Series C. *Vol. VI. Fascicle 1.*

PALÆONTOLOGIA SINICA

Editors:

V. K. Ting and W. H. Wong

The Cretaceous Dinosaur from Shantung

BY

CARL WIMAN

UPSALA

Published by the Geological Survey of China

Peking 1929

Translator: Nadja Insel, University of Michigan, Department of Geological Sciences, Ann Arbor, Michigan USA.

Translation Editors: Jeffrey A. Wilson and John A. Whitlock, University of Michigan, Museum of Paleontology & Department of Geological Sciences, Ann Arbor, Michigan USA.

31 July 2007

INTRODUCTION

The Chinese geologist, Dr C.H. T'an, has described the geology of the Chinese field area and the history of discovery of dinosaurs in East Asia in a work that was published in 1923 in Beijing (32. S.95). For more information see that work; I want to present only a very short report about the historical data and the geological age of the dinosaurs.

HISTORY

T'an (32. S.122) writes about the oldest fossil records of dinosaurs in east Asia: "The first scientific note, communicated by Dr. A. N. Kryshtofovich, on the occurrence on the Amur of vertebrate remains which later proved to belong to Dinosaurs was published in 'Annuaire de minéralogie et géologie de la Russie' par N. J. Krischtafovitsch in 1902, where it is stated that bones from these beds were known to the local cossacks and that some specimens were brought to the museum of Blagoweshchensk as 'bones of mammoth'." In 1914, Dr. A.N. Kryshtofovich found strata with dinosaurs in it on the right side of the Amur river, below the estuary of the left tributary Burreya[1]. The discovery led to excavation from the Russian survey during the summer 1915-1917. Results were published in a brief report by A. Riabinin (28).

In ~1913, Father R. Mertens found a skeleton of a Dinosaur near Ning Chia Kou in the Meng Yin district. In 1916, part of the specimen was presented by the German mining engineer, W. Behagel, to the head of the geological survey of China, Dr. V.K. Ting. At that time, it was not clear where the sample came from. It was not possible to find the sample locality until the end of 1922, when Prof. J.G. Andersson (1) together with Dr. T'an went to Shantung and relocated the sample locality. That led to the discovery of new localities and to the excavation in 1923 of Otto Zdansky and Dr. T'an. That material that is described below.

During the summer of 1922, the famous excavations of the American expedition in Mongolia[2] (2) started. This material was described in the American Museum Novitates and in several other publications.

---

[1] [Eds.]: "rechten" and "linken", literally "right" and "left"

[2] [Eds.]: Central Asiatic Expeditions of the American Museum of Natural History

GEOLOGY

Shantung has an area of ~149,000km^2 and is a little smaller than south Germany and Switzerland together. Due to the large size of the study area and the short study time, T'an made only a very cautious estimate of age determinations.

Following T'an, the dinosaurs come from three different formations:

1. The *Meng-Yin-Series* is from the Lower Cretaceous. Dinosaurs were found in the lower and middle level of gray sandstone. The strata occur in the central part of Shantung. Beside dinosaurs, turtles, fish, lake mollusks, and land plants were found.

2. The *Ch'ing-Shan-Formation* is equivalent with the upper and middle part of the Meng-Yin-Series, and therefore these dinosaurs come probably from the middle part of the Meng-Yin-Series. The formation is located in eastern Shantung, the dinosaur-bearing rock is red clay.b

3. The *Wang-Shih-Series* is from the Upper Cretaceous, the dinosaurs are from the middle part of red clay, red and clay-rich sandstone and conglomerate. The series is found in eastern Shantung and also includes lake mollusks.

DESCRIPTION OF SPECIES

SAUROPOD

Helopus zdanskyi n. g. et n. sp.

Pl. I-IV,

Two complementary specimens, a and b, exist for this species. Both were excavated by Dr. Otto Zdansky. The specimen a is labeled: Zdansky, April 1923, Shantung, Meng-Yin-Hsien, NW 40 li, Ning Chia Kou, W 2 li. It comprises parts of the skull, the articulated vertebrae II-XXV, cervical ribs, pectoral rib from vertebra XX, a fragmentary coracoid (not mapped), and a left femur. Dr. Zdansky told me that Father Alfred Kaschel, who lives near the sample locality, told him where Father Mertens excavated parts of the exemplar. These vertebrae are part of specimen a. Other parts of the skeleton probably exist, but I didn't attempt to find them, because there were probably spoiled during the excavation.

Specimen b is labeled: Zdansky, March 1923, Shantung, Meng-Yin-Hsien, NW 39 li, Ning-Chia-Tung-Kou SE 1 li. The locality is ~2-3 km from the location of specimen a. It comprises the vertebrae XXII-XXXVII, the entire pelvis, and the femur, tibia, fibula, astragalus, metatarsals I-IV, and seven loosely lying phalanges (three of them are unguals) from the right posterior leg.

Below I describe the material.

Specimen A

Pl. I-III.

The Skull

The skull was disarticulated, but the appropriate elements were lying on top of each other and side by side within a small, limited area in front of the axis. In several cases, the bones lay so close to each other that it was difficult to separate them, especially because some were very thin. Perhaps it is because the skull disarticulated before being buried and crushed by the overlying sediment that the bones are so undeformed that the skull, when rebuilt, is only slightly more asymmetrical than it would have been in life.

The premaxilla is narrow and tall, and has a process along the mid-line of the snout. If the process were not broken, it would be covered by the nasal at the dorsolateral[3] margin of the naris. This process is thickened at the front margin, but otherwise thin as cardboard. Four teeth are in the premaxilla, and a fifth is at the boundary between the premaxilla and the maxilla (Pl. II. Fig. 2). A hole or small foramen is located below the narial opening, at the clearly visible boundary between the premaxilla and the maxilla.

The maxilla is fragmentary, because the posteriormost part, where the lacrimal and the jugal should abut, is broken off or eroded. Only a small upturned point exists that holds up the lacrimal (Pl. II. Fig. 1-4). A thin process that becomes thinner stretches to the top and the back and separates the narial opening and antorbital fenestra, which must have been bordered posteriorly by the lacrimal. This process has two narrow facets at its upper boundary. The inner facet is connected with the nasal and the outer one with the prefrontal (Pl. II. Fig.2). In addition to the above-mentioned tooth from the boundary between maxilla and premaxilla, each maxilla bears nine other teeth that were worn and positioned very close to each other. The part of the maxilla containing the big teeth with long roots is robustly built, while the rest of the bone is so thin that it is similar to the light structure of a pterosaur.

---

[3] [Eds.]: literally “upper outer”

The vomers (Pl. II. Fig. 8-11) were not considered in earlier studies about sauropod, as far as I know. The form resembles the same bone from *Sphenodon*, but the posterior and laterally-directed thin part is more fan-shaped and restricted by the palatine laterally and by the pterygoid posteriorly.

The pterygoid, the quadrate and part of the quadratojugal were prepared out in their original articulation (Pl. II. Fig. 5-7). The quadratojugal is incomplete. The process that should be connected to the jugal is lost. On Pl. II. Fig 6 the line is visible that borders the front part of the quadratojugal, which is pressed against the processus pterygoideus of the quadrate. From the back, a big foramen quadrati is visible between the quadrate and the quadratojugal. The eardrum was located above this foramen and was outstretched between the quadratojugal (in front) and the quadrate (above). It was relatively small.

The quadrate forms a thin bar, which swells at the lower end to a thick part of joint against the lower jaw and enlarges at the upper end to a flat bowl with sharp edges where the eardrum was located. To the front and within the bar forming part of the quadrate rises a thin sheet, the processus pterygoideus, to the skull.

Posteromedial to the anteriorly pointed pterygoid process [of the quadrate] is the pterygoid. Slightly anterior, where the pterygoid loses the connection with quadrate, a curved process is directed outward (Pl. II. Fig. 5 and 6), which accommodated the ectopterygoid. The anterior, disc-shaped part of the pterygoid is almost vertical and towers into the skull (Pl. I Fig.1, Fig.2, Fig.3, Fig.4). Although the bone has the same position in Osborn's (26. S. 287) and Gilmore's (9. S. 454) figures of *Camarasaurus*, I have difficulty believing that this is the correct position. Probably the bone has experienced a rotation around its axis as a result of the pressure of the overlying strata, so that the front part with the quadrate and its own back part end up parallel to each other, instead of being influenced by the curvature of the palate.

The postorbital-postfrontal (Pl. I Fig 9 and 10) is primarily made up of three processes: a small ventrally-directed one that is positioned in front of the ascending limb of the jugal, a triangular posterior one, located in an appropriate cavity at the outside of the squamosal, and a broken dorsal directed one, which comprises the postfrontal and on which fragments of the frontal or parietal are attached. The postorbital borders the posterodorsal margin of the orbit with its anterior margin, abuts the upper temporal fenestra along its upper margin and meets the uppermost corner of the laterotemporal fenestra with its lowermost corner.

The lower limb of the squamosal, which should connect to the quadrate, was lost. The consequence is an uncertainty in the reconstruction of the skull. At the exterior of the anteriorly-directed process of the squamosal is the above mentioned triangular cavity for the posterior arm of the postorbital visible. The upper, very thin part of the bone is positioned above the supraoccipital. A sharply demarcated cavity is located ventrally[4]. The front edge of the bone is also the back rim of the upper [temporal] fenestra.

From the lower jaw only the dentary and the surangular and angular of the exterior is obtained.

The teeth resemble those of *Camarasaurus*, and show wear not only against their antagonists but also against their neighbors (Pl. II. Fig. 13, 20, 22). That shows that the teeth are not positioned separately as in carnivores (as Versluys (34) supposed based on Osborn's figure), but densely packed like in Gilmore's figure. This represents the typical tooth type for sauropods. Although I have a large number of in situ and shed teeth I couldn't find differences that indicate whether the teeth were come from the premaxilla, maxilla, or the lower jaw. I can only differentiate between older and younger teeth. The abrasion of the antagonistic teeth is strong as seen in Pl. II. Fig. 12, 14, 19.

Reconstruction of the skull. Although many bones are missing, including the entire braincase, prefrontals, nasals, lacrimals, jugals, and palatines, it is not really difficult to reconstruct the exterior of the skull with the claim of a high degree of certainty. That is based on the available bones that have a lot of the sutures from the missing neighbors. The strongest uncertainty comes from the fact that the lower process of the quadrate is missing. Needless to say that during the reconstruction I didn't work only in two dimensions (drawing), but in three (modeling). Everybody who worked on that type of project with a lot of fixed points can admit that in our case a high grade of certainty is expected, and that also differences of similar forms can occur. The skull might be a little bit higher atop above the frontal or a little bit lower in the back above the supraoccipital than shown in my figures, but different uncertainties may occur also by complete pieces.

---

[4] [Eds.]: "underside"

The reconstruction proceeded in the following way. First, the upper jaw was put together. The lower jaw was put against the upper jaw, and I found that if the lower jaw limbs were put together the same way as they meet at the symphysis, the width of the jaw pairs were the same. Therefore, length, width, and minimum height of the skull were determined. The next step was to put the quadrate with the connected pterygoid on top of the lower jaw joint. Then, we tried to find the position of the squamosal and postorbital, which fit together. After that it wasn't difficult to model the missing bones. The last step was to open the mouth. The modeled bones are indicated. Of course, the work from Osborn and Gilmore was a big help during my own reconstruction.

In terms of the practical adjustment: I incorporated the pieces that were modeled in plaster in the stand and put the bones loosely on top of it.

Although smaller uncertainties may exist, we observed discrepancies between the skull of the *Helopus* and the skulls of the two *Camarasaurus* specimen. The parietal is toroid, the entire skull is lower and the snout is stronger displaced than in these types.

The Vertebral Column

Thanks to the extraordinary carefulness and accuracy of Dr. Otto Zdansky at the time of the excavation, we have recovered the entire series of 25 vertebrae in undisturbed sequence and with all vertebrae in juxtaposition to each other.

