidenced by pieces of the sternum, and pieces broken away from the caudal vertebrae. The distal thickening of the ribs is specific to *Zeuglodon* and has no analogy with pinniped ribs, since the ends of pinniped ribs are horizontally cut off.

So much for d'Arcy W. Thompson! There are not only numerous errors, but also, there is a methodological weakness that has to be pointed out. He makes gross generalizations and covers up other important evidence. We will no longer consider his work here.

If it has been determined above that zeuglodonts are not pinnipeds, but are cetaceans, we can examine how they are related to other members of this family; specifically, how can we clarify their divergent characteristics? With v. Zittel and Lydekker, I treated zeuglodonts as cetaceans that had not yet reach a level of specialization, as is the case of the younger toothed whales, which were adapted to water. That fact that the toothed whale, the bearded whale, and the siren, all live today in water, yet stemmed from land animals, can be supported by the research of Weber and Kükenthal. The opinion offered by Albrecht³², that cetaceans were closest to Promammalia, whose anatomical and osteological characteristics, which allow them to appear more basely organized than the typical land mammal, can only be only be handled by a researcher who works from a point of view of comparative anatomy and from a geological one.

³² Ueber die cetoid Natur der Prommamalia. (*Anatomischer Anzeiger* I, 1886. p. 338 ff)

Not only must Albrecht's comparative anatomy, but also Weber's³³ refutation of the same, must be taken under consideration. If cetaceans are to be considered as ancient mammals, then their descendents must also be understood to be marine animals, since today's cetaceans must have inherited this characteristic directly. All studies made by paleontologists contradict this. Remains in all formations of marine vertebrates dating back to the Paleozoic times are known, and many previously-unidentified species have been noted. Based on previous findings, it would be unexplainable how a trace of a marine mammal could be found in the Tertiary. How could their skeletons be transported so as no trace of them could be found? Why don't they appear near the Ichthyopterygia, Sauropterygia, Mosasauria, and other Mesozoic sea dwellers who had similar life styles to the cetaceans?

From a geological standpoint, Albrecht's hypothesis does not stand up. Neither does it from an osteological standpoint if we, as Albrecht, look at both recent cetaceans and their ancestors. We can mention the toothed whale, which, has been through an array of developmental phases, which evidence how animals went from land to water. The well-known characteristics of today's cetaceans, especially the toothed whale, are either present or developing in zeuglodonts. The phases they went through in development are clear. In any case, we must free ourselves of all ideas that zeuglodonts have any phylogenetic relationship to pinnipeds. If J. Müller and other researchers have arrived at this conclusion, it is based on the formation of the rear teeth. We must, however, remember, that when these writers did their studies, there was no discussion of phylogenetics or of the development of convergence, where external similarities in shape without relationship to other skeletal similarities were sufficient to establish a relationship. From this emerged the notion that, with the exception of whales,

³³ Ueber die cetoide Natur der Promammalia Anzeiger II, 1887, p. 43 ff) *Apäont. Abh.* N.F. 1 (der ganzen Reihe V), Bd., Heft 5.

pinnipeds are the only marine mammals that need to be considered and were thus linked to them. D'Arcy W. Thompson has made such a linkage between zeuglodonts and pinnipeds, which I hope I have conclusively refuted. Since pinnipeds no longer enter into the dynamics, then it can be further questioned as to which mammals must be considered. The answer can still not be given today, and we must make a comparison with an ideal mammal, that has developed similar typical characteristics. The zeuglodont characteristics of this rubric are, above all, the formation of the nasals, frontals, and parietals. These are still similar to land mammals. It is not difficult to find, in the case of the cetacean skull, the beginning of later formation of the lengthening of the snout into a rostrum. The same can be found in the significant lengthening of the inter-maxillary bone in front of the nasal opening, through which this was thrust at approximately one-third the entire length of the bone. This had progressed a good deal of the way towards the tip of the snout which, in the case of young cetaceans, comprised the lengthening of the inter-maxillary bone. The bordering of the snout by the upper jaw, the stunt of the nasal bone, the emergence of the maxillary over the frontals, are all strong changes in form and placement of the skull bones, which occur in cetaceans and are in evidence here. For an animal that definitively lives in water, a pointed, long nose to cut through water when swimming fast and, if it breathes with lungs, a high-positioned nasal opening to get air are necessary. Today's cetaceans have attained both. Both are evidenced on the zeuglodont skull. The part of the skull that held the brain did not keep up with these developments. It is so similar to terrestrial ancestors of zeuglodonts that if we study remains without teeth, we can assume, as d'Arcy W. Thompson did, that the pterygoids had shapes similar to carnivores. In one aspect, the rear half of the skull had developed a typical cetacean trait—a completely developed tympanic bulla. This is developed to marine life; the cochlea has the 2½ coils of land mammals.

Although to a lesser extent than the skull, the lower jaw shows ancestral characteristics. Its development into a odontocete lower jaw is complete. The giant alveolar foramen that increases in height from front to back, the joint surface for the squamosal, the lack of an angular process, the weak crown extension, and finally the beak-like lengthening with long symphyses on the front end give the zeuglodont lower jaw a marked similarity to *Physeter*, which is intensified by the right angle at which the two rami behind the symphyses diverge.

Only the teeth are considerably different between the two. While recent odontocetes and the fossils of their close descendants—like dolphins and platanistids³⁴—are completely homodont and polydont, zeuglodonts were heterodont and oligodont. However, one can see in the teeth the initial transformation from land to marine mammal. In the first, the function of teeth in one and the same bite are different—the front teeth grasp and the rear make the food smaller—whether by tearing as is the case with carnivores or by grinding, as is the case with herbivores. This difference is lacking in odontocetes. In this case, the food is grasped and killed by biting, or swallowed alive. In any case, it is not made smaller. There is no need for differentiating the biting teeth, and one finds homodontology. Moreover, the teeth, which are no longer used to grab or break down food, become a means of entrapment. They do not need complicated cusps and indentations. What is needed is a simple tapered tooth, which does the job better. We note that polydontology also occurs, as in the case of dolphins, which have fully developed this. In sum, we can state that oligodonty with heterodonty is the norm for land animals, and polydontology, with homodonty for carnivorous marine mammals is required.

The dentition of zeuglodonts can be explained through this paradigm.

³⁴ One half, or approximately one half, of all toothless odontocetes, such as physeterids, cannot be classified as odontocetes, but rather, as a later, specialized, sub-branch.

The emergence of homodonty is apparent in that the incisors and canines have the same form and size. If we assume that the last single-rooted tooth is the front-most premolar, then this has already gone through morphological processes. Moreover, the first three and the last three of the double-rooted teeth are similarly constructed. Even if their cingulum and the frontal thickening coincide with land mammals, we cannot deny that by reason of side compression and the cusps on the upper border, the teeth have become quite similar, so that the whole dentition has only two forms of teeth. It must also be noted that the rear teeth, in comparison to those of typical land mammals, are constructed very simply—all secondary protuberances and cusps are missing, and the crown forms a side-compressed triangle with border cusps having been reduced. Between the front five and the rear six teeth, there is a clear connection, in that the presence of denticles on the front border has almost disappeared and the front halves of the single-rooted teeth have become more similar. To a greater extent, this would be the case if the above-mentioned pair of teeth (J. Müller, *l.c.* vol. 23, p. 4) were both pre-molars. In this situation, the fronts would have an insignificant denticle on the rear border.

If we assume the above position, that the first three double-rooted teeth of *Zeuglodon osiris* correspond to the premolars, one can summarize as follows: first the incisors take the form of canines, as single-rooted, single-cusped teeth; at the same time, the difference among the premolars on the one hand and the molars on the other disappears; both groups become closer, due to side compression and the presence of border denticles; the premolars are already more fully developed, while the molars still show clear traces of the cingulum and have not attained front compression. Subsequently, homodonty moves from the tip of the jaw to the end, both above and below. This appears in close tandem with transformations in the skull, namely, the lengthened premaxilla and the resulting back positioning of the nostrils, with the skull cover

remaining similar to that of land mammals; only in this aspect does the lower jaw reveal a difference from the one that I have shown in the cetaceans, as can be evidenced by the mandibular foramen and the shape of the joint.

Similarly, there is scarcely any evidence of polydonty. This can be seen in the 4 incisors, which are not present in placental mammals.³⁵

The passage to water life is clearly evidenced by the spinal column. Only in the mobility of the head, which, at least in the case of *Zeuglodon osiris*, still has a well-developed odontoid process of the axis, as evidence for its development from the vertebrae of land animals. The particular, cushion-like thickened joint surface of the axis is specific to *Zeuglodon*. We can see it to be merely a transitional state, which reveals how metamorphosis takes place. In literature, we frequently hear of the cervical vertebrae of the zeuglodont, which is similar to land animals. I have been unable to prove from which author this myth has been handed down. J. Müller (*l.c.* vol. 13, pp. 3-5) describes his *Zeuglodon* cervical vertebra and states that it is constructed like that of a whale. He admits that it is thicker, but does not make generalizations about the neck of *Zeuglodon* and that of the cetaceans. He only states that “it is longer and freer than in whales and dolphins.” That does not provide enough certainty to claim that the cervical vertebrae are “considerably long” or “similar to the dorsal vertebrae,” with which they have nothing in common. Our Plate IV [XXXIII] should help put such a myth to rest. The still-uncontested cetaceans of the more recent geological ages, such as *Priscodelphinus*, clearly had cervical vertebrae like that of a *Zeuglodon*, as mentioned above. The fact that these have not melded together can be easily explained: in the case of the oldest odontocetes. We have not encountered the final level of specialization. Neck movement from head to the lower body is present in some,

³⁵ If the tooth formula provided by J. Müller for *Zeuglodon macrospondylus* is correct, then this type would constitute a significant step on the way to polyodonty. This has not been proven.

but not in all late cetaceans. The somewhat thicker cervical vertebrae fall into this rubric. The fact that the thoracic vertebrae are through the form of the centrum, the upper curve, and the rib joints has been developed above. J. Müller has already described the small peculiarities that have been taken from land ancestors. There is no need to repeat these here.

The significant lengthening of the lumbar vertebrae in the *Zeuglodon macrospondylus* is completely foreign to land animals. To this effect, there is also a complete difference, which, evidenced in more recent cetaceans, is still perceived here. This involves the need to consider the cartilage plate and the thick epiphyses between the centra of the vertebrae. This has made the spinal column considerably more elastic than it had been in the case of zeuglodonts. In the lengthening of the lumbar vertebrae, we can see the development of the larger, cetacean body dimensions. The thoracic vertebrae do not evidence this lengthening. This can be explained by the fact that the ribs are further apart, so that the thorax loses part of its solidarity.

In the case of the caudal vertebrae, there is no longer any difference between zeuglodonts and cetaceans. In form, relative size, development of the upper curve, and the vertical, diagonal extensions, there is complete coincidence. This has also been shown by J. Müller (*l.c.* vol. 21, p. 8). Lastly, we can only negatively consider the fact that never has a trace of a pelvis or femur been found, while we have encountered of upper body parts. It would also be hard to explain that a sacrum with a pelvis has never been found, although they must have been especially big and easily preservable.

We must now mention the remains of scapula and humerus. Lydekker discusses a still more generalized cetacean scapula; the loss of the spine and the development of a large coracoid process, which were acquired rather than inherited.

D'Arcy W. Thompson, in what concerns the humerus, "has shown a wise discretion, from his point of view, in making no reference to the humerus," as Lydekker (*I.c.* p. 560) appropriately comments. There has previously been no possibility for discussion of this matter. He has, as is well known, a specimen that deviates the most from other mammals of which many different opinions have emerged. These do not need to be discussed here. The peculiarity lies in the contrast between the construction of the head with that of the trochlea. The first is completely normal and is suitable for a strong joint in the glenoid cavity of the scapula. The latter is reduced to a narrow, concave surface, without any trace of division into two condyles, and is in sharp disjunction with a strong, developed head. This reduction of the trochlea also involves the distal quarter of the shaft portion, which suddenly dwindles under the deltoid crest. If we consider such a humerus in light of the above, then it implies a complete transformation between land and water mammals in the tendency of the trochlea to lose and give up the joint between upper and lower arms³⁶. Lydekker thus frames the matter when he states, "that between the zeuglodont and cetacean humerus there is a very pronounced resemblance; both having a very large head, directed outwardly in the natural position, a more or less flattened shaft, and the distal terminating in fore-and-aft facets for the radius and the ulna. It is true that in the zeuglodonts the head is relatively smaller, the shaft longer and more flattened, and the distal facets more rounded than in modern cetaceans; while the latter have lost the distinct deltoid crest of the zeuglodonts,

³⁶ In his description and depiction of the humerus of *Zeuglodon caucasicus*, Lydekker is considerably more specialized than that of *Zeuglodon marcospondylus* and *brachyspondylus*, in so far as the trochlea, in this case, is divided into two facets for radius and ulna. The shaft is also notably shorter. I would be more inclined to agree with this if there were no doubt as to the above-mentioned type belonging to zeuglodonts. The last teeth stand widely apart for each other, which indicates a squalodont. If Lydekker were to base his zeuglodont determination on the placement of the border of the teeth and the equally sized cusps in front and behind (which the illustration does not clearly show), or with reference to J. Müller's depictions (*I.c.* vols. 23 and 24), which he has provided for *Squalodon ehrlichii*, *scillae*, and *grateloupi* from Linz and Malta. The form of the denticles is, in the rear teeth, similar to *Zeuglodon caucasicus*. Nothing will be said about this that implies that the latter form belongs to a squalodont, which is contradicted by the eight teeth of the lower jaw. Instead, it could be a new type of species that had the dentition of a squalodont and the high lower jaw of a zeuglodont and which suggests, by means of the above-mentioned humerus, a link between the two.

and the two tuberosities have become confluent. These differences appear, however, to me to be precisely those which we should expect to meet within a generalized form; and how it is possible to imagine that an animal with a humerus of this type, and a true paddle, in place of an ordinary fore limb, can have 'the closest possible relation' with the seals, passes my comprehension."

It is very regrettable that there remains nothing of other parts of the forelimbs. I have not yet studied the pieces that J. Müller identified to be phalanges or as elements of the sternum and cannot venture a final opinion. J. Müller, on the other hand, determined this immediately. Nothing is known of the forearm, and therefore, the two pieces in the Teyler Museum, which were entrusted to me for study, were of special interest. They are two hatchet-shaped, flattened bones which widen towards the bottom. These, in their distal ends to the radius and the ulna, are very close to cetaceans. Whether this explanation is correct can be determined once a zeuglodont limb with its parts in natural relationship is found. Accuracy notwithstanding, its forearm would be completely cetacean in nature, as Lydekker also assumes.

If we put all of this together, the zeuglodonts comprise a sub-category of odontocetes, which developed from land animals and are closer to these than geologically younger squalodonts and typical odontocetes, for which the denomination Euodontoceti has become commonly used. Therefore, they carry more characteristics of land animals. No less important is the specialization and the adaptation to water life, which is so extensively advanced, that we clearly place them in the category of Odontoceti, which will be discussed as follows.

We also learn from the level of specialization that the individual body parts have reached where they fit into evolution. It has been shown that the rear body, through the construction of the caudal and lumbar vertebrae and in the loss of the rear extremities, has developed most of the characteristics of the younger cetaceans, and that the upper body, through the formation of the

rostral region, shows the beginning of homodonty. The skull, the atlas, the axis bear more than does the ocular region. Namely, the lower jaw is very generalized. It is the least developed. We know too little of the front extremities to render judgment. We can determine something about the level the cervical vertebrae have reached.

Marine mammals, as in the case of typical fish, have their main propulsion strength in the rear part of the body. Former sites of propelling now function as steering devices and as means of maintaining balance³⁷. In the case of zeuglodonts, this type of movement is complex and shows that the adaptation to water life first involved the development of rapid and powerful movement to help catch prey. Like most odontocetes, nourishment was taken from the animal world. Movement was the most significant, since their prey also swam. In second place came the seizure of the prey, which explains why the part of the skull devoted to sight is adapted to such necessities, yet is not as developed as the rear part of the body. The head, upper extremities, and ribs have been the least modified due to the need for catching and holding the prey. The adaptation to water life thus found its beginnings at both ends of the body, and most rapidly at the rear portions, the motor pole, which developed faster than the nutritive pole. These were followed by the middle portion of the body.

If the claim that zeuglodonts as odontocetes took more of the characteristics of their land ancestors is correct, then the younger representatives of this order must have lost more and more of these characteristics. This assumption should now be tested.

Squalodon follows *Zeuglodon* of the old Tertiary in the Miocene and Pliocene of both hemispheres. We only have skull remains and teeth of *Squalodon*. It is difficult to establish how the odontocetes of the second development period went through such transformations compared

³⁷ This is demonstrated by Küenthal in his essay Ueber die Anpassung der Saugthiere an das Leben im Wasser (*Zoologische Jahrbücher* Vol. 5, 1890, p. 373 ff).

to their ancestors and descendants. Compared to the skull of *Zeuglodon*, the *Squalodon* skull shows a marked step forward. It has reached in all essential points the developments of recent odontocetes. Only on the lower jaw, as is the case with *Zeuglodon*, does it still have three incisors on each side. Also, in the dentition, it has made a significant advance; polydonta is notably developed and homodonta is fostered, whereby there are only two types of teeth. V. Zittel offers for *Squalodon* the tooth formula $3.2.4-5.7/3/1/4/7$, so that there are 15-16 above and 15 below. In all, there are 60-62 teeth, more than double the number of *Zeuglodon*, and somewhat half of that of recent odontocetes, such as *Platanista* and *Inia*, while as others, such as *Phocaena*, *Orcella* and *Orca*, retain approximately the same or demonstrate a somewhat reduced number of teeth.

Of special interest is the type in which homodonta developed later. We saw, in the case of *Zeuglodon*, that the incisors and canines had taken the same shape and size, that pre-molars and molars, although of the same type, were still sharply separated from each other. In *Squalodon*, we find, instead of this, two types of teeth. The single-cusped single-rooted tooth form appears in the premolars, and the molars have all attained the same form. The types of *Zeuglodon* molars described on (S. 9 [195]) have disappeared. We also note that *Zeuglodon* had strong progress toward homodonta from front to back. Clearly, a front group of teeth leaves its mark on the next younger form.

If this law of development of homodonta from front to back is valid, it must also define the relationship between squalodonts and euodontocetes. And this is the case. Here there is homodonta up to the end of the teeth. The single-rooted, single-cusped tooth form, which was characteristic of the zeuglodont incisors and canines, has spread in squalodonts to the premolars

and to the molars of the euodontocetes. There is no longer a difference, and a distinction between premolars and molars is impossible to make³⁸.

Of greatest importance for the proof of the above is an observation made by Kükenthal, in which he finds in a *Phocaena communis* embryo that was near birth, the 18 teeth of each jaw half being all cusped in the same way, the rear 7, in contrast, being rounder, and clearly showing two or three denticles on individual teeth. In this case, “the lack of similarity in the dentition, heterodonty, is clear.” This ontogenetic indication brings forth the desired confirmation of the above phylogenetic comments and lends credibility to the belief that homodonty develops from front to back, since only the rear teeth of the *Phocaena* embryo still have the cusps.

It directly follows, that the dentition the dolphin is not, as many authors such as Schlosser, have assumed, the original form of all mammal teeth, “which have been most closely preserved in dolphins”³⁹, rather, that we will agree with W. Kükenthal when he states⁴⁰ “Doubtless, the dentition of the bearded whale as well as the toothed whale can be considered an adaption to water life. Further discussion is offered by O. Jaekel⁴¹ in a historical study of the enamel of zeuglodont teeth. He claims, “that the same attains a height of organization, which is characteristic only of higher mammals,” and further that “If we thus find highly developed enamel in old cetaceans, then this is certain proof that they have developed from advanced mammals...”

³⁸ In this case, only typical dolphins have been considered and not other forms such as monodont, mesoplodont, etc., which have had, through further specialization, a reduction in teeth.

³⁹ Die Differenzirung des Säugthiergebisses (*Biologisches Centralblatt*, vol. 10, 1890, p. 238). Schlosser also writes that the length of the jaw is also characteristic of the original form, which I cannot agree with. The opposite has been demonstrated in my analysis. When we find in amniotes a long jaw formed into a rostrum, it is still a marine animal (*Ichthyosaurus*, *Mosasaurus*, *Champsosaurus*) which developed from land mammals. Nothing can be further discussed to this effect. I believe, however, that the passage of reptiles to water life must fully be discussed.

⁴⁰ Ueber des Ursprung und die Entwicklung der Säugethierzähne (*Jeaische Zeitschrift für Naturwissenschaft*, Vol. 26, N.F. vol. 19, p. 277). In this important article, we find very useful observations for paleontology regarding the dentition of whales. Once again, d’Arcy W. Thompson’s belief in the pinniped nature of zeuglodonts is sharply contradicted.

⁴¹ *Neues Jahrbuch für Mineralogie*, etc. 1891, 1, p. 198

Thus, I am, on geological-paleontological grounds, able to come to the same conclusion as Kükenthal/Weber. The fact that this former research arrives at a very different conclusion for cetaceans is due to the state of affairs of knowledge of the migration of these animals to water. Much material was available to them for analysis. Such details are not available to a paleontologist. Thus, I could not address this part of Kükenthal's research since he drew his conclusions regarding the adaptation to marine life on things that cannot be proven from a paleontological perspective. He deals with the development of the frontal extremities and the increase in number of the phalange, which are virtually unknown in archaocetes and squalodonts. I must only mention that the geologically-studied osteological development of the odontocetes⁴² has come to similar conclusions as the anatomical studies. I believe this confirms the correspondence of the individual skeleton parts.

Let me briefly explain my methodology. I tried to determine that zeuglodonts, squalodonts and euodontocetes represented three phases on the path from land to sea, and that these three phases can be grouped into three sub-categories. If we look at the impressive system reviews for cetaceans⁴³, we see that each other drew upon divergent factors. Brandt looked at the heterodont teeth of zeuglodonts and squalodonts to determine their relationship to the toothed whale. The construction of the skull was, for most other researchers, used to support Brandt's claims, among these Cope, Lydekker⁴⁴, who link squalodonts more closely to odontocetes, and zeuglodonts are distinguished from both. Both support my suppositions that not all of the characteristics of the three groups have the same weight.

⁴² I also agree with Kükenthal, that the whale is of diphyletic origin; his conclusions appear completely justified. From a paleontological perspective, this question cannot yet be approached.

⁴³ In v. Zittel's *Handbuch der Paläontologie* IV, pag. 184, such matters are discussed. The assumption that zeuglodonts are between seals and whales, or merely seals, prevails and is no longer considered here.

⁴⁴ Lydekker (*Catalogue of the Fossil Mammalia in the British Museum (Natural History)*, Part V, 1887, p. 75) speaks of the Squalodontidae, which he deems a family of odontocetes. "The cranium resembles in essential characters that of the Delphinidae and differs entirely from that of the Archaoceti, although the teeth differentiate into groups as in the latter.

Zeuglodonts are, through their skulls which are similar to land animals and the oligodont dentition, clearly and sharply separated from squalodonts; but they are equally separated from odontocetes through the placement of the inter-maxillary on the tooth-bearing part of the rostrum and through a heterodont dentition. There is no connection between the two. The homodont dentition of odontocetes can serve as evidence of a new and final phase of assimilation, in the same way the transformation of the skull of *Squalodon* surpassed *Zeuglodon*. All in all, *Squalodon* is in osteology and odontology equally close to or far from *Zeuglodon* on the one hand as to dolphins on the other, and thus we can identify three suborders, namely:

ODONTOCETI

1. Suborder: Archaeoceti – oligodont and heterodont
2. Suborder: Mesoceti⁴⁵ – polydont and heterodont
3. Suborder: Euodontoceti – polydont and homodont

IV. Regarding the dermal armor of zeuglodonts

Although there are no remains of the dermal armor of the Egyptian zeuglodonts, we can nonetheless make some comments regarding the question of whether pieces of plate found with the Alabama zeuglodonts are parts of the dermal armor.

The question has emerged through Kükenthal's important discovery⁴⁶. He observed a living toothed whale belonging to *Neomeris phocaenoides* in the Indian Ocean, whose skin on

⁴⁵ I give the above name for squalodonts to underscore the position of the second sub-classification between the first and third sub-classifications. Squalodontidae must be used for the family. A complete justification for these sub-classifications is unnecessary here since it has been provided by v. Zittel.

the back revealed a series of plates with spikes which covered a long area; there were also similar plates on the front flippers and on the spray opening. He thus rightly concluded that the odontocetes stemmed from land animals that had armor. This was an argument against the monophyly of the Bearded and Sea Whales, who have no trace of such armor, yet have hair.

Are the zeuglodonts thus forefathers of the odontocetes? If so, they must also have skin armor. I was able to compare such remains from Alabama with remains in the Teyler Museum and have been able to determine this with certainty. Since the skin armor in zeuglodonts comes in the form of irregular hand-sized pieces, the question of whether they belong to zeuglodonts can only be answered through macroscopic and microscopic comparison with other vertebrates. They will be compared to species having polygonal plates, such as glyptodonts, turtles, especially *Psephophorus*, and the controversial *Psephoderma* of the Alpine Triassic. Of these, the glyptodonts have, through their strong sculpture, have regular plates which zigzagged from the front. *Psephoderma* is only occasionally considered in the same light. The American skin armor is, as we have learned from J. Müller⁴⁷, and V. Carus, of unequal size, having irregular polygonal borders.

CAPTION ON PAGE 220 OF GERMAN TEXT

Vertical micro-section of the upper part of a piece of dermal armor of the Eocene from Alabama.

⁴⁶ Ueber Reste eines Hautpanzers bei Zahnwalen (*Anatomischer Anzeiger* V, 1890, p. 237). *Paläont Abh.* N.F. 1 (Complete Series V) Issue 5.

⁴⁷ I note that in many handbooks, for instance, in von Zittel, there is the belief that J. Müller asserted that this belonged to the zeuglodont. J. Müller, however, states (l.c. pag. 36), "to which animal, and whether this belongs to the zeuglodont, is clearly unclear." The error can be contributed to the fact that, in a footnote, he states that he saw a *Dermatochelys* which had skin armor in the form of a bone shield.

The smooth surface actually is close to the armor of *Psephophorus*, which, in other important points, is insignificant. Secondly, the *Psephophorus* plates are much thicker and stronger, and are of the same dimension with relatively regular borders, and finally they are considerably more loosely connected one to the other. Individual, naturally-bordered plates can be separated, which is not the case for the other. Other differences can be found in the histological structure. I refer to discussions of the chelonians of the north German Tertiary, where there are depictions of the objects found. I am providing here only the depiction made by Dr. O. Jaekel, of a microscopic section of skin armor found with a *Zeuglodon*. He was so kind as to provide a description of it, which I quote here:

“The state of preservation of the bone weaving leaves a lot to be desired. The smaller canals are, for the most part, not visible by indirect light. They are unrecognizable when the micro-section is even slightly blown up. . Most of them reveal the central cavity, but not the offshoots. On the above illustration, the parts belonging to the outer zones of the armor are especially well preserved, so that we can see them clearly on the left side of the illustration and can thus determine their placement.

The picture has a second defect. Many cracks and fissures are present in the bones and give the impression of canals or natural stratification lines. By blowing the image up, I believe that we can identify two systems of fissures which encircle the Haversian canals concentrically, and which radiate from this radial. The first ones show the division of lime around the canals only in strong quantities, and thus do not distort the image, while the second type of fissure crosses through the canals and tunnels and dulls the illustration. If we take into consideration the state

of preservation, then we can see the following structural relationships in the picture:

The large central cavities, which appear black due to having been filled with secondary material, are the cross-section of a Haversian canal. The same are smaller and less thick in the zones lying under the surface as in the deeper positions of the upper zone. There remain only thin walls between the central cavities in the lower zones.

The lime substance around these canals is concentric. This aspect is similar to the case of turtle shells.

The bones are quite regular and are distributed through the lime weaving, but less so under the surface. Their size comprises 2–3 micromillimeters. By and large, they are deformed lengthwise, not only near the Haversian canal, where they are 5 times as long as they are wide, but also, to a lesser extent, in the central parts of the intermediary substance. Their offshoots are not particularly numerous, but can be clearly observed.

The lime intermediary substance is thickest under the surface and has almost no fissures. Further underneath, there is a more organic substance between the lime salt, and here one sees evidence of the development of a fissure system. In the deepest level, the layer of the intermediary substance can only be evidenced by its border. The interior is only lightly filled with lime.

Under the surface, we find irregular canals of the same diameter which can be deemed *Mycelites ossifragus* Roux.”

Beyond a doubt, the skin armor we have discussed belongs to a zeuglodont. This determination is evidenced by macro and microcopy studies of these and the skin armor of other species. This discovery also speaks to the emergence of younger odontocetes from zeuglodont-like animals as well as for the emergence of the later from armor-bearing land animals, as Kükenthal has already determined (*I.c.* p. 383). He states that further studies must be made to determine closer relationships, *i.e.* toothed whales with ungulate and carnivorous animals. These studies should focus on a time period in which land animals bore such armor. I am not in agreement with the last point. Zeuglodonts emerged in the early Tertiary. Their evolution from land animals must have appeared in the Cretaceous Period. An animal, which has slowly adjusted to a new life style, enters into competition with those who were already adapted to water life. But neither in the Cretaceous Period nor in the Jurassic did we have mammals with armor. We must seek out the ancestors of the odontocetes in the armor-bearing land mammals of the Mesozoic Era, about which we know nothing. We must conclude that the phylogenetics of this species still remains unclear.

EXPLANATION TO PLATE I [XXX].

Zeuglodon osiris Dames

Fig 1a. Lower jaw from the outside, 1b from the inside, 2c from above in actual size

P. 5 [191]

The original is to be found in the geological-paleontological collection of the Royal Museum of Natural Science in Berlin.

EXPLANATION TO PLATE II [XXXI]

Zeuglodon osiris Dames

Fig. 1a Atlas from behind, 1b from the right side, 1c from underneath, 1d from above in actual size. The dark, smooth triangle on the joint in Fig. 1a as well as on the odontoid process in Pl. 1d are gypsum-filled holes in the original. P. 11 [197].

The original is to be found in the geological-paleontological collection of the Royal Museum of Natural Science in Berlin.

EXPLANATION TO PLATE III [XXXII]

Zeuglodon brachyspondylus J. Müller

Fig 1a Atlas from in front, 1b from behind in actual size. P. 11 [197]

The original is to be found in the geological-paleontological collection of the Royal Museum of Natural Science in Berlin.

EXPLANATION TO PLATE IV [XXXIII]

Zeuglodon brachyspondylus, J. Müller

Fig 1a Third cervical vertebra from in front, 1b from behind, 1c from underneath in actual size P. 13 [199]

Fig. 2 The axis depicted in Plate III [XXXII] from underneath P. 13 [199]

The original is to be found in the geological-paleontological collection of the Royal Museum of Natural Science in Berlin.

EXPLANATION TO PLATE V [XXXIV]

Fig 1a Lumbar vertebra from above, 2b from underneath in actual size P. 13 [199]

The original is to be found in the geological-paleontological collection of the Royal Museum of Natural Science in Berlin.

EXPLANATION TO PLATE VI

Zeuglodon osiris Dames

Fig. 1a lumbar vertebra from in front, 1b from above, 1c from underneath in actual size P. 14 [200]

The original is to be found in the geological-paleontological collection of the Royal Museum of Natural Science in Berlin.

EXPLANATION OF PLATE VII [XXXVI]

Fig 1a Caudal vertebra from in front, 1b from above, and 1c from underneath in actual size P. 14 [200]

The original is to be found in the geological-paleontological collection of the Royal Museum of Natural Science in Berlin.