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Introduction.

The following notes are the result of studies in various Museums. They deal with *Palaeohatteria*, *Deuterosaurus*, some Nothosaurians, two Tortoises, two Dinosaurs and the classification of the *Crocodylia*.

These studies were only possible with the help of numerous Gentlemen and Ladies, who permitted me to investigate the material contained in various Museums and facilitated my work also in many other regards. I am especially indebted to: Madame AMALITZKY (Petrograd), Prof. ARTINI (Milano), Dr. F. A. BATHER (London), Prof. M. BOULE (Paris), Dr. R. BROOM (Douglass, S. Africa), Prof. L. DOLLO (Bruxelles), Prof. O. JAEKEL (Greifswald), Dr. KAHLER (Klagenfurt), Prof. KARPINSKY (Petrograd), Prof. KOSSMAT (Leipzig), Prof. KRUSCH (Berlin), Prof. LULL (New Haven), Prof. MARIANI (Milano), Prof. MOUCHKETTOFF (Petrograd), Dr. RJABININ (Petrograd), Prof. SOLLAS (Oxford), Prof. STILLE (Göttingen), Prof. STROMER (Munich), Dr. TRAUTH (Vienna), Dr. YAKOWLEW (Petrograd), Prof. WATSON (London) and Sir A. S. WOODWARD (Haywards Heath, Sussex).

While editing some parts of these notes in English, I was greatly assisted by Lady WOODWARD who helped me to bring, at least some parts of the paper, into proper English.

Owing to illness and to the fact that Dr. ST. MAJER (editor of *Palaeontologia Hungarica*) had delayed the publication of this paper in a quite unjustifiable manner for more than two years, till it was withdrawn from his hands, the recent literature could no more be properly referred to.

I. REDESCRIPTION OF *PALAEOHATTERIA*.

Although *Palaeohatteria* has been successively studied by CREDNER (II 272)¹, BAUR (II 35), A. S. WOODWARD (II 624), HUENE (VIII 236), JAEKEL (II 389) and WILLISTON (II 608) nevertheless a renewed investigation brought out several points of interest. The possibility of these discoveries was principally due to the fact that several of CREDNER's type specimens had recently been prepared by Professor JAEKEL in a remarkable manner. With incredible skill Professor JAEKEL has completely removed the fractured bony substance in many pieces and now the casts of these negatives reveal the most minute structure of the former bones. For casting a boiling mixture of about equal parts of gelatine and glycerine was used, to which, during its boiling, a fairly large quantity of zinkwhite powder has been added. This powder colours the translucent and elastic mass and by making it opaque renders it suitable for photography. Acting at the same time as a desinfectant it prevents mould. The same material was also used for casting the pieces figured on Plates II, III and IV. These casts were afterwards painted with water colours.

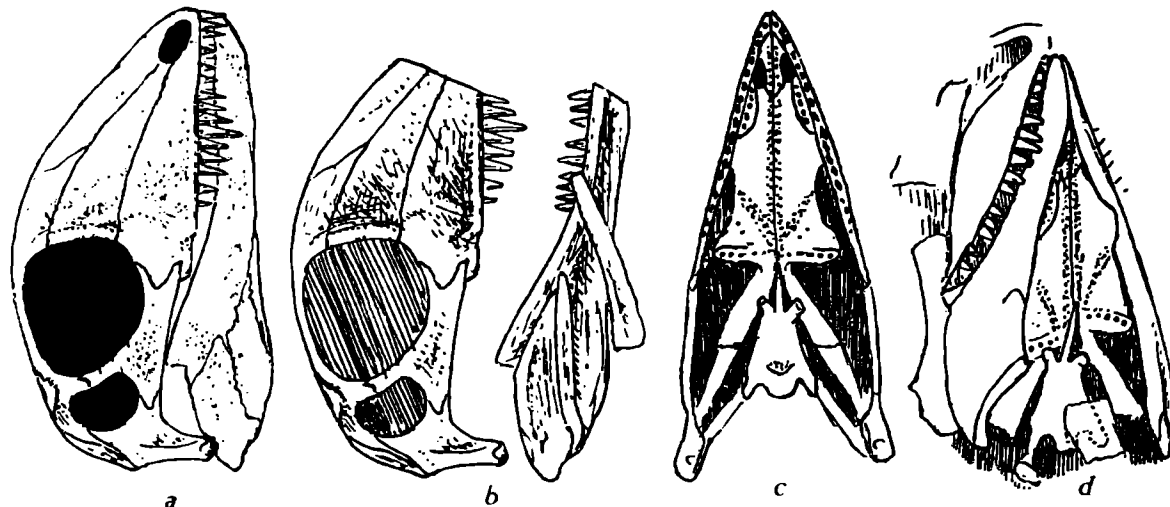


Fig. 1. Skull of *Palaeohatteria* (nat. size). — a) reconstruction of lateral view; b) actual specimen (lower jaw from the interior); c) reconstruction of the palate; d) actual specimen.

The principal pieces that served as basis for the following description are the casts of the skull figured by CREDNER (II 272) on Plate XXV figure 4, and of a hitherto undescribed palate.

The first named piece shows, that the lateral view of the skull of *Palaeohatteria* is more nearly complete than has hitherto been suspected, for the drawing figure 1b) is an actual tracing of the original cast and by no means a reconstruction. The single bone that has been omitted in the drawing is the displaced frontal.

1) The numbers in brackets refer to the chapter and the current number under which the exact title of the paper referred to can be found in my book „Osteologia Reptilium fossilium et viventium (Fossilium Catalogus, pars 27, Berlin 1926.). The roman number refers to the chapter, the arabic number to the number of the paper.

The maxillary is a low and elongated bone the upper margin of which is but indistinctly traceable on the specimen studied. Other pieces, as the one figured by CREDNER on Plate XXV fig. 3 and the piece figured in his memoir as textfigure 3 show, that the superior border of the maxillary was gently convex, the greatest height being obtained above the longest teeth. Its shape recalls generally the maxillary of *Varanops* (II 596) and *Edaphosaurus* (II 575) and to some extent the maxillary of *Galepus* (II 125).

The lacrymal is a remarkably long bone extending, as already noticed by WILLISTON (II 608), probably as far as the nares. Its shape is by no means the same as indicated in CREDNER's drawings (Pl. XXV fig. 1 and 3) or in JAEKEL's reconstruction (II 389). GREGORY showed in his monograph on the lacrymal bone (II 326) that a large lacrymal is a very primitive feature and occurs principally among the *Cotyloauria*. A large lacrymal comparable with the lacrymal of *Palaeohatteria* occurs however also in *Varanosaurus* (II 54), *Pantelosaurus* (XIII 59) and in *Edaphosaurus* (II 575).

As in *Sphenacodon* (II 613) and *Diopaeus* (II 581) the prefrontal is a longish, narrow, triangular bone. It is very different from the short prefrontal in the *Dromasauroida* (II 125). It is placed on the highest point of the skull as in *Sphenacodon* (II 581), as in some *Dromasauroida*, for example *Galepus* (II 130) and as in some *Anomodontoida*, for example *Diaelurodon* (II 127) and *Lystrosaurus* (II 488). The prefrontal and lacrymal show in front of the orbits a deep fossa as visible also in *Sphenacodon* (II 581), *Diopaeus* (II 581) and *Varanosaurus* (II 581). This fossa is separated from the orbits by a sharp, projecting ridge.

In the skull forming the basis of this description the jugal is preserved in situ and its median and posterior part is certainly complete. It is altogether a slender, triradiate bone. In front two small bifurcating projections are visible, the origin of which may, however, be attributed to lesion. In the middle a slender, ascending process is given off, that separates the temporal opening from the orbit. Posteriorly the horizontal bar of the jugal is applied against the squamosal. The jugal recalls the same bone in *Mycterosaurus* (II 610). It may be emphasised that in the specimen studied the inferior margins of the temporal and orbital cavities are complete.

Not the slightest trace of interruption is visible where the jugal touches the squamosal. The latter forms the posterior and inferior border of the temporal opening. It has the shape of a T laying on its side. As may well be seen in CREDNER's figure 1 on Plate XXIV, the squamosal finishes below in a thin and rod-like process that bears a little knob. This knob ends distally in a smooth, small, but well marked surface. The latter corresponds to the place where the lower jaw articulated with the quadrate.

As in *Scalopsosaurus* (II 125), *Ictidorhinus* (II 142), many *Dinocephalia* (II 571), the *Dromasauroida* (II 125, 130), *Pantelosaurus* (XIII 59), *Edaphosaurus* (II 575) and as in some *Pelycosauria*, so *Sphenacodon* (II 581) and *Dimetrodon* (II 581), the articulation of the lower jaw was situated far below the level of the alveolar margin of the maxillary. This important character of *Palaeohatteria* has not been brought out in any reconstruction.

A T-shaped, pendant squamosum occurs only in the primitive Theriodont *Scalopsosaurus* (II 125), and the *Dromasauroida* (II 125). In *Pantelosaurus* (XIII 59) the low position of the articulation of the mandible is due to an elongation of the quadrate as in *Edaphosaurus*.

The postfrontal and postorbital of *Palaeohatteria* are likewise both preserved in situ. This can be deduced from the even curve of the posterior outline of the skull and from the regular outline of the upper part of the temporal cavity. Unfortunately the suture between the postfrontal and the postorbital can not be traced. Exactly above the ascending process of the jugal the postfrontal and the postorbital show a small projection that bears dorsally a flattened surface. This indicates that in this region the top of the skull was broad and flat. The incision indicated at this place in CREDNER'S drawing of this piece (plate XXV fig. 4) does in reality not exist. The development of the squamosal, the postfrontal and the postorbital prove together that *Palaeohatteria* was a monozygocrotaphous reptile. This has already been pointed out by WILLISTON (II 613) in 1918.

The lateral position of the single temporal opening brings *Palaeohatteria* closer to the *Pelycosauria* than to the higher *Theromorpha*. The conspicuously large size of the orbits in *Palaeohatteria* is to be met with in *Glaucosaurus* (II 609), *Pantelosaurus* (XIII 59) and the *Dromasauria* (VIII 58, II 125, 130). Contrarily in the more specialised *Pelycosauria*, *Anomodontia* and *Theriodontia* they are comparatively small.

Where the postfrontal touches the squamosal the lateral process of the parietal was applied against this bone. In the lateral aspect this part has a splint-like outline.

In the skull studied the frontal is strongly displaced and thrust into the orbit. In the adjoining figure No 1 this element has been purposely omitted. Its general shape is well shown in CREDNER'S figure (plate XXV fig. 4) published in 1881 (II 272).

The nasals are large, the premaxillaries feeble and narrow. They resemble to the premaxillaries in *Galechirus* (VIII 58), *Scaloposaurus* (II 125) and *Varanosaurus* (II 54). They differ from the premaxillaries in the more specialised Theriodonts as *Scylacops* (II 136), the more specialised *Anomodontoidea* as *Dicynodon* (II 389) and the more specialised *Pelycosauria* as *Dimetrodon* (II 191) in not having such a thick inferior border as these.

The teeth of *Palaeohatteria* are protothecodont as is the case in the primitive *Pelycosauria*, they are however thecodont in the specialised *Pelycosauria* and in all *Theriodontia*.

The new specimen of *Palaeohatteria* exhibiting the palate shows the vomers, palatines, pterygoids and the base of the skull. Drawings of the palate of *Palaeohatteria* are given in figures 1 c and d the former being a reconstruction, the latter a drawing of the actual specimen.

The vomers are short and slender bones, each bearing, as in many primitive reptiles, a row of teeth. They do not extend beyond the choanae and form their median borders. Medially their posterior projections enter between the pterygoids as in *Diadectes* and *Seymouria* (II 579). Similar vomers as in *Palaeohatteria* are to be met with in *Dimetrodon* (II 191), *Pantelosaurus* (XIII 59), *Edaphosaurus* and *Proterosuchus* (II 136). The vomers of even the most primitive *Theriodontia* (II 136) differ to a great extent.

The palatines are narrow at both ends and broaden in the middle. They bear numerous teeth of which the median ones are larger than the rest. The palatines likewise recall the same elements in *Dimetrodon* (II 191) and *Proterosuchus* (II 136).

The pterygoids show exactly the same shape as in *Dimetrodon* (II 191) and recall at the same time strongly the pterygoids of *Sphenodon*. They differ well from the pterygoids in *Pantelosaurus*

(XIII 59). They reach the choanac as is the case in *Broomia* (VII 749) and *Dimetrodon* (II 367). In their present state of preservation they are somewhat displaced and touch each other as in *Sphenodon* in the middle line of the skull, it may however be, that in the living animal they were separated by a narrow cleft. Such a cleft is visible in *Howesia* (VIII 56), *Broomia* (VI 794), *Proterosuchus* (VIII 51), *Dimetrodon* (II 191) and *Limnoscelis* (II 596).

This cleft might account for the two zones of numerous small teeth which, as in the animals just mentioned, border their median margins. Apart from these zones of teeth on the pterygoids of *Palaeohatteria* yet two other teethbearing regions can be discerned. One zone of diminutive teeth extends obliquely forward and outward, another is placed transversely to the long axis of the skull. In this second zone the teeth are much stronger than in the other two. A row of strong teeth placed transversely to the long axis of the skull occurs also in *Limnoscelis* (II 596), *Pantelosaurus* (XIII 59) and *Dimetrodon* (II 191). By the absence of a transversum *Palaeohatteria* resembles *Dimetrodon* (II 367) and differs from *Proterosuchus* (VIII 51) the palate of which otherwise shows a similar structure.

The basisphenoid and the basioccipital, that have been well figured by CREDNER are altogether flat, long and large. Basioccipital tuberosities are absent. As a whole this part differs from the same region in *Dimetrodon* or in the *Theromorpha*, but recalls somewhat *Casea* and is much the same as in all reptiles having a primitive metakinetic skull. In accordance the basiptyergoidal processes are very well developed.

The shape of the mandible is well shown in figure 1, but can also be made out in CREDNER'S figure 1 on his Plate XXIV. The upper margin of the mandible shows a well marked projection that is formed by the posterior part of the dentary bone. Such a projection is always absent in the *Pelycosauria*, but it characterises one of the *Dromasauroida* [*Galepus* (II 130)] and all the *Theriodontia* (II 558). The rest of the mandible is likewise built on the Theriodont pattern. Behind the projection of the dentary a large surangular can be made out. Under the surangular a long slender and somewhat rectangular bone stretches obliquely upward and forward. It is identical with the prearticular in *Scymnognathus* (II 389). Under this bone follows the angular, that forms the inferior part of the jaw. The inferior border of the angular of *Palaeohatteria* differs from *Scymnognathus* but resembles *Galepus* (II 125) and *Varanosaurus* (II 54).

A small, displaced, splint-like bone, laying in front of the angular is probably the splenial. A separate coronoidal bone can not be detected, but unfortunately the region, where it ought to be looked for, is not well preserved.

Since the vertebrae of *Palaeohatteria* have all been well described by CREDNER it is needless to give a redescription. Their number is about the same as in *Pantelosaurus* (XII 69).

The scapular arch recalls *Varanops* (II 596) but is less ossified than in this genus. A good outline drawing of this part has been given by WILLISTON (II 608). From the pelvis of the *Dromasauroida* (II 156) the pelvis of *Palaeohatteria*, as reconstructed by WILLISTON (II 608), differs only in having much smaller foramina obturatoria; the small size of these foramina indicates however only a lower degree of specialisation.

The ileum of *Palaeohatteria* differs markedly from the same bone in most of the *Pelycosauria*

(*Pantelosaurus* included) for in these it is generally elongated and extends obliquely downward and forward, but it resembles in a high degree the ileum of the *Dromasauroida* (VIII 58, II 125, 156).

The pubis shows, as may be well seen on CREDNER'S drawings, an incision for the obturator nerve. It differs markedly from the pubis of the *Pelycosauria*. In these as in the *Parapsida* the foramen obturatorium always passes through the pubis. The pubis of the *Theromorpha* shows the same type as the pubis of *Palaeohatteria*, for in the latter the obturator nerve always passes between the pubis and the ischium.

The humerus of *Palaeohatteria* is a slender bone showing no special dilatation at either end. It resembles the humerus of the *Dromasauroida* and differs strongly from the dilatated humerus of the *Pelycosauria*.

The occurrence of a foramen entepicondyloideum brings *Palaeohatteria* near to the *Cotylosauria*, the *Pelycosauria*, the *Dranitesauria*, most of the *Theromorpha* and the primitive *Ichthyopterygia*. It separates *Palaeohatteria* from the *Testudinata*, *Parapsida* and *Diaptosauria*. In the latter a foramen ectepicondyloideum prevails.

The following tabula gives a good summary view of the development of the humeral foramina in different groups of reptiles.

III no Foramen		<i>Ichthyopterygia</i> (<i>Ichthyosauria</i>)		<i>Dranitesauria</i> (<i>Plesiosauroida</i>)	<i>Mammalia</i>		
II only Fossa entepicondyl.				<i>Dranitesauria</i> (<i>Placochelys</i>)			
I For. entepicondyl.	<i>Cotylosauria</i>	<i>Ichthyopterygia</i> (<i>Mesosauria</i>)	<i>Pelycosauria</i>	<i>Dranitesauria</i> (<i>Conchiosaurus</i>)	<i>Theromorpha</i>		
II For. entepicondyl. + For. ectepicondyl.			<i>Pelycosauria</i> (<i>Naosaurus</i>) <i>Parapsida</i> (<i>Pleurosaurus</i> , <i>Araucelias</i>)		<i>Theromorpha</i> (<i>Dinocephalia</i> , <i>Cynognathidae</i>)	<i>Diaptosauria</i> (<i>Sphenodon</i>)	
III Fos. entepicondyl. + For. ectepicondyl.						<i>Diaptosauria</i> (<i>Sapheosaurus</i>)	<i>Prepubici</i> [<i>Atoposaurus?</i>]
IV only For. ectepicond.	<i>Testudinata</i>		<i>Parapsida</i> (<i>Squamata</i>)			<i>Diaptosauria</i> (<i>Champsosaurus</i>)	
V only Fossa ectep.	<i>Testudinata</i> (<i>Chelone</i> , <i>Podocnemis</i> , <i>Testudo</i>)					<i>Diaptosauria</i> (<i>Champsosaurus</i> , <i>Belodon</i> , <i>Proterosaurus</i>)	
VI no Foramen			<i>Parapsida</i> (<i>Camelotritinae</i> , <i>Mosasaurinae</i>)			<i>Diaptosauria</i> (<i>Pseudosauchoidea</i>) <i>Dinosauria</i>	<i>Prepubici</i> (<i>Crocodylia</i> , <i>Pterosauria</i>)

As may be seen, the *Ichthyosauria* and *Plesiosauria* lost their humeral foramen simply by a reversal, some *Squamata* and many *Archosauria* lost however these foramina only after the animals had shifted the function of the principal bloodvessels and nerves from the one side of the arm to the other.

The two enlarged proximal elements of the carpal and tarsal bones of *Palaeohatteria* recall to a certain degree the same bones in the *Pelycosauria*, their feeble ossification prevents however a further comparison.

The immature condition of *Palaeohatteria* is clearly shown by a microscopic investigation of the structure of its bones. The rib-fragment, that was investigated (compare plate II fig. 6), is hollow and shows a large, well defined marrow cavity of irregularly elliptical outline. The diameter of this cavity is about half of that of the whole bone. On account of the rib not being everywhere equally thick, the outer outline of the rib does not agree with the outline of the marrow cavity itself. Where the exterior outline runs more or less parallel to the one of the marrow cavity, the outer surface of the bone shows numerous semicircle-shaped bays or inlets of which the diameter is only a trifle larger than the diameter of the Haversian canals met within the bony mass. Evidently these small, but very well marked bays are all only impressions of those bloodvessels of the periostic layer, that were just in the course of being included into the bone. Contrarily to this in those regions of the rib where the outlines of the marrow cavity and the exterior surface do not agree, the exterior surface shows irregular projections and even a very diminutive piece of bone, that is detached in the section from the rib itself. These angular projections show even more clearly than the incision of the periostic vessels, how rapidly in *Palaeohatteria* in the moment of its untimely death, boneformation was going on.

The Haversian canals in the rib of *Palaeohatteria* are all of equal size, they have all more or less rounded and somewhat elliptical outlines, and their diameter is but 7—8 times larger than the one of a bone cell. Secondary Haversian laminae are nowhere visible. The distribution of the Haversian canals throughout the bone is quite irregular and in this regard *Palaeohatteria* recalls very strongly a young *Lystrosaurus* and to some extent also the other *Dicynodontidae*, furtheron the *Diadectidae*, the *Pareiasauroidea* and some *Gorgonopsoidea*, it differs however by the distribution of its Haversian canals very well from *Labidosaurus*, *Limnoscelis* and all the *Pelycosauria*. From the bone structure of the *Squamata* and the one of all *Archosauria* the bone structure of *Palaeohatteria* differs to a great extent. Details will be given at an other occasion.

The bone cells of *Palaeohatteria* are all remarkably large, their cross-section is generally egg-shaped and in such places their distribution is quite irregular, in some places however the diameter becomes elongated and the bone cells group to short and irregularly interrupted rows. These rows seem somehow to twist along between the Haversian canals.

The whole of this redescription proves beyond all doubt that BROILI'S (II 629) statement, according to which *Palaeohatteria* unites pelycosaurian and theromorphous characters, is essentially correct. The pelycosaurian characters of *Palaeohatteria* have already been recognised by HIBENE in 1910 (VIII 236), the theromorphous characters have been pointed out by WATSON (unpublished observations communicated to the author in spring 1923).

The relationship of *Palaeohatteria* to the likewise permian *Haptodus* (II 303) could only be

made out during a stay in Paris. For the possibility of doing so I am indebted to Professor M. BOULE. Contrarily to THEVENIN's opinion (II 543) the resemblance between *Palaeohatteria* and *Haptodus* is but feeble. In *Haptodus* the somewhat crushed skull is elongated and low, the parietals are much the same as in *Varanops* and as a whole this skull recalls *Varanops* and *Varanosaurus*. The vertebrae have no notochord and the humerus of *Haptodus* is expanded at both ends. Thus *Haptodus* agrees with the *Poliosauridae* but differs from *Palaeohatteria*. While this paper was in the hands of ST MAJER, in Paris PIVETEAU came to the same result¹⁾.

The precise systematic position of *Palaeohatteria* can only be fixed after separating the generally primitive characters of this animal from those, that indicate its trend of evolution.

The primitive characters of *Palaeohatteria* are: the size of the lacrymal bone, the weak premaxillary, the extensive dentition of the palate, the strong development of the anterior part of the pterygoids, the presence of a notochord, the presence of ventral ribs and the small size of the foramen obturatorium. In more than one of these points *Palaeohatteria* is not only more primitive than any known theromorphous Reptile but even more primitive than most *Pelycosauria*.

The trend of evolution of *Palaeohatteria* is indicated by the T-shaped squamosum, the structure of the mandible, the shape of the pelvis, the position of the foramen obturatorium and the shape of

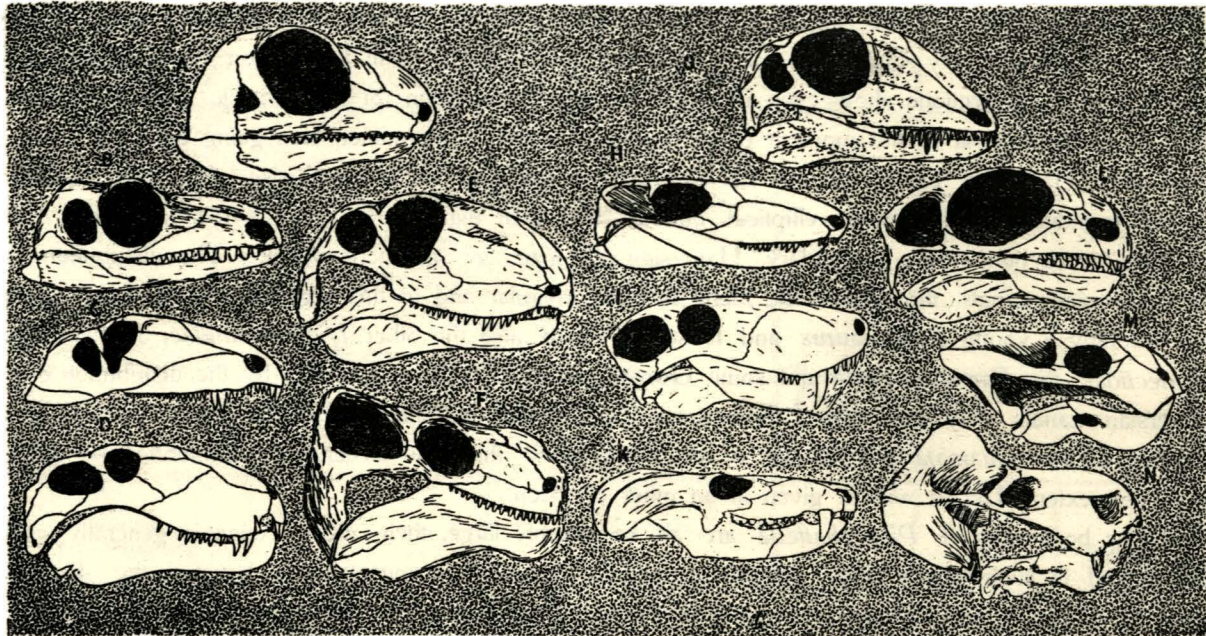


Fig. 2. Skulls of *Theromorpha*:

A) *Glaucosaurus*; B) *Mycterosaurus*; C) *Diopaeus*; D) *Dimetrodon*; E) *Pantelosaurus*; F) *Edaphosaurus*; G) *Palaeohatteria*; H) *Scaloposaurus*; I) *Scymnognathus*; K) *Protacmon*; L) *Galepus*; M) *Emydopsis*; N) *Kaunemeyeria*.

the humerus. These points indicate that *Palaeohatteria* was developing on the same lines as the *Theromorpha*. On account of the presence of ventral ribs, the shape of the pelvis, the shape of the squamosum and the shape of the humerus, *Palaeohatteria* approaches the *Dromasauroides*, it differs however

¹⁾ PIVETEAU, J.: Étude sur quelques Amphibiens et Reptiles fossiles. Annales de Paléontologie, Vol. XVI. Paris 1927.

from these in the dentition and the shape of the root of the tail. *Palaeohatteria* has evidently to be placed near the primitive *Dromasauria* and the *Theriodontia* but as a representative of a special suborder. This suborder has to be called *Palaeohatteroidea*. It is characterised and distinguishable from the *Dromasauroides* and *Therocephaloidea* by its notochord, by a metakinetic skull, by large lacrymal bones, by a pelycosaurian palate, by protothecodont teeth and by a long tail, thick at the root.

The discovery of this suborder is of very great importance. It proves that in their present extent the *Pelycosauria* on the one side and some of the *Theromorpha*, as Theriodonts and probably also Dicynodonts on the other, form two diverging groups of reptiles that evidently arose from a common stock. Because of their showing a strikingly parallel development in their braincase the one group seems to have arisen from the other; this relationship is however only apparent. In reality the one group is but further advanced than the other.

In the foregoing textfigure 4 thirteen skulls of some *Pelycosauria* and some *Theromorpha* have been placed side by side and have been all reduced to about equal size.

In the first horizontal row side by side with the skull of *Palaeohatteria* the skull of *Glaucosaurus* (A) has been figured. Both are characterised by laterally compressed, high and short skulls, long lacrymal bones and enormously developed orbits. Under the skull of *Glaucosaurus* the skull of *Mycterosaurus* (B) has been figured, for *Mycterosaurus* is a primitive member of the family *Poliosauridae*. The orbits in this genus are yet large, the skull is yet laterally compressed, but the lacrymals are smaller and the facial part is already elongated. *Diopaeus* (C), in which the whole outline of the skull recalls *Mycterosaurus*, is evidently another direct descendant of the primitive *Poliosauridae* and *Dimetrodon* (D) again is a descendant of *Diopaeus*. *Dimetrodon* shows a short lacrymal, huge maxillaries and an excessive carnivorous specialisation. This is combined with a relative immobility of the body.

An other phylum of *Pelycosaurians* represented in the diagramm is the one leading over *Pantelosaurus* (E) to *Edaphosaurus* (F).

Although generally classed among the *Pelycosaurians* these *Edaphosauroides* differ from the typical *Pelycosauria* in many important points as: the long lacrymal bone combined with a great specialisation of the teeth, the long pedunculate articulation of the lower jaw and the double perforation of the humerus. In many of these points this unit approaches *Palaeohatteria* to such an extent that *Palaeohatteria* may somehow well be considered as an ancestor of the group. Apart from this *Palaeohatteria* (G) seems to be however also related to the *Theromorpha*.

As *Palaeohatteria* so *Galepus* is characterised by strongly enlarged orbits, the lacrymal is however short as in all *Theriodontia* and the dentition is much weaker. On account of the latter character the posterior part of the mandible, where the muscles of mastication insert, also shows a rather different structure. In this point *Galepus* (L) approaches the *Anomodontoides*. The skull of a moderately specialised Anomodont, *Emydopsis* (M) is also in the figure. In this type the feeble dentition of *Galepus* gave way to the formation of a beak, the temporal muscles became enormous and the orbit became comparatively small. These features are still more exaggerated in *Kannemeyeria* (N). Similar changes as among the carnivorous *Pelycosauria* occur among many *Therocephaloidea*. In these it is easy to trace a line leading from *Palaeohatteria* through *Scaloposaurus* (H) to *Scymnognathus* (I) and from there to *Protacmon* (K). Also along this line a diminution of the orbit and a development of a carnivorous

dentition can be observed, but the carnivorous adaptation of these reptiles follows an other line than in the *Pelycosauria*. Instead of an elongation one remarks a reduction of the quadrate. Contrarily to this the *Dinocephalia*, that are also classed among the *Theromorpha* and that also arose from the *Pelycosauria*, evolved on a line of their own, but this will be dealt with in the following note. So the „*Pelycosauria*“ seem to be polyphyletic.

II. ON SOME FOSSIL REPTILES FROM THE COPPER-BEARING PERMIAN STRATA OF RUSSIA.

Owing to the permission of Prof. D. MUSHKETOFF I had, during a stay in Petrograd (Leningrad) in 1925 the opportunity to study at the Mining Institute the different type specimens of *Deuterosaurus* and *Rhophalodon* and some other pieces of the copper-bearing Permian of Russia, that had hitherto escaped attention.

Regarding first of all the skull described and figured by SEELEY (II 516) as *Deuterosaurus*, it was soon discovered that it is generically distinct from the piece described and figured under the same name by EICHWALD (II 281), therefore it needs

a new name. Because of this discovery having been made during the festivities commemorating the 200 years jubilee of the Russian Academy of Science, I propose to call SEELEY'S specimen *Mnemeiosaurus jubilaei*, the word *μνήμειον* meaning in ancient greek „token, remembrance“

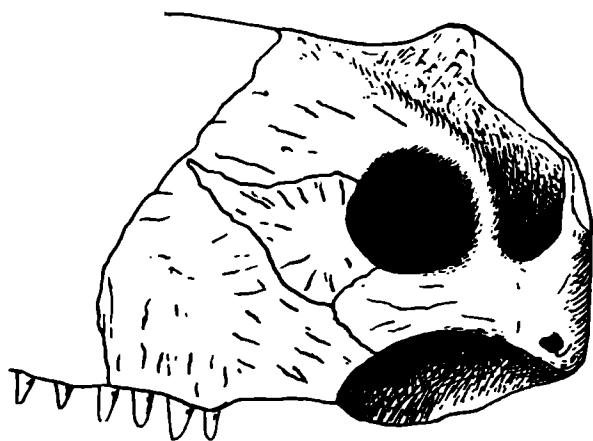


Fig. 3. Skull of *Mnemeiosaurus jubilaei* nov. gen., n. sp.

It is to a certain extent deplorable to have to rename such a well known specimen as SEELEY'S *Deuterosaurus*, of which the figure passed into so many textbooks of Palaeontology, but on account of SEELEY'S reconstruction being in many points wrong, the disappearance of his figure and

even of his family *Deuterosauridae* will produce only a passing inconvenience.

The renewed investigation of SEELEY'S specimen showed, that there does not only exist no proof for the skull having been so short as figured by that author, but that on the contrary even indications exist, showing that the facial part of the skull was at least as long as in any *Dinocephalian*. It is especially the way how the jugal arch curves upwards and forwards, the pointed outline of the huge lacrimal and the lack of a nasal bone that point in this direction. What SEELEY considered to be the posterior border of the premaxillary I take to be a crack. *Mnemeiosaurus* had furtheron as all *Dinocephalia* a large, funnelshaped pineal canal (II 571) that opened on the top of a well developed and truncated cone and a very deep hypophysis, recalling the one of the *Tapinocephalian* skull figured by

HAUGHTON (II 341). In the lower and posterior region of the skull in *Mnemeiosaurus* a small but well marked foramen is present, that seems to pass between the jugal and the quadratojugal. It is surely directed from outside inward and not as a foramen quadrati would be: from behind forward. A similar foramen has been figured by BROOM in *Delphinognathus*. As far as the sutures of the lacrymal and the jugal are concerned, SEELEY's drawings are correct, there is however no evidence of an especially strong canine having existed. SEELEY must evidently have arrived to this conclusion by the investigation of some other pieces. These have, as shall be shown furtheron, nothing to do with *Mnemeiosaurus*. Contrarily to *Deuterosaurus*, *Mnemeiosaurus* has numerous maxillary teeth.

Altogether the outline of the skull of *Mnemeiosaurus* is very different from the one given by SEELEY and this is the reason, why it was considered good to give a new drawing of the piece (fig. 3).

As visible from this drawing, the enormous lacrymal recalls to a good extent the reconstruction of *Delphinognathus* as given by BROOM. The temporal opening looks upwards as in most *Dinocephalia* and the curious cone for the pineal organ of *Mnemeiosaurus* likewise occurs in this group. All this leads to the conclusion that *Mnemeiosaurus* is a tapinocephalian reptile, but a genus in which the pachyostosis of the skull bones had not yet set in. This is the principal character forcing one to give the specimen a new name.

The second genus studied was *Rhopalodon*. This reptile turned out to be a true Gorgonopsian. Perhaps the most important conclusion arrived to was, that the long suture, drawn by SEELEY (II 516) as separating his „interparietal“ from his „parietal“ is but a muscular impression and that the true interparietal is but a small triangular bone, placed with its point turned downward on the upper margin of the vertical occipital surface. This surface forms, as in many *Gorgonopsoidea*, a nearly right angle with the upper surface of the skull. Far back on the upper surface of the skull a small pineal foramen can be detected, which is to be found in this position only in some highly specialised *Pelycosauria* (*Dimetrodon*) and some *Gorgonopsidae* (*Arctops*, *Gorgonognathus*). In *Rhopalodon* the frontal partakes to some extent in the bordering of the orbit, the palate has no suborbital vacuities and the posterior part of the mandible has a small but well marked process, directed downwards and outwards, recalling the analogous but much stronger process of the typical *Gorgonopsidae*.

By the fairly complete and but slightly differentiated dentition, by its strong sclerotic plates, by the high profile of the skull and by the feeble development of the mandibular flange *Rhopalodon* is, as has already been recognised by WATSON (II 581), a good deal more primitive than the S. African *Gorgonopsidae*, a closer relationship with the *Titanosuchoidea* can however not be detected.

A third Russian piece of no small interest is the small palate attributed by SEELEY to *Deuterosaurus*. The piece is

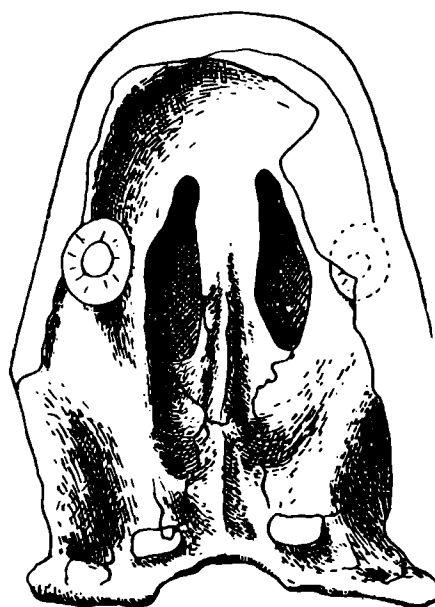


Fig. 4. Palate of *Uraniskosaurus* n. g.

much too small to belong to the type described by SEELEY under this name, and from the palate of *Rhophalodon* it differs considerably.

By the shortness of the presumed palatines and of the pterygoids, as well as by the median tongue-like projection of the median part of the pterygoids towards the vomer, this palate recalls to a good extent the palate of some *Gorgonopsidae* as *Arctognathus*.¹⁾ The *Titanosuchus*-like *Burnetia* (II 166) is said to have a palate recalling the *Theriodontia*, but on account of the palate of the *Titanosuchoidea* and *Burnetia* being only very little known, it seems premature to unite this interesting piece with *Mnemosaurus*. The presence of a large tusk-like canine points to a dentition of Gorgonopsian type. Because of the difference of interpretation, that I give to the different parts of this palate and that SEELEY gave, a drawing of the palate is given in figure 4. What SEELEY considered to be the transverse bone, I consider only to be a part of the pterygoid and SEELEY's small bone I take to be the true transversum. Unfortunately the sutures between the palatine and the maxillary, between the maxillary and the premaxillary and those between the vomer and the premaxillary can not be made out, the occurrence of a large canine on either side shows however at least where the suture between the maxillary and the premaxillary is to be sought for. It is curious that on the right side, in spite of its being better preserved, not the slightest trace of any tooth occurs posterior to the canine, although of the canine itself nearly the whole cross-section is preserved.

Owing to the decidedly Gorgonopsian type of this palate, it does not seem probable that it will turn out to be the palate of *Deuterosaurus*, and it is also unlikely that it belongs to the genus *Mnemosaurus*, consequently it deserves a new name. On account of only the palate (*ὄδραντιον* in greek) being known, I think it best to call it *Uraniskosaurus watsoni*, commemorating the important contributions of M. D. S. WATSON on the *Theromorpha*.

The fourth piece studied in Petrograd, and by far the most important, was discovered nearly accidentally, for it was only by cleaning away the matrix from a rather unpromising lot of bones labelled in an old German handwriting as «undeterminable skullfragments» that the posterior part of that skull was discovered, of which the anterior part had been figured by EICHWALD (II 281) as the type of *Deuterosaurus* nearly eighty years ago (Plate I fig. 4, 5). The reason why these two pieces had remained apart for so many years is evidently due to the fact that they were preserved in different Museums and labelled as coming from different localities. Even so their belonging together was only discovered after my having left Petrograd when my attention was attracted by the shape of the anterior fracture of the specimen I had cleared myself from matrix, that showed exactly the inverse shape of the posterior fracture of the dentigerous piece figured by EICHWALD, *Lethaea Rossica* (Plate LVIII fig. 1) and also by OWEN (II 485). After this discovery I wrote to Professor A. RJABININ asking him to try and bring both pieces together. This succeeded and now his kindness enables me to give on Plate I fig. 1, 2 for the first time a photograph of the nearly complete skull of *Deuterosaurus*. As visible the greater part of the skull is comparatively well preserved, for except of a part of the snout that was lost after the first description, only its upper part is missing. The old piece comprised, as known, the anterior parts of the upper and lower jaws, the new piece shows a fragment of the maxillary, the almost complete jugal,

HAUGHTON, S. H. On some Gorgonopsian skulls, *Annals S. Afric. Museum* 1924.

the quadratojugal, the quadrate, the squamosal, the greater part of the interparietal, the whole supraoccipital, one exoccipital, the basioccipital and the greater part of the right mandible. All bones are beautifully preserved and the sutures generally very well visible.

When complete the outline of the skull must have been somewhat elongated as in *Moschosaurus* (II 337).

The jugal is a triradiate, broad and flat bone, that borders the lower half of the orbit and the anterior part of the temporal fossa. In front of the orbit it ascends rather high upwards. The bar between the orbit and the temporal fossa is remarkably slender. GREGORY¹⁾ pointed out that in the *Dinocephalia* the thickening of the postorbital bar is a mark of specialisation. The temporal fossa is directed outwards as in *Scapanodon* (II 166) and *Diopaeus* (II 581) and not upwards as in *Mnemeiosaurus* or *Mormosaurus* (II 581). The general shape of the jugal differs from the jugal in *Dinocephalia* and recalls *Dimetrodon*. Its anterior bar adheres to the maxillary, the superior bar ascends between the orbit and the temporal fossa to meet the postorbital, the posterior bar touches above the squamosal and below an irregular bone, that may perhaps pertain to the jugal, but may already just as well be a part of the quadratojugal. In this manner the lower part of the temporal fossa is bordered in front by the jugal and behind by the squamosal, thus as in *Pelycosauria* (II 125, 151) and not as in *Dinocephalia*. The slenderness of the postorbital bar separates *Deuterosaurus* well from most *Dinocephalian* but recalls *Mnemeiosaurus*. The lower border of the jugal is to the greater part somewhat mutilated, but it does not seem to have reached much lower than shown in the figure; perhaps an exception is to be made for the region where it touches the quadratojugal. The structure of the jugal and its relation to the other bones is such as to prove that HUENE (XIII 207) was right, when he assumed that in the *Dinocephalia* the simple temporal fossa had secondarily shifted upwards. For our conception of the origin of the different temporal fossae of reptiles this is of remarkable theoretical importance, for it shows that in some groups of monozygocrotaphous reptiles the fossa, that at present appears to be an upper one, originated as a lower fossa. Thus it is, at least in some cases, not necessary to fall back into the hypothesis of a polyphyletic origin of the temporal fossae of reptiles, as has been done by VERSLUYS.²⁾

The squamosal. The border between the jugal and the squamosal is situated beneath the anterior part of the temporal opening, and thus in the squamosal two regions can be distinguished: an anterior region under the temporal fossa, where a flange of the squamosal extends over the jugal, and a posterior region more behind than under this fossa, in which the squamosal bulges somewhat outward so as to form an elongated hood over the quadrate and the quadratojugal.

An anterior flange-like process of the squamosal, as in *Deuterosaurus* is also indicated in *Delphinognathus* (II 125) and strongly developed in *Scapanodon* (II 166). In the latter also the same contrast is visible between the two regions of the squamosal as in *Deuterosaurus*. Unlike in *Scapanodon* the flange of the squamosal is however separated in *Deuterosaurus* from the postorbital by the jugal and in this regard therefore *Deuterosaurus* differs from all *Dinocephalia* and recalls the *Pelycosauria* (II 185).

The exterior side of the hood-shaped, somewhat bent part of the squamosal shows a rather well marked, almost vertical ridge, that may be considered as a faint indication of the strongly projecting crest,

¹⁾ GREGORY, W. K.: The skeleton of *Moschops capensis* Bullet. Amer. Mus. Nat. Hist. Vol. LVI. New-York, 1926.

²⁾ VERSLUYS, J. Über Phylogenie der Schläfengruben und Jochbögen. Sitz. Ber. Heidelberg. Akad. d. Wiss. 1919.

that characterises the squamosal of *Pnigalion* (II 571) and other specialised *Dinocephalia*¹⁾. The overlap of the squamosal over the quadrate and quadratojugal, although clearly visible, is not as strong as in the carnivorous *Pelycosauria* or as in the *Dinocephalia*. A foramen at the junction of jugal and quadrate, as visible in *Mnemeiosaurus*, is wanting in *Deuterosaurus*.

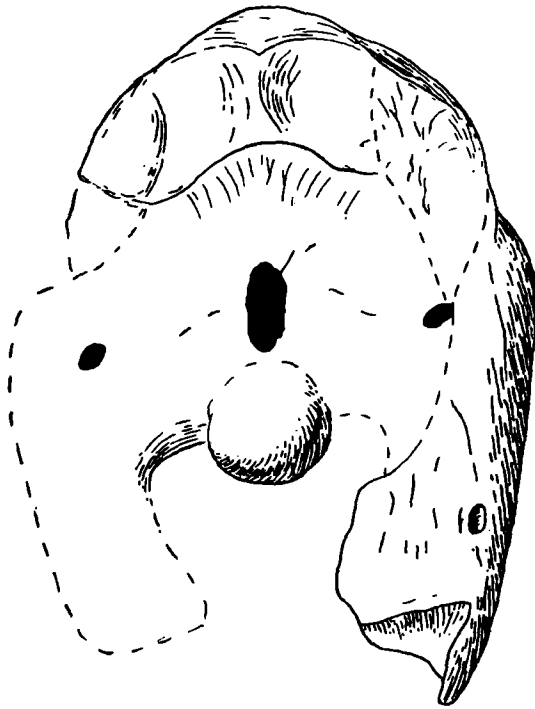


Fig. 5. Posterior aspect of skull of *Struthiocephalus* (?).

according to BROOM, to *Struthiocephalus*, of which he was so kind to send me an unpublished drawing. With his special permission this drawing is reproduced in figure 5. On account of this feature occurring only in the more specialised *Pelycosauria*, the less specialised *Dinocephalia* and the *Thecodontia* it seems to have originated at least twice independently. In this way its occurrence can to a certain extent be considered as one proof more that the evolution of all three groups is influenced by some common agent forcing them to develop more or less on parallel lines (latent homoplasy).

The quadrate is a rather long and very strong, pillar-like bone, that is directed with its lower end somewhat forwards. A similar elongation of the quadrate as in *Deuterosaurus* is known in the more specialised carnivorous Pelycosaurians (II 457, 581), but in all these it is laterally much more overlapped by the squamosal. It is only in the shell-eating Pelycosaurians as *Pantelosaurus* (XIII 59) and *Edaphosaurus* (XIII 59) that the quadrate and the quadratojugal are more exposed to the view. Distally the quadrate is transversally expanded as in *Struthiocephalus* (?) and bears here the very large, double articulated surface for the mandible. Curiously enough this surface is not more or less horizontal as in most Reptiles, but almost vertical and looks, consequently, nearly forwards. On account of the elongation of the quadrate, the articulation of the lower jaw is far beneath the occipital condyle. By this character *Deu-*

¹⁾ GREGORY, W. K.: The skeleton of *Moschops*, loc. cit.

terosaurus again resembles more to the specialised than to the primitive *Pelycosauria*, furtheron to *Scapanodon* (II 166), *Moschops* and *Moschognathus* and differs from *Titanosuchus* (II 571), *Mnemeiosaurus* and all the pachyostotic *Dinocephalia* that cluster round *Mormosaurus*. Owing to the overlapping of the squamosal and the development of the quadratojugal the quadrate is only visible from behind.

On the side of the squamosal and in the middle line of the skull the large, hemispherical and well preserved basioccipital condyle is seen and above this the triangular foramen magnum. This opening is comparatively small and is bordered laterally by small, triangular and rather pointed exoccipital bones. The supraoccipital seems only to partake to a slight degree in the formation of its border. On the side of the skull the supraoccipital reaches with a moderately slender process to the squamosal, in the middle of the skull its superior border is formed by the long, nearly straight and horizontal suture, that separates it from the interparietal. Laterally and between the squamosal and the interparietal the supraoccipital was in contact with a well developed tabulare, this bone is at present however entirely broken away.

In the middle of the skull the supraoccipital shows a vertical ridge that dies away towards the foramen magnum, but is continued upwards on the interparietal. Laterally of this ridge on each side of the supraoccipital a thumb-shaped impression is visible, that is likewise continued upwards. Evidently this impression served as place for the insertion of the cervical muscles. A long and horizontal supraoccipital—interparietal suture, as in *Deuterosaurus*, occurs in some carnivorous *Pelycosauria* as *Diopaeus* (II 581), in some *Dinocephalia* as *Lamiasaurus* (II 571) and in some *Gorgonopsioidea*, as *Arctops* (II 572) and *Galesuchus*.¹⁾ In the more specialised *Pelycosauria*, to which the jugal region and the suspensorium mandibuli of *Deuterosaurus* recalls, the occiput is built on an altogether different plan.

A small splint-like bone placed in front of the region from where the tabulare broke away and above the squamosal is probably a part of the supratoral. It is only visible in the side view and in the upper aspect of the skull. In the lateral temporal opening an irregular mass of bone comes out from under the matrix, and shows a foramen leading into the braincase. The nature of this bone can not be fixed with certainty, but it does not seem improbable that the foramen is the opening of the fifth nerve. The top of the skull being broken away, the braincase itself is exposed to view. This part has the shape of a large, vertical canal of elliptical cross-section and shows that a great part of the braincase ascended vertically as characteristic for *Dimetrodon*.

Under the condyle an other somewhat irregular mass of bone is visible, that forms a descending wall as in some *Dinocephalia*, the elements of this wall can, however, not be determined.

The posterior part of the mandible of *Deuterosaurus* is broad and high. It is altogether dinocephalian. It is characterised by the almost unique position of the surface of articulation, by the abrupt ascent of its posterior and superior margin and by the low and strongly rounded, but nevertheless well developed coronoidal process. The inferior border of the mandible is to the greater part missing, the equal thickness of the parts preserved indicate however that it was relatively straight. A retroarticular part was not developed.

Sutures of three mandibular elements are clearly visible. The whole posterior part is formed by one strong bone corresponding to the fused articular and surangular, the lower and inferior part is covered

¹⁾ HAUGHTON: On some Gorgonopsian skulls, loc. cit.

by a smaller piece representing a part of the angular and the rest is formed by the dentary bone. As far as preserved the posterior piece of the dentary is devoid of teeth. From the upper edge of the concave surface of articulation on the outer side of the mandible a curved ridge extends upwards and forwards, that forms the upper convex border of a well marked and slightly concave surface. This surface was probably the region where a pterygoido-mandibular muscle or some other similar muscle inserted, which was used for closing the jaw and at the same time for pulling the jaw against the surface of articulation. A very similar impression seems also to occur on the lower jaw of *Moschops capensis*, but here it seems to have shifted much further upwards so as to cover a greater part of the jaw.

As evident from this description, the posterior part of the skull of *Deuterosaurus* resembles in so many important points to the *Pelycosauria* and differs so strongly from the *Dinocephalia* that one would even hesitate to place it among these, would not the anterior part of the skull prove its dinocephalian nature.

Of the maxillary on the new piece only the posterior and inferior part touching the jugal is preserved. This part is not very characteristic. As far as preserved it is edentulous and has a triangular outline. Posteriorly it thins out under the jugal much as in *Diopaeus* (II 581). The rest of the maxillary is contained in the old piece. It is a high and robust bone. It shows in the anterior and superior part a concavity indicating the place where the nares were situated. Under this place a large canine is visible. It indicates where the suture between the maxillary and the premaxillary is to be sought for. Apart from the canine only two smaller teeth seem to be present in this bone.

The premaxillary is at present practically wanting, for only alveoli with five teeth are preserved, that were implanted very obliquely in the bone.

A step between the maxillary and the premaxillary, as characteristic for the higher carnivorous *Pelycosauria* and some lower *Theriodontia*, is wanting in *Deuterosaurus*. EICHWALD's figure shows that the anterior end of the premaxillary ended very abruptly.

In accordance to the posterior part also the anterior part of the lower jaw is very high and comparatively short. It ends in a strong and vertically descending chin. The symphysis is very strong and both rami of the lower jaw are firmly coossified with each other. In this regard *Deuterosaurus* differs somewhat from the *Pelycosauria*, for in these the symphysis mandibuli is generally weaker. Evidently this is in correlation with the shape of the incisors.

The teeth of *Deuterosaurus* are very characteristic and truly dinocephalian. The dental formula is: $\frac{3}{4} i \frac{1}{1} c \frac{2}{1} m$. The teeth are slender, about conical and slightly curved. Those of the left side are preserved better. On the right side one can distinguish far behind a very small molar with a blunt conical crown, that is constricted quite markedly at its base. On the left side EICHWALD's figure shows a strong canine, that is missing on the plastercast at my disposal and in front of this follow two very obliquely placed slender premaxillary teeth. In the lower jaw there exists a strong canine and then follow in each mandible four incisors the size of which increases towards the symphysis. By having a concavity on the inner surface of the crown the second incissor shows the shape characteristic for the *Dinocephalia*. The compression of the incisors is somewhat lateral, while the molar is slightly compressed in linguo-labial direction.

Unluckily nothing is known of the palate of this specimen.

The feebly differentiated, but nevertheless characteristic dentition of *Deuterosaurus* proves that this reptile is a Dinocephalian, but it differs from the South African types in many important points. The differences concern especially the jugal, the quadratojugal, the quadrate and the occipital region. In all these points *Deuterosaurus* approaches the more specialised *Pelycosauria*, as *Diopaeus*, *Dimetrodon* and the *Edaphosauroides* and differs from the *Dinocephalia*. Probably the resemblances in the occipital and in the jugal region are the inheritance of a common descent, but the elongation of the quadrate and the formation of a foramen quadrati seem rather to be a convergence between *Pelycosauria*, *Deuterosaurus* and *Thecodontia*. Together with the investigation of *Palaeohatteria* the study of *Deuterosaurus* shows that the *Theriodontia* and the primitive *Pelycosauria* arose from a common stock, while the *Dinocephalia* are probably descendants of some rather specialised *Pelycosauria*. This pleads for including the *Pelycosauria* in the *Theromorpha*.

The genus *Deuterosaurus* forms at present a family of its own, that has to be called *Deuterosauridae*. This family is altogether different from the *Deuterosauridae* of SEELEY. The latter family has to vanish, for it is only based on the erroneous reconstruction of a skull that is now recognised as tapinocephalian.

The *Deuterosauridae* of SEELEY 1882 (sensu NOPCSA 1926) have to be defined as titanosuchian reptiles in which the squamosal is not yet in contact with the postorbital, the quadrate and the quadratojugal are elongated and a foramen quadrati is present.

Baron FEJÉRVÁRY, the well known authority on international rules of nomenclature, was so kind to inform me that, according to the international rules, for the fossil skulls of the Russian copper-bearing strata following generic names have to be used :

1. *Deuterosaurus* EICHW. 1848 (sensu NOPCSA 1926 ; synonym : *Deuterosaurus* part. SEELEY 1893) belonging to the family *Deuterosauridae* SEELEY 1893 (sensu NOPCSA 1926) synonym : *Deuterosauridae* part. SEELEY 1893.
2. *Mnemeiosaurus* NOPCSA 1926 (synonym : *Deuterosaurus* part. SEELEY 1893, nec EICHW. 1848) belonging to the family *Tapinocephalidae* WATSON 1914 (synonym : *Deuterosauridae* part. SEELEY 1893)
3. *Rhophalodon* EICHW. belonging to the primitive *Gorgonopsoidea* and more precisely to the subfamily *Akidognathinae*.
4. *Uraniscosaurus* NOPCSA 1926 (synonym : *Deuterosaurus* part. SEELEY 1893) belonging to the family *Gorgonopsidae* and the subfamily *Gorgonopsinae*.

As is well known, apart from the skull remains also numerous vertebrae and other bones have been found in the copper-bearing strata of the Ural. In some of these, as for example in a humerus with two foramina, their pertinance to the *Dinocephalia* is evident, it seems however at present premature to associate any of these isolated bones with the different skulls. As result it is at present best to register each separate piece provisionally yet under the name under which it has originally been described. When in the course of future discoveries it will finally become possible to associate the various limb-bones with the different skulls, of course all these different names will have to be revised.

The recognition of the primitive dinocephalian nature of *Deuterosaurus*, furtheron the determination

of *Mnemeiosaurus* as a true, but not yet pachyostotic Dinocephalian and of *Rhophalodon* as a primitive Gorgonopsian, are of far reaching stratigraphical importance.

The copper-bearing strata, that yielded these remains, are situated below the beds of the northern Dvina, that contain *Pareiasauridae*, *Dicynodontidae*, *Gorgonopsoidea* and *Therocephaloidea*. Somewhat over the niveau containing the Pareiasaurians follows in Russia a niveau containing primitive *Cynognathidae* (*Dvinia*, *Permocynodon*)¹⁾ and these beds are again overlaid in the governments Vologda and Kostruma by beds containing *Thecodontosaurus* (IX 523) or some other Archosaurian. There exists no conclusive evidence for *Dicynodon* occurring in Russia already in the niveau containing the *Dinocephalia* and so altogether the succession of the different faunas of the Russian Permian is quite the same as that in the Karroo. In South Africa the Eccla-beds and the lowermost Beaufort-beds (*Tapinocephalus-zone*) contain predominantly *Dinocephalia*, the next beds (*Endothiodon-zone*, *Cistecephalus-zone*) *Pareiasauridae*, *Dicynodontidae*, *Gorgonopsoidea* and *Therocephaloidea*, then follows a niveau rich in *Cynognathidae* (*Cynognathus-zone*) and uppermost come the Red-beds with different Archosaurians. This sequence makes it possible to parallelise the continental strata of northern Europe with those of the Karroo. The strata of the shores of the Dvina represent evidently the Lower and Middle Beaufort-beds and those of Vologda seem, at the first glance, to represent the South African Red-beds. In reality they are somewhat older than the Red-beds, for the Vologda-beds of Russia are of lower triassic age (Werfenian), while the *Thecodontosaurus* beds of Germany and those of South Africa belong to the Middle Triassic. Because of both the *Dinocephalia* and the one Gorgonopsian of the copper-bearing strata of Russia being more primitive than the reptiles of the South African *Tapinocephalus-zone*, the copper-bearing strata may be considered to be an equivalent to the Eccla-beds.

So altogether it makes the impression, as if all the different faunae of the Karroo would have originated somewhere north of Africa, and, consequently, the collecting of further fossil reptiles in the copper-bearing strata of Russia would be of utmost scientific importance. It is here that we may hope to discover all those types, that are necessary to bridge over the gaps observable between the types known from Texas and those known from the Karroo.

III. ON SOME NOTHOSAURIAN REPTILES FROM THE TRIAS.

The discovery of some new specimens of small Nothosaurian reptiles made it desirable to revise all the smaller genera of this group and the more so as G. von ARTHABER's recent revision of these genera (V 31) was based more on speculations than on investigations of the types. The consequence of his method was, that conclusions were arrived at, which are frequently open to criticism. Some of his drawings are likewise inexact.

The pieces that form the basis of the following paper are: The type specimens of *Pachypleurosaurus* (*Pachypleura*), *Anarosaurus* and *Neusticosaurus*; BOULENGER's and MARIANI's specimens of *Lario-*

¹⁾ HUENE, FR.: Ein Cynodontier aus der Trias Brasiliens. Centralbl. Min. Geol. u. Palaeont. (B). Stuttgart 1928.

saurus, a new specimen of *Dactylosaurus*, a fossil representing a new genus *Psilotrachelosaurus* and a second specimen of *Pachypleurosaurus* from the Senckenberg Museum. Prof. BROILI was so kind to send me a magnificent gelatine-cast of *Rhäticonia*¹⁾ A review of those Nothosaurian genera, that cluster more or less closely around *Nothosaurus* and are only known by skulls, as *Conchiosaurus*, *Pistosaurus*, *Cymatosaurus* and *Germanosaurus* (= *Eurysaurus*)²⁾ was purposely omitted. These genera have already thoroughly been dealt with by SCHROEDER. *Partanosaurus* was also omitted because the type of *Partanosaurus* can no more be found in the collection of the Austrian Geological Survey and finally the types of *Phygosaurus* and *Marcomerosaurus* were out of reach.

In the following lines the data concerning *Lariosaurus* refer, when not especially mentioned, always to MARIANI'S (V 296) specimen of *Lariosaurus* (B), in which the proportions agree very well with those of ZITTEL'S specimen (A) and BOULENGER'S (V 58) specimen (C). Both the dimensions and the proportions of all three specimens can very well be made out from the following data :

1. Dimensions.

Size in millimeters:	A	B	C
Length of skull	91 mm	55 mm	43 mm
„ presacral part of vertebral column	440	277	135
„ „ humerus	72	36	20
„ „ ulna	33	20	11
„ „ manus	56	31	20
„ „ femur	90	43	24
„ „ fibia	38	19	12
„ „ pes	60	37	25

2. Body proportions.

	A)	B)	C)
Proportion of skull to presacral part of vertebr. column	20·7 : 100	20·2 : 100	31·8 : 100
„ humerus to ulna	10 : 4·7	10 : 5·5	10 : 5·5
„ humerus to ulna+manus	10 : 12·3	10 : 14·1	10 : 15·5
„ femur to fibia	10 : 4·2	10 : 4·4	10 : 5·0
„ femur to fibia+pes	10 : 10·8	10 : 13·0	10 : 15·4
„ humerus to femur	10 : 27·2	10 : 21·5	10 : 21·8
„ „ hu+ul+ma : fe+fi+pes to posterior extremity	10 : 11·6	10 : 11·3	10 : 11·9

As visible, the changes of proportions are very gradual and thus only such that are due to growth-rate. A very fine, hitherto undescribed primitive Nothosaurian reptile, that is reported to come from the trias of Hueska, exists in a private collection in Spain.

For *Pachypleura* and *Eurysaurus* new names had to be adopted, for the name *Pachypleura* CORNALIA (1854) was preoccupied, as LYDEKKER pointed out, by WHITE in 1853 and FRECH'S name *Eurysaurus* (1903) was preoccupied by GAUDRY in 1878. It is a great pity that all this escaped G. v. ARTHABER'S attention, when he wrote his comprehensive memoir on the *Nothosauria*. For *Pachypleura*

¹ BROILI, F.: Ein Sauropterygier aus den Arlbergschichten. Sitz. Ber. Bayr. Akad. d. Wiss. math. naturw. Abt. München 1927.

² NOPCSA, FR.: The genera of Reptiles; Palaeobiologica, Vol. I. Wien 1928.

in the following paper the new name *Pachypleurosaurus*, and for *Eurysaurus* the name *Germanosaurus* is used. Curiously enough the name *Pachypleurosaurus*, that I used for the first time in my paper „The Genera of Reptiles“ in 1928, was used by BROILI independently for the same fossil in the same year. This shows better than anything else, how appropriate this name is.

A) Redescription of *Pachypleurosaurus* NOPCSA.

I agree with BROILI that that specimen has to be considered as the type of *Pachypleurosaurus*, which has been described as „the smaller specimen“ of *Pachypleura* by CORNALIA in 1854 (V 119). It belonged then to the collection Borromeo, it is now in the Museo Civico di Storia Naturale in Milano and represents, as other pieces show, a semiadult individual. Owing to the courtesy of the Professors ARTINI and MARIANI, I was permitted not only to investigate but also to prepare the specimen and owing to this preparation the specimen now shows several characters that were hitherto obscured. When I began the study of the fossil, its greater part was covered by a thin layer of calcareous material that had to be removed by the joint action of a lithographic needle and of phosphoric acid.

The skull, the posterior part of the trunk, the entire tail and most of the bones of the extremities are well preserved. Some are visible from the back, others from the side. Of the cervical and of most of the dorsal vertebrae as well as of the scapular arch only the impression of the ventral side is preserved.

The entire length of the specimen is 29 cm. Judging from the length of the back of the Frankfurt specimen, that belongs to a full grown individual, adult specimens attained a length of 40 cm.

The skull of the type specimen (Pl. II fig. 2) that has, to some extent, been described by CORNALIA is 27 mm long and 14 mm broad. The premaxillaries are cleft at the distal end, as is frequently the case in *Simosaurus*, they are however firmly united in their proximal half. At this place they are prolonged into a slender rod-shaped process that separates the nasals and enters even slightly between the frontals. Such a prolongation of the premaxillaries is known in *Cymatosaurus* (V 432) and quite frequent among the *Plesiosauria*. Each premaxillary bears four cylindrical teeth that are separated by large diastemata from each other. In the present state of preservation these teeth protrude strongly outward as in *Anarosaurus*, in lifetime they were however probably directed obliquely downward and forward. The small nasals seem to touch the large prefrontals of which each has the shape of half a crescent. The frontals are fused in the median line and longer than broad. Backward they diverge strongly and join the postfrontals and the paired parietals. The postfrontals do not reach the prefrontals and extend from the orbit to the temporal fossa. They are sigmoid-shaped and receive on their outer border a small, tongue-like process of the postorbitals. The suture between the postfrontals and the parietals is clearly visible. The parietals are paired and enclose a large pineal foramen. They are the largest bones of the skull and remarkably broad. Posteriorly on the outer side each parietal has a spur-like projection that joins the squamosal along a longish suture. Owing to the breadth of the parietals, the supratemporal openings are far asunder. The triangular squamosals project far backward and partake only to a slight degree in the formation of the broad temporal bar. This bar is formed to the greater extent by the postorbital. Contrarily to all the other *Sauropterygia* with small temporal openings in *Pachypleurosaurus*, as in *Plesiosaurus*, the skull is broadest in the region of the temporal fossae. Between the squamosals and

behind the parietals a part of the occiput is visible from above. It shows that this part consisted in a large plate of bone pierced evidently only by very small post-temporal fossae. Beneath the postoccipital surface the posterior ends of both mandibulae are visible, showing a well developed retroarticular process.

Anterior parts of the mandibles are visible under and within the very large orbits, but curiously enough, the lateral border of the orbits could nowhere be detected. Because of this border being absent on both sides, it must evidently be surmised, that the orbits opened to a good extent sideways, so that their inferior border came to lay nearer to the median line of the skull than the median part of the orbit. Something similar can be observed sometimes among recent *Lacertilia*, for example in many *Geckonidae*.

The entire length of the presacral part of the vertebral column (Pl. II fig. 3) is 112.5 mm. On account of only the impression of the relatively short neck being preserved, not much can be said about the cervical vertebrae. To the utmost 15 cervicals seem to have been present. They are shorter than broad and by no means elongated, as in the reconstruction of *CORNALIA*. Backwards they increase markedly in size and recall in general somewhat the cervicals of *Dactylosaurus*.

The number of dorsal vertebrae can only be deduced from the number of dorsal ribs that are present in the specimen. Their borders are obliterated by the impression of the numerous, well developed ventral ribs, thus the impression of the centra of the dorsal vertebrae are difficult to distinguish. The ventral riblets reach forward to the ninth dorsal. The number of dorsal ribs is 20. Even the last dorsal vertebra bore a strong and well developed rib. The Francfort specimen (Pl. IV fig. 3) shows the arches of the dorsal vertebrae in a magnificent state of preservation. These are all broader than long, they show a nearly horizontal upper surface and a low neural spine that extends from one end of the arch to the other. The arches are the broadest and longest in the anterior part of the back. Their size diminishes somewhat towards the sacrum. On account of the length diminishing more rapidly than the breadth, the posterior vertebrae seem abbreviated. In *CORNALIA*'s type the pelvic girdle is born by three well developed sacral ribs that converge towards the ilium.

After the sacrals follow seven strong caudal vertebrae with moderately low and broad neurapophyses, that bear strong, long, straight, cone-shaped costoids. After these come five vertebrae in which the neurapophyses are yet broad but the costoids much smaller. On the top of the eleventh caudal vertebra the anterior and superior border of the neurapophysis shows a small step-shaped incision. This incision increases in size in the twelfth vertebra and in the thirteenth it attains already such a size as to reach down to the niveau of the praecygapophyses. It reduces the neurapophyses to a narrow blade of bone situated on the posterior part of the neural arch. On the fourteenth vertebra the reduction has made still more progress and the neurapophysis is only a very small and sharply pointed spine arising on the posterior part of the neural arch. On all the following 28 caudals no traces of the neurapophyses or of the costoids can be detected and thus the tail, however elongated, certainly did not serve as rudder. In this part of the body, the cross-section of the tail was evidently circular, while it was transversely elliptical in the region situated further in front.

The scapular girdle is curious. Its impression shows the ventral side and figure 4 on plate II shows a cast of this impression. On the right side of the figure a well preserved and characteristic

scapula can be discerned, showing a broadened glenoidal part and a thin but well developed scapular blade. On the left side the glenoidal part of the scapula is visible from above, but the suprascapular process is broken off. In front of the right scapula a relatively large, nearly rectangular bone can be detected, that is yet in union with the scapula. This must evidently be a clavicle of peculiar shape and the same bone, but in worse state of preservation, left its impression also on the other side of the body. Between these two bones extends a broad and very strong bone that lays in the middle line of the body. Evidently this is the interclavicular bone that was transversely elongated as in the *Nothosaurus* figured by KOKEN and in ARTHABER's (V 31.) reconstruction of *Lariosaurus*. Nothing certain is known about the coracoidea of *Pachypleurosaurus*, it may however be, that an elongated impression, visible near the humerus on the left side of the figure, is a trace of one of the elongated coracoids. In the Francfort specimen the scapula and the clavicle are visible from above. Of the scapula not much can be said, except that it had on the dorsal side a spine which is however at present broken off. On the ventral side it seems to have been somewhat longer than broad. The part of the clavicle laying on the dorsal and inner surface of the scapula is a trifle more dilated than the rest.

Owing to the fact that in the type the pelvis is visible from the dorsal side only, the ilium is exposed to view (Pl. II fig. 5). This bone is stout in the acetabular region, but thins out markedly upward. Above it curves backwards and recalls thus strongly the ilium of *Metrioichynchus Morelli* (V 25). The ventral elements of the pelvis are very well visible in the Francfort specimen. The pubis that is visible from above, is an irregularly quadrangular bone. The side facing the acetabulum is the shortest and feebly convex, the side placed in the median line is much longer and very strongly convex, the two other sides are concave, the anterior of these two being the shorter. The obturator passes through a notch on the posterior border and near the acetabulum. Altogether this bone recalls the pubis in *Proneusticosaurus*, it is however somewhat longer. It differs well from the pubis of *Phygosaurus*. The ischium is very narrow in the acetabular half, but beyond the middle it expands very rapidly towards the median line. Altogether it has nearly exactly the same shape as in *Anarosaurus* and is very different from the ischium in *Lariosaurus*.

The limb bones are not very characteristic. The humerus of the type is a 17.5 mm long, straight and rod-like bone, only feebly dilatated at either end. It has a nearly circular cross-section in the middle. Radius and ulna are both also slender, rod-like bones. The radius, that is the longer of the two, measures 10 mm. Two of the elongated carpals are arranged as in *Dactylosaurus*. The metacarpals are very slender and the phalanges are rather short. The entire length of the manus was about 11 mm. Altogether in the fore limb a certain resemblance to *Neusticosaurus* can be detected, but in the latter, as in *Anarosaurus*, the humerus is more dilated at the distal end.

Of the two feet, visible in the type specimen, the one shows the palmar, the other the dorsal side (Pl. II fig. 5). The femur of *Pachypleurosaurus* has been well figured by CORNALIA. It is 14.5 mm long. The tibia (9.5 mm), the fibula and the proximal tarsal bones have also been well figured by CORNALIA, but his figure of the metatarsals is not exact. Four of the metatarsals of *Pachypleurosaurus* are slender and of nearly equal size, but the first is strongly abbreviated and thus recalls *Proneusticosaurus*. The digital formula can no more be made out, it is however important to note that the small

distal phalanges of one of the fingers were flattened and broadened at either end and strongly contracted in the middle. Thus they have the shape of an hour-glass rolled flat. Thin, but sharp and well defined black lines separate at both ends of all phalanges the epiphyses from the rest of the bone. The total length of the pes was 19.5 mm.

B) *Dactylosaurus Schroederi* nov. spec.

The new specimen of *Dactylosaurus* was discovered at Gross-Stein and belongs to the Prussian Geological Survey. It consists of two slabs showing the ventral and dorsal impression of a nearly complete reptile. On the slab showing the impression of the dorsal side of the skeleton the skull, the posterior cervical and all the dorsal vertebrae, both anterior extremities, parts of one posterior extremity and the middle part of the tail are preserved. On the other slab, besides these parts, also the anterior cervicals, one complete and one incomplete posterior extremity and the root of the tail are visible. Owing to the kindness of Prof. STILLE, this slab could be compared with the type specimen of *Anarosaurus*, that shows a good deal of resemblance. Figures of *Dactylosaurus* and *Anarosaurus* are given on plates III and IV.

The skull is well preserved (Pl. III fig. 3, 4). The paired parietals are somewhat longer than broad, thus somewhat longer than in *Anarosaurus* and decidedly longer than in *Pachypleurosaurus*. The pineal foramen is small and situated in the middle of the parietals. The posterior margin of the parietals, that is nearly straight in *Pachypleurosaurus*, is sharply concave as in the type specimen of *Dactylosaurus* and more concave than in *Anarosaurus*. The frontals are very long and slender as in *Pachypleurosaurus*. Behind they are lyriiform and somewhat broader than in front. The suture with the parietals is the same as in *Anarosaurus* and very characteristic. The frontals do not diverge backwards as in *Pachypleurosaurus*, but remain rather straight throughout their length. The postorbital and the postfrontal are fused and form the anterior part of the temporal fossae. These fossae are small and elliptical as in *Anarosaurus*. They are elongated in cranio-caudal direction and narrow transversely. Their inner margin is formed by the parietals, their posterior by the squamosals. In the middle of the temporal bar the skull is narrower than at its beginning or at its end; thus *Dactylosaurus* recalls to a good degree *Anarosaurus*. The triangular prefrontals can be well made out. Their slender posterior end is well separated from the splintlike anterior end of the postfrontal, the large orbits are therefore bordered by frontals, prefrontals and postfrontals. The longitudinal diameter of the orbits is greater than the transverse. Owing to the remarkable narrowness of the frontals, the orbits look to a good extent upward, but with their lower part also somewhat sideward.

The paired nasals are somewhat elongated and are, to the greater part, separated from each other by a slender process of the premaxillary, this process does however not reach the frontal. In *Anarosaurus* this process seems to be much shorter than in *Dactylosaurus*, while it is longer in *Pachypleurosaurus*.

The premaxillaries and maxillaries are invisible from the dorsal side of the skull. On the ventral side on the left two rows of numerous conical teeth are visible. Of these rows, the exterior one belongs to the maxillary and premaxillary, but the complete number of the maxillary teeth could not be fixed, because their row is frequently interrupted by the interior row, that pertains to the mandible.



Fig. 6. Inferior aspect of skull of *Rhäticonia* (nat. size).

The palate is rather difficult to understand. Posteriorly the palate is narrow and consists evidently of two pterygoids that are built on the plan of *Cymatosaurus Friedericianus* (V 187.) or *Neusticosaurus*. They reach right to the condyle and show at their posterior end two concave excisions with a small spur between them. By this small spur *Dactylosaurus* differs well from *Rhäticonia*, of which I am enabled by the kindness of Prof. BROILI to give in fig. 6. a better drawing than he gave in his original paper. In *Dactylosaurus* this part is more slender than in *Anarosaurus*. Towards the region where the transverse bone is to be expected, the pterygoids become broader, but owing to several cracks that cross over the well closed palatal vault and to the fact, that the palatal vault has been pressed against the bones of the roof of the skull, so as to show, en relief, the outlines of the orbits, the components of this vault can not be recognised. Far in front two rather large openings are visible that are evidently the internal nares. Suborbital openings, as present in *Neusticosaurus* and *Lariosaurus*, are surely missing.¹⁾

The mandible is slender, but not well preserved, nor very characteristic: its detailed description can therefore easily be neglected.

The vertebral column is well preserved (pl. III., fig. 1, 2). Altogether 36 presacral vertebrae are present, of which 16 belong to the neck and 20 to the body. The impressions of the first three cervicals are preserved both on the slab and on the counterslab: the next six are preserved only on the slab showing the ventral aspect of the skeleton, the following seven are again visible on both slabs.

The neural arches of the foremost cervical vertebrae are badly preserved, the centra can however be made out very clearly. These centra are nearly three times as long as broad or high. Owing to a longitudinal furrow, their base is transversely and longitudinally concave and margined on each side by a sharp ridge. Above this ridge, rather high up on the centrum and equally far from both ends of the vertebra, from an elongated base a small, stout and blunt projection arises, bearing a concavity at its distal end. This is the parapophysis for the cervical rib. Parts of the neural arches of these vertebrae are visible from below. They show that the arches were a good deal broader than the centra. Backwards the cervical vertebrae gradually become much broader but only a trifle longer, thus they are stouter than those situated further in front. On the last six cervical vertebrae, at the posterior end of the base of the centrum, a small hyapophysial knob is visible. In comparison to the size of the centrum, in all cervicals the parapophysis is very large. The neural arches of the posterior cervicals interlock very closely. They are somewhat longer than broad and broader than in the vertebrae situated further in front. In the last two cervicals they are as long as broad. By their length they differ somewhat from the neural arches of *Anarosaurus*. All cervical vertebrae have low neural spines that extend from the anterior end of the arch to the posterior and partake in the formation of a rather strong zygosphenial articulation. The prezygapophyses and the postzygapophyses are everywhere nearly horizontal.

¹⁾ At this point it may be remarked that G. v. ARTHABER's (V 31.) reconstruction of the palate of *Neusticosaurus* is entirely fanciful. On the type itself, as shown on the enlarged photograph of the piece given on plate IV fig. 4, no sutures can be detected. All sutures are obliterated and what ARTHABER took to be sutures, are in reality only cracks.

The cervical ribs, of which the three last are preserved on the left side of the animal, are strong and stout and rapidly increase in length. They are one-headed (?) and by showing a small projection extending in front of the head, somewhat, hammer-shaped.

The seventeenth vertebra can be considered as a sort of transitional vertebra between the cervicals and the dorsals. Apart from this vertebra, nineteen dorsals are present. The centra of these vertebrae are barrel-shaped, somewhat longer than broad and bear on the side and in the middle the large conical parapophysis. The neural arches of the dorsals have the same shape as those of the cervicals, but their breadth increases backward, so that on the posterior dorsals the breadth of the neural arch is nearly twice as great as its length. All dorsals bear well developed ribs that thicken slightly at the proximal end, but are otherwise slender and one-headed as in all other *Nothosauroidae*. They are equally curved throughout their length and differ thus from the more angular ribs of *Anarosaurus*. Being comparatively short, they indicate that the body of *Dactylosaurus* was rather cylindrical.

Dactylosaurus had, as all *Nothosauroidae*, well developed ventral ribs, but it was not advisable to remove these delicate, nearly hair-like bones from the original slab so as to get their cast. The result is that their impression is missing on the cast figured on plate III. fig. 2, and therefore they were also left away in the figure. The ventral ribs consist of a median, V-shaped piece that opens broadly backwards, and slender rod-like pieces. Probably as in all *Nothosauroidae*, two rods followed on each side.

The exact number of the sacrals can not be fixed, but it makes the impression as if four sacral ribs would have carried the ilium. These ribs are stout and blunt on both ends. The first sacral rib is somewhat flattened distally, the second and third are throughout cylindrical or only feebly thickened proximally, the fourth is thickened at the distal end. These characters can, to some extent, also be observed in *Proneusticosaurus*, but in the latter genus they are much more marked. Because of the vertebra following the fourth sacral also having a strong attachment for a rib, perhaps this vertebra also yet belonged to the sacrum. Contrarily to *Dactylosaurus* in *Proneusticosaurus* six sacral vertebrae are present.

The complete number of the caudal vertebrae is unknown; it was more than 18 and probably not more than 26, for the eighteenth vertebra is already very small. The centra of the anterior caudals are about as high as long. They have strong neural arches and rather high, strong and moderately broad neurapophyses. The total height of an anterior caudal is about 6 mm, its length 4 mm. The transverse processes of these vertebrae are feeble. Further back in the tail the length of the centra remains the same, but the height and breadth decrease very rapidly; thus the centra of the posterior caudals have an elongated appearance. In the eighth or ninth caudal vertebra the transverse processes disappear and the neurapophyses are very low. Thus the total height of these vertebrae is but 3 mm by 4 mm length. The eighteenth vertebra has a length of 4.5 mm and a height of 2 mm. On this vertebra the neural arch is reduced to a small roof, limited to the middle part of the vertebra. This structure is the same as in the distal caudals of some *Sauropoda* and probably due to degeneration.

On the slab showing the dorsal aspect, from the sixth caudal vertebra to the eleventh, chevron bones are visible. The chevron between the sixth and seventh vertebra is short but broad in cranio-caudal direction, those under the tenth and eleventh vertebra are ventrally elongated and narrow.

The scapular and pelvic arches are both comparatively well preserved. The scapula is a robust bone. It consists of a dorsal elongated and pointed process, measuring 11.5 mm and a ventral

saddle-shaped, inferior part that is 5 mm broad and 8.5 mm long. The posterior end of the inferior part is thickened and bears, together with the lateral end of the coracoid, the glenoidal fossa.

The coracoid is broadened at the glenoidal fossa, constricted further towards the middle and flattened and somewhat dilated in the median line. It is decidedly longer than broad. It recalls strongly the coracoid in *Nothosaurus* (V 327) and differs from *Anarosaurus*. The clavicle covers with its lateral end the dorsal and anterior end of the scapula and is placed at right angles to the long axis of the body. It is club-shaped at the lateral end and thins out towards the middle. Altogether it recalls the clavicle of *Phygosaurus* (V 131, 31) and differs considerably from the thick clavicles in *Lariosaurus* or the boomerang-shaped clavicles of *Psilotrachelosaurus*. Of the interclavicle only a fragment is preserved, that is laying on the posterior end of the centrum of the second dorsal.

The pelvic elements are strongly displaced. The ilium is better visible on the left side of the body. It is a small and decidedly hood-shaped bone that recalls the ilium of *Phygosaurus* (V 131), it is however somewhat higher. On the slab giving the ventral aspect of *Dactylosaurus*, the left pubis is complete but so displaced, that its median margin looks outward and its posterior margin looks forward it is therefore clapped over in such a manner as to show its dorsal surface. Its general outline is well shown in the figure. It is irregularly pentagonal and slightly concave on the posterior border. In this aspect the obturator foramen is entirely surrounded by bone and not an incision.

In this regard the pubis of *Dactylosaurus* agrees with the pubis of *Anarosaurus* and it is highly probable that, as in this genus, the foramen obturatorium passed obliquely downward and backward so as to leave the pubis on its inferior and posterior margin. That this was the case in *Anarosaurus* becomes evident by the comparison of the figure 1 giving a ventral and figure 2 giving a dorsal view of the pubis on plate IV. In the ventral aspect this pubis seems notched as in most *Nothosauria*, in the dorsal aspect it shows however a foramen. The lack of any constriction of importance in the middle of the bone and the absence of a dilatation on the median margin are two rather conspicuous features of the pubis in *Dactylosaurus*. A processus prepubicus, as present in *Anarosaurus*, is missing in *Dactylosaurus*.

The ischia are both preserved. They are somewhat rod-shaped in the acetabular half, but flat and strongly expanded in the median line. Their shape is to some extent similar to the one in *Anarosaurus*.

All four extremities are more or less well preserved. The humerus is present on both sides and shows the dorsal and the ventral aspect. Altogether the humerus is a rather slender and straight bone with well developed articulating surfaces and well developed ridges for muscular attachments. There is a slight indication of the long axes of the proximal and of the distal ends being placed at right angles to each other. By the lack of a curve the humerus of the new reptile can easily be distinguished from the humera of *Lariosaurus* and *Nothosaurus* and by the strong muscular ridges from those of *Pachypleurosaurus*, *Phygosaurus* and of the genus to be described later on as *Psilotrachelosaurus*. The humerus of the new fossil recalls to a good extent the humera figured by HERMANN von MEYER, without special names in his magnificent „Fauna der Vorwelt (Saurier des Muschelkalkes)“ on plate 31 fig. 1—3, 5, 7, 10 (V 327). As in these humera the proximal end of the new humerus shows a well rounded articulating surface, that is even more marked than in H. v. MEYER's specimens. On the dorsal and inner side of the condyle a small tuberosity is visible and exactly dorsally a rounded ridge

descends, that dies out in the middle of the bone but reappears again towards the distal end. Laterally the insertion for the pectoralis shows, as in H. v. MEYER's specimens, a strong projection with a small pit at its apex. Under the projection of the pectoralis, the shaft of the humerus is constricted and nearly circular in section. The distal end of the humerus is expanded and dorso-ventrally somewhat compressed. It differs from the nothosaurian humerus by not being rounded at its lower end but by giving off under the entepicondylar foramen an oblique process. The lower margin of this process forms an obtuse angle with the surface against which the ulna and the radius abut. Ulna and radius are both nearly straight and slender bones of about cylindrical cross-sections. The radius is markedly longer than the ulna.

The carpus is preserved in situ. It consists of four disk-like bones of very different size and of considerable thickness. They are all situated on the ulnar side of the manus. The centrale is very thick, so that it is disk-like when viewed from above or from below, but rod-like when viewed from the side. Exteriorly to this bone two smaller, disk-shaped bones occur, of which the upper one is the larger and touches the ulna. This is evidently the ulnare, while the smaller, that articulates with the fourth digit, is surely a carpal. The pisiforme is a diminutive, ball-shaped bone, situated exteriorly of the radiale, but likewise under the ulna. The first metacarpal is very short and thick; the three next are of about equal length, the middle one being however a trifle longer. The fifth metacarpal is longer than the first, but shorter than the second and very slender. The phalanges are rather slender, the impressions of the last phalanges are exceedingly feeble and have been omitted in the figure; the digital formula seems to have been 2, 3, 4, 4 (?), 3, as in *Lariosaurus*. This formula of *Dactylosaurus* does not agree with the formula 2, 3, 4, 5, 3 as given by ARTHABER (V 31), while the figure published by GURICH (V 188) seems to indicate the formula 2, 3, 4, 3, 3.

Not much can be said about the femur, in spite of its being preserved on both sides. The femur of the right is to its greater part covered by the pubis, the femur on the left side shows its proximal end on the one slab and its distal end on the other. The proximal end of this bone is deeply concave and indicates that the superior epiphysis is missing. A section of the shaft of the bone is circular at the upper end and in the middle, but dorso-ventrally slightly compressed at the distal end. By showing a circular cross-section at the upper end, the femur of *Dactylosaurus* differs from the corresponding bone in *Nothosaurus*, for in this genus the upper end shows a projecting ridge. On the distal end there exists an indication of two very feebly developed trochleae. They are about as much developed as in *Trionyx*. Tibia and fibula are slender, cylindrical, rod-like bones of nearly equal length. As in *Dactylosaurus* and contrarily to *Lariosaurus* or *Nothosaurus*, there is no large spatium interosseum. The tibia is thicker than the fibula. The proximal row of the tarsus consists of a small, button-shaped fibulare and a second large and very robust element, the tibiale. The latter touches proximally the tibia and to a slight degree also the fibula. Laterally it touches the fibulare and distally the digits one and two. From the fourth digit the tibiale is separated by a small spherical bone that is one of the tarsalia. As a whole, the structure of the tarsus recalls *Nothosaurus Raabi*, but this resemblance is evidently only due to the fact that in both specimens the ossification is incomplete.

The first metatarsal is much shorter than the others and somewhat thickened. The following three are of equal length and slender, the fifth is likewise slender, but somewhat shorter than the middle ones. The digital formula was most probably 2, 3, 4, 5, 4; the number of the phalanges in the second

and third toe can, however, not be made out clearly and in the fourth at least one phalange is missing. The first toe evidently bore a well developed claw, on the other toes strong claws seem to have been absent.

The generic position of the animal just described can be determined by the shape of its skull and by the proportions of the limb bones. That it is a Nothosauroidan beyond all doubt.

As already pointed out during the description of the skull, the small temporal fossae, the relatively narrow parietal and a deeply concave outline of the back of the skull point all to *Dactylosaurus*. Because of the proportion of the humerus to the radius also being the same in both genera, in spite of the new Berlin fossil being nearly twice as large as the type of *Dactylosaurus*, there can be no doubt that it belongs to the same genus. On account of the greater elongation of the cervical vertebrae in the new specimen it is specifically distinct from GÜRICH'S (V 188) *Dactylosaurus gracilis*, therefore I propose to call it *Dactylosaurus Schroederi*, to commemorate SCHROEDER'S well known work on the *Nothosauria* of the Trias. (V 432) The largest of the *Dactylosaurus*-like humera that have been figured by H. v. MEYER (V 327) evidently also belongs to a genus allied to *Dactylosaurus*, it is however easily distinguished from *Dactylosaurus Schroederi* by the stronger development of the aeras and rugosities for the musculus latissimus dorsi and the musculus supracoracoideus. Regarding the development of the latissimus dorsi H. v. MEYER'S large „*Dactylosaurus*“ foreshadows the genus *Nothosaurus*. It seems as if the largest dactylosaurian humerus figured by H. v. MEYER would belong to *Proneusticosaurus*. Both in *Proneusticosaurus* and *Dactylosaurus* the centra of the dorsal vertebrae are barrel-shaped, the proportions of the femur to the tibia are similar and finally the presence of well developed muscular ridges on the femur of *Proneusticosaurus* indicates that muscular ridges were probably also present on the humerus of this genus. The importance of this identification will be dealt with later on.

It is very instructive to compare the genus *Dactylosaurus* with *Anarosaurus*. As visible from the figure 2 on plate IV the skull of *Anarosaurus* has been quite well figured by JAEKEL. It can easily be remarked that the structure of the entire skull is essentially that of *Dactylosaurus*, for the outlines of the skull are somewhat alike and the temporal openings, the structure of the palate and the course of the frontoparietal suture are very similar. ARTHABER'S criticisms of JAEKEL'S figure are entirely unfounded (V 235). In spite of its being a good deal shorter, somewhat straighter and more slender, the humerus of *Anarosaurus* likewise recalls the humerus of *Dactylosaurus* and it is only when one turns to the vertebral column and to the scapular and pelvic arches that one finds greater differences. The number of presacral vertebrae differs very strongly, being 42 in *Anarosaurus* and only 36 in *Dactylosaurus*.

HOW ARTHABER (V 31) manages to state, that in *Anarosaurus* only 15 cervical vertebrae are preserved, is a perfect puzzle. It is true that on the *Anarosaurus*-slab showing the upper view of the skull, only 15 large cervical vertebrae are visible on the top of the slab, but the arches of two and the centrum of a third vertebra are visible on the side. These vertebrae have been added to the figure 2 on plate IV. in their right position, but they have been separated from the rest of the figure by a black line. It does not seem likely that more than one vertebra is missing between the pieces visible on the top of the slab and those on the side, thus *Anarosaurus* surely had 18, and must probably not more than 19 cervical vertebrae. ARTHABER'S (V 31) ideas about the number of dorsal vertebrae, although coming nearer to the truth than the ideas of DAMES (V 128), are just as erroneous. On the slab already mentioned, 16 left ribs are preserved in a continuous line. The first belongs to the last of those vertebrae

that are preserved on the side of the slab. After these ribs follows a vertebra without a rib, after that follow before the sacrum two more vertebrae bearing ribs and then two more without ribs. This gives a maximum of 21 dorsal vertebrae. Thus *Anarosaurus* had altogether surely 39, but probably 40 presacrals.

The shape of the vertebrae of the two genera in question is also very different. They are barrel-shaped in *Dactylosaurus*, but slightly constricted in the middle and therefore somewhat hourglass-shaped in *Anarosaurus*. The barrel-shape does not seem to be in connection with the pachyostosis, for in *Dactylosaurus* the ribs are normal. Of course it may be surmised that the pachyostosis first set in on the vertebral column and only after that spread onto the ribs.

The coracoid of *Anarosaurus* is broader in the median line than in *Dactylosaurus*, the part of the ischium nearer to the acetabulum is more rod-shaped and the pubis is much more constricted in the middle.

All these characters prove the generic difference of the two types. *Proneusticosaurus* differs from *Dactylosaurus* by having a greater number of sacral vertebrae and still broader ischia and pubes. By the lack of a constriction in its middle, the pubis of this genus recalls more *Dactylosaurus* than *Anarosaurus*, but nevertheless altogether it makes to a certain extent the impression, as if a phyletic line were leading from *Dactylosaurus* over *Anarosaurus* to *Proneusticosaurus*. It is not impossible that the *Proneusticosaurus* of the Lower Muschelkalk will turn out to be identical with *Simosaurus*, known from the Lettenkohle to the Upper Muschelkalk. Basing a calculation on the data given by VOLZ and assuming *Proneusticosaurus* to have had 21 dorsal and something like 20 cervical vertebrae, assuming furtheron that the proportion of the neck to the body was the same or about the same as in *Anarosaurus*, this gives for the presacral part of the vertebral column of *Proneusticosaurus* a length of 60 cm, and for the skull a length of about 12 cm. The large temporal openings of *Simosaurus* and the broadness of the ventral elements of the pelvis of *Proneusticosaurus* both indicate that these genera were rather specialised, consequently it may be presumed that both had a relatively large skull. This conclusion agrees very well with the size of the skull of *Simosaurus Guillielmi* of the Lettenkohle that measures 14 cm in length. As in this skull of *Simosaurus* (V 214) the temporal openings are relatively somewhat smaller than in the later species of the Muschelkalk, there exists also an indication that in the genus *Simosaurus*, in the course of time, the size of the temporal openings augmented.

Probably the *Proneusticosaurus*-like Muschelkalk limb bones, alluded to in the foregoing lines (MEYER, plate 31, fig. 1—3, 5, 7, 10) will turn out to belong to the Muschelkalk skulls of *Simosaurus*, while other limb bones of the Muschelkalk, as those figured by MEYER on Plate 48, fig. 1 and Plate 49, fig. 1 will probably turn out to belong to *Cyamodus*, for they recall *Placochelys*.

C) *Psilotrachelosaurus* nov. gen.

The third Nothosauroidan specimen to be described was found as far back as 1844 and belongs to the Klagenfurt Museum.

The exact locality, at which the fossil was found, is not known, a geological reconnoitering done by Mr. KAHLER tends however to show, that it was found in the Stadlbach-Graben 2 kilometers west of Töplitzsch, for the fossil is imbedded in such a dark and bituminous limestone, as occurs near Töplitzsch only at this locality. This limestone belongs to the alpine „Muschelkalk“-series.

The specimen (Pl. II fig. 1) comprises nearly the whole neck in a rather bad state of preservation, the whole body, the root of the tail, scapular and pelvic arch and all four extremities. The specimen is laying on its back, thus most of the skeleton is visible from the ventral side. The anterior cervical vertebrae have broken off, so these show the dorsal impressions of their neural arches.

Apart of the partially preserved impression, of an eighth vertebra, impressions of seven cervical vertebrae can be clearly distinguished. About the shape of their neural arches only so much can be said that each bore a longitudinal and laterally compressed, thin and blade-like neural spine, extending over nearly the whole of the length of the neural arch. All the vertebrae are practically of equal size.

To show the impressions of these anterior vertebrae more clearly, they have been touched up in the plate with darker paint. At the base of the neck a fracture traverses the bone in such a manner that of the four last cervicals the neural arches themselves are preserved, showing their pedicles and between them the impression of the dorsal part of the neural arch. These vertebrae all are longer than broad and thus the fossil of Töplitsch differs well from *Pachypleurosaurus*, *Macromerosaurus* (V 123), *Lariosaurus* (V 58) and to a certain extent also from *Phygosaurus* (V 131), for in all these genera the last cervicals are abbreviated. On the right side of the slab, close to the last of the four vertebrae, lays the fragment of a small cervical rib. All cervical vertebrae are of nearly equal size, thus built as in *Neusticosaurus* (V 444). They serve well to distinguish the fossil from *Dactylosaurus*, *Anarosaurus* and *Macromerosaurus* (V 123), which have relatively large posterior cervicals.

By bearing well developed and long ribs, the following nineteen vertebrae differ very markedly from the preceding cervicals. In most of these vertebrae the centrum is badly damaged and especially so on the left side. At these places the ventral smooth surface of the matrix filling the neural cavity is exposed to view. On the right side here and there parts of the centra are preserved, but it is only in the second dorsal that the centrum is complete. In this vertebra the shape of the centrum is longish, narrowing slightly forward. Its base is longitudinally and especially transversely concave and bordered by two blunt ridges that converge slightly forward. This vertebra bears, as the preceding one, on both sides a strong and quite well preserved rib. This rib is only a trifle thinner than the following ones and already markedly pachyostotic at its proximal end. Of the preceding first dorsal rib only the head is visible, but this seems to indicate that this rib was probably not pachyostotic or, if so, only very slightly.

The vertebrae following the second dorsal have at present a rather curious outline, because laterally of the neural canal the vertebrae bulge out at the anterior end, while they are strongly constricted at the posterior. This outline recalls the one that has been given by ARTHABER for the dorsals of *Proneusticosaurus carinthiacus* (V 31). Owing to the bulging out, the breadth of all these vertebrae exceeds the length. The adjoining tabula gives a review of the number of vertebrae of different *Nothosauroidae*.

Genus	cervical vertebrae	dorsal vertebrae	total
<i>Pachypleurosaurus</i>	15	20	35
<i>Dactylosaurus</i>	16	20	36
<i>Psilotrachelosaurus</i>	12+x (18 ?)	19	(37 ?)
<i>Rhäticonia</i> ¹⁾	18	21 (20 ?)	39

¹⁾ BROU, F: Ein Sauropterygier aus den Arlbergschichten. Sitz. Ber. mat. naturw. Abt. Bay. Akad. d. Wiss. München 1927.

Genus	cervical vertebrae	dorsal vertebrae	total
<i>Nothosaurus</i>	19	21	40
<i>Anarosaurus</i>	19	21	40
<i>Macromerosaurus</i>	21	21	42
<i>Lariosaurus</i>	18	23	41
<i>Phygosaurus</i>	22 + x	24	?
<i>Neusticosaurus</i>	20	24	44

The dorsal ribs are pachyostotic at their proximal end as in *Pachypleurosaurus*, *Rhäticonia* and *Neusticosaurus*. Along the curve the total length of a middle dorsal rib is, 8 mm and the thickness at the thickened proximal end nearly 2 mm. At the thinner distal end the thickness is scarcely 1 mm. The curve of the rib is the strongest at the proximal part and diminishes gradually towards the distal end. As shown by the study of the Dolichosaurians, the presence or absence of pachyostosis is of only very small systematic value. The great transverse diameter of the dorsal vertebrae brings the new fossil rather close to the type of the genus *Pachypleurosaurus*, *Rhäticonia* and separates it well from *Dactylosaurus* and *Phygosaurus* (V 131). The small number of sacrals separates it from *Proneusticosaurus* (V 31, 476), *Lariosaurus* (V 269) and *Macromerosaurus* (V 123).

Very fine, nearly hair-like riblets show that the whole of the belly from the coracoids right to the pubis was covered by well developed and very numerous ventral ribs, the number of these bones and their arrangement can, however, not be fixed.

Considering the distance between the last rib-bearing dorsal and the first caudal vertebra, three sacral vertebrae seem to have been present, but the place occupied by the first sacral is covered by the pubes and that of the last to some extent by the two ischia.

Owing to these circumstances only the rib of the middle sacral vertebra can be made out. It is a strong bone that stands out nearly at right angles on the left side, but is displaced and shifted somewhat forward on the right. The shape of the first sacral vertebra can not be well made out, it seems however to be thick and bulging out as the last dorsal, for at the place, where it is laying under the pubes, the latter show a boss. This boss is evidently due to a post mortem deformation, suffered by the thin pubes when they were pressed onto the thick underlying vertebra. The second and third sacral vertebra have rather elongated centra, as the anterior caudals.

In spite of ARTHABER's elaborate argumentations (V 31) I do not think that any systematic importance may be attributed to the number of sacrals in the primitive *Sauropterygia*, for even in the *Plesiosauroidea*, that evidently are their more specialised descendants, the number of sacrals varies. It is four or five in *Rhomaleosaurus* (V 27), three to four in *Muraenosaurus* and *Cryptoclidus* (V 22), finally only two in *Plesiosaurus* (V 159). So both in the *Plesiosauroidea* and in the *Nothosauroidea* some of the chronologically later forms have more sacral vertebrae than the earlier.

Several caudal vertebrae are present in the Töplitsch fossil, but only the first, the second and the third are in such a state of preservation as to deserve description; all the other caudals are strongly mutilated and muddled up together. As in nearly all dorsals, also in the anterior caudals the centra of the vertebrae are mutilated. the strong transverse processes are however well preserved. The latter show a cit-

cular cross-section and are stout at the base and pointed at the other end. So they form straight and gradually tapering, very slender cones. The root of the tail is, as a whole, not very strong. It recalls more *Neusticosaurus* (V 444) than *Macromerosaurus* (V 123) or *Pachypleurosaurus*.

The scapular arch is rather peculiar, as is the case in all *Sauropterygia*. The clavicle is shown on the right side, the scapulae are preserved on both sides. Of the coracoids only the proximal and distal end of the right coracoid has been preserved. The middle part of the right coracoid broke away, but left a neat impression. To bring this part of the shoulder-girdle out more clearly, later on this impression has carefully been filled up with plaster and afterwards painted black. Thus the general outline of the bone is well shown (Pl. II fig. 1).

The clavicle is a flat and relatively broad, rather boomerang-shaped bone with parallel anterior and posterior borders. On the ventral smooth surface, at equal distances from the anterior and posterior border and near the median end a weak, but quite well visible and rather marked crest arises, that curves towards the middle line of the body. Caudally of this crest a small pit follows. Evidently this pit served to receive the lateral wing of the interclavicle. On the distal end, towards the glenoid cavity, the blade of the coracoid narrows, owing to a convex indentation on each border and so it joins the scapula only by a narrow bridge of bone. It is very different from the short clavicle of *Pachypleurosaurus*. Of the scapula on the right side of the slab and thus on the left side of the animal, the dorsal thin triangular part is preserved which has a length of 4.5 mm and tapers rather abruptly towards the upper end. On the left side of the slab the proximal and ventral part of the scapula is shown, which is, in its present state, flat and irregularly pentagonal. Unfortunately the entire shape of this bone can not be made out for it is partially covered by the coracoid. The coracoid, as reconstructed, is a flat, rather thick and very gently curved bone of 14 mm length that expands slightly towards its median end. It recalls in a rather marked degree the coracoid in *Chelone* and *Dermochelys* (III 1005). The slender shape of the coracoids and the lack of a median dilatation separates our fossil well from *Dactylosaurus*, *Nothosaurus* (V 327), *Phygosaurus* (V 131) and *Lariosaurus* (V 58), and brings it closer to *Pachypleurosaurus*, *Macromerosaurus* (V 123) and *Neusticosaurus* (V 444). The coracoids are directed strongly backwards and have thus somewhat the same direction as in *Macromerosaurus*. This shows that the position of the coracoidea in Nothosauroidan reptiles varies more than supposed by ARTHABER (V 31) in his different reconstructions. This author drew in his reconstructions the coracoidea of all genera nearly at right angles to the long axis of the body. This shifting of the coracoidea backward and the existence of a great median aperture between the anterior elements of the shoulder-girdle and the coracoidal symphysis is to some extent a „chelonian“-like character of the primitive *Sauropterygia*, but the anterior elements of the shoulder girdle are however acromia in the *Chelonidae* (III 510) and clavicles in the *Sauropterygia*, thus the resemblance is only superficial. It is of great mechanical and of biological interest, but not of genetical importance. The similar bone-arrangement shows that in both groups the humera must have moved in very much the same manner.

Up to the present it is yet an unsolved problem from what a type of shoulder-girdle the shoulder-girdle of the *Sauropterygia* was derived from. On account of *Triassochelys* (III 159) showing that the more or less elongated coracoidea of the other tortoises were derived from broad and nearly rectangular coracoidea, one may presume that this was also the case in the forerunners of the primitive *Sauropterygia*,

The pubes are preserved in the new Töplitsch reptile on both sides, but in both pubes the median part is missing. Judging from the parts preserved, the pubis was in its complete state nearly twice as long as broad; thus it was more slender than in *Nothosaurus* (V 432), *Proneusticosaurus* (V 476) or *Lariosaurus* (V 58), but broader than in *Neusticosaurus* (V 444), *Macromerosaurus* (V 123) or even in *Phygosaurus* (V 31). Close to the acetabulum and on the suture of the ischium a very small but marked indentation can be observed, through which the obturator nerve evidently passed outward. This indentation is visible in nearly all primitive *Sauropterygia*, but a true foramen obturatorium is present only in *Nothosaurus* (V 327), *Dactylosaurus* and *Anarosaurus*. The shape of the pubis separates the Töplitsch fossil well from *Lariosaurus* and *Proneusticosaurus* (V 476), in which the pubes are much broader, and just as well from *Neusticosaurus*, in which the pubis is narrower. In *Anarosaurus* the pubis has a prepubic process and is more constricted in the middle, in *Pachypleurosaurus* the acetabular part of the pubis is narrower, *Phygosaurus* and *Rhäticonia* have, however, a rather similar pubis.

The ischia are somewhat triangular bones that have a broad neck near the acetabulum and expand towards the middle. The left ischium is especially well preserved, although somewhat displaced on the right side of the slab. In the Töplitsch fossil the ischium is medially more expanded than in *Neusticosaurus* (V 444) or *Nothosaurus Raabi* (V 432), but not as much as in some other species of *Nothosaurus* (V 175) or in *Proneusticosaurus* (V 476). By being broad near the acetabulum the ischia of the Töplitsch fossil recall *Neusticosaurus* and *Dactylosaurus*, but the lack of a marked median dilatation separates them clearly from the ischia of *Dactylosaurus* and *Proneusticosaurus*; from the ischia of *Anarosaurus* and *Pachypleura* they differ even more. It is with *Neusticosaurus* that they can be compared best.

Owing to the histological discovery of *Nothosaurus Raabi* being but an immature individual of some other species of *Nothosaurus* (unpublished observations of the author), evidently in some primitive *Sauropterygia* no great weight may be laid on the relative expansion of the ischium. This indicates furtheron that probably also the breadth of the pubis of the *Nothosauroides* may likewise have frequently changed with age. So these characters can not be used when classifying *Nothosauroides*.

The right humerus is complete, the left is mutilated at the upper end. The shaft of this bone is straight, slightly constricted in the middle and expanded at both ends. At the distal end the expansion is much more marked than at the proximal. As a whole the humerus recalls *Pachypleurosaurus* and is much more slender than in *Phygosaurus* or *Neusticosaurus*. By its straightness it is easily distinguishable from the humerus of *Anarosaurus* (V 128), *Lariosaurus* (V 31) and *Nothosaurus* (V 442, V 486). The upper end lacks a well developed condyle and is straight, as if the end was cut off with a knife. As in all primitive *Sauropterygia*, a foramen entepicondyloideum is present on the distal end; tuberosities for muscular attachments, as present in the humera of *Dactylosaurus* and *Nothosaurus* are altogether absent.

Ulna and radius are short and slender bones, rather closely applied against each other; the radius is the longer of the two. Distally of the ulna two small carpal bones are visible on both extremities, that show the same relative position to the bones of the forearm as in SEELEY'S (V 444) specimen of *Neusticosaurus* or SCHROEDER'S (V 432) specimen of *Nothosaurus*. To a certain extent their

arrangement also recalls that of the carpal bones in *Dactylosaurus*, as figured by GURICH in 1886 (V 188) and *Pachypleurosaurus*. It is difficult to reconcile these observations with the reconstructions of the different nothosauroidan carpals published by ARTHABER (V 31).

The five metacarpals are nearly all long and slender and with exception of the first, nearly all of equal length. The phalanges are remarkably slender but the digital formula can not be made out. In *Dactylosaurus* the formula is, according to ARTHABER (V 31) 2, 3, 4, 5, 3; in *Lariosaurus* and *Proneusticosaurus* it is 2, 3, 4, 4, 3. Probably the latter was also the formula in *Nothosaurus*, although ARTHABER publishes the formula 2, 3, 4, 5, 4 and gives according drawings. It is true that in spite of this he states at an other place, contradicting his own drawings, that the formula was probably the same as in *Lariosaurus*, but this contradiction is evidently only due to an unfortunate slip that occurred during the revision of the paper before it went to print. However it may be, recent observations show that the digital formula of reptiles has no systematic value whatever, because even in some recent Lacertilia (*Trachysaurus*) the digital formula is 2, 3, 3, 3, 3.

The femora of the new Töplitsch reptile are both very well preserved. They are of about the same length as the humera, but still more slender. They are straight and lack all tuberosities for muscular attachments, thus they differ well from the femora in *Proneusticosaurus* (V 173), *Dactylosaurus* and *Nothosaurus* (V 327, 432). To a certain extent they differ in this regard even from the femora of adult individuals of *Lariosaurus*. Tibia and fibula are both very short but slender, and diverge distally, leaving a large spatium interosseum between them. In the pes only the two large tarsal bones are present. One articulates with the fibula, the other, that is closely beside it, touches the fibula on the one side and the inner corner of the tibia on the other. A special ossified tibiale does not seem to have occurred, but, as there is a free space under the exterior and inferior part of the tibia, probably this place was filled by a cartilagenous tibiale. Quite the same arrangement as in the Töplitsch fossil can be seen in *Dactylosaurus*, *Pachypleurosaurus*, *Proneusticosaurus* and in both specimens of *Neusticosaurus*. Therefore all the reconstructions that ARTHABER gives for the tarsus of different *Nothosauroidae* are decidedly wrong. All metatarsals are of nearly equal length and therefore quite characteristic.

The long and slender digits of the left pes are beautifully preserved and the digital formula 2. 2 + x, 4, 5, 2 + x could be established beyond doubt. Evidently the complete digital formula must have been 2, 3, 4, 5, 4 and thus the same as in all *Nothosauroidae* in which the digital formula of the pes is surely known (V 31). Both in the third and fourth finger the last phalange is much smaller than the rest and very short and blunt.

Owing to the lack of the head, it is especially by the proportions of the limb bones that the systematic position of the new fossil can be determined. The data that serve for such a comparison, are given in the following tabula.

Genus	humerus : antibrachium	femur : tibia	humerus : femur
<i>Dactylosaurus</i>	10 : 5	10 : 5·9	10 : 8·5
<i>Neusticosaurus</i>	10 : 4·1	10 : 6·6	10 : 7·1
<i>Pachypleurosaurus</i>	10 : 5·7	10 : 6·5	10 : 8·2

Genus	humerus : antibrachium	femur : tibia	humerus femur
Töplitsch fossil	10 : 5·4	10 : 5·4	10 : 10
<i>Nothosaurus</i>	10 : 5·2	10 : 4·4	10 : 11
<i>Lariosaurus</i> .	10 : 5·5	10 : 4·4	10 : 12
<i>Rhäticonia</i>	10 : 5·5	10 : 5·2	10 : 13
<i>Anarosaurus</i>	—	—	10 : 13
<i>Macromerosaurus</i>	10 : 4·2	10 : 3·6	10 : 14

As visible at a glance, the general proportions of the limbs, furthermore of the humerus to the antibrachium recall in the new fossil to some extent *Pachypleurosaurus* and *Lariosaurus*, but not so strongly as to warrant a generic identity. From *Lariosaurus* the new fossil can easily be distinguished by the shape of the humerus and the number of the sacrals, from *Pachypleurosaurus* by the longer and more slender neck and by the shape of the shoulder girdle. The shoulder girdle of the Töplitsch fossil and its long and slender neck both recall strongly *Neusticosaurus*, but from this the genus Töplitsch fossil differs again rather much by the number of dorsal vertebrae and by the proportions of the limb bones. The equal length of all five metatarsals separates the Töplitsch fossil from all other *Nothosauroidae*.

Thus altogether the Töplitsch fossil deserves a new generic name and on account of its long and slender neck I propose to call it *Psilotrachelosaurus*. As specific name the adjective „töplitschi“ can be used best.

It seems as if a well preserved, medium-sized, pachyostotic Nothosaurian, of which a plastercast is in the Natural History Museum in Madrid, likewise belongs, in spite of its being much larger, to the genus *Psilotrachelosaurus*. The proportions of the body and of the extremities of this specimen, that may have been found in Spain, are much the same as in the type of *Psilotrachelosaurus*, but owing to the small size of the photograph at my disposal and to the fact that considerable parts of the skeleton of this specimen are yet covered with matrix, this is all that can be said about the piece at present. The completeness of the specimen and its well preserved skull with large temporal openings bring it about, that the piece deserves thorough investigation and description.

D) General remarks on the classification of the *Nothosauroidae*.

The renewed study of *Pachypleurosaurus*, the investigation of MARIANI's specimen of *Lariosaurus* and of *Anarosaurus* and the discovery of a new *Dactylosaurus* and of *Psilotrachelosaurus*, all naturally tempt one to try once more, in spite of BROILI's scepticism, to classify the primitive Sauropterygians. This is all the more necessary, because the classification given but lately by G. von ARTHABER does not seem satisfactory.

The following characters can each be considered as giving a basis for a classification :

1. The occurrence of infraorbital foramina ;
2. The size of the temporal fossae ;
3. The relative size of the skull to the presacral part of the vertebral column ;
4. The length and thickness of the neck ;

5. The proportions of the extremities ;
6. The number of presacral and sacral vertebrae ;
7. The development of the tail ;
8. The histology of the bones, as derived from the study of the ribs.

Ad 1. Infraorbital foramina occur in *Neusticosaurus* and *Lariosaurus* and are absent in *Anarosaurus*, *Nothosaurus*, *Dactylosaurus*, *Simosaurus*, *Pistosaurus* and in the genera allied to *Nothosaurus*, as *Germanosaurus* and *Cymatosaurus*. In the *Theriodontia* these foramina occur in various groups. They are present, for example, in *Scaloposaurus* (II 488), *Icticephalus* (II 155) and *Akidognathus* (II 341), but closed in *Whaitsia* (II 341) and all *Gorgonopsoidea* (II 451), with the possible exception of *Galesuchus*. This leads to the conclusion that also in the *Sauropterygia* the presence or absence of suborbital vacuities may perhaps occur independently in different systematic units.

Ad 2. Temporal openings. In *Anarosaurus*, *Pachypleurosaurus* and *Dactylosaurus* the temporal openings are small, in *Simosaurus*, *Nothosaurus*, *Pistosaurus* and *Lariosaurus* they are large. This increase in size can be considered as a sign of specialization, for it occurs also in the *Theriodontia*. In these it is in correlation with the size of the canine. This becomes evident from the following list, that shows the approximate relation of orbits and temporal openings and in which the presence of elongated jaws or of well developed canines is marked by an asteric.

Proportion of the orbit to the temporal opening.

Nothosauroidae	Therocephaloidea	Gorgonopsoidea
<i>Anarosaurus</i> 10:4 . .		
<i>Dactylosaurus</i> . 10:4.5 .		
	<i>Scaloposaurus</i> 10:7	
<i>Pachypleurosaurus</i> 10:8 .		* <i>Galesuchus</i> . 10:10
	<i>Icticephalus</i> 10:11 .	* <i>Scylacops</i> 10:16 (II 136)
	* <i>Alopecognathus</i> 19:18 .	
<i>Simosaurus</i> } 10:18		
* <i>Pistosaurus</i> .		
<i>Germanosaurus</i> . 10:20 .	* <i>Glanosuchus</i> 10:20 (II 82)	
<i>Cymatosaurus</i> .		
<i>Lariosaurus</i> 10:21	* <i>Ictidosuchus</i> 10:22 (II 66)	
* <i>Nothosaurus</i> } 10:26		* <i>Scymnognathus</i> 10:26 (II 581)
10:30	* <i>Whaitsia</i> 10:45	

The perusal of this list leads to the conclusion that also the increase of the size of the temporal openings may have occurred independently in different phyla of *Sauropterygia*.

Ad 3. The proportions of the skull to the presacral part of the body and the proportions of the neck to the body can be made out from the following lists that allow also a comparison with some longnecked aquatic Lacertilians.

A) Proportion of the skull to the presacral vertebral column.

Nothosauroidae.		Dolichosaurinae.	
<i>Macromerosaurus</i>	12:42	<i>Opetiosaurus</i> (VI 459)	14:42
<i>Nothosaurus Raabi</i>	11:42	<i>Aigialosaurus</i> (VI 367)	12:42
<i>Rhäticonia</i>	10'6:42		
<i>Pachypleurosaurus</i>	10:42		
<i>Anarosaurus</i>	8'3:42		
<i>Lariosaurus</i>	8:42		
<i>Dactylosaurus Schroederi</i>	7'3:42		
<i>Neusticosaurus</i>	7:42	<i>Pontosaurus</i> (VI 457)	7:42
		<i>Dolichosaurus</i> (?) (VI 626)	4:42

B) Proportion of the neck to the body.

<i>Nothosaurus Raabi</i>	10:8
<i>Nothosaurus mirabilis</i> (?)	10:10
<i>Lariosaurus</i>	10:10 to 10:13
<i>Rhäticonia</i>	10:12
<i>Neusticosaurus</i>	10:15
<i>Macromerosaurus</i>	10:15
<i>Psilotrachelosaurus</i>	10:16 (?)
<i>Dactylosaurus Schroederi</i>	10:19
<i>Anarosaurus</i>	10:19
<i>Pachypleurosaurus</i>	10:21

The proportion of the neck to the body in *Pachypleurosaurus* recalls somewhat the proportions in the longnecked *Dolichosaurinae*, for in these it is about 10:25.

Ad 4. Shape of the neck. The neck is thick at its base in *Macromerosaurus* and *Rhäticonia*, moderately thick in *Anarosaurus*, *Lariosaurus*, *Pachypleurosaurus* and *Nothosaurus* and thin in *Psilotrachelosaurus* and *Neusticosaurus*.

Ad 5. Proportions of extremities. The antibrachium is comparatively long in *Dactylosaurus* and *Pachypleurosaurus*, moderately long in *Nothosaurus* and *Lariosaurus*, but short in *Neusticosaurus* and *Macromerosaurus*.

The tibia is relatively long in *Neusticosaurus* and *Pachypleurosaurus*, but short in *Lariosaurus*, *Macromerosaurus* and *Nothosaurus*.

The femur is shorter than the humerus in *Pachypleurosaurus* and *Dactylosaurus*, but longer than this bone in *Rhäticonia*, *Macromerosaurus* and *Lariosaurus*. It is as long as this bone in *Psilotrachelosaurus* and *Nothosaurus*. At this point it has to be remarked that a decided reduction of the anterior extremity can very well be observed among the longbodied semiaquatic and aquatic *Lacertilia*, as has been already emphasised by various authors.

The ratio of the limbs to the length of the body (without neck, sacrum and tail) shows in the different *Nothosauroida* as follows:

Genus	body: fore limb	body: hind limb
<i>Rhäticonia</i>	100:40 (?)	100:57 (?)
<i>Psilotrachelosaurus</i>	100:45	100:54
<i>Neusticosaurus</i>	100:48	100:60
<i>Nothosaurus</i>	100:54	100:71
<i>Lariosaurus</i>	100:57	100:71
<i>Dactylosaurus</i>	100:60	100:60
<i>Macromerosaurus</i>	100:63	100:74
<i>Pachypleurosaurus</i>	100:72	100:72

The proportions of the anterior to the posterior extremity of different *Nothosauroida* and some aquatic *Squamata* are shown in the following list:

Nothosauroida.		Dolichosaurinae.	
		<i>Carsosaurus</i> (V 458)	10:10
<i>Psilotrachelosaurus</i>	10:10·6		
<i>Pachypleurosaurus</i>	10:10·9		
<i>Macromerosaurus</i>	10:11		
<i>Lariosaurus</i>	10:11		
<i>Dactylosaurus</i>	10:11·2		
<i>Nothosaurus</i>	10:12		
<i>Rhäticonia</i>	10(?) : 14 (?)		
<i>Neusticosaurus</i>	10:14		
		<i>Adriosaurus</i> (VI 586)	10:15
		<i>Actaeosaurus</i> (VI 558)	10:16
		<i>Pontosaurus</i> (VI 457)	10:20

This list shows that in the very highly modified *Dolichosaurinae* not only the reduction of the skull, but also the reduction of the anterior limbs has made further progress than in the *Nothosauroida*. Contrarily to this the elongation of the neck made more progress in the *Nothosauroida*, than in the *Dolichosaurinae*.

Ad 6. The number of presacral vertebrae is the smallest in *Pachypleurosaurus* (35) and *Dactylosaurus* (36), it is possibly somewhat greater in *Psilotrachelosaurus* (37) and *Rhäticonia* (39), still greater in the larger headed *Anarosaurus* (40) and *Nothosaurus* finally it rises in *Lariosaurus* to 41 and in *Macromerosaurus* and *Phygosaurus* to 42. In the rhätic *Neusticosaurus*, the number is even 44. This shows that there is a general tendency to augment the number of the presacral vertebrae, it has however to be considered that this may be brought about independently in different systematic units.

The number of sacral vertebrae is six in *Partanosaurus* (V 455) and *Proneusticosaurus*, five in *Lariosaurus*, four in *Dactylosaurus*, according to my observations three or four in *Rhäticonia* and only three in the rest of the *Nothosauroidae*. The number varies, as has already been pointed out, in the same manner as in the *Plesiosauroidea*, therefore the augmentation of the number of the sacrals must also be considered in the *Nothosauroidae* as a sign of specialization. In the aquatic *Squamata* the number of the sacrals is never augmented but the reason is obvious. In this group the locomotion was not done to the greater part by the hind limbs but, contrarily to the *Nothosauroidae*, by the tail, for in this group this organ was stronger from the beginning. The consequence was that in the *Dolichosaurinae* a rigid fixing of the hind limbs to the body was less needed than in the *Nothosauroidae*.

Ad 7. Development of the tail. In spite of but few data being available about the structure of the tail in the *Nothosauroidae*, this part is therefore of some importance, for it is most improbable that a tail undergoing reduction should again be rejuvenated without its possessor changing its mode of locomotion. Thus the size of the tail can give some phylogenetic data. A review of the principal characters of this organ is given in the following list:

Genus	number of caudal vertebrae	caudals carrying neuropophyses	caudals carrying costoids
<i>Pachypleurosaurus</i>	42	14	12
<i>Rhäticonia</i>	30 (?)	(?)	12
<i>Lariosaurus</i>	40	—	9
<i>Dactylosaurus</i>	18	6	9
<i>Neusticosaurus</i>	25	—	8

These data are too poor to draw many conclusions, they show however that in the primitive *Sauropterygia* the tail was undergoing a gradual reduction.

Ad 8. Histology. Regarding the histology, it has first of all to be mentioned that the histology of the rib of *Neusticosaurus* and of adult specimens of *Pachypleurosaurus* is much the same. In both cases the rib consists only of markedly undulated, concentric layers of laminated, primary bone that are traversed by numerous radial canals, while Haversian canals are absent or only very scarce.

In *Anarosaurus* the structure is different. There exists an exterior, moderately thick zone of concentric laminated but not undulated bone and an interior somewhat cartilaginous core. Radial canals and Haversian canals are both entirely wanting. *Proneusticosaurus carinthiacus* shows somewhat the same structure, for also in this genus an exterior laminated and an interior cartilaginous zone can be distinguished. The difference is that the laminated zone is relatively thinner and the cartilaginous structure more pronounced. In *Proneusticosaurus carinthiacus* the cartilaginous core has several Haversian canals filled

up to some extent with Haversian laminae. A figure of a microsection of such a rib is given in figure 5 on Plate IV. In the larger *Proneusticosaurus silesiacus* the laminated zone is still thinner and the cartilage still more pronounced; the arrangement of the Haversian systems is, however, quite the same.

Lariosaurus differs from both types hitherto described. Already the young individuals have very numerous, but small Haversian canals and in these, with growing age, secondary bone-lamellae are developed. This type of structure is the same as in *Nothosaurus Raabi* and some other Nothosauroids, it differs however from the one in *Nothosaurus Strunzii*. The latter recalls by the persistence of cartilage somewhat *Proneusticosaurus*; perhaps therefore *Nothosaurus Strunzii* is no *Nothosaurus* at all, but some other genus. Altogether the histology of the ribs indicates three types of Nothosauroids.

Conclusion:

As it has already been remarked, that *Dactylosaurus*, *Anarosaurus*, *Proneusticosaurus* and probably *Simosaurus* form a well defined group, characterised at its beginning by small temporal openings, first of all *Pachypleurosaurus* has to be compared with this group, for also in this genus the temporal openings are very small. By having comparatively long anterior and posterior extremities of nearly equal length, *Pachypleurosaurus* recalls a good deal *Dactylosaurus*, but the smaller number of presacral and sacral vertebrae as well as its longer tail and its histology indicate that it is a more primitive type. Nevertheless there exist no important characters preventing one to place *Pachypleurosaurus* into the same systematic unit as *Dactylosaurus*.

It is more difficult to fix the systematic position of *Neusticosaurus*. The suborbital vacuities, the great number of presacral vertebrae and the abbreviation of the anterior extremities separate *Neusticosaurus* at once from the pachypleurosaurian group, but the narrowness of the coracoidea, the great length of the femur, the slender neck, and the histology of the rib show a good amount of resemblance. Unluckily the size of the temporal fossae is unknown.

The reptiles that cluster round *Pachypleurosaurus* differ well from those that recall *Lariosaurus*. This second group comprises *Psilotrachelosaurus*, *Phygosaurus* and *Lariosaurus*. In this group the anterior extremities are comparatively short, frequently a large spatium interosseum is present and the humerus is always relatively short. In the one genus in which the skull is known, suborbital vacuities are present. These are accompanied by large temporal fossae. Taking the number of vertebrae as a leading mark, *Psilotrachelosaurus* with only 22 dorsal and sacral vertebrae turns out to be more primitive than *Lariosaurus* with 28 vertebrae.

Nothosaurus with comparatively short anterior extremities having a broad spatium interosseum, with a relatively short humerus and with a neck that is comparatively long recalls to a good amount *Lariosaurus*, to which it resembles also by the structure of its ribs, it has however no suborbital vacuities and less presacral and sacral vertebrae. In a certain sense *Nothosaurus* is therefore in the same relation to *Lariosaurus* as *Neusticosaurus* to *Pachypleurosaurus*.

It is very difficult to fix the systematic position of *Rhäticonia*. The outline of the skull proves that it is a distinct and well defined genus allied to *Macromerosaurus*. The shortness of the humerus brings it close to *Anarosaurus*, *Lariosaurus* and *Macromerosaurus*. The number of cervicals (18) and dorsals (21) is about the same as in *Anarosaurus* and smaller than in *Lariosaurus* and *Macromerosaurus*, the shape of the limb bones is however more that of *Lariosaurus* and *Macromerosaurus* than

that of *Anarosaurus*. Finally the proportion of the limbs to the body are those of *Psilotrachelosaurus*. At present it seems best to place *Rhäticonia* provisionally among the primitive *Sauropterygia* that cluster around *Psilotrachelosaurus*.

Summing up all, it seems best to distinguish among the *Nothosauroida* two groups; one for the type *Pachypleurosaurus*, the other for the type *Lariosaurus*. The *Pachypleurosauridae* comprise the genera *Pachypleurosaurus*, *Dactylosaurus*, *Anarosaurus*, *Simosaurus*, *Proneusticosaurus* and, provisionally, *Neusticosaurus*. In the *Nothosauridae* the genera *Psilotrachelosaurus*, *Phygosaurus*, *Macromerosaurus*, *Lariosaurus*, *Nothosaurus*, *Cymatosaurus* and *Germanosaurus*, have to be placed together. *Pistosaurus* differs to some extent from *Nothosaurus*, but only the skull is known, thus nothing positive can yet be said about this genus and the same holds good for *Partanosaurus*, of which only the vertebral column is known. Anyhow, *Pistosaurus* may belong somehow to the *Nothosauridae*.

If one accepts these ideas the basis of a classification, the different systematic units of *Nothosaurians* must be defined as follows:

Suborder Nothosauroida.

Family *Pachypleurosauridae*; anterior outline of skull oval, antibrachium relatively short.

Subfamily *Pachypleurosaurinae*; temporal openings small, no suborbital vacuities.

1. *Pachypleurosaurus*: neck short, 15 cervical, 20 dorsal and 3 sacral vertebrae; tail long; humerus straight and longer than femur.

2. *Dactylosaurus*: neck elongated, 16 cervical, 20 dorsal, 4 or 5 sacral vertebrae; tail long; humerus with tuberosity and longer than femur; coracoid narrow; ischium and pubis broad.

3. *Anarosaurus*: neck long; 19 cervical, 21 dorsal vertebrae; humerus with tuberosity and shorter than femur.

Subfamily *Neusticosaurinae*: suborbital vacuities present; skull somewhat elongated.

1. *Neusticosaurus*: 20 cervical, 24 dorsal, 3 sacral vertebrae; humerus longer than femur; anterior extremity somewhat shortened.

Subfamily *Simosaurinae*: suborbital vacuities closed, temporal openings relatively large, humerus and femur with strong muscular attachments, six sacral vertebrae, ventral pelvic elements broad.

1. *Simosaurus*: only skull known: definition as above.

2. *Proneusticosaurus*: only body known, definition as above.

Family *Nothosauridae*: temporal openings large, fibia relatively short.

Subfamily *Lariosaurinae*: suborbital vacuities present, skull not elongated.

1. *Psilotrachelosaurus*: 19 dorsal vertebrae: coracoid narrow; pubis and ischium broad; incompletely known.

2. *Phygosaurus*: 24 dorsal vertebrae: coracoid slightly expanded; humerus short and broad but not curved; ischium and pubis moderately expanded.

3. *Lariosaurus*: outline of skull oval; 18 cervical, 23 dorsal, 5 sacral vertebrae; humerus shorter than femur and well curved; coracoid broad; ischium and pubis broad.

4. *Macromerosaurus*: outline of skull oval premaxillary somewhat constricted; coracoids narrow, 21 cervical, 21 dorsal vertebrae; humerus shorter than femur and only slightly curved.

5. *Rhäticonia*: premaxillary forming a rostrum; 18 cervical, 21 praesacral, 4 (?) sacral vertebrae, pelvis moderately broad; humerus nearly straight and shorter than femur.

Subfamily *Nothosaurinae*: suborbital vacuities closed; skull elongated;

1. *Nothosaurus*: facial part of skull strongly elongated; nasals meeting in median line; median part of pterygoidea extending far backward; 19 cervicals, 21 dorsals, 3 sacrals; coracoid broad; humerus strongly curved and about as long as femur; anterior extremity somewhat abbreviated.

2. *Germanosaurus*: snout relatively short; nasals separated in median line by premaxillaries; median part of pterygoidea extending far backward; frontals bordering orbits; skeleton unknown.

3. *Cymatosaurus*: snout relatively short; nasals separated in median line by premaxillaries; median part of pterygoidea extending far backward; frontals excluded from orbits by prefrontals and postfrontals; skeleton unknown.

4. *Pistosaurus*: snout strongly elongated; pterygoidea not extending backward in median line; skeleton unknown. (This genus may have the rank of a subfamily or may be related to *Rhäticonia*.)

It seems premature to discuss the genetic relations of the different *Nothosauroides* for the trend of evolution in the different groups is yet obscure, but it seems as if a very strong and not even adaptive radiation would be splitting up the whole group in a perfectly irregular manner. The same has been observed in the *Dolichosaurinae* and is considered to be due to arrostic changes.¹⁾

IV. HELOCHELYDRA AND HYLAEOCHELYS, TWO LITTLE KNOWN TORTOISES FROM THE WEALDEN AND PURBECK FORMATIONS.

A) *Helochelydra*.

The remains, on which the new genus *Helochelydra* is based, are the specimens of the British Museum (Nat. Hist.) bearing the register number R. 171 that have hitherto been included in the genus *Tretosternum*. These pieces have been described in a joint paper by LYDEKKER and BOULENGER (III 626). They were all found at Brook on the Isle of Wight in a Wealden stratum which has only yielded, according to verbal information given to the author of this paper by the late Mr. R. W. HOOLEY, remains of this one genus of tortoises and an isolated cervical vertebra of a *Pterosaurian*.

The reason for separating the genus of tortoises occurring in the Wealden at Brook from the Purbeck remains called *Tretosternum* will be discussed at the end of this paper.

The type specimen of *Helochelydra* consists of four neuralia, the nuchal bone, the pygal bone, several rib plates, and several marginal bones, the hyo-, hypo- and mesoplastron, the entoplastron, one sacral vertebra and practically the whole of one side of the scapular and pelvic girdles.

Supplementary pieces coming from the same spot as the type specimen are in the HOOLEY collection, and consist of rib plates, marginal plates, and the upper end of one humerus.

The general outline of the carapace of *Helochelydra* is shown in figure 7 A. Figure 8 B shows the outline of the plastron including the xiphiplastra, which have been added according to evidence afforded by the allied genus *Helochelys* (III 688).

¹⁾ NOPCSA, F.: Heredity and evolution. Proc. Zool. Soc. London, 1926.

As seen in fig. 7 A the general outline of the carapace in *Helochelydra* is much the same as in *Chelydra* and *Chelone*, with the exception that the posterior part is more rounded in the new genus. The nuchal is deeply excavated and the first marginal bone on each side curves rapidly backward.

After having joined the two foremost marginals to the nuchal bone it became evident, that the process which had been considered as the costiform process of the nuchal was in reality the upper anterior and interior end of the axillary buttress reaching remarkably far forward (Fig. 7 C). A similar structure is visible in *Kallokibotium* (III 734) and to some extent also in *Tholemys* (III 31). The marginals abutting against the nuchal are already deeply excavated and form the anterior boundary of the sternal chamber.

The pygal bone is much broader than long and broadens rapidly backward. It recalls the pygal in *Helochelys* and differs markedly from the pygal in *Peltochelys* (III 274). The marginals touching the pygal are moderately excavated, their inferior rim is, however, thick and smooth and shows that this part was not in contact with the plastron.

In the penultimate marginal the excavation is much stronger and the inferior borders are serrated; thus these marginals evidently already reached the plastral buttress. All the other marginals were likewise joined to the plastron by suture.

The excavation on all the marginals is deep and V-shaped. The broadened parts of the rib plates were all in close contact with the marginal bones. Fontanelles, as for example in *Chelydra*, were certainly absent. The free distal and narrow ends of the ribs were fixed as in *Chelydra* in grooves on the marginal bones. The last rib plate was remarkably broad and had the rib on its anterior border; the first rib plate was likewise somewhat broader than the rest but not as broad as the last. Since none of the intermediate rib plates show the sulci for the dermal shields, their exact position in the carapace is open to some doubt.

The neural bones are indented behind, the breadth is greater in the anterior than in the posterior ones. All resemble very much the neuralia in *Helochelys*. The centra of the dorsal vertebrae are relatively short. They are laterally compressed in the middle, but strongly expanded at both ends. Their compression recalls rather the *Pleurodira* and some *Amphichelonoidea* than the *Cryptodira*, for in the latter a lateral compression is frequently wanting, while it occurs among the *Pleurodira*. This feature seems to vary among the *Amphichelonoidea*.

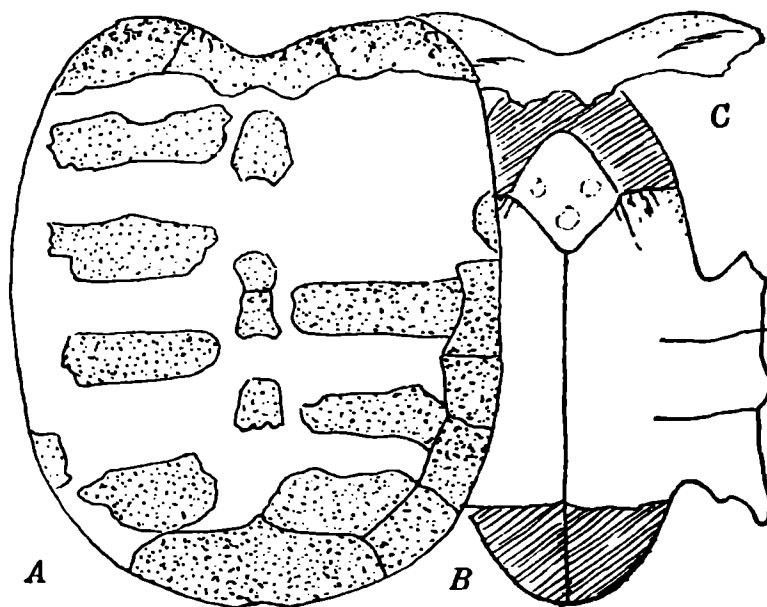


Fig. 7. Carapace and Plastron of *Helochelydra*. A) Carapace from above; B) Plastron; C) Nuchal from inside.

One of the sacral vertebrae bore a strong sacral rib, having a rather thick median end. This again recalls some *Amphichelonoidea* (*Glyptops*, *Baena*, III 473) and the *Chelydridae*.

The plastron is comparatively well preserved.

The large diamond-shaped entoplastron recalls the same bone in *Naomichelys* and to some extent the entoplastron in *Helochelys*. It differs from the Purbeck entoplastron (76325) assigned by LYDEKKER to *Tretosternum* (III 517). The exterior and anterior margin of the hyoplastron is much the same as in *Helochelys*. Some digitate impressions on the anterior and interior part of the hyoplastra show that the epiplastra extended far backwards. This occurs in *Dermatemydidae*, *Chelydridae* and primitive *Trionychidae*.

Since the whole skeleton of *Helochelydra* is disintegrated along the sutures of the bones, and since one line of separation crosses the plastron transversely behind its middle and another such line is visible further in front on the left side, a distinct and broad mesoplastron seems to have been present. Such a mesoplastron occurs in *Helochelys*, *Trachydermochelys* (III 29) and many *Amphichelonoidea*. The bridge of the plastron was very broad.

An isolated rib showing exceptionally the margins of the dermal scutes, indicates that the neural scutes were not very broad. Inframarginal scutes seem to have been present.

The shoulder girdle (fig. 8 b) has a long rod-like scapula (*sc*) broadening just a little towards its base, heavy comparatively short, distally club-shaped acromia (*a*), that are decidedly triangular at their distal ends and thus resemble the acromia in *Chelys* and *Chelodina*. The coracoids (*co*) are remarkably broad and short. Such coracoids

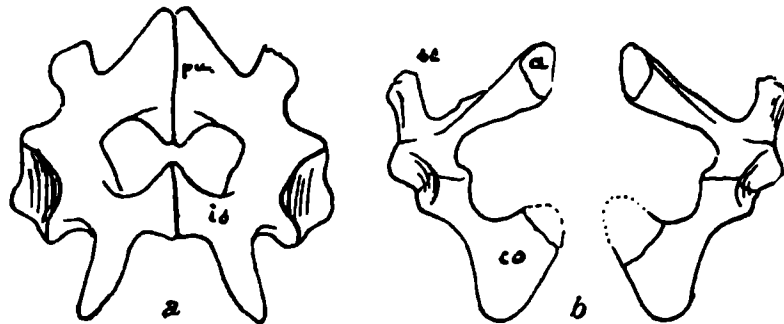


Fig. 8 Pelvis (a) and scapular girdle (b) of *Helochelydra*.

suggest those of the *Amphichelonoidea* and the *Testudinidae*. There exists no neck-like constriction between the glenoidal cavity and the rest of shoulder girdle as is, for example, visible in the *Pleurodira*. In this again *Helochelydra* recalls some — but not all — *Amphichelonoidea*, for example *Kallokibotium*, and the recent *Chelydridae*. In the figure the long scapula is perspectively shortened.

The upper part of the humerus marked 27^h in the HOOLEY collection, which was found at Brook and evidently also belongs to *Helochelydra*, agrees well in size with the scapular arch of the type and shows *Chelydroid* build.

The pelvis (fig. 8 a) is also built on the same plan as in *Chelydra* but it also recalls some *Amphichelonoidea*. The ischia and pubes are not bent downward at their distal ends as in the *Pleurodira* or in *Kallokibotium*, but are situated in a nearly horizontal plane, as in *Glyptops* and the *Chelydridae*. The obturator foramen was large. As in *Chelydra* there seems to have existed, no median osseous bridge between the ischia and the pubes, and even if such a ridge was present it can only have been very narrow. This distinguishes *Helochelydra* from *Glyptops* and *Baena*.

The pubes are elongated, the ischia are narrow and have each a strong and pointed posterior process, as have those of the *Amphichelonoidea* and the *Chelydridae*.

The sculpture in *Helochelydra* is the same on the carapace and on the plastron, and very characteristic. It consists of very small, comparatively high, cylindrical bony bodies, the size of which may vary according to the different regions. Their upper end is always decidedly hemispherical and their transverse diameter is frequently less than their height. When becoming detached from the bones beneath, these cylindrical bodies always leave a well-defined concave scar, and the formation of this scar proves that the texture of these bodies is denser than that of the underlying bone.

The cylindrical bony bodies are always very distinctly separated from each other and a fusion of two such bodies has never been observed.

The sulci marking the borders of the different dermal plates cannot be made out clearly in the specimen No. R. 171, but on the rib already mentioned one can see that such a sulcus consists of a narrow zone devoid of cylindrical bodies.

As evident from this description, the sculpture in *Helochelydra* is exactly the same as in *Helochelys* and *Naomichelys* (III 473) and recalls to a certain extent *Tretosternum* and *Trachydermochelys*. From the two latter *Helochelydra* differs, for in these types the bony tubercles are much flatter, their transverse diameter is much greater than their height, and because in the latter the separate tubercles have a tendency to agglutinate. This is well shown on the type specimen of *Tretosternum Blackwelli* figured by MANTELL in 1827 (III 633) and can also be seen on some fragments of *Trachydermochelys*. Since the tubercles produce also in *Trachydermochelys* a scar when broken of, they recall *Helochelydra*. Among recent tortoises a sculpture recalling the one in *Helochelydra* is only seen in the genus *Emyda*.

On account of the presence of a broad mesoplastron, the probable presence of axillary and inguinal buttresses, a very broad coracoid, and a humerus and pelvis of chelydroid type, *Helochelydra* and the allied *Helochelys*, and probably *Naomichelys*, belong to the *Amphichelonoidea*. Since they more resemble *Glyptops* and *Baena* than *Plesiochelys*, *Kallokibotium*, or *Thalassemys*, they must be classed among the *Pleurosternidae*. Together with *Trachydermochelys* and the poorly known *Tretosternum* they seem to form a small natural unit that may be considered a special subfamily equal to *Pleurosterninae* and *Baeninae*. This subfamily must be called *Helochelydrinae*. The following are the distinctive characters of the hitherto known members of this group:

1. *Helochelys*, MEYER. Entoplastron somewhat broader than long. Anterior part of carapace with wide and rather shallow excavation. Sculpture with high cylindrical tubercles. Cenomanian, Germany.
2. *Helochelydra*, NOPCSA. Entoplastron as broad as long. Carapace with very deep nuchal excavation. Sculpture with high cylindrical tubercles. Wealden, Isle of Wight.
3. *Naomichelys*, HAY. Entoplastron longer than broad. Sculpture with small short little tubercles. Morrison formation, N. America.
4. *Trachydermochelys*, SEELEY. Entoplastron broader than long. Carapace straight in front. Sculpture consisting of round large flat tubercles that rarely agglutinate. Cambridge Greensand, England.
5. *Tretosternum*, OWEN. Entoplastron posteriorly lyriiform and longer than broad. Outline of carapace unknown. Sculpture consisting of small round low tubercles that sometimes agglutinate. Wealden, England.

The Belgian *Peltochelys* (III 274), which has been identified with *Tretosternum*, differs, as

L. DOLLO kindly informed me, from *Helochelydra* by the different shape of the first marginal bone, by the whole structure of the pygal region, by the lack of a mesoplastron and by the completely different sculpture. After an examination of the type specimen I can only confirm Prof. DOLLO's view. From *Tretosternum Peltochelys* differs in the shape of the entoplastron and by its sculpture. *Peltochelys* is evidently not an Amphichelonoidean, but may be a primitive Dermatemydean. GAUDRY's *Tretosternum ambiguum* (III 361) from the Cretaceous of the Mont Aimée likewise does not belong to the genus *Tretosternum*. Owing to the courtesy of Professor BOULE, the type specimen could be studied. Only the plastron is known. This is covered with numerous broad and shallow anastomosing furrows that to some extent run transversely over the plastron. The bridge is covered with broad, flat tubercles, that are formed by the close joining up of the anastomosing furrows. This sculpture recalls to a certain extent that of *Puppigerus parvitecta* from the American Eocene (III 473). *Tretosternum ambiguum* has no mesoplastron, no inframarginal scutes and shows on the entoplastron traces of four dermal sulci that touch each other. *Tretosternum ambiguum* evidently does not belong to the Amphichelonoidea, but probably to the Emydinae. A piece that does belong to the genus *Helochelydra* is a fragment described and figured by SAUVAGE (III 861) under the name *Tropidemys*.

B) *Hylaeochelys*.

During a visit to the Geological Department of the University Museum at Oxford, my attention was attracted by a large and well preserved Chelonian from the Purbeck of Swanage. The total length

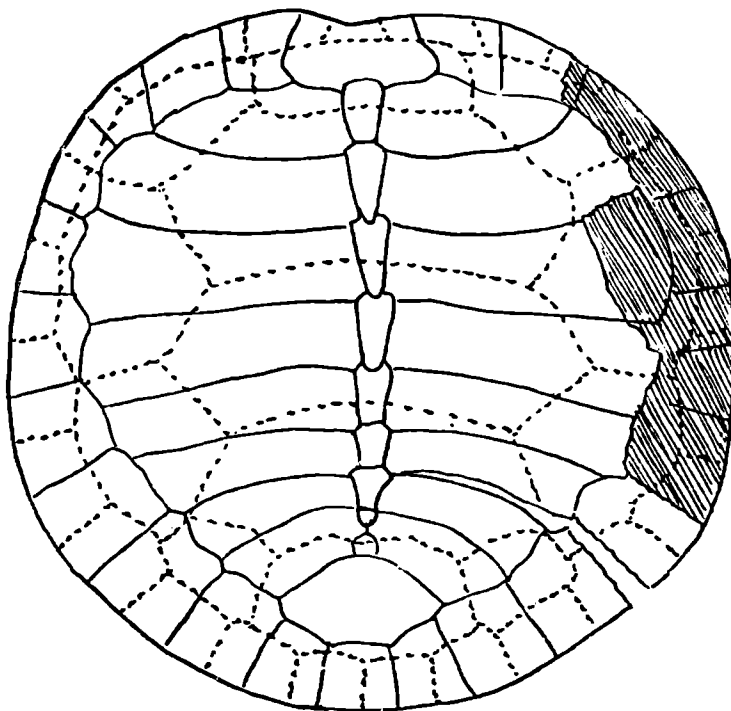


Fig. 9. Carapace of *Hylaeochelys Solassi* n. sp.

of the specimen in the middle line of the body is 46 cm, the breadth 48 cm. By being just a trifle broader than long, the new specimen is at once well distinguishable from *Pleurosternum*. Except when dealing with full grown specimens, however not too much weight should be attributed to the proportion of the length and breadth, because it varies considerably with age. As in some species of *Pleurosternum* and in *Plesiochelys*, the outline of the shell is equally rounded with a small emargination for the neck.

The specimen (fig. 9) shows nine neurals, the nuchal, the pygal and twenty-nine marginal bones. The neurals one to seven are all longer than broad. The second, third and fourth are the narrowest and longest; the first

and the fifth are equally broad but both shorter than the intervening neurals. Number seven is nearly as broad as long and has the shape of a lyre. The eighth neural is a small, somewhat quadrangular bone with convex posterior outline. It is separated from the ninth neural bone by the eighth pair of ribs meeting for a short distance in the middle line of the body. The last neural is as small as the eighth and has a pentagonal outline, with the apex of the pentagon directed forward. The length of neurals one and five is about 4 cm, the length of the second, third and fourth about 5 cm. The seventh is only 3 cm long and the eighth and ninth finally attain each only a length of approximately 1.5 cm. The breadth of the neurals varies from 2.5 to about 1.5 cm. The reduction of the last neurals at once separates this fossil from *Pleurosternum*, *Glyptops* (III 277), and many other genera of this group and places it close to the genus *Plesiochelys* (III 277), where such a reduction seems to occur in *Plesiochelys vectensis* (III 502). It is however only in the *Thalassemydidae* that such a reduction is frequent. The eight costal bones are nearly equally developed, for the breadth of the first pair is not much greater than that of the other anterior ones. The breadth of the first pair of costal plates near the middle line of the body is 6 cm, that of the costal bones two to five about 4 cm, and that of the costals six to eight about 3 cm. The ribs two to seven are broader on their distal ends. From the fifth rib a gradual curving backwards can be noted, that is more marked in the posterior ribs. A similar relative breadth of the costals as in the new specimen is to be found in different *Pleurosterninae*, *Baeninae* and in the *Plesiochelyidae*. In the new fossil and in most *Plesiochelyidae* the narrowness of the last three costals is however more marked than in the other groups.

In *Hylaeochelys* (III 768) to which the new specimen resembles in the development of narrow neural bones and of broad vertebral scutes, the first rib is not broader than the rest and the narrowing of the posterior ones is somewhat less marked. Curiously enough the pygal is a simple bone and not double, as in most *Amphichelonoidea*. Exceptions are however to be met with in *Plesiochelys Hannoverana* (III 801), *Baena antiqua* and *Compsemys parva*. Consequently the simple nature of the pygal may be considered as an individual variation, or variation produced by age. The nuchal bone is much broader than long, it recalls the nuchal of *Hylaeochelys* and differs somewhat from the nuchal in *Plesiochelys*. The latter is generally less broad. Most of the other *Amphichelonoidea* show a less abbreviated nuchal.

The most characteristic feature in the new *Plesiochelys* is to be found in the development of the scutes. The vertebral scutes are broader than in any known tortoise. Short vertebral scutes, in which the breadth exceeds the length, can be found in many primitive mesozoic tortoises, for such scutes occur in *Triassochelys*, *Proterochersis*, *Kallokibotium*, some species of *Plesiochelys*, *Hylaeochelys* and some *Thalassemydidae* (III 734), in no species however, is the disproportion between breadth and length marked to such an extent as in the Oxford fossil. In the young *Plesiochelys minima* (III 738) and *Hylaeochelys* (III 768) which are both characterized by very broad vertebral scutes, the ratio of the length to the breadth in the third vertebral scute is only somewhat more than 1:2, while it is about 1:3 in the new fossil. The broadening of the fourth vertebral scute is so great in the new fossil, that its lateral point touches the ninth marginal bone. Thus on this bone five scutes meet, which fact is unique among tortoises. Considering the great variety of the shape of the vertebral scutes in the different species of

Plesiochelys, the very great width in the Oxford specimen can scarcely have more than specific importance. It is enough to refer, in this instance, to the narrow vertebral scutes in *Plesiochelys vectensis* (III 502) in *Plesiochelys Brodiei* (III 621), in *Etalloni* (XIII 112), in *Plesiochelys Jaccardi*, to the broader scutes in *Plesiochelys Hannoverana* (III 801), *Plesiochelys Choffati* (III 864), *Plesiochelys Soloturensis* (III 850) and *Plesiochelys Langhi* (III 850) and to the very broad scutes in *Plesiochelys minima* (III 738). It is true that the latter does not seem to be a full grown individual and that the broadness may therefore be due to age, for in many young tortoises the vertebral scutes are broader than in the adult specimens. The first vertebral scute of our fossil is remarkably small, short and broad and recalls *Hylaeochelys*.

The sulcus between the costal scutes and the marginal scutes is situated exclusively on the marginal bones, as is the case in all *Plesiochelyidae*, but not in *Pleurosterninae*. It is further away from the costo-marginal sutures than in the *Baeninae*.

The costal scutes are remarkable for their small size that is brought about by the widening of the vertebral scutes. Especially the fourth costal scute is very small, as in *Tholemys* (III 31), *Hylaeochelys* (III 768), *Kallokibotium* (III. 734) and as in some species of *Plesiochelys* [*Pl. Jaccardi*, *Pl. Soloturensis* (III. 850). *Pl. Hannoverana* (III. 801).]

With regard to the systematic position of the Oxford fossil, there can be no question about its belonging to the genus *Hylaeochelys*. The differences that can be remarked on the skeleton consist only in the broader development of the first rib in the new fossil and in the different structure at the end of the last neural bones. In the scutes only those somewhat variable differences are more accentuated which separate *Hylaeochelys* from *Plesiochelys*.

The relative breadth of the neuralia varies a good deal in recent tortoises according to age, and the same is the case in the different species of *Plesiochelys*. They are elongated in some species, as *Pl. Etalloni* and *Soloturensis* (III 112), but much shorter in others as *Pl. vectensis*, or *Pl. pumilis* (XIII. 112). The shape of the nuchal is also subjected to great changes, being broad and short in *Plesiochelys Choffati*, but long and narrow in *Pl. Brodiei*, and some similar changes are observable in the vertebral scutes of the *Plesiochelyidae*. In consequence of all this, none of these characters in *Hylaeochelys* can alone be used for a generic separation, but altogether they are enough to separate *Hylaeochelys* on the one side and *Plesiochelys Brodiei* on the other from the rest of the *Plesiochelyidae*.

For *Plesiochelys Brodiei* the new generic name *Brodiechelys* may be created; in *Hylaeochelys* one may perhaps distinguish the older species *H. latiscutatum* and the new species *H. Sollasi*. The Oxford specimen is the type for the latter species. A genus evidently closely allied to *Plesiochelys* is the genus *Tholemys*.

How far the differences remarkable in those species of *Plesiochelys*, that have not been established by RUTIMEYER but by other authors, are due to sex and age, will perhaps be elucidated when once the new material collected in Solothurn and the splendid material collected at Bückeberg by Professor BALLERSTEDT will have been exactly studied.

V ON THE SKULL OF THE UPPER CRETACEOUS
DINOSAUR *EUOPLOCEPHALUS*.

At present not less than seven types of skulls of armoured Dinosaurs are known. These are *Scelidosaurus* (IX 917), *Stegosaurus* (IX 318), *Tröodon* (IX 340), *Panoplosaurus* (IX 974), *Ankylosaurus* (IX 91), *Protoceratops* (IX 343) and the different Ceratopsidians. The skulls of *Scelidosaurus*, *Stegosaurus*, *Tröodon*, *Panoplosaurus* and different Ceratopsidians have been described in detail, of the skulls of *Protoceratops* and *Ankylosaurus* hitherto only preliminary accounts were given. Owing to this it seems advisable to give the description of an isolated skull (Pl. V fig. 1—4) belonging to the *Ankylosaurus* group, that is preserved in the Natural History Museum in London, under the register-number R. 4947. It was found by the late W. CUTLER in the Belly River Beds of Red Deer River, Alberta, Canada.

This skull is in a very good state of preservation. It recalls in a general way *Ankylosaurus* and still more *Euoplocephalus* (called by GILMORE *Europocephalus*, XI 337). The posterior portion of the skull is flat above. On each side this flat surface is bordered by another flat surface, that descends obliquely outward and downward. Its posterior margin is straight. In consequence of this arrangement this part of the skull resembles to such an extent to *Pareiasaurus* (II 586) that there is no doubt that if the posterior part of this skull would have been found in rocks of unknown age, it would have been put down as *Pareiasaurus*. In the anterior part the skull slopes forwards and sideways. The anterior contour of the skull is broad and rounded. The nostrils are placed forward and but very slightly sideways. They are rather large. The orbits are placed sideways and are about round. They are comparatively small and behind the middle of the skull. The whole upper part and the side of the skull is covered by dermal plates, covering all the sutures. The arrangement of the plates is exactly the same as in the skull described by GILMORE as *Europocephalus*. The jaw is protected by three large plates and the projecting large nasal scute, characteristic for *Europocephalus* is also present. The posterior and inferior part of the side of the skull is protected by a large dermal plate, having a thickened and rounded inferior border. This plate adheres firmly to the quadratojugal. Spine-like squamosal projections, as characteristic for *Ankylosaurus*, are missing.

Viewed from behind, the skull is even more pareiasaurian than from above. To prove this resemblance, it has been found appropriate to place drawings (fig. 10) of the posterior aspect of the skull of a Pareiasaurian (*Embrithosaurus*)

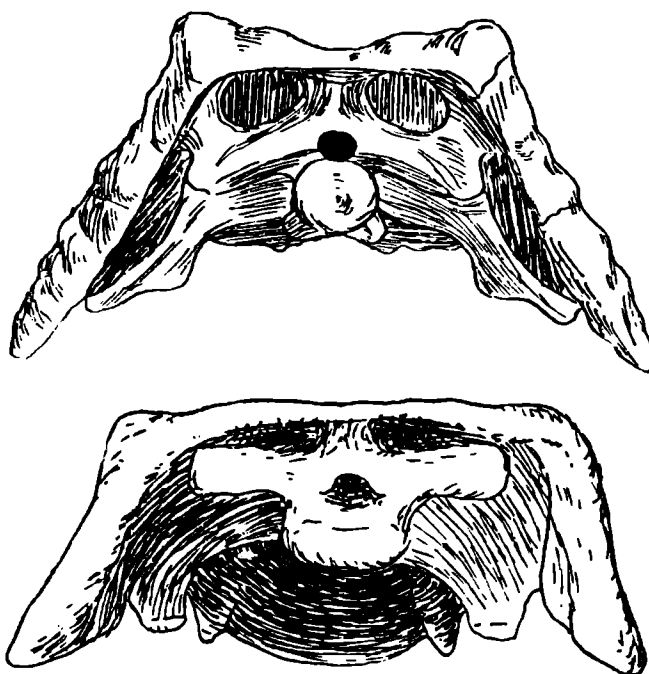


Fig. 10. Skull of *Embrithosaurus* (above) and *Euoplocephalus* (below) from behind.

thosaurus) and that of the posterior aspect of the skull of *Euoplocephalus* side by side. The single differences that become remarkable at the first glance are, that *Euoplocephalus* has above the foramen magnum two oval tuberosities that are absent in *Embrithosaurus* and that the pterygoidal part of the quadrate is developed otherwise. The differences in the altitude of the skulls of the two genera are due to a post mortem deformation in *Euoplocephalus*.

All the bones of the base of the skull are traversed by numerous cracks, while the sutures are all very well closed. The result of this is that an identification of the elements of this region encounters greatest difficulties. The large condyle is clearly visible. It is somewhat flattened and directed obliquely backward and downward. This indicates that in the normal position the skull was carried so as to make an obtuse angle with the neck. The foramen magnum opens backward and the condyle does not project beyond the foramen magnum. The basioccipital is not much longer than broad and its transverse section is about rectangular. Its sides are bordered below by two short, stout and rounded ridges with a longitudinal shallow groove between them. These ridges run from the condyle to the paired tubera basioccipitalia. The basipterygoidal processes of the basisphenoid were not far in front of the tubera basioccipitalia and can only have been very short. On account of fragments of the pterygoids laying upon them and reaching backwards to the tubera basioccipitalia, their shape can no more be made out.

Laterally of the condyle and somewhat above of it the exoccipitals are given off in a nearly horizontal direction. These join again by means of the paroccipital process to the upper end of the quadrate. The quadrate is a long, straight and not very thick bone, the upper head of which was evidently lodged rather freely in the squamosum. Its lower part is slightly inclined forward and bears on the lower end the very flat and small articulating surface for the mandible. This shape of the articulating surface of the quadrate is, as shall be shown furtheron, in good correlation with the feeble function of the jaws. On the interior part of the quadrate a huge wing is attached, that joins the posterior part of the pterygoid. The squamosal is visible on the right side of the skull from below. It is a deeply concave bone, that caps the upper end of the quadrate and has, inside of this cup, a curious triangular process that is turned downward. This process is placed at right angles to the long axis of the skull and placed quite near to the opisthonic. Its meaning is not easy to make out, it seems however likely that after the closing of the upper temporal fossae it served as a surface of attachment to some of the muscles of the lower jaw.

The pterygoids are not quite easy to describe. Behind and on the sides they consist of an elongated, rather narrow wing that extends backward and outward and joins the quadrate. Further in front and on the side they consist of a vertical plate of bone that is placed transversely and gradually curves in such a way inwards towards the middle line, that its concave side is directed forward. Near the middle line of the skull two likewise vertical laminae of bone occur, that are directed straight forward and seem to be placed just in front of the basipterygoid processes. These plates extend far forwards but their median part is missing. They likewise yet belong to the pterygoid. On each side of the skull the exterior and anterior plate of the pterygoid shows a very large perforation.

Laterally the pterygoid reaches about to the place where the jugal and the maxillary meet, but a separate ectopterygoid can not be distinguished. It was probably present as a separate bone but now it is included in that part of the pterygoid that is situated behind and outside of the large foramen perforating the anterior and exterior part of the pterygoid. The vertical position of the anterior branch

of the pterygoid gives to the roof of the mouth a very curious appearance. The mouth has the shape of an enormous vault that is separated in the middle by two longitudinal septa. It is very difficult to say whether two triangular plates, that are placed inside and in front of the pterygoids and near the middle line of the skull actually belong to the pterygoids. Anteriorly they give off two narrow elongated processes, that reach nearly to the inner choanae. Behind they seem to continue each in a vertical bony lamina that is missing to the greater part, but seems to have joined those vertical median laminae that were given off by the pterygoids at the basypterygoidal processes. If this reconstruction of the palate is right then one must assume that the large openings placed in front of the concave wings of the palate and on the side of the median vertical laminae were everywhere bordered by the pterygoids. In such a case they correspond to a certain extent to those apertures, that are visible in the anterior parts of the pterygoids in *Tyrannosaurus* (IX 870). According to this explanation the difference in the structure of the pterygoids of both genera would chiefly consist in the enormous inferior hollowing out of each pterygoid in *Euoplocephalus*. Having thus identified the median part of the palate, it becomes relatively easy to determine the nature of those two crook-shaped bones that are placed laterally of the anterior prolongations of the pterygoids and interiorly of the maxillaries. These two comparatively small, flat bones, that are at present just a little out of position, can only be the palatines. They abut against the maxillary near the anterior end of the alveolar fossa. The vomera are too much broken up and too much restored with plaster to deserve description and the sutures between the vomera, the maxillary and the premaxillary can neither be detected. The large inner choanae are situated in front of the region, where the vomers are suspected.

The anterior outline of the skull is broad and rounded, recalling thus *Embrithosaurus* and to some extent *Whaitsia* (II 341). It is edentulous and armed with a horny beak. The inside of the lower surface of the premaxillary is rather flat. The maxillary bears on its interior slope a shallow alveolar fossa, that has a slightly sigmoidal curve. It is very remarkable that the row of teeth is not placed on the lower border of the maxillary bone but on the interior slope (IX 337). The margin of the maxillary bone shows near the anterior end of the alveolar fossa and outside of it an elongated bony projection, as occurs in the tuskless *Dicynodontidae*. Both the interior position of the evidently strongly reduced teeth as this projection of the jaw strongly recall the jaw of the *Endothiodontidae*. The premaxillary was surely edentulous.

Together with the transferring of maxillary teeth to the inner margin of the jaw, the development of the projection at the suture between the premaxillary and the maxillary is a remarkable case of convergence between *Euoplocephalus* and some *Anomodonts*, as *Esotherodon* (II 101), *Endothiodon* (II 488), *Chelyrhynchus* (II 340) and all the tuskless *Dicynodonts*. This convergence is all the more surprising as the feeble articulation of the mandible and the broadly rounded outline of the skull in *Euoplocephalus* are in marked contrast to the more pointed beak and the strong articulation of the lower jaw of the *Anomontoidea*. Together with the fact, that remains of *Anomontoidea* of different size are comparatively frequent, while remains of *Euoplocephalus* are rare, this contrast is of biological importance; it shows that, although the locomotion of both types was practically the same, the diet and hence the mode of living must have been very different in the two types.

As evident by the description, *Euoplocephalus* is closely allied to *Ankylosaurus* and somewhat less to *Panoplosaurus*, while it differs well from *Scelidosaurus*, *Stegosaurus* and all the *Ceratopsidae*.

From *Panoplosaurus* *Euoplocephalus* differs by the much greater number of the frontal and parietal

dermal scutes, by the more rounded outline of the mouth and the flatness of the skull. In the heavily armoured *Thyreophoroidea Tröodon* and *Struthiosaurus* the skull is built on altogether different lines.

Struthiosaurus that is a quadrupedal Dinosaur closely allied to *Tröodon*, is going to be described in part V of „Dinosaurierreste aus Siebenbürgen“ while the body-skeleton of an armoured Dinosaur, that is somewhat allied to *Euoplocephalus* forms the subject of the following note. In this note also a more detailed discussion of the relationship of all those *Thyreophoroidea* will be given, that cluster round *Euoplocephalus*.

VI. *SCOLOSaurus CUTLERI*, A NEW DINOSAUR.

The specimen that forms the subject of this note was discovered, as the skull of *Euoplocephalus* by the late W. E. CUTLER on the banks of the Red Deer River, Alberta, Canada. Professor PARKS of Toronto informed F. A. BATHER, the Keeper of the Natural History Museum in London, that according to information gained from Mr. LEVI STERNBERG „it seems that the specimen was found in the Belly River series, Upper Cretaceous, about one half mile below «Happy Jack» ferry on the Red Deer River. This would make the location in Dead Lodge Canyon, where the erosion valley is narrow and the banks steep. The canyon is nearly 400 feet deep and the skeleton was found about halfway up“ The specimen belongs to the British Museum (Natural History Museum). Its register number is R. 5161. and it was first referred to in an article published in the Illustrated London News on Sept. 11. 1926.

This specimen is the finest armoured Dinosaur ever discovered and the single one in which nearly all parts of the dermal armour are preserved in situ. The specimen surpasses, as far as I am aware, all similar specimens preserved in the various American Museums. In consequence of its unique state of preservation it is of greatest scientific importance and I consider it as a very high mark of estimation, that I was permitted by F. A. BATHER, the Keeper of the Geological Department of the Natural History Museum, to give the first description.

The piece forms the type of the new genus *Scolosaurus*, this name being derived from the greek *σκολος* (thorn) to indicate the spiny nature of the creature, as already alluded to in its first description. The specific name *Cutleri* is given to commemorate the late W. E. CUTLER by whom it was discovered.

When discovered, the skeleton of *Scolosaurus* was laying on its back. It is imbedded in a very fine sand which is, as a microscopic investigation showed, of aeolian origin. In some places this sand passes into a fine clay that evidently originated from finer dust. In the bodycavity of the animal a well preserved leaf of *Platanus* sp. indet. was found, which shows, as a dried leaf generally does, an undulated surface. Both the nature of the sand and the shrivelled state of the leaf show that the skeleton of *Scolosaurus* did not get imbedded in the sediment under water, but on some dry place, otherwise the leaf would have flattened out.

The removal of the skeleton from the spot, where it was discovered, to the Natural History Museum, was done with the greatest care in a series of large blocks and it was only after that these had again been fitted together and the working out of the skeleton had begun, that the impression of the entire skin of the animal was discovered.

The preparation, that demanded the greatest care, was carried on with interruptions from 1915 to 1926. Many technical difficulties had to be overcome but the »Mason« of the Geological Department, L. E. PARSONS again gave a magnificent proof of his masterly skill and patience. With exception of the head, an unknown part of the tail and the extremities of the right side, the skeleton is complete. Apart from the lower arm and manus of the left side, of which the bones have been twisted backwards and dislocated, all bones are more or less in natural connection.

The fossil is at present 398 cm long and 170 cm broad. The neck is somewhat bent to the left, the upper arm is stretched horizontally outward in natural position, the forearm is bent at a right angle to the upper arm. In spite of being dislocated by a twist it is directed vertically downwards. The femur is laying, as the humerus, horizontally and its distal end points obliquely forwards. The tibia is likewise placed horizontally and forms a rather sharp angle with the femur. The bones of the foot are yet in connection with the lower leg, but pressed against the vertebral column. The clumsy tail forms the straight continuation of the body. On the whole dorsal part of the skeleton the impression of the skin is marvellously preserved and contains all its different elements in situ. On the ventral side parts of the skin are preserved on the neck and on the upper arm and traces of the skin are visible on the ventral side of the tail.

A) Description.

Vertebrae and ribs. Twenty presacral, five sacral and thirteen caudal vertebrae are preserved. Owing to the lack of the head and even of the axis and to the fact, that the transitory vertebra between the cervical and dorsal series is imbedded in the matrix, the exact number of the cervical vertebrae can not be determined. Centra of six cervical vertebrae are clearly visible. Probably a seventh occurred, which is laying in front and above the coracoidea, at present however this vertebra is not exposed to view. The centra of the six cervicals form an arch of 130 degrees. Being articulated with each other, they indicate a fairly great flexibility of the neck. The length of the centrum of a cervical vertebra is 7.5 cm, but nothing can be said about its shape.

The neural arch is only visible on the second, fifth and sixth cervical but even here only to a limited extent. From the parts visible in the fifth and sixth cervical it is evident, that in these two vertebrae the arches were short and very high and had zygapophyses strongly elevated above the centrum. Judging from the cross-section of the first cervical, which is visible on the anterior end of the specimen, it seems as if this vertebra would have had a somewhat lower arch with powerful diapophyses, that were directed straightly outward. A cervical rib is preserved on the fourth vertebra and the caudal end of another, that may belong to the first known vertebra or to one further in front, is preserved far in front. The distal end of this ribs is straight and flattened and 12.6 cm long at the proximal fractured end. It is 3.8 cm broad and tapers towards the other end. The rib of the fourth cervical is at the tuberculum 5 cm broad and also straight, but too incomplete to give any further indication about its original shape.

Behind the cervical vertebrae follow nine free dorsal vertebrae and behind these yet four others that are fused so as to form a solid rod of bone. This rod is again coalesced with the sacrum. In spite of their

carrying well developed ribs, the four fused dorsals may be termed, to distinguish them at once from the free dorsals, lumbaroid vertebrae. Similar vertebrae occur also in other armoured Dinosaurs.

The centra of the dorsal vertebrae are visible on the inferior side of the specimen, the tops of their neural arches on the superior surface. The centra of the free dorsals are well preserved. They are nearly equally rounded on the base and on the flanks and expand gradually but quite remarkably towards both ends. Their length is 11.5 cm and in the transverse diameter at the thinnest part 7.8 cm. At their expanded ends they are 15.6 cm thick. Altogether these vertebrae are similar to those in *Stegosaurus* (IX 318), *Triceratops* (IX 380) and *Polacanthus* (IX 818). Their distal expansion is stronger than in *Struthiosaurus* (IX 1007), or *Acanthopholis* (IX 837). In the lumbaroid vertebrae the expansions at the distal ends are missing, as is always the case, when dorsal vertebrae fuse. As an example it is enough to quote *Polacanthus* and *Glyptodon*.

The neural spines of all the dorsal and lumbaroid vertebrae are feeble. They are thin and blade-like, scarcely thickened at their upper end and fairly apart from each other (Plate VII fig. 1).

The shape of the ribs (Plate VII fig. 1) varies in the different regions of the body. The foremost dorsal ribs show a very curious cross-section, for to the posterior surface of the elliptical rib a thin flange of bone is attached which adheres to the rib with a concave surface. This flange can only be a processus uncinatus. It gives the rib a cranio-caudal breadth of 13 cm by a maximal thickness of only 2 cm. The dorso-ventral dimension of the processus uncinati could not be determined.

Ossified processus uncinati have not yet been discovered in Dinosaurs, their occurrence in *Scolosaurus* is however evidently in correlation with the strong dermal armour of this genus, for they serve to distribute the weight of the great spines of the shoulder region evidently onto all the anterior ribs.

On the posterior dorsal ribs, which are not overlaid by gigantic spines, processus uncinati seem to be absent. The posterior dorsal ribs have a roughly triangular section with a flat superior surface and a strongly rounded base. These ribs are 3.5 cm thick and 4 cm broad above.

A microscopic investigation showed, that these ribs are entirely built up of secondary and tertiary Haversian systems, as is nearly always the case in specialised upper-cretaceous Dinosaurs. The somewhat irregular size and shape of these systems in *Scolosaurus* deserve especial notice. Contrarily to all other upper-cretaceous specialised *Orthopoda*, in which the elements of the Haversian system are round or, in consequence of touching each other, polygonal with a rounded center, in *Scolosaurus* the outlines of these systems are frequently elliptical. Thus they remind more of the Haversian system of the *Sauropoda*, than of those of the *Orthopoda*.

Both the lumbaroid ribs as well as the preceding ones are transversely but moderately curved and indicate a body that was flat and broad above and had abruptly descending flanks.

The lumbaroid ribs are all more or less modified. They are all broader than the dorsal ribs. Their distal ends are overlapped by the preacetabular part of the ilium. The inner margin of this latter bone runs obliquely forward and outward, and thus from above the first lumbaroid rib seems the longest and the last the shortest. The three anterior lumbaroid ribs are only a trifle broader than the last dorsal rib, for even near the vertebral column their cranio-caudal breadth is only 5 cm. Towards the ilium they become even thinner. The last lumbaroid is broader and strongly modified. It is narrower near the vertebral column and broadens towards the ilium. In this regard it resembles very strongly to the follow-

ing sacral ribs, but whereas these have all got a ventral part, which unites the centra of the sacral vertebrae with the ilium, in this lumbaroid rib such a ventral part is absent. Near the vertebral column the cranio-caudal breadth of the last lumbaroid rib is 5 cm and near the ilium 8 cm.

Dorsally all five sacral vertebrae as well as their corresponding sacral ribs are well visible (Plate VII fig. 1), the centra of the sacral vertebrae are however strongly mutilated. The ends of most of the centra of the sacral vertebrae are preserved and show, that here these vertebrae were strongly expanded.

The sacral ribs show their dorsal and ventral surface. On the dorsal side the sacral ribs one to three have the same shape as the last lumbaroid rib, the succeeding ribs, four and five, are narrower than these. The first sacral rib is the longest, the last the shortest. On the ventral side (Plate VI fig. 2) the sacral ribs are vertical laminae of bone, that are about 2.7 cm thick from fore to aft. The dorso-ventral total height of a middle sacral rib is about 10.5 cm. Owing to the ventral thinness of the sacral ribs, the foramina that are placed between these ribs are all very large. They are all of equal size and have an elliptical outline. In this regard *Scolosaurus* recalls strongly *Dyoplosaurus* and to a certain degree also *Scelidosaurus*.

Thirteen caudal vertebrae are preserved (Plate VI fig. 3) and an unknown number (about 3 or 5) are missing. The centrum of the first caudal is 8.5 cm long and 9.7 cm broad in the middle. It is not fused with the sacral vertebrae, but the strong transverse processes of this vertebra are directed obliquely forward and touch, as in *Dyoplosaurus*, on both sides the postacetabular process of the ilium. The transverse processes of the following vertebrae are likewise yet directed somewhat forward, owing to their shortness they do however not reach to the ilium. It seems quite likely, that in one or two of these caudals the gap between transverse processes and the ilium was filled up by a ligament joining these two parts together. The size of the transverse processes gradually diminishes backward, a small transverse process is however present even on the thirteenth caudal.

The chevron bones begin only on the fourth caudal. They are very strong bones, that are open at their upper end and fused with this part to the posterior half of the centrum of the foregoing vertebra. In *Orthopoda* a fusion of the chevrons to the centra of the caudal vertebrae is comparatively rare. It is known in *Dyoplosaurus* (IX 927), furtheron in a caudal, that has been described by OWEN (IX 917) as *Cetiosaurus* and that was later on called by MARSH and LYDEKKER, but probably erroneously, *Morosaurus brevis*. Finally this character has been observed in some of the distal caudals of *Acanthopholis* (IX 837). Chevron bones that open at the upper end are furtheron known in the *Ceratopsidae*. In all the other systematic units of the superorder *Dinosauria* at least the anterior chevron bones are closed above. The pedicles of all chevron bones of *Scolosaurus*, even those of the thirteenth caudal, are remarkable for their stoutness. They seem to indicate that either a good part of the tail, perhaps a club as in *Dyoplosaurus*, is missing or that the tail finishes abruptly as in some of the fossil South American sloths.¹)

Ossified tendons, as known in all orthopodous Dinosaurs occur also in *Scolosaurus*, but it is only in the tail that traces of these are visible and consequently nothing can be said about their distribution or arrangement.

¹ LYDEKKER, R: The extinct Edentates of Argentina. Ann. Mus. La Plata, Palaeont. Argentina. III. 1895.

Scapular and pelvic arches. Without endangering the precious impressions of the skin, the scapular arch of *Scolosaurus* could not be entirely freed from matrix, and thus only the coracoids are well exposed to view. The scapulae are to the greater extent imbedded in matrix, their upper ends however visible on the dorsal side of the specimen, and their lower ends appear below. These observations enable one to fix the approximate length and the position of the scapulae. The length is about 56 cm, the upper ends of both scapulae are 78 cm far apart, their lower ends approach each other at present to 40 cm; in lifetime they were probably even somewhat nearer. This shows that the scapulae diverge backward. Their blades are laying even at present flat on the ribs and their exterior surfaces look nearly vertically upwards. This shows that the ribs below evidently retain their normal position and this is again of importance for the reconstruction of the transverse section of the fossil. If any remarkable displacement of the scapulae would have taken place this would have affected the folding of the skin.

The shape of the glenoidal cavities and their surroundings is most peculiar. Whereas in all other Dinosaurs, with two exceptions, the long axis of the glenoidal fossa is parallel to the long axis of the scapula and circular only in *Panoplosaurus* and *Polacanthoides*¹⁾, in the new Canadian fossil the long axis of the glenoidal fossa is at right angles to the axis of the scapula and therefore horizontal and not, as generally, vertical.

In this way the long axis of the glenoidal fossa of *Scolosaurus* is directed from fore to aft and attains 13 cm. The short axis is dorso=ventral and only 7 cm. *Panoplosaurus* and *Polacanthoides*, in which the glenoidal cavity is circular, link *Scolosaurus* to the rest of the Dinosaurs.

The curious shape of the glenoidal cavity of *Scolosaurus* not only separates this genus well from *Panoplosaurus*, but it shows also how the humerus was placed. Among all reptiles, living and extinct, a glenoidal cavity, elongated in cranio=caudal direction occurs only in the *Pareiasauridae* where it is, as WATSON (II 577) has pointed out, in close correlation with the movement of the humerus: it forces this bone to move in horizontal plane only. Both in *Scolosaurus* and in *Pareiasaurus* the glenoidal cavity is directed outward and even to certain extent backward. How much of the glenoidal cavity of *Scolosaurus* is formed by the scapula and how much by the coracoid can not be fixed at present and the presence or absence of an acromion on the lower part of the scapula must likewise remain an open question.

The presence of an enormous acromion in *Polacanthoides* and of a small acromion in *Hylaeosaurus* (IX 917), *Ankylosaurus* and *Struthiosaurus* (IX 1007) make it probable that a large acromion is present also in *Scolosaurus*.

The coracoides are two flat, large, strong and twisted bones of about 2·8 cm thickness. The median part bends in a bold curve inwards and towards the middle line of the body (Plate VI fig 1) so that the exterior surface of this part of the coracoid looks very nearly forward. Beyond the twist the greater part of the bone is placed parallel to the long axis of the glenoidal fossa.

The median border of the coracoids is somewhat thicker than the rest of bone and not rounded as

¹⁾ This new genus is based on the scapula 2584, the humerus 1106 and the tibia 1107 of the British Museum (Natural History) These pieces were all found in the Wealden at Bolney and were successively described by HULKE and MANTELL. A renewed description of the pieces is going to appear as part VII. of my Notes on British Dinosaurs in the Geological Magazine.

the margin of a bone generally is, but straight as if cut off with a knife. In this regard it recalls for instance the upper margin of the scapula of a young Mammal. This shows, that in lifetime there followed a very great mass of cartilage, which united the two coracoidea firmly in the median line. At present the median rims of the coracoidea are 11 cm far apart, but it seems perfectly reasonable to suppose that they were in lifetime somewhat nearer. Evidently they were then not pressed against the cervical vertebrae as at present. Allowing for these displacements of the coracoidea, in lifetime the glenoidal fossa was evidently further away from the vertebral column than at present and probably it looked also a trifle more downward.

One sternal bone is preserved, it is however displaced and shifted into the abdomen. It is a triangular bone, in which all three sides are of nearly equal length. Its shape is about the same as in *Stegosaurus* (IX 318). One of the margins is gently concave and here the bone is the thickest. At the opposite corner the bone is the thinnest. The two other margins are straight, but owing to the thinness of the bone their edges are somewhat mutilated.

The pelvic arch of *Scolosaurus* is to the greater part only exposed on the left side. On the right side only the ischium deserves particular attention. With exception of the foremost part of the preacetabular process and of the greater part of the pubis, the pelvic arch is complete.

The ilium (Plate VI fig 2) is a great, elongated, flattened but curved bone, that shows a very strong transverse expansion and an insignificant dorso-ventral thickness. Its length is at present 96 cm and on one side of the acetabulum it projects 29 cm beyond the outer rim of this surface. It is broadest by the acetabulum and recalls in a general manner the ilium of *Dyoplosaurus*, *Nodosaurus*, *Polacanthus*, *Kentruosaurus* (IX 409) and a photograph of an undescribed ilium of *Ankylosaurus*. To some extent it recalls even the ilium of *Omosaurus* (IX 917). Its preacetabular part is a slender bone of 45 cm length, which is longitudinally concave below. The postacetabular part is somewhat triangular and only 26 cm long. As has already been mentioned, the postacetabular part meets the transverse process of the first caudal. The acetabulum is a wide shallow and circular fossa which is directed nearly vertically downwards as in all armoured Dinosaurs. The general shape of the ilium in the *Thyreophoroidea* allied to *Scolosaurus* has been dealt with by ROMER¹⁾.

Both ischia are preserved. The one on the left side is complete (Plate VI fig 2), of the other one only the proximal end is preserved (Plate VII fig 1), but this one in a splendid state. The ischium is a flat and long bone which is narrow in the middle and in its distal part, but strongly expanded at the proximal end. The borders of the ribbon-like middle and distal part are nearly parallel. In this region the bone is only 6.7 cm wide, at the proximal end it expands to 22 cm. On the outer surface the proximal end is concave and forms a part of the acetabulum. Owing to the ribbon-like outline of its distal part this bone recalls strongly the same bone in *Polacanthus*, but whereas in *Polacanthus* the distal end is strongly curved, in *Scolosaurus* it is flat throughout. In lifetime probably in both genera the ischium was less curved than at present in *Polacanthus*, but somewhat more than at present in *Scolosaurus*. In *Ankylosaurus*²⁾ the ischium is somewhat more curved than in *Scolosaurus*. Perhaps even the degree of curvige can be taken as a sign, that the belly was more rounded in *Polacanthus* and flatter

¹⁾ ROMER A. S. The pelvic musculature of Ornithischian Dinosaurs; Acta Zoologica Vol VIII Stockholm 1927.

²⁾ ROMER A. S. loc. sup. cit. 1927.

in *Scolosaurus*. The length of the ischium is 50.5 cm, it is therefore evident, that originally the ischium can not have been directed very strongly backward, else it would not meet its opponent. To the utmost the angle that it formed with the longitudinal axis of the body can have been 45 degrees. This shows, that in *Scolosaurus* the ischia formed a transverse bridge placed rather far in front. This bridge evidently supported the belly and besides it united the acetabula firmly with each other. Such a union became necessary on account of the great breadth of the acetabular region, the remarkable dorso-ventral flattening of the ilium and on account of the great weight of the lumbar shield. To a certain extent in this regard *Scolosaurus* can be compared with the recent Lizards, in which the sacro-pelvic union is comparatively feeble. *Scolosaurus* differs from all bipedal *Orthopoda* by having the symphyses of the ischia much further in front than these.

The acetabular margin of the ischium is remarkably straight. The pubic and ischiadic pedicles of the ilia being about 30 cm apart, the space that was filled by the pubis can scarcely have exceeded 10 to 12 cm. Unfortunately about the pubis itself practically nothing is known. Under the head of the femur only a small fragmentary bone is seen, which is probably the pubis, but nothing can be said about its shape. The absence of a pubis of considerable size is therefore of importance, because in *Ankylosaurus* the pubis is likewise remarkably small, in *Polacanthus* it neither seems to have been very large. Evidently both the pubis as well as its pseudopectineal process are reduced in all Dinosaurs allied to *Scolosaurus*.

As will be shown further on, when discussing the femur, the reduction of the pseudopectineal process is due to the position of this bone. There is a good amount of evidence to show that at least in *Scolosaurus* and *Struthiosaurus* the femur was placed with its long axis in a nearly horizontal plane and with its distal end obliquely outward. Owing to this thoroughly changed position of the femur, naturally all those muscles which worked from the pseudopectineal process to the femur had to shift their position (IX 964) and this alone can already quite well account for the reduction of this part. Apart from this it has yet to be considered that, as in all slowly moving quadrupedal reptiles in which the feet are wide apart, there existed no reason for a strong development on the musculus ambiens, or for a strong pubo-ischia femoralis¹⁾ and lastly it has to be considered that the presence of a marked pseudopectineal process would greatly have hindered the movement of the femur. All this can explain its reduction. As for the reduction of the posterior part of the pubis, this is quite frequent among the *Orthopoda*.

Limb bones. With exception of the femur and of the phalanges of the anterior limb the limb bones are comparatively well preserved. They are neither crushed nor distorted. The humerus is by far the most massive bone of the entire skeleton. It is 44 cm long and bears an enormous deltoid crest. This crest gives the humerus a total width of 20 cm and descends for 25 cm along the anterior and median part of the bone. It is 3.5 cm thick. Where the deltoid crest ends rather abruptly, the shaft of the humerus is 7.5 cm thick, but this region is only very short for very soon the humerus again expands and at its lower end it is again 18 cm broad.

Among the humeri of mesozoic reptiles is especially the humerus of the poorly known *Polacanthoides*, which resembles the Canadian fossil and a nearly similar, but lesser likeness can also easily be

¹⁾ ROMER A. S. loc. sup. cit. 1917.

detected with the humerus of *Panoplosaurus*. Other heavily armoured *Orthopoda* as *Omosaurus*, *Stegosaurus* (IX 318), *Kentrurosaurus* (IX 408) and the more specialised Ceratopsidians (IX 303) have humeri, which are built in much the same manner, but as a rule their deltoid crests are not as strong.

Comparing now these massive bones with the more slender humeri of *Scelidosaurus* (IX 917), *Leptoceratops* (IX 101) or *Centrosaurus*, it is very easy to remark that the humeri of the second type recall somewhat the humeri of the bipedal *Orthopoda* and thus the thickening of the humeri of the more advanced types of armoured Dinosaurs is surely a mark of specialisation.

The humerus of the *Scolosaurus* does not however only recall the humerus of specialised *Thyreophora*, but apart from the fact, that it has no entepicondylar foramen, also the one of many primitive reptiles as for example the *Dicynodontidae*. This is due to its very massive nature, its enormous deltoid crest and its expansion at the lower end. Together with the shape of the glenoideal fossa this striking resemblance goes to prove that in *Scolosaurus* and in *Polacanthoides* the humerus was carried normally in a horizontal position. Bearing now in mind that in *Scolosaurus* this horizontal position is a secondarily acquired character, one naturally must conclude, that this was also the case in many other allied types. The importance of this conclusion lays therein, that it sheds a good deal of light on the evolution of the *Thyreophoroidea*. Originating from forms, in which the anterior limb was originally comparatively slender and not placed straight under the body, and in which the palms were probably rotated somewhat inward, it seems as if the armoured Dinosaurs, in spite of their newly acquired quadrupedal locomotion would have been incapable to shift the elbow under the body as is the case in Mammals. This was probably the reason why the pectoral muscles were continually strengthened, but it is likewise quite natural that such an unpractical manner of specialisation finally was detrimental to locomotion. Thus the unpractical and consequently very slow and unyieldish manner of moving the forelimbs may to some extent account for the extinction of this group.

The fact that the humerus of *Stegosaurus* and *Scolosaurus* shows the same trend of evolution as the humerus of the *Ceratopsidae*, prevents me from accepting the explanation given by J. TAIT and BARNUM BROWN¹⁾ for the shape of the humerus in the latter group.

In the fossilised skeleton of *Scolosaurus* the ulna and the radius (Plate VI fig. 1) have retained the normal position to each other, owing to a twist they lost however the contact with the upper arm. In comparison to the humerus the ulna, which is but 33 cm long is comparatively short but on account of a pathological malformation it is very thick. Even at the thinnest place the transverse diameter of the ulna is yet always 9.5 cm. Contrarily to the smooth surface of the humerus and radius, the surface of the ulna is everywhere uneven and covered with irregularly distributed furrows and vascular apertures. The fibres of the bone are also very irregular and follow undulating lines. All this seems to indicate that up to the death of the animal, probably in consequence of a laesion of the periosteic layer and in consequence of a strong inflammation due probably to infection, all over the ulna rapid but irregular bone formation was going on. Not only does this new formation of the bone give the entire ulna a clumsy shape, but it alters even the olecranon. Here even the part facing the humerus lost its original even surface and became a remarkably deep pit that has a subtriangular shape (Fig. 4).

¹⁾ TAIT J. and BARNUM BROWN: How the Ceratopsia carried and used their head. Trans. Roy. Soc. Canada, Ottawa, 1928.

The radius is 6 cm shorter than the ulna. Its maximal thickness is only 4.5 cm and its entire surface is smooth. The normal way in which it yet always articulates to the ulna shows in a conclusive manner that the lower arm had become dislocated by a twist from the upper part. It is quite interesting to note, that the ratio of the humerus to the ulna is approximately 2:1 for this may in future give a clue for the distinction of different species. The radius as a whole can not be said to show any characteristic features. Its ends are but very slightly expanded and it recalls the radius of the more specialised *Ceratopsidae* (IX 380).

The manus is unfortunately very strongly mutilated, only two metacarpals being well preserved. Each metacarpal is about 9 cm long, 7 cm broad at either end and 6 cm broad in the middle. Dorsoventrally the metacarpals are somewhat flattened and thus they indicate a plantigrade and comparatively broad foot. Compared with the metacarpals of *Panoplosaurus* (IX 1048) those of *Scolosaurus* are much broader and shorter. On account of the metatarsals being 15 cm long, while the metacarpals attain only 9 cm, one may conclude that the manus of *Scolosaurus* was much smaller than the pes. Unfortunately both the number of digits as well as the phalangeal formula of *Scolosaurus* can not be determined.

Of the femur (Plate VI fig. 2) only the two ends on the left side are preserved, but the preservation of both ends in situ enables one to get some idea about the entire bone. In the specimen the missing part has been restored in plaster. The length of the femur must have been 60 cm and thus its ratio to the humerus is about 3:2. The distal and proximal ends of the femur are expanded, but the shaft seems to have been rather slender but not as slender as in the restoration. Owing to the expansion at its ends, the femur differs well from the pillar-like femora of *Stegosaurus*, *Kentrurosaurus* and even *Omosaurus*, and recalls *Polacanthus*, *Nodosaurus*, *Ankylosaurus*, *Hoplitosaurus* and to some extent *Struthiosaurus*.

Laying, as it does at present, with its lower end directed downward and outward and the proximal end close to the acetabulum, the femur is entirely beneath the preacetabular process of the ilium. This seems also to have been about the normal position of the femur when the animal was alive. Probably a dipping of its anterior end for scarcely more than 20 cm would be enough to make up for the post mortem displacement. That in lifetime the horizontal position was the normal one, can be deduced from the observation, that on the femora of *Struthiosaurus* (IX 118), *Nodosaurus* (IX 631) *Hoplitosaurus* (IX 318) and *Polacanthus*, which are all flattened from fore to aft, the cartilage covering the articulating surface is not placed, as in *Iguanodon* or *Stegosaurus* equally on both flanks of the upper end of the femur, but to a great part of its anterior surface. This shows that the former anterior side of the upper end of the femur faced the ilium and bore the weight. Naturally such a position is only possible, when the femur is placed in a more or less horizontal plane with its distal end directed outward and forward.

As already mentioned, the distal end of the femur of *Scolosaurus* was dilatated and it may therefore be presumed that it was similarly built as in *Nodosaurus* etc. Contrarily to the *Stegosauridae* and to the *Sauropoda*, in which the distal part of the femur is but slightly expanded and smooth, in *Nodosaurus* and its allies the inferior part of the femur has remarkably strong ridges.

This is the region where the muscles of the lower leg are attached and thus evidently a great strain must continually have acted on the knee and this again shows that normally the knee was flexed, that

the tibia constantly met the femur in a more or less right angle and that it had continually to be kept in position by muscular strain. Thus also the study of the structure of the distal end of the femur of the *Scolosaurus* corroborates the conclusions arrived to by the study of the upper end.

The tibia of *Scolosaurus* (Plate VI fig. 2) is less characteristic than the femur. It is, as in all armoured Dinosaurs, strongly expanded at both ends. It is 41.5 cm long, 9 cm thick in the middle, 23 cm thick at its upper end and 17 cm thick at its lower. The proportion of the tibia to the humerus of *Scolosaurus* is much the same as that of the similarly built bones in *Polacanthoides*. The ratio of the femur to the tibia is about 3:2, that of the tibia to the humerus about 100:93. The latter proportion is therefore of importance, because it serves to distinguish *Scolosaurus* from *Panoplosaurus* for in the latter this proportion is 100:88.

Unfortunately the fibulae are missing on both sides of the type of *Scolosaurus*. The tarsal bones are likewise absent but, probably their absence is due to their incomplete ossification. The argument for this supposal is to be found in the position of the metatarsals. Two of these retained their position to the tibia as well as their position to each other, but in spite of that, there is no trace of any bone in the gap between the metatarsals and the tibia. (Plate VI fig. 2).

Each metatarsal is 15 cm long, about 8 cm thick at each end, but only 4 cm thick at the thinnest part. Antero-posteriorly the metatarsals do not seem to be greatly flattened and this indicates that they were placed rather upwards.

With one of the metatarsals three phalanges are yet in connection and form an entire toe. The length of this toe is about 14 cm and its components diminish forward rapidly in size. The first phalange is only 5 cm long and nearly 8 cm broad but only 5 cm thick, thus it is rather strongly flattened. A similar flattening is also observable on the following phalanges, which are also all broad, short and flat. On account of their broadness diminishing forward very rapidly, the flattened and rounded claw is even at its base only 4 cm broad.

Together with the presence of a broad and flat claw this flattening of the phalanges shows that the phalanges were placed parallel to the ground and formed thus the angle with the metatarsals. Altogether there is no decided fossorial adaptation, although the feet might occasionally have been used for scraping.

Skin and dermal armour. The most remarkable feature of the new Canadian Dinosaur is the preservation of the impression of its dorsal skin and of innumerable dermal ossifications in situ (Plate VII). The dermal covering or at least its impression is entirely preserved on the back of the neck, on the back of the body, on the top of the tail and on the dorsal (exterior) side of the upper arm. Traces of the dermal covering are visible on the ventral side of the neck down to the coracoids, then on the left side of the body behind the humeral articulation and on the anterior part of the upper arm. Very poor traces of the dermal covering can be detected on the ventral side of the middle of the tail.

Three types of skin covering can be distinguished. The first type is an evidently thick but flexible skin, in which numerous small granular ossifications were imbedded much in the same manner as in *Neomyiodon* or *Heloderma*. This type of skin is folded and occurs in many regions of the body. Professor W. J. SCHMIDT, to whom some of the granules and a part of the skin were sent for investigation, gave

an account, but the manuscript of this account is yet in the hands of St. MAJER, who in spite of being assistant at the Budapest University, is not ashamed of preventing its publication. The second type of skin consists of the impression of what must have formerly been flat, polygonal, rigid horny scutes, (Plate VI and Plate VII) of some centimeters in diameter. This type of skin was evidently incapable of being folded and as in Rhinoceroses, formed a rigid cuirass. In this second type are imbedded numerous large dermal ossifications, which are the third type of dermal cover (Pl. VII). To be able to distinguish these three types easily in the following detailed description, the first type will be called the granular skin, the second the polygonal skin, while for the third type the terms „dermal ossifications“ or „dermal bones“ will be used.

The first and second type alternate in *Scolosaurus* in such a manner that the body becomes transversely segmented. (Pl. VII).

The foremost part of the neck is covered by a very narrow zone of granular skin, then follows on the back of the neck a large and symmetrical dermal bone (Pl. VII fig. 1 nu. p₁) that has a sharp ridge on each side and descending flanks, which are placed under the sharp ridges. The lateral parts of this great nuchal plate consist in reality on each side of a special roof-shaped bone, of which the one side is fused to a central dermal plate, while the other side forms the descending flank (l. p₁).

This first nuchal bone is flat from fore to aft, but transversely slightly convex above and concave below. Its outline is somewhat irregular. In front it is nearly straight, its sharpened sides slope backward in an undulating line and behind it is again nearly straight. The upper surface is not quite even, for laterally of the median line and on the posterior half of the bone on each side a low and blunt boss or protuberance occurs. This protuberance evidently represents a trace of that pair of blunt but well marked ridges that characterise the nuchal plate of *Panoplosaurus* (IX 574). The cranio-caudal length of the first nuchal plate of *Scolosaurus* is 18 cm, its greatest breadth 46 cm.

The height of the roof-like crest on the margin of the nuchal plate gradually increases backward, so that it attains its maximum on the posterior end. A cross-section of the roof-shaped crest is not quite symmetrical. The flank below the crest is more concave than the part above. The descending flank is of considerable size and evidently protected the side of the neck. The textfigure 11 is intended to give an idea of the entire cross-section of this nuchal plate.

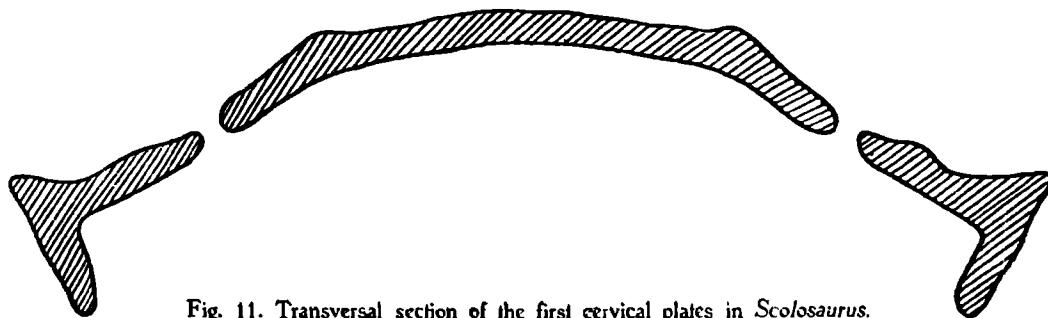


Fig. 11. Transversal section of the first cervical plates in *Scolosaurus*.

Behind the first nuchal plate again a zone of granular skin follows. This zone is 22 cm long and more than 28 cm wide. Here the skin shows several very well preserved deep and well marked folds. They run transversely over the neck and indicate a good amount of flexibility in this part.

Two huge, nearly flat plates of bone (Plate VII n. u.), that are fused along the median line, each with a slightly elevated boss on his posterior part, are the next dermal elements to be dealt with. They cover the middle of the posterior part of the neck and are homologous to the flat median bone further in front. The breadth of these two posterior nuchal plates together is 47 cm, their cranio-caudal length only 22 cm. On its outer, slightly convex border each of these bones touches a large, roof-shaped plate (l. p.), which is similar to the roof-shaped part of the former segment. In the case of the second nuchal plate the lateral element is however not fused with the median piece. The one flank of the lateral piece again abuts against the flat median plate, the other flank again descends on the side of the neck. On account of the flank, that descends on the side of the neck, being also more concave than the other side, a transverse section of this roof-shaped plate is likewise symmetrical. Viewed from above, the outline of the roofed plate is elliptical and the crest on the top forms the long axis of this ellipse. From a point that overhangs the posterior border of the bone the top of the crested roof slopes gradually forward and downward. The inferior base of the piece is deeply concave. On account of the basal outline of the lateral piece being elliptical, and the lateral border of the median plate being somewhat convex, these two dermal elements do not join very closely and especially on the posterior border a sharp triangle remains open, into which the granular skin, following behind both plates, enters.

The region of the granular skin situated behind the second ossified nuchal segment indicates the region, where the neck and the body meet. This region is 17 cm long and 71 cm broad and has an irregular outline. On the two sides this region shows strongly concave excisions, into which the armour of the upper arm enters. In front on each side a triangle projects forward which enters, as already mentioned, between the different dermal ossifications of the second cervical segment. The posterior margin of this granulated region is deeply concave in the middle line of the body and curves backward on either side. Thus laterally in the scapular region the granulated skin extends rather far back.

The third zone of granular skin is likewise crossed by symmetrical, transverse folds. Owing to the light falling straight on to the specimen, they are unfortunately invisible on plate VII. The first fold runs straight across the median part of the neck, but on the sides it curves somewhat forward, so as to run everywhere parallel to the posterior border of the median dermal bones of the second nuchal segment. The second and third fold cross the neck straight from one side to the other, the fourth fold finally runs likewise straight across the median part of the neck, but on both sides it turns in a sharp angle backward and outward. Owing to the flatness of this region of the back, this fold is confined to the upper surface of the body. By turning sharply backward the last fold runs to a certain extent about parallel with the median borders of the scapulae and it extends backwards beyond their posterior end. This arrangement enabled the rigid skin, that overlayed the scapula, to move together with this bone.

The scapular transverse fold forms the anterior border of what may well be called the dorsal cuirass (Plate VII). This cuirass is divided into two halves: an anterior flexible half covering the dorsal vertebrae and a posterior rigid one, that covers the lumbar and sacral. On the anterior half five transverse segments can be distinguished, each of which corresponds to about two vertebrae. The relation of the segments to the vertebrae underneath is in so far not quite exact, as the first segment is somewhat broader than the space occupied by the first vertebrae, while the last is somewhat narrower than the underlying parts. The length of the first segment is 32 cm, that of the second 24 cm, that of the third 22

cm and that of the fourth only 21 cm. All four segments are built up of what has been called polygonal skin and the space between them is filled by granular skin. The cranio-caudal length of the intervening zones of granular skin is in the average 3 cm. Beyond the last zone of granular skin follows the rigid lumbar shield. This shield is covered to the greater part by polygonal skin. Each segment of the body carries one transverse row of dermal ossifications, that will be dealt with later on, while the lumbar shield has three transverse rows. This seems to indicate that the lumbar shield originated by the coalescence of three segments.

The dermal ossifications are spines, bosses and plates. The principal spines on the back of the animal are so arranged as to form on each side two longitudinal rows running from fore to aft; between these two principal rows a third, smaller row is intercalated. This third row begins only on the third segment.

Owing to the fact, that on the first segment a dermal bone is met with, which is placed behind the elbow and exteriorly of the lateral marginal row, one may perhaps take this as an indication that one more exterior row of dermal bones existed, but conclusive evidence for this hypothesis is yet wanting. The distance between the two median rows of dermal ossifications is 28 cm on the first dorsal segment and only 25 cm on the lumbar shield.

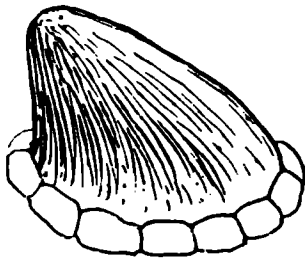


Fig. 12. Dorsal spine of *Scolosaurus* (anterior margin to the right).

The shape of the dermal ossifications of the back varies a good deal according to the different regions. In the median row the ossifications of the first segment are robust and high but blunt spines (fig. 12). On the second segment they are low spines and on the following ones they gradually turn to flat and round plates. The first spine rises from an elliptical base, 27 cm long and 16.8 cm broad, the spine itself is 15 cm high. The spine of the second segment is at base about 16 cm long and only slightly broader and attains a height of only 4 cm. On the fifth segment the median pair of dermal ossifications consists only of two flat and nearly round bones, each of which is 12.5 cm long and 11.5 cm broad.

In the lateral row of dermal ossifications the variations are greater. The lateral ossification of the first dorsal segment (Plate VII l. p._a) recalls the lateral ossification of the last nuchal segment. It is an elongated plate of asymmetrical triangular outline. At its base it is 27.5 cm long and 13 cm broad, and deeply concave below. Above it carries a sharp crest, that arises laterally of the median longitudinal axis. This crest is low on the front end, but it rises at the posterior end to a height of 10.5 cm. On the second and third segment of the body this crested ossification is replaced by a flat bone of asymmetrical elliptical outline. This bone is 15 cm long and 13 cm broad.

The ossifications of the intercalated row are all only flat plates of more or less circular outline. The outermost dermal bone, which is placed behind the elbow, differs from all the others. This element is but a vertical plate of bone thickening at its base, which is elongated in cranio-caudal direction and is 12 cm long but only 1.4 cm thick. At the upper edge this bone is very thin. Its height is about 8 cm and its summit longitudinally but very slightly convex.

The polygonous impressions of the cuirass, that are evidently impressions of smooth and flat horny shields, are rather uniform in size and show only slight variations. Near the folds covered by the granular

skin, the polygons become smaller and are somewhat elongated parallel to the folds (Plate VII fig. 2) whilst around the larger dermal ossifications the rounded polygons are grouped in concentric rows (Plate VI fig. 4).

The tail of *Scolosaurus* is segmented in a manner analogous to that of the body and is covered with the same sorts of dermal elements as the back. Unfortunately on the root of the tail, even on its dorsal side, the dermal parts are badly preserved. It makes however the impression, as if formerly in