The skeleton was not excavated too much, but instead was protected in blocks of rocks. The joints of both the rocks and the bones were preserved. Each block was marked with a sign that defines how it fits with another block. A plan was made that described the position of the blocks. After arrival in Upsala and the beginning of preparation, there was no doubt how the blocks and the embedded vertebrae were fit together.

Here we have the case that the number of cervical vertebra was determined with certainty. If I do not take into account the so-called[5] "proatlas", but instead take the atlas as the first vertebra, the amount of cervical vertebra is 17. In comparison, the appropriate number is 12 for *Camarasaurus lentus* (after Gilmore). The same author presented 15 vertebrae for *Apatosaurus louisae* and *Diplodocus*.

---

[5] [Eds.]: in text as "s.g.",which is probably the abbreviation for "so genannt", literally "so-called"

The atlas was not found. Based on the appearance of the anterior articular surface of the axis, it was concluded that the atlas comprised a crescent-shaped intercentrale[6], a free centrale[7] that was not fused to the axis, and a dorsal arch. We don't know whether the two ossification centers of the upper arch were fused.

The axis shows the indication of the suture, in which the centrale and the intercentrale were fused. At the lower outer edge is a small parapophysis that is not dominant, because it is a little bit damaged. In Plate III. Fig.5 you can see the boundary between the intercentrale and the centrale, above is the neural canal and above is again the real neural spine. I say "real neural spine" because I don't consider the "split neural spine" as a neural spine. In my mind, the "splitting" of the so-called "neural spine" has nothing to do with the element itself, but is a regeneration within the upper arch that I don't regard homologous with the neural spine. If you see the vertebra from the posterior, the real neural spine is only a barely seen, sublime, vertical line in the back of the backward dorsal alcove. What was, up to now, interpreted as the posterior split part of the neural spine is not the neural spine, but consists of the postzygapophysis and the posterior part of the Lamina neurozygapophysica[8]. The posterior part of this lamina is the only one that was fully developed, other than the posterior laminae from the cervical vertebra mentioned below.

I will talk about the rest of the cervical vertebra and start with an overview of the system of laminae and the cavities and coels they bound that is characteristic for the vertebrae of the Sauropoda. It helps to make the vertebra lightweight in comparison to their size and therefore exceed the vertebra of the pterosaurs.

There is a widely used terminology to describe the supporting construction. See Hatcher for *Diplodocus* (10) and *Haplocanthosaurus* (11), Lull for *Barosaurus* (20), and Osborn and Mook for *Camarasaurus*. I prefer Latin names that are used in all languages. I named the laminae after the vertebra they connect.

The *Lamina neurozygapophysica* run near the neural spine between the pre- and postzygapophyses.

The *Lamina praediapophysica* connects the prezygapophysis and the diapophysis.

---

[6] [Eds.]: atlantal intercentrum

[7] [Eds.]: probably atlantal pleurocentrum (odontoid)

[8] [Eds.]: all names for laminae remain as written, see Wilson (1999) for a revision of laminar terminology

The *Lamina postdiapophysica* connects the postzygapophysis and the diapophysis.

The *Lamina centrodiapophysica* (*Lamina horizontalis Auctorum*) connects the diapophyses with the centrum and runs horizontal along the cervical vertebra to the back, and along the thoracic vertebra vertical down.

The *Lamina diaparapophysica* connects the diapophysis with the parapophysis.

The *Lamina parapophysica* contains the parapophysis.

It is the upper, often quite tall process of the *Lamina neurozygapophysica* that was interpreted as a process of the split neural spine. I call that process P*rocessus pseudospinosus.*

It seems to me that the limbs of the split neural arch were not formed from the two bone centers that build the upper arc of the neural spine, but are regeneration from the bone centers of the zygapophyses. I assume that the zygapophyses emanate from special ossification. I did not want to dissect a vertebra, but the bone fibers of the zygapophyses are built together with the ones of the Lamina neurozygapophysica as a whole that has nothing to do with the neural spine. In contrast, I have seen fibers that pass each other at right angles without mixing. Even though the Lamina neurozygapophysica does not form from a different ossification center than the zygapophyses[9], it must formed out of a different part of the upper arch of the neural spine. I don't assign it to the neural spine, but as a recreation of different source.

The real neural spine ends for *Dicraeosaurus* at the place where the presumed split occurs.

Something similar occurs for the Zeuglodonts (22), where the neural spine is completely reduced, but characteristic paired Processus obliquiomammilares developed.

The cavities that are limited at the cervical vertebra by the above mentioned laminae, are named as follows:

The *Cavitas dorsalis anterior*, the frontal dorsal fossa lies between the frontal parts of the Laminae neurozygapophysicae.

The *Cavitas dorsalis posterior*, the posterior dorsal fossa lies between the posterior parts of the Laminae neurozygapophysicae.

[9] [Eds.]: uncertain translation here

Between the two fossae lies the neural spine that sometimes forms a vertical ridge or a barely raised ridge band in the depressed surface of the fossa. On Pl. III. Fig. 16 of the cervical vertebra XIV, you can see next to the neural canal and below the dorsal fossa a pair of accessory cavities. On the posterior side of the same vertebra (Fig 15) you can see similar cavities, but they are located a little bit higher and below the posterior dorsal fossa. These cavities were also seen on different cervical and thoracic vertebrae, but were also sometimes missing.

The *Cavitas lateralis superior* lies between the Lamina neurozygapophysica and the Lamina postdiapophysica.

The *Cavitas lateralis media* lies between the Lamina postdiapophysica and the Lamina centrodiapophysica.

The *Cavitas lateralis inferior* lies between the Lamina centrodiapophysica and the Lamina parapophysica.

The *Cavitas ventralis* lies between the two Lamina parapophysicae.

In the *Cavitas lateralis superior* is a small accessory, almost horizontal lamina.

This system of laminae and cavities is found on all cervical vertebrae except for the following cases.

The frontal dorsal fossa is missing on the axis. The raised ridges of the axis, the third, forth, and maybe the fifth cervical vertebrae, which define the lateral cavities can not be called laminae, but could be called tuberosities. The ventral cavity does not start to dominate until the fourth cervical vertebra. The third cervical vertebra, without a ventral cavity, has some small holes between the parapophyses (Pl. III. Fig. 2).

The system of laminae continues all the way to the dorsal region, to the seventeenth and last cervical vertebra, where the different elements are as follows:

The Lamina neurozygapophysica is still present in the 25th vertebra, but changes its habitat at the last cervical vertebra XVII, and much more at the first thoracic vertebrae.

The Lamina praediapophysica loses the character of a Lamina at the first thoracic vertebra.

The Lamina postdiapophysica exists up to the 25th vertebra, but shortens and loses its character already at the 19th vertebra.

The Lamina centrodiapophysica is preserved over the entire length, but in the same way the diapophysis moves atop, the lamina becomes vertical.

From the Lamina parapophysica you can only find a weak indication at the first thoracic vertebrae that is already missing at the next vertebra.

The cavities are similar to those described previously.

The dorsal fossae exist up to the XXV vertebra.

Small, undivided neural spines can be seen from the 16th cervical vertebra and then further back in the depressed surfaces of these fossae and between the Processus pseudospinosi.

The upper side cavity is already strongly reduced at the last cervical vertebra and is also split by the small accessory lamina. At the first thoracic vertebra, XVIII, the reduction is advanced, but then the holes stay as far as the material goes.

The middle side cavity is merged to a part of the backside of the vertebra at the 20th vertebra.

The lower side cavity is conserved, but moves atop and is strongly changed at the 20th vertebra.

The ventral cavity disappears at the 19th vertebra, when the parapophyses migrate dorsally.

As I mentioned above, the laminae lose their character as laminae at the thoracic vertebrae and are more like supported tuberosities[10].

At the thoracic vertebrae form new supported elements due to the disappearance of the normal elements of the vertebrae. Together with the movement of the diapophysis and parapophysis[11] a tuberosity forms that connects the diapophysis with the parapophysis. On Pl. III. Fig. 3 you can see it on the 20th vertebrae, but in Fig. 4 you can already see it at the 19th vertebrae. It begins to develop on the 16th vertebra and strongly developed on the 17th.

At vertebrae XXIII and XXIV it runs below the Lamina praediapophysica and is parallel with it. On the left side of vertebra XXI, you can see a accessory lamina that runs from the lower part of the diapophysis to the prezygapophysis and therefore separates the cavity between the Lamina prediapophysica and the Lamina diaparapophysica.

More accessory supported tuberosities or laminae come along and give a characteristic look to the neural arches of the thoracic vertebra. This appearance is not

---

[10] [Eds.]: “Wülst” = bulge, tuberosity, swelling

[11] [Eds.]: “Rippenapophysen” = rib-bearing processes

necessarily symmetrical on both sides of the same vertebra, but is characteristic to identify part of the backbone from another specimen.

Now I talk about the part that I assume is the real neural spine. First, I refer to Fig. 1, 3, 5, 6, 17, and 18 on Pl. III, where you can see the neural spine. Actually, the neural spine was seen very often, but never interpreted as such. For example, Hatcher (10) 1901 called the neural spine “median spine”, not interpreting it as the neural spine. On several figures of *Haplocanthosaurus* Hatcher doesn’t label the neural spine, but instead labels it as a whole as “neural spine” and only part of it as the “median spine”. In 1914, Janensch showed the neural spine for *Dicraeosaurus*, but called the Processus pseudospinosi the dorsal process. Lull (1919) labelled[12] the neural spine “postspinal” and “prespinal” laminae in *Barosaurus*. In 1921, Osborn and Mook also do not label the neural spine for *Camarasaurus supremus* and *Amphicoelias*, but instead referred to the whole “neural spine” (also Hatcher’s “neural spine”) as “spine” .

If we examine how the neural spine for the *Helopus* appears on the different vertebrae, I already mentioned that it is visible at the axis anteriorly and dorsally; the same for the third vertebra. For the remaining cervical vertebrae it is completely or partly embedded between the Lamina neurozygapophysicae. If the neural spine is not completely covered, it is seen in as a narrow band in the depressed surface[13] of the dorsal cavities. For cervical vertebra XVI and the vertebrae posterior to it, you can it also see dorsally. For the cervical vertebrae III – XV, the neural spine can seen in the dorsal fossae, but is covered by the Laminae neurozygapophysicae with its Processus pseudospinosi. These two come together above the neural spine. The bone fibers of the lamina run parallel to the backbone and form a right angle with the fibers of the neural spine. From the last cervical vertebra the neural spine is seen from the front and the back.

The entrance to the pleurocoel is not a gradual increase in size of the lower lateral cavity, but instead an independent formation. It is present on all vertebrae beginning with the axis and does not migrate, while the diapophysis and parapophysis and the lower lateral cavity move. In the cervical vertebrae, it is a flat, cone-shaped depression in the lower lateral cavity. The point of the cone runs to the pneumatic cavity in the interior of the

---

[12] [Eds.]: “nennt”, literally “named”

[13] [Eds.]: “hintergrund”, literally “background”

vertebra. The walls of the coel will be steeper at the last cervical vertebra, but beginning with the first thoracic vertebra, XVIII, the coel changes into a sharply demarcated hole with rounded-off edges. You can see the alteration on Pl. III. Fig. 3. The hole leads to the interior of the vertebra, but not into an entire chamber as in other sauropods, but instead to a complex of small pneumatic cavities that fill all parts of the vertebra except the thinnest regions of the laminae. That formation of the spongiosa, if you want to called it that, is similar to the pneumaticity seen in the skull of a horse or elephant.

The joint areas of the zygapophyses are almost horizontal in the cervical region, but start to tilt medially between the 16th and 17th vertebra, a position that is maintained as far as the specimen goes. There is no hyposphene-hypantrum articulation.

The diapophyses keep their position throughout the entire cervical region, and migrate dorsally starting in the thorax region.

The parapophyses keep their position to the external trending bottom line of the vertebra through the entire cervical region until the first thoracic vertebra, XVII. At this first thoracic vertebra the parapophysis lies lower than the aperture of the pleurocoels. Between vertebrae XXI and XXII the parapophysis moves up to the neural arch, and reaches the final position at vertebrae XXIV.

The cervical ribs II and III are free, all the others are fused with the vertebrae and can reach a length of 2.5 vertebrae. The rib of the last cervical vertebra, XVII, is a little bit damaged, but was probably not longer than the vertebra.

The thoracic rib that belongs to vertebra XX is preserved. The ribs probably take the position that is typical for Sauropoda, and show that the chest was tall and narrow.

The femur is poorly preserved. For the measurements, I refer to the table after description of *specimen b*. The fourth trochanter is well-developed but short. The bone is very massive and its lumen is only 2 cm wide and filled with spongy bone.

SPECIMEN B

Pl. IV.

The Vertebral Column

Before I start with the description of that specimen, I want to explain the reason for my opinion that the vertebrae XXII – XXV are present in both specimens.

1. The vertebrae of the different specimens of Sauropoda are different, although in general they are all constructed in a similar way. In particular the system, with supported laminae and tuberosities is different for each specimen. Because there are infinite possibilities for the arrangement of the laminae and tuberosities, we can expect that the system is also very different for very similar specimens. In contrast, it is interesting that a pattern that also can change from vertebra to vertebra in the same individual is so constant throughout the same specimen (at least for the same age). Therefore, there are no doubts that these patterns are characteristic for the specimen. Comparison between the figures 3 and 4 from Pl. III and the figures 1 and 2 from Pl. IV should convince that specimens *a* and *b* are the same species.

2. The next step is to identify the four thoracic vertebra that are present in both specimens with the greatest certainty. The good thing is that in both specimens the location of these vertebra is where the parapophyses migrate dorsally the fastest. On Pl. III Fig. 3 and 4, you can see that on vertebra XXI the parapophysis is still attached to the centrum and a little bit higher than the aperture of the pleurocoels. On vertebra XXII the parapophysis has jumped to the neural arch. The vertebra XXII is the first that is conserved on specimen b, Pl. IV. Fig. 1 and 2. Because the vertebra is deformed by pressure, the position of the parapophysis in the figure changed and does not show the convincing similarity to the same vertebra of *specimen a*. Therefore, I created a small table with the movement of parapophysis on the vertebrae XXII – XXVIII.

Table (in cm), position of the parapophyses on the vertebrae XXII – XXVIII

Numbers represent distance between the ventral-most point of the suture[14] between the parapophysis and the anterior, dorsolateral edge of the vertebrae.

vertebral position	Specimen a		Specimen b		average	
					Sp. a	Sp. b
XXII	5.1	6.8	4.7	5.5	6	5.1
XXIII	6.5	7.9	5.7	6.8	7.2	6.3
XXIV	8.4	9.5	8.4	8.5	9	8.5

[14] [Eds.]: "Unterkante der Gelenkenfläche", literally "lower edge or border of the joint or suture"

XXV	9.1	11.2	9.5	10.8	10.2	10.2
XXVI	—	—	9.5	10.7	—	10.1
XXVII	—	—	9.5	10.7	—	10.1
XXVIII	—	—	8.4	10.3	—	9.4

If you also compare the configuration of the vertebrae elements and the size ratio that you can find in the Table on page 21[15] you can see that the existing differences are based on the heterogeneous deformation of the vertebrae.

If I am correct with the combination of the specimens, I can conclude that *Helopus zdansky* had 15 thoracic vertebrae including the last thoracic vertebra that functioned as sacral vertebra. Therefore it had 32 presacral vertebrae.

From the backbone of specimen b vertebrae XXII – XXXVII are present, and vertebrae XXII – XXXII are thoracic vertebrae. Except for the posteriormost vertebrae that is attached to the sacrum, all vertebrae are morphologically similar[16] after the parapophysis moves to its final position.

You can see the changes in the size of the diapophysis from Fig. 3 and the table.

The medially-directed tilt of the joints of the zygapophyses increases posteriorly, but never reaches vertical, not even between vertebrae XXXI and XXXII.

The neural spine is visible on thoracic vertebrae XXII - XXX from the front, the top and the back, but is covered on the

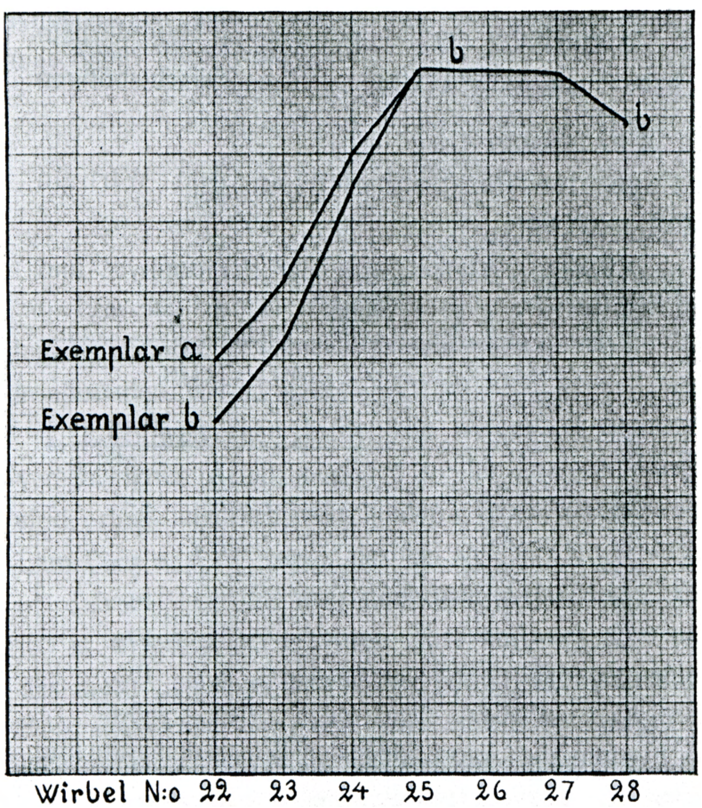

Fig. 1. *Helopus zdanskyi*. Curve showing the position of the parapophysis in vertebrae XXII-XXVIII. Natural size.

[15] [Eds.]: refers to pagination in the original

[16] [Eds.]: “etwa dasselbe Aussehen”, literally “look about the same”

side by the Laminae neurozygapophysica. Like in specimen a, it is discontinued in the Processus pseudospinosi, but the distal extremities are blunted. Like in specimen a, the neural spine and the Processus pseudospinosi form a quadrangular figure that becomes wider in the back when viewed dorsally.

The pattern between the vertebrae and the dia- and parapophyses that is formed by the supported laminae and tuberosities changes gradually, as you can see in the figures.

The posteriormost thoracic vertebra, XXXII, differs in appearance. The opening of the pleurocoels has the same position as for the other thoracic vertebrae, but is not visible in the figures. The diapophysis behaves as in the foregoing vertebrae. The upper edge of the parapophysis is at the same height as in the foregoing vertebrae, but extends to the lower end so far on the vertebrae that the lower edge is at the same height as the opening of the pleurocoels, which naturally fits with the different shape of the appropriate thoracic rib.

Size of the vertebrae in cm

vertebral position	vertebral body						the whole vertebra					
	length, excluding anterior convexity		posterior width		posterior height		height above neural spine		width above outer edge of postzyga-pophyses		width above diapo-physes	
	a	b	a	b	a	b	a	b	a	b	a	b
II	9.4	—	3.3	—	3.7	—	13.2	—	6.7	—	5.2	—
III	13	—	3.6	—	4.8	—	10.8	—	7.3	—	8.3	—
IV	22.2	—	4	—	4.1	—	15	—	8	—	8.5	—
V	23.4	—	4.6	—	6.5	—	15.8	—	8.8	—	9.1	—
VI	23.8	—	5.5	—	7.5	—	16.4	—	9	—	10	—
VII	26	—	6.6	—	8.2	—	20.2	—	9.4	—	11.6	—
VIII	26.2	—	7.2	—	9.3	—	22.1	—	10	—	12.2	—
IX	27.4	—	7.4	—	99.6	—	23.3	—	10.7	—	13.7	—
X	28.2	—	8.9	—	11	—	26	—	11.5	—	15.3	—

XI	28.3	—	9.3	—	11.5	—	27.4	—	12.6	—	15.8	—
XII	27.6	—	10	—	13.9	—	29.2	—	12.8	—	16.3	—
XIII	26.8	—	11.3	—	12.7	—	31	—	13.4	—	19.4	—
XIV	26.3	—	11.3	—	13.9	—	33.2	—	14	—	21	—
XV	26.3	—	12.3	—	14.2	—	33.7	—	16.5	—	23	—
XVI	20.3	—	12.7	—	12.9	—	29.7	—	16.6	—	25.5	—
XVII	18	—	14.8	—	14.2	—	27.3	—	17	—	31.1	—
XVIII	14.2	—	13.1	—	14.2	—	27.9	—	17.5	—	32.3	—
XIX	12.8	—	12	—	13.2	—	31.1	—	16.3	—	37.2	—
XX	10.1	—	11	—	13.2	—	32.1	—	15.8	—	38	—
XXI	11.6	—	9.8	—	13.3	—	35.1	—	12	—	37.4	—
XXII	12.2	10.3	9.2	13.3	13.3	14.5	39.3	29.8	12.1	16.2	32.6	46.6
XXIII	12.8	12	9.2	12	13.8	12	44	31.6	11.3	12.7	29.5	41.5
XXIV	12.7	11	—	11.8	—	11	44.2	32.3	10	13	24.2	37.9
XXV	—	11.2	—	11.2	—	11.9	—	35.8	9.4	12.4	21.6	34
XXVI	—	10.3	—	13.2	—	12.3	—	36.7	—	11.3	—	30.7
XXVII	—	8	—	11.3	—	14.1	—	37.1	—	11	—	26.6
XXVIII	—	9.3	—	11.6	—	13.8	—	38	—	—	—	25.4
XXIX	—	10.3	—	13.8	—	14.4	—	—	—	10.2	—	—
XXX	—	9.6	—	19.9	—	15.1	—	—	—	9.8	—	25.4
XXXI	—	11.1	—	13.8	—	11.8	—	40.5	—	10.1	—	24.6
XXXII	—	10	—	14	—	—	—	43.4	—	—	—	31.5
XXXIII	—	—	—	—	—	—	—	42.1	—	—	—	29.8
XXXIV	—	—	—	—	—	—	—	40.9	—	—	—	29.5
XXXV	—	—	—	—	—	—	—	39.2	—	—	—	29.5
XXXVI	—	—	—	—	—	—	—	38.4	—	—	—	—

The Processus spinosi of vertebrae XXXI – XXXVI merge together, so that they build a plane that is visible from top and from the sides, where it is not covered by the Laminae neurozygapophysicae and its Processus pseudospinosi. For the posteriormost thoracic vertebrae, the neural spine is visible in anterior, dorsal, and lateral views. To the back it is merged with the neural spine of the first sacral vertebra. For the posteriormost thoracic vertebrae and the sacral vertebrae, the Processus pseudospinosi and the neural spine form an oblique rectangular figure seen from the top.

The Sacrum. During the preparation, I left the pelvic girdle attached to sacrum and also left the matrix in the pelvis lumen, seen in Figures 3, 4, and 5.

Therefore, I am forced to abstain from a complete description of the sacrum. I summarize the vertebrae XXXXIII – XXXXV as sacral vertebrae. They follow the thoracic vertebra that merges into the sacrum. The diapophyses of the sacral vertebrae behave[17] as the last thoracic vertebra, and the same is probably true for the parapophyses.

The first caudal vertebra, XXXVI, is subsumed[18] into the pelvis and is similar to the last thoracic vertebra. It seems like that the second caudal vertebra, XXXVII, is also a part of the pelvis, but the specimen is too poorly preserved to be sure.

The Ribs

I already mentioned a frontal lying thoracic rib, XX, in *specimen a*. In this specimen, a fragment of a thoracic rib is found on vertebra XXII. This rib is substantially different from rib XX, because the tuberculum is shifted downward, separating itself from the neck of the rib. It is similar to the ribs that belong to vertebrae XXIX, XXX, XXXI and that are preserved on the right side, Fig. 3. They were pushed to the back against the ilium. The rib of the posteriormost thoracic vertebra, XXXII, has the form of a sacral rib, Fig. 4BR, and forms a big, almost triangular plane anteriorly. The joint of the tuberculum and the diapophysis is not bigger than seen in the rest of the thoracic ribs, but the joint of the capitulum is very tall and extends from the normal height of the parapophysis ventrally to the centrum. Distally, that rib separates into two short limbs that are both attached to the ilium (Fig 4). The upper limb is

---

[17] [Eds.]: “verhalten”, literally “behaves”

[18] [Eds.]: “engagiert”, literally “engaged with”

more narrow and is seen in dorsal view in Fig 3. The lower limb is wider. Between the two limbs is a hole that can be seen in Fig. 4 from both sides.

The sacral ribs and the caudal rib that is fused to the sacrum are probably similar, at least they are visible from the top, where they connect the diapophysis with the ilium.

The Pelvis

The pelvis does not differ significantly from other Sauropoda.

The ilium is short and if you put the greatest length of the bone horizontal, the entire acetabular part is in the back part. The pubic peduncle is long and forms a right angle with the long axis of the bone, and the acetabular joint of the peduncle coincides with the midline of the bone. The ischial peduncle is a little bit damaged, but was probably only little projected. The acetabulum is pierced, but it seems like that it is not, unlike Osborn and Mook's figures of *Camarasaurus supremus*, without a bottom. The position of the ilium in the living animal was such that the connection between the interfaces of the two peduncles against the lower pelvic bone was horizontal, because that is the position with the biggest support of the ilium.

Insertion areas for muscles were described by Romer (30 S. 606). We can observe the following: The long crista for the Ilio-tibialis, the wide cavity of the Ilio-femoralis, the pronounced deepening of the ilio-fibularis and in the front on the pubic peduncle, the rough area of the ambiens.

With the exception of the rim of the acetabulum, the entire ilium is very cavernous and has slightly larger cavities than the vertebrae. In contrast, the other two pelvic elements are more massive.

The proximal plate of the pubis is bent and takes part in the formation of the pelvic cavity. The *foramen pubicum* pierces the proximoposterior limb of the pubis. The biggest area of the distal part of the pubis is set with an angle (compare Fig. 1, 2, 4, and 5). The most distal part of the bone (the most frontal part), was not fused with the opposing pubis, instead there is a small slit. Dorsally, the pubis was not fused with the ischium, but on the lower side of the girdle, the four bones, pubes and ischia, were complete fused, without even a fontanelle open.

On the pubis, you can see the origins for the following muscles: the flat, rough area of the ambiens and the big, at least in the lower part flat area of the pubo-ischio-femoralis externus.

The ischia are flat and discoidal and form a trench whose frontal part takes part in the building of the girdle. In the most distal part, the two ischia were not fused. The angle between the proximal and the distal part of the ischium is more obtuse than for the *Camarasaurus supremus*. Therefore, the distal part of the bone was not curved as much as in this specimen. It is possible that the strong backward bending of the ischia is based on deformation. If you test particular assemblies of sauropod skeletons, you can find the following pattern: The ischium is bent dorsally, the tail was bent downward and in the middle of the back opening of the pelvis is a haemal spine (probably displaced) that would have split the egg or cub into two pieces, and that is probably incorrect. Life pictures of sauropods are based on similar skeleton configurations, with the result that the egg or the cub could not have been born without a cesarean.

On the ischium you can see the following insertion areas for muscles: the small ridges for the different limbs of the flexor tibialis internus, the long ridge for the adductor 2 femoris and the big field where the pubo-ischio-femoralis externus 3 is attached.

The Hind Leg

When the pieces arrived here, the head of the femur was still in the socket of the pelvis. The femur terminates proximally[19] with an attachment site for cartilage. The greater part of the head and of the trochanter majus were probably composed of cartilage, which decreases the load capacity of the joint. The bone has the usual form that is oblate from the front to the back. The fourth trochanter is not long, but very strong and lies at the inner part of the back side and almost completely above the midline of the bone. Anteriorly, the tibial and fibular condyles are roughly the same size. Posteriorly, both are significantly smaller, especially the fibular condyle that is not positioned above the fibula, but further medial near the intercondyloid fossa. Perhaps one must regard the outer part of the fibular condyle as the lateral epicondyle. The bone is very massive and has a lumen of around 2 cm width that is, like the end of the bones, filled with a spongy bone.

---

[19] [Eds.]: “endet oben”, literally “ends on top”

The tibia and fibula are totally free from each other and do not show areas where they have could be connected. The tibia has the usual sauropod appearance. The femoral joint is very flat and suggests a thick cartilaginous cap in the knee joint. The cnemial crest is strong, is bent laterally, and encloses the fibula.

Dorsally, the fibula is very anteroposteriorly elongate. Above the center is, as usual, a rough flat area for the attachment of an especially strong muscle that caused a knee-formed bending of the bone that was also observed for other sauropods. The fibula extends farther distally than the tibia and must have been in connection with the two external metatarsals. When I talk about an elongated fibula, I do not hypothesize the fate of the fibulare. Because the ankle joint of the dinosaurs does not lie between the lower leg and the tarsals, but within the tarsus itself, there are different possibilities. The fibula of the sauropod, *Diplodocus* is in articulation with the tibiale[20]. Therefore I conclude that the fibulare and the fibula are fused[21]. If (like here) this articulation is not present, it is also possible that the fibulare is contained in the thick cartilaginous coat of the distal end of the fibula and is therefore not ossified.

The astragalus, tibiale, is ossified as usual and includes the three internal metatarsals. In term of dinosaurs we are in general talking about metatarsals, but it is also possible that we are talking about tarsometatarsals, because the distal-most tarsals are missing. Because there is a strong trend toward reduction within the sauropod leg, it is also possible that the distal-most tarsals were completely reduced.

As I mentioned above, the bones of the right hind leg were not connected to each other distally. The metatarsals, from which I-IV are present, are not difficult to identify and position. They show that the foot was very flat. The fifth metatarsal and a not determined number of phalanges are missing.

Phalanges. I strongly emphasize that my reconstruction of the foot is completely arbitrary in several ways. But it is a possibility that shouldn't be ignored. If we compare the hind legs of *Apatosaurus* and *Diplodocus* (10 S. 511 and 52), we can find that the second phalanx in digit II is strongly reduced in both feet, most strongly in *Diplodocus* where the element is not visible dorsally. An obvious next step of that reduction would be the

---

[20] [Eds.]: Wiman is probably using tibiale here as a synonym for astragalus

[21] [Eds.]: it is ambiguous as to whether he means *Diplodocus, Helopus*, or both

disappearance of the element. That possibility was the one I tried to consider in my reconstruction. If we examine digit III of *Brontosaurus*, we can see that phalanges 2 and especially 3 are strongly reduced. If they would disappear, ungual 4 would be, as I reconstructed, in contact with phalanx 1 in that toe. The argument for that comes from the observation that two of the three unguals that I have got are so wide. Maybe something similar happened in the outer digits of the posterior legs of sauropods, but the reduction has already progressed so far that it is hard to say what really happened.

That reduction in the hind foot of *Helopus* is only an assumption, but I return back to solid ground. I found a phalanx that I labeled I 1, because it was farthest away[22]. It is strongly oblate at the outer side and is bent medially. Proximally, it also has a big, wide joint that only matches with the first metatarsal and distally, there is a small, but pronounced joint that probably carried a small ungual. The external margin of that phalanx gives the impression that the inner side of the feet was covered by horny skin. I don't know such a phalanx from other sauropod feet and it gives that foot a specific character.

Now I talk about the unguals. The big ungual, Figs. 12, 13, 21, and 22, cannot be connected to the above mentioned phalanx I 1, because it is too wide, and its position is uncertain. The composition of the joint, Fig. 22, the form of the phalanx and the impression of the blood vessel on the ventral surface indicate that the phalanx was not vertical, but flat.

Diplodocus has similar phalanges that I attempted to position vertically, which I found to be impossible. After I reconstructed the phalanges horizontally, I studied the skeleton of *Diplodocus* in Frankfurt am Main. That skeleton was recently constructed and it was found out that this type of phalanges should be horizontal.

I positioned a strongly reduced ungual, Figs. 12, 13, 23, and 24, with pronounced step area, Figs. 23, on toe 3. A smaller ungual, Fig. 25 – 27, that has also a pronounced step area, Fig. 26, was not positioned.

---

[22] [Eds.]: Meaning here is unclear

Length of the pelvis and the posterior leg in cm

	Specimen a	Specimen b
Ilium, greatest length	—	57
height above acetabulum	—	27.4
height above pubic peduncle	—	48.5
Pubis, greatest length	—	63
width at acetabulum	—	23.4
width at distal end	—	13.8
thickness at distal end	—	8.7
Ischium, greatest length	—	64.7
width at acetabulum	—	21.1
width at distal end	—	19
thickness at distal end	—	8.7
Femur, greatest length	90	95.5
width on top	—	29.4
width on bottom	—	26.1
circumference above fourth trochanter	42	43.1
smallest circumference below fourth trochanter	37.5	40
smallest width below fourth trochanter	14	14.8
smallest thickness below fourth trochanter	8.8	9.2
thickness above tibial condyle	—	17.1
thickness above fibular condyle	—	13
Tibia, length	—	60.2
width on top	—	20.4
width above cnemial crest	—	19.2
width, distal end	—	16.5

	Specimen a	Specimen b
smallest width	—	9.4
smallest circumference	—	26.4
thickness at the proximal end	—	12.7
thickness at distal end	—	11.3
Astragalus, length	—	14.7
width	—	9.6
Fibula, length	—	61.8
width above	—	15
width at the bottom	—	10.2
thickness on top	—	5.6
thickness at the bottom	—	6
smallest circumference	—	18.4

AFFINITY TO OTHER SPECIES

Diagnosis. Skull small, lightly built, very similar to *Camarasaurus lentus* (Marsh). Nostrils high, but not retracted to the forehead. Teeth in premaxilla, maxilla and lower jaw shaped similarly, not spike-shaped, but strong, anterior and posterior edges sharp, lingual side is oblate, similar to *Camarasaurus*, positioned in complete closed lines. Number of presacral vertebrae 32, cervical vertebra 17, thoracic vertebrae including the dorso-sacral vertebra 15, sacral vertebrae 3. All vertebrae, including the anterior caudal vertebrae strong, almost hemispherical formed, opisthocoelous, highly pneumatized with lots of pleurocoels that open laterally to uniform cavities. All vertebrae are relatively short. Strongly developed system of support laminae, similar to *Camarasaurus supremus* (Cope). Processus pseudospinosi slightly taller than the Processus spinosi. Pelvis and posterior leg very similar to *Camarasaurus*. Hind foot developed as swamp foot[23].

---

[23] [Eds.]: a reference to later statements comparing the feet of *Helopus* to snowshoes or *trugor*

What we can see from the diagnosis and the description is that it is not possible to classify *Helopus* into one of the known species of sauropod. That is also true, if we establish six different species like v. Heune did (15). For *Helopus* we have to establish the new family Helopodidae. Whether we can also put other, less known species into Helopodidae, is not yet known.

It is also possible that there is not enough information for a systematic classification of Sauropoda, although it is possible to differentiate between different forms. Only very few species are more well-known known and it seems to me that it is difficult to judge the value of characters.

Helopus shows great similarities to *Camarasaurus* in terms of the teeth and the form of the skull, but is very different from *Diplodocus*. The backbone is more similar to cetiosaurids, like *Cetiosauriscus* and *Brachiosaurus*, than to *Camarasaurus*. The neural spine[24] of the presacral vertebrae is undivided in *Cetiosauriscus* and *Brachiosaurus*, but divided in *Camarasaurus*. The systematic importance of the of the Processus pseudospinosi over that of the neural spine in *Helopus* is doubtful. For the *Camarasaurus* specimen the Processus pseudinosi are also not very high. The neural spines of the thoracic vertebrae are also much taller in *Brachiosaurus* than in *Helopus*. *Helopus* is in this regard more similar to *Camarasaurus supremus*. The number of cervical and thoracic vertebrae do not agree with any known sauropod. The pelvis is similar in form to different families. The ilium is very short and probably lacks completely the posterior process[25] and is thus still similar to Cetiosauridae. The pubes are not constricted like in *Diplodocus*, but instead flat and wide, but not in the same form like *Cetiosauriscus leedsi* or *Camarasaurus supremus*. The ischia are also flat and not constricted, but are bent in the back part to the exterior. They are not as wide and short as in *Cetiosauriscus*, but wider than in *Camarasaurus supremus*. The bones of the posterior leg are of little systematic use, they are not as thin as for *Diplodocus* and the fibula has the most pronounced muscle process above the center, which is absent in the specimens of Cardiodontidae of the Cetiosauridae (v. Heune). The hind foot shows a similarity with *Diplodocus*, but is more developed as a swamp foot. With one word, *Helopus* seems to take an independent position.

---

[24] [Eds.]: “dorsal process” in text

[25] [Eds.]: “Hinterspitze”, literally “back spike”; probably refers to the postacetabular process.

BIOLOGY

In this chapter, I try to summarize some adjustments of the sauropods and especially of the *Helopus*. I start with the feet. The name *Helopus* means swamp foot, and I draw attention to the big step area of the posterior leg.

Before I go further, I must make a small departure toward another topic.

In the northern half of Sweden more than one third of the area are swamps. If a geologist travels through these areas during the summer, there is no day without passing a swamp and it happens that the shoes never dry. Most of the swamps are passable, but it happens that this is not the case. Then people use a very old apparatus that is called trugor or trygor (singular: truga or tryga). Other Swedish words are skarbagar or snoskor. The names show that these things are also used for snow. If plants that live in water, e.g. *Equisetum*- and *Carex* specimen, are harvested for food, people also wear trugor, that are called snow shoes. Horses also learn easily to go on trugor, which is especially important by the movement of heavy stuff.

After that ethnographic excursion, I go back to our sauropod feet. The understanding of the feet is based on my personal experience with snow shoes on soft ground during the summer. In the German language we can use the name “Tellerfusse[26]” for this kind of foot.

Although the plate foot is not so clearly seen in other animals, there are some similar feet. Most often mentioned are probably the wide claws of reindeer. They increase the load capacity of the foot on snow. The increase seems to be too small to be of significance, but it was observed that a man can pass snow without problems, while a 10 kg lighter woman has more difficulty because she has smaller feet. That shows that a small increase in the area of the foot is enough to get the desirable effect.

It is also possible that another effect played a role for the increased size of claws in reindeer. Their feet are capable of shoveling snow to the side to uncover the ground. In zoos animals have sometimes very long claws due to the lack of usage.

After that description the feet of different antelopes should be unambiguous. Brehm wrote about swamp horses, *Limnotragus*: “the hooves are extraordinarily long, often three times as long as wide. The toe elements are very flexible. The middle toes spread far away,

---

[26] [Eds.]: literally “plate-foot”

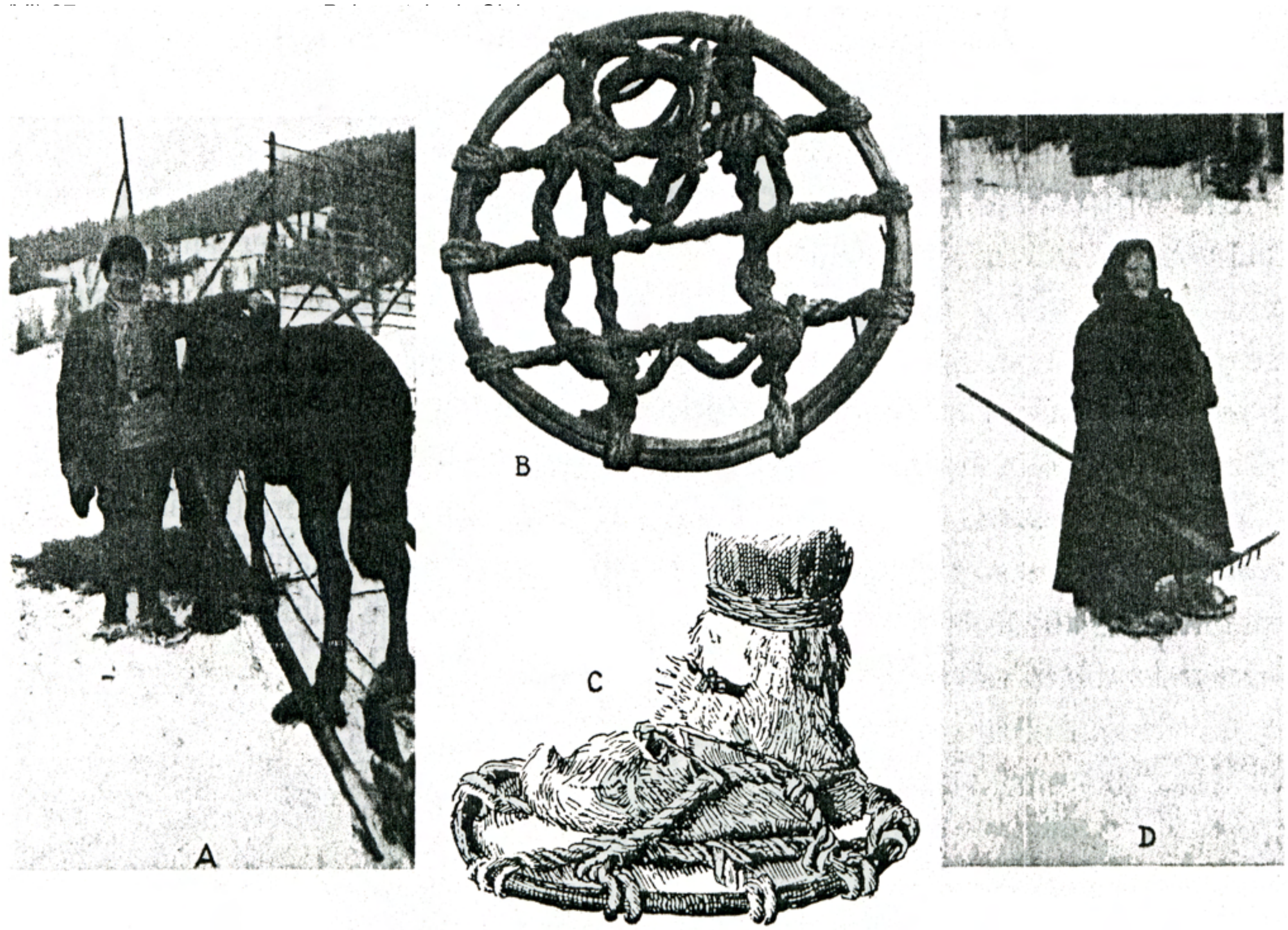

Fig. 2. Man and horse with snowshoes. B. Circular snowshoe for horse. C. Finnish shoe with connected snowshoe. From Hansen (21). D. Woman with snowshoe.

the lower part bear on the ground, hairless and covered with horny skin. The side hooves are in touch with the ground. This specific foot composition is a natural adaptation to the soft swamp ground where the animals live and enables them to walk on it, without sinking". For two water horse species, *Kobus kob* and *K. leche*, the hairs on the feet between the hooves and the side hooves are missing. That should be the same adaptation as in the case of the swamp horses.

In the Berlin zoo, I observed *Limnotragus gratus* and other antelopes that walked over loose sand. The animals do not step with splayed middle toes horizontal on the ground, but instead bend the splayed toes strong to the ground and stick their feet into the ground. On swamp ground they need roots etc. between their toes, to impede sinking. But because the center of gravity is at the intersection of the foot, the toes should gradually become horizontal with advanced sinking and then the foot could act as plate foot. If the latter is not the case, it is only the fork form of the foot that counteracts the sinking.

The foot of a hippo provides a very interesting comparison to the plate foot of sauropods. The posterior toes are strongly developed and are in the same plane as the middle toes. Therefore, a wide plate foot is created that does not sink easily. Sinking is also avoided due to the webs between the toes. That this foot is also practical for swimming does not counteract its nature as plate foot. That the hippo is really an adaptation to a life in a swamp is seen, if you compare it to the dwarf river horse, *Choeropsis liberiensis*, that is less adapted to the swamp and where the side hooves barely hit the ground.

Maybe it is the life in a swamp that resulted in the original three- to four toed feet of the tapirs.

For camels, we are not talking about sinking in the swamp, but sinking in the sand. The alignment is different. First, the canon[27] is split on the bottom, in order to split the toes apart. Next, not only the ungual, but also the previous phalanges are attached to a large callus pad. FInally, the toes are widened by this elastic pad and the horny sole of the foot.

None of these types of plate feet or swamp feet is so close to the idea of the *Helopus* feet as is the foot of the mammoth. In the past, analogies were made between the extremities of sauropods and elephants, so it is probably not an accident to find more similarities.

Recent elephants have a padded step base that is widened laterally and posteriorly. That widening is not so significant that we can talk about a plate foot, but it was in the case of the mammoth. Tolmachoff was probably right when he interpreted the observations and descriptions from Vollosovich (37) and Neuville (24) of the "presence of rimes[28] or horny excrescences surrounding the soles" as "an adaptation to the marshy tundras" on which the mammoth graze during the summer. The widened plate feet were also usable on snow.

The forefeet of *Helopus* are not known, but we can see from other sauropods that the soles of the forefeet also have to be big. The metacarpals are significantly longer than the metatarsals, and they are more vertically oriented, but they still form a cone, the base of which has the same size as the sole of the posterior feet. The carpus sits higher than the tarsus.

---

[27] [Eds.]: canon-bone

[28] [Eds.]: possibly a reference to an "ice rime", a blocky or chunky concretion of ice that may resemble these soles texturally

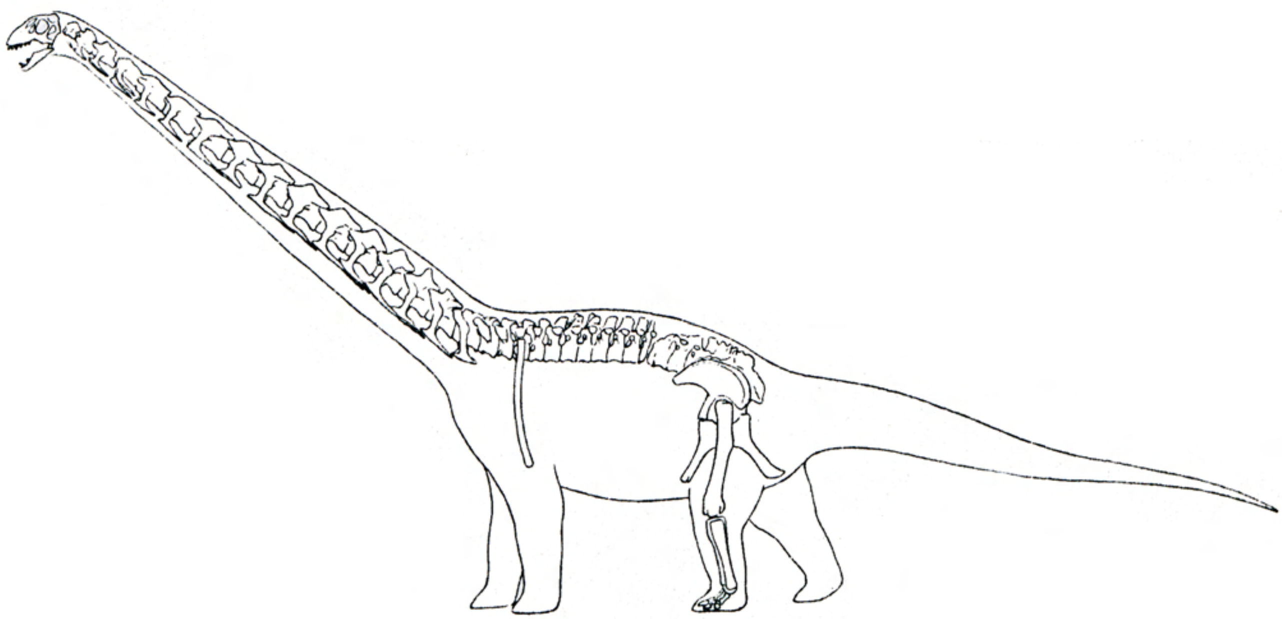

Fig. 3. *Helopus zdanskyi*. The preserved skeleton in the most probable position and with body outline. Scale is 1/70.

It is not impossible that sauropods that really used their claws, for example to dig or tear, had also plate feet. But it is also possible that not all of the sauropods lived similar.

I want to combine the adaptation of the feet with the so-called[29] waterline of the sauropods. As I mentioned, the skull, vertebrae, and the ilium of *Helopus* are very lightly built, whereas the pubis, the ischium, and the limb bones are massive and heavy. That does not mean the waterline was lower, but only that the balance point of the body was lower, as for a diver in a diving suit. The animal went under water on the sea bottom, as in *Diplodocus*. The skull of *Diplodocus*, where the nostril, the eyes and the eardrum lies high, is a periscope, but a periscope that does not only account for face, but also for smell, hearing and air. For *Helopus* and *Camarasaurus* the periscope nature of the skull is less significant than for *Diplodocus*, but there is no doubt that it served that purpose.

The idea that the sauropods lived under water and went on the sea bottom is not new. In the museum of London are postcards on which *Cetiosaurus* is drawn like that. This idea is highly debated.

That sauropods had a high upright position is clear, because the chest is relatively high and narrow. It is not common that you can find such an arrangement of extremities for an animal like a crocodile. Everything accounts for a vertical position of the extremities. The

[29] [Eds.]: "s.g." in text, see footnote 5 for details

ends of the extremity bones are so fragmentary that it is not possible to get an realistic idea about their form. The amount of cartilage present in the extremities makes it improbable that sauropods were land animals, because for such a heavy body to move through air, it would be necessary to ossify the joints. Several times it was also emphasized that sauropods are water animals. The form of the feet show unambiguous that the legs were vertical (like Marsh and Abel observed).

As I mentioned above, the dentition is unambiguously formed for eating plants, and exactly the same dentition is found in *Camarasaurus* and most of the other sauropods. For

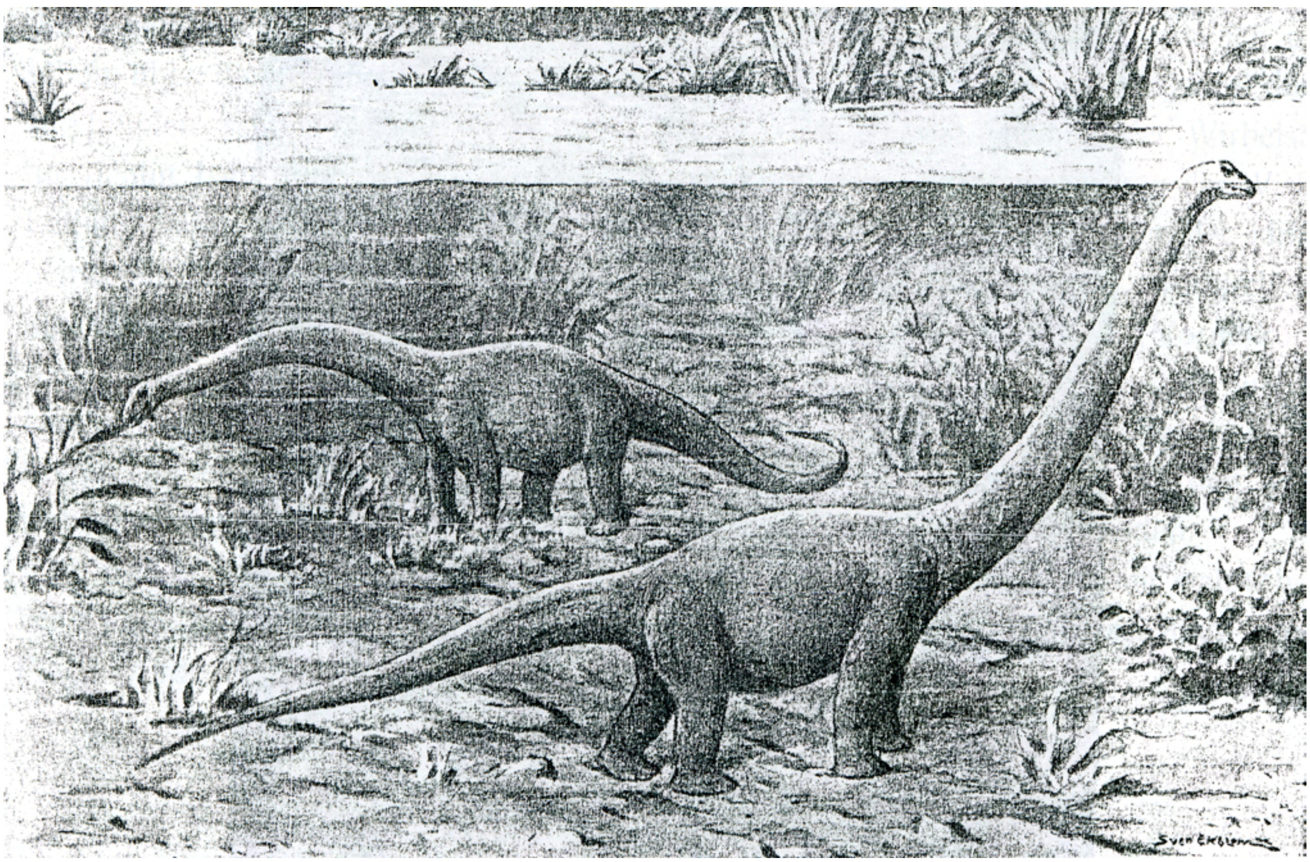

Fig. 4. *Helopus zdanskyi.* One individual biting a fruit collection; and the second lifts its head above the water surface to breathe and look around. Scale of the front individual 1/70.

this correlation, I don't talk about *Diplodocus*, because his dentition is still strange. From the beginning it was clear that sauropods lived on plants, especially water plants. In recent literature they were called plant-eating dinosaurs, a name that is unfortunate, because all ornithischians are probably plant eaters to a much higher degree. Because water plants were assumed to be not very nutritious, researchers had difficulty explaining how the huge bodies of the sauropods can exist, when the food is so restricted. There are two different ways to get out of the problem. First, there is the idea that water plants might be more nutritious then they were assumed. That didn't work. Since 1878, we have called them "succulent water plants". The condition of being succulent is an adaptation for retaining water during drought and is therefore not developed in water plants. I also do not assume

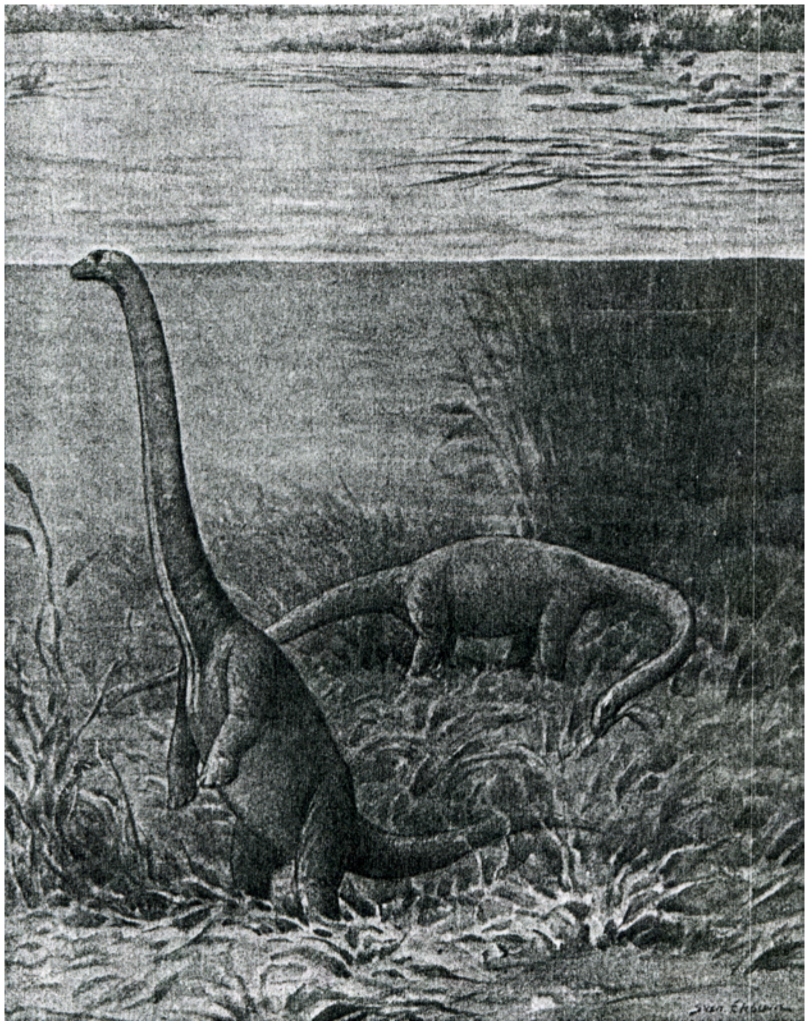

Fig. 5. *Helopus zdanskyi.* One individual in an upright position to breathe for a short moment. The other uproots a plant. Scale of the front individual 1/70.

that succulent plants are very nutritious. They were eaten by animals but it is more a drink than food. Despite protests, this 'contradictio in adjecto'[30] persisted until today, when they are now called lush water plants. Lush means water rich, but the more water a water plant has, the less nutritious it is.

---

[30] [Eds.]: Latin, "contradiction in itself"

The second idea was to supplement the diet of sauropods with fish (34).The dentition of *Diplodocus* was used to expand on that idea. I do not know the dentition from my own experience, but looking at the figures, I would say instead that the teeth do not completely suggest this. Of course it is possible that *Helopus*, *Camarasaurus*, and other sauropods with similar dentition caught fish and other animals, but it is not possible to make this assumption on the base of the dentition. I can not accept why it should be impossible that sauropods lived on water plants. They had a lot of time to digest, and although they couldn't chew the meal, Barnum Brown and Janensch (16) showed that they had grindstones in their stomach. Recent research published in agricultural literature shows that not all water plants are so poor in nutrients. For example *Sparganium fluitans* and *Menyanthes* are not so bad as food. Some other plants that are not so nutritious could be also good food, only because the animals loved to eat. I can also remember that during the war a lot of easy accessible roots of water plants, like *Scirpus, Cyperus, Phragmites, Butomus, Calla, Nuphar, and Nymphoea*, were recommended as nutritious flour substitutes. It is easy to extract these roots. Fruits are also very nutritious. All these things account for present day plants, but during the Cretaceous the *Phanerogamen* were already highly developed.

Maybe the sauropods could extract the roots with their claws. At least for *Helopus* the neck seems too long to allow a good interaction between the mouth and the forefeet.

I want to give some notes about the assembly of the Frankfurt examples of *Diplodocus*. I believe that the position of the backbone is correct, not only because the things I mentioned above about the egg and the pelvis, but also because the vertebrae fit together very precisely. On the other hand, I think the position of the scapula and the position of the hint legs are incorrect. I would like to put the scapula more oblique, therefore the socket for the humerus opens more posteriorly and the fore body drops a little bit. The hind legs should be more vertical and elephant like. These changes would result in a more convex form of the tail and the similarity with the very improbable reconstruction of *Brachiosaurus* would vanish.

In Fig.3, I put the skeleton part of *Helopus* in my favored position and drew the sketch for the body. This figure was used as the basis for the life pictures.

Isolated sauropod bones

Cervical Vertebra

The specimen is labeled as followed: T'AN. 15 Apr. 1923. NE of T'ien-Ch'iao-T'un. Lai-Yang-Hsien. The rock is a red clay, the sample location belongs to the Wang-Shih-series, upper Cretaceous.

The exemplar is not well enough preserved to bother illustrating it. The neural spine is compressed and the centrum is oblate. The centrum is 57cm long, 23.5 cm wide and 12 cm high. The animal had almost the same height as *Diplodocus*. The apophyses are only fragmentary. The same for the Lamina neurozygapophysica, but this one is at least preserved dorsally well enough to assume that the spike of the neural spine was covered from atop. It is unclear, whether the Processus pseudospinosi existed. The Lamina postdiapophysica is a little bit better conserved and also the Lamina centrodiapopysica and the Lamina parapophysica. These laminae are very thin and high.

Thoracic Vertebra

Pl. VII. Fig. 1 and 1a

The specimen is labeled: T'AN. 14 Apr. 1923. Shantung. Lai-Yang-Hsien. T'ien-Ch'iao-T'un, NE. The sample location belongs, after T'an, to the Wang-Shih-series, upper Cretaceous. The surrounding rock is a red clay.

The vertebra is fragmentary. The following measurements were taken:

Centrum	
length	98.5+ cm
height	15 cm
breadth	47.5 cm
Greatest height of the fragmentary parapophysis above the lower edge of the vertebra	40.5 cm
" " diapophysis	51 cm

The ratio between length and width is very high for a thoracic vertebra of a sauropod. It is similar to *Bothriospondylus elongatus*, Owen (27. Pl. 7), that is of equal size. The vertebra is opisthocoelous with a strongly convex articular surface. The opening of the pleurocoels is tall and pear-shaped antero-posteriorly. The network of laminae[31] in the

[31] [Eds.]: "maschige Gewebe", literally "retiform tissue".

pleurocoels is like that in *Helopus*. The parapophysis is high on the neural arch. The diapophysis is relatively thin and is supported by normal laminae. On the outer side of the arch, below the apophysis, is an oblique ventrally-directed line of four holes that are separated by accessory laminae, like on the thoracic vertebra of *Diplodocus* from Hatcher (10) in fig. 10, Plate 7. The neural channel is not as high as my fig 2 is visualizing, but has to be much lower.

From the figures and the above description we can assume that we are talking about a posterior thoracic vertebra, due to the dorsal position of the parapophysis.

Caudal Vertebra

Pl. VI. Fig. 13-13b

The specimen is labeled: T'AN. 24 March 1923. Shantung. Lai Yang Hsien. Ch'ing Shan, SE. The sample comes from the Ch'ing-Shan-formation, Lower Cretaceous. The rock is very fine grained and brown and contains isolated smaller boulders.

The vertebra is not very well preserved and was damaged in several places.

The centrum is procoelous, short and full of erratic holes. The opening of the pleurocoel is a deep circular funnel at half height of the vertebra. The neural channel is triangular, wider than high and very narrow. The upper arch is wide and short. Central within the arch is the neural spine and on both sides of the neural spine are the two Laminae neurozygapopysicae that run up to the spine. The frontal and back parts of that laminae form an acute angle with each other. The neural spine is supported by four laminae and the upper part is visible from the front and the back. The diapophysis or transverse process lies low and is connected to the prezygapophysis by the Lamina praediapophysica.

The vertebra is an anterior caudal vertebra. A more specific identification of the placement is not possible. The third caudal vertebra of *Barosaurus* described by Lull (20) is very similar, but almost double in its length.

	Length in cm
Centrum	
total length	16cm
length on the side	9cm
height	24.5cm

breadth	28cm
Breadth above the diapophysis	41+cm
Breadth above the upper end of the prezygapophyseal joints	17.7cm
“ “ for the postzygapophyses	16.7cm
Total heigh of the vertebra	61cm

Femur

The specimen is labeled: T’AN. 22 April 1923. Lai-Yang-Hsien. Chiang-Chun-Ting. 1 li NW. The sample belongs (after T’an) to the Wang-Shih-series, upper Cretaceous. The bone is grey outside, but reddish inside.

The bone is fragmentary on top and on the bottom, but from what is left, the bone could belong to *Helopus zdanskyi*, although the level[32] is different.

	Length in cm
Length	98.5+cm
Smallest width below the fourth trochanter	615 cm
Circumference above the fourth trochanter	47.5 cm
Smallest circumference	40.5 cm

THEROPODA

Vertebra

Pl. VI. Fig. 14, 14a, 16 and 16a

We could find only very isolated fragments of predatory dinosaurs. Four vertebral fragments are labeled as follows: T’AN. 20 Apr. 1923. Shantung. Lai-Yang-Hsien. Chiang-Chun-Ting. SW 1 li. The pieces are from the usual red clay of the Wang-Shih-series, upper Cretaceous.

The pieces are of the same size. One of them is not specifically identified. The second one is a cervical vertebra. It is too poorly preserved to illustrate. The entire piece is compressed from all sides. The vertebra is 9.5cm long, 5.5cm high, and 4.5 wide. In the front, it is relatively deeply concave, posteriorly it is flat or, seen in lateral view, slightly concave, therefore it is amphicoelous. It can be assumed that the posterior joint consisted of

[32] [Eds.]: “Niveau”, literally “level”, referring to the stratigraphic level the bone comes from.

cartilage and therefore the vertebra would be procoelous. The apophyses are broken off and sit on the frontal one-third of the vertebra. The diapophysis is on the neural arch, and the parapophysis on the side of the centrum, on the ventral half. Because the neural spine is broken off, the height is not determined, but the length is 4cm and the width at the broken side is 0.8cm. From the diapophysis runs a Lamina centrodiapophysica to the upper back edge of the vertebra, and a bulge, similar to the Lamina neurozygapophysica of the sauropod, connects the zygapophyses on the the same side. The vertebra is less similar to *Antrodemus valens* (7. S. 34) than it is to *Plateosaurus* (14. Pl. II. Fig. 1).

The thoracic vertebra (fig 14) is better preserved and seen in the figure.

	Length in cm
Centrum	
length	6.2 cm
breadth	6.2 cm
height	6.8 cm
Height of entire vertebra	18 cm
Width above diapophysis	14.6 cm

PLATE I.[33]

Helopus zdanskyi

Specimen A.

Fig. 1. Skull from the right side. 1/3.
“ 2. Skull from left side. 1/3.
“ 3. Skull from the front 1/3.
“ 4. Skull in dorsal view. 1/3.
“ 5. Right lower jaw from inside. 1/2.
“ 6.Left lower jaw from inside 1/2.
“ 7. Squamosum from outside. 1/2.
“ 8. Squamosum from inside 1/2,
“ 9. Postorbital-Postfrontal from inside 1/2.
“ 10. Postorbital-Postfrontal from outside 1/2.

Missing bones are labeled with points.

Pm Premaxilla, Mx Maxilla, Na Nasal, L Lacrimal, Pf Prefrontal, F Frontal, Po Postfrontal-Postorbital, P Parietal, So Supraoccipital, Exo Exoccipital, Co Condylus, Sq Squamosum, J Jugal, Q Quadrate, Opo Opisthotic, Pt Pterygoideum.

N Nares, A Orbit, PD antorbital fenestra, OD Supratemporal fenestra, UD lateral temporal fenestra.

[33] [Eds.] All plates were scanned, cleaned up, and assembed by Bonnie Miljour, Museum of Paleontology, University of Michigan

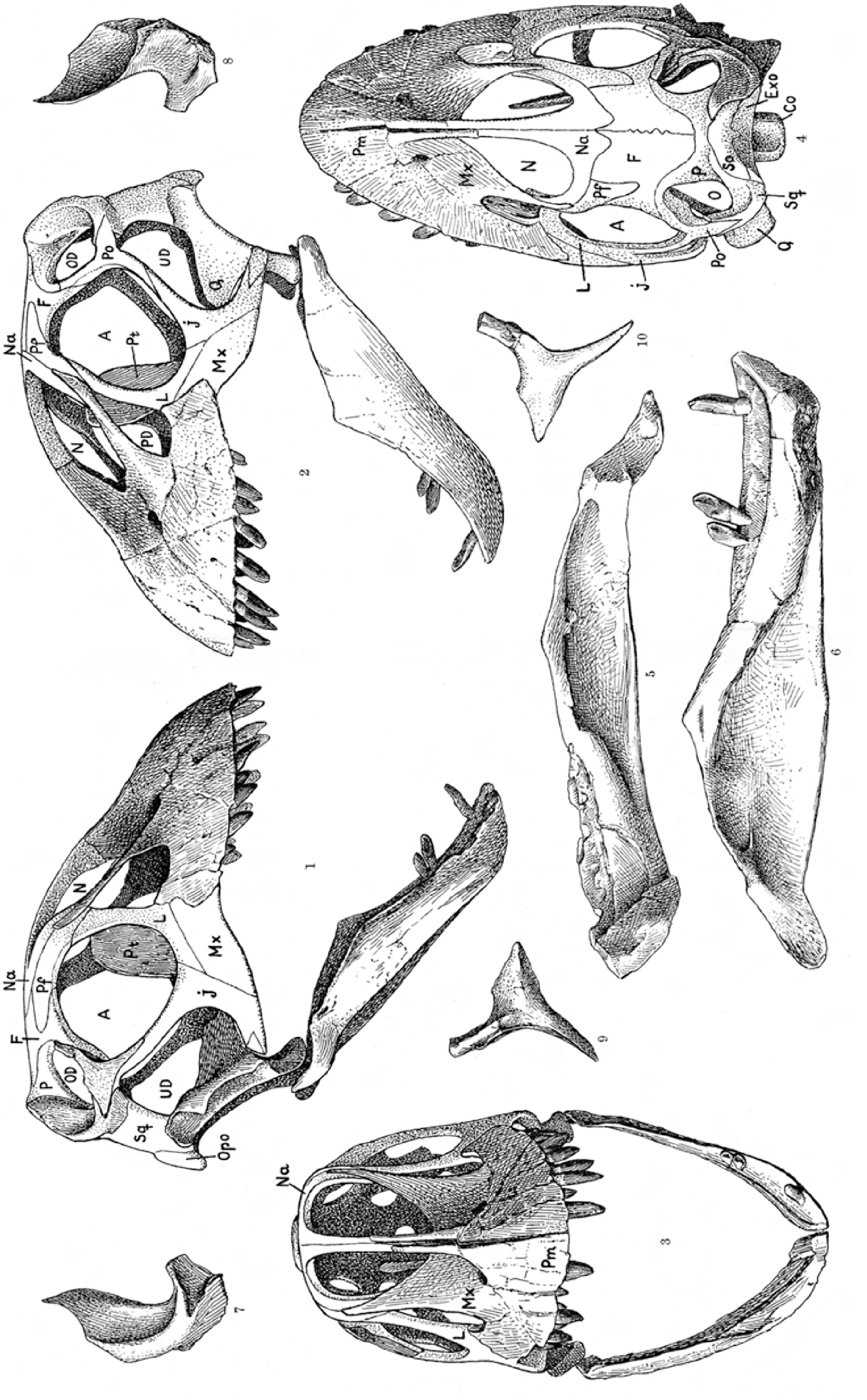
1
2
3
4
5
6
7
8
9
10
Na
Pf
F
P
OD
A
Pt
j
Mx
L
N
UD
Sq
Opo
Po
Q
PD
Pm
Exo
Co
So
O

PLATE II

Helopus zydanskyi

Specimen A.

Fig. 1. left upper jaw external view. 1/2.

“ 2.” “ internal view. 1/2.

“ 3. Right upper jaw external view 1/2.

“ 4. “ “ internal view. 1/2.

“ 5. Right quadrate from inside. 1/2.

“ 6. Right quadrate from outside 1/2.

“ 7. Right quadrate and quadratojugal from behind. 1/2.

“ 8. Right vomer from above 1/2,

“ 9. Right vomer medial view 1/2.

“ 10. Right vomer from below 1/2.

“ 11. Left vomer from below 1/2.

“ 12-23. Teeth. Natural size

“ 24. Profile of a tooth (FIg. 16). Natural size.

Pm Premaxilla, Mx Maxilla, Q Quadrate, Qj Quadratojugal, Pt Pterygoideum.

L suture with Lacrimal, + Pt suture with the Pterygoid, Pa suture with the palatine, Tr transverse process of the Pterygoid, T edge of the eardrum.

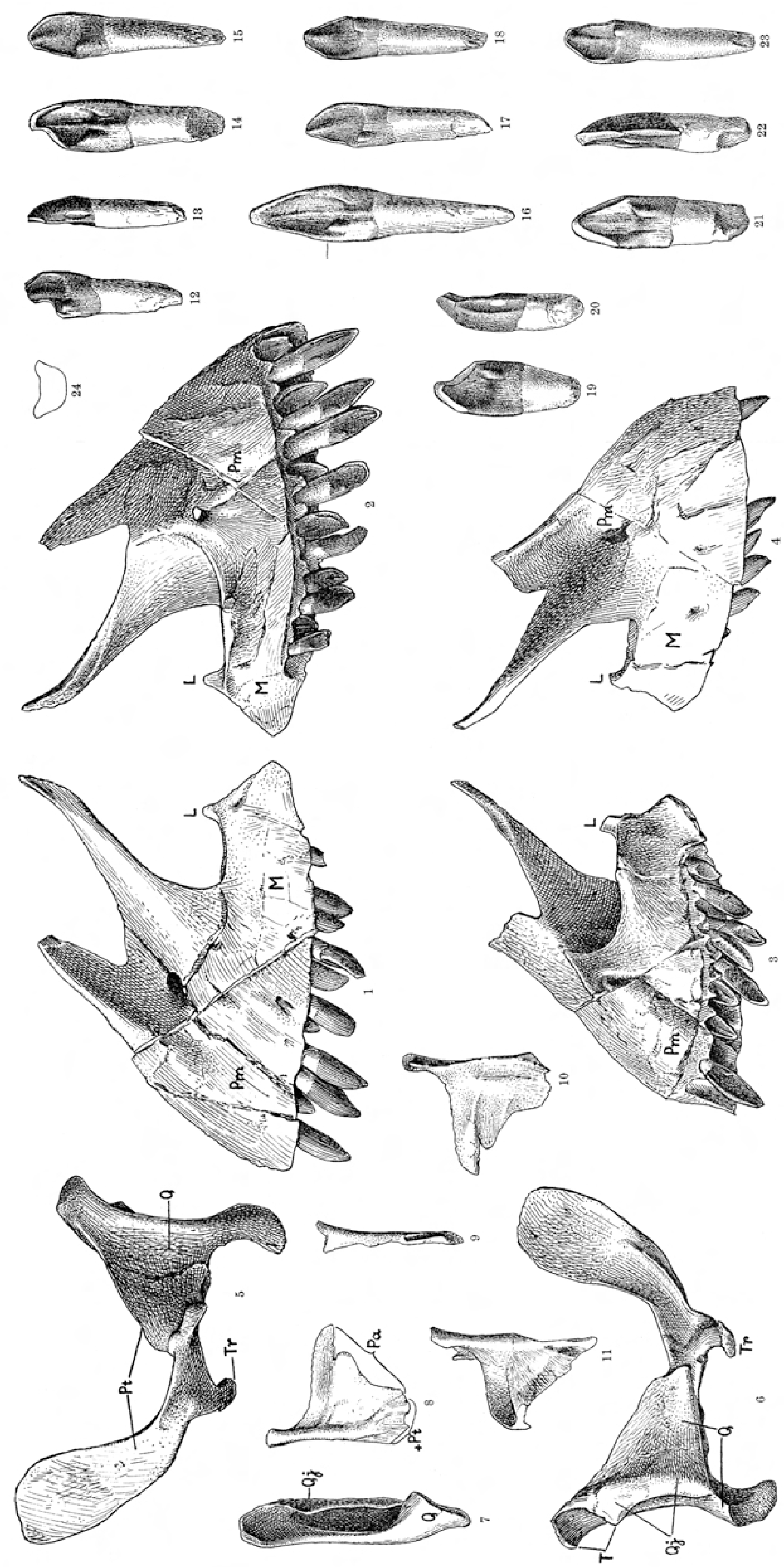
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
Pm
M
L
Q
Pt
Tr
Qj
Pa
T

PLATE III

Helopus zydanskyi

Specimen A

1/10 Natural size

Fig. 1. Backbone from above. Vertebrae II-XXV
" 2. "" from below
" 3. " " from the left side
" 4. Vertebrae XIX-XXV from the right side
" 5. Axis from the front
" 6. Third cervical from the front.
" 7. " " from behind
" 8. Fourth cervical from the front
" 9. Eighth cervical from behind
" 10. Ninth cervical from the front
" 11. Tenth cervical from the back
" 12. Eleventh cervical from the front
" 13. " " from behind
" 14. Twelfth cervical from the front
" 15. Fourteenth cervical from behind
" 16. " " from the front
" 17. First dorsal from the back. Vertebra XVIII
" 18. Second dorsal, XIX, from front. Behind the third thoracic vertebra, XX, with the appropriate thoracic rib
" 19. Thoracic rib 3 of vertebra XX
" 20. Left femur from the side
" 21. " " in lateral view
" 22. " " from the front
" 23. ' ' in medial view

C centrale of the axis, Ic intercentrale of the axis, N "real" neural spine, Processus spinosus[34], Ps Processus pseudospinosus, D diapophysis, P parapophysis, Pz prezygapophysis, Ptz postzygapophysis.

Lnz lamina neurozygapophysica, Lpd Lamina postdiapophysica, Lcd Lamina centrodiapophysisca, Lp lamina parapophysica.

VN anterior dorsal fossa, HN posterior dorsal fossa, OK upper pleurocoel, MK middle pleurocoel, Cavitas laterales media, UK Lower pleurocoel, a accessory coel.

H, dorsal rib.

---

[34] [Eds.]: no abbreviation given in original

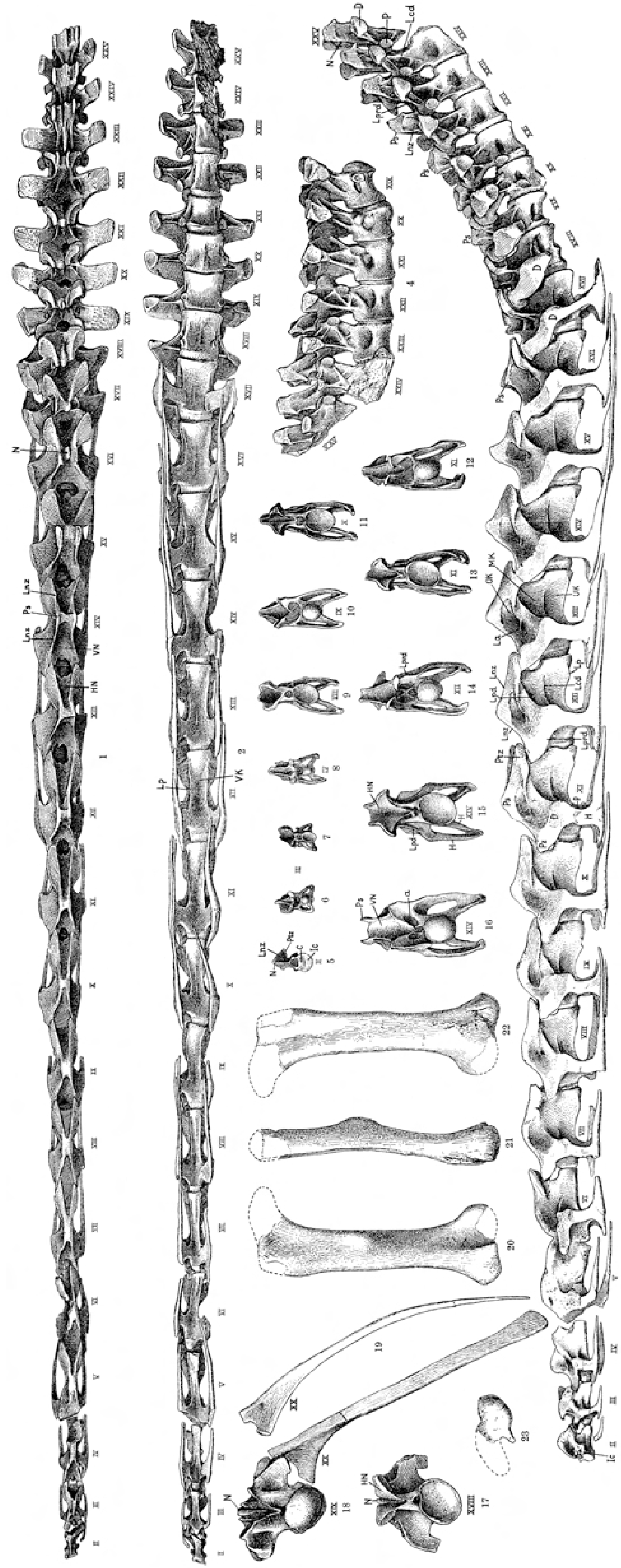

PLATE IV

Helopus zydanskyi

Specimen b

Fig. 1. Entire specimen from right side 1/10
“ 2. Backbone and pelvis from left side 1/10
“ 3. Backbone and pelvis from above 1/10
“ 4. Entire specimen from front 1/10
“ 5. “ “ from behind 1/10.
“ 6. Fifth thoracic vertebra, XXII, from front 1/10.
“ 7. Upper end of right femur from above 1/10
“ 8. Lower end of right femur from below 1/10
“ 9. Upper end of right Tibia and Fibula from above 1/10
“ 10. Left astragalus and lower end of tibia, right lower end of fibula, from below 1/10
“ 11. Upper ends of metatarsals I-IV of the right hind foot 7/30
“ 12. Right hind foot from above 7/30
“ 13. Right hind foot from above and front 7/30
“ 14. Right metatarsal I internal view 7/30
“ 15. Right metatarsal II internal view 7/30
“ 16. Right metatarsal III internal view 7/30
“ 17. Right metatarsal IV internal view 7/30
“ 18. First phalanx of the first toe of the right hind foot, ventral view 7/30
“ 19. “ “ posterior view 7/30
“ 20. “ “ from the front 7/30
“ 21. Ungual of the second toe on the right hind foot, ventral view 7/30
“ 22. Joint of the same phalanx 7/30
“ 23. Ungual of the third toe on the right hind foot, ventral view 7/30
“ 24. “ “, internal view 7/30
“ 25. Ungual of the fourth or fifth toe of the right hind foot, dorsal view 7/30
“ 26. “ “, ventral view 7/30
“ 27. “ “ internal view 7/30

Sacr sacral vertebrae, N neurapophysis, D diapophysis, BR and B thoracic vertebrae, SR sacral rib, I ilium, P pubis, Is ischium, Fe femur, F fibula, Tr IV fourth trochanter, T tibia, A astragalus, I-IV metatarsals I-IV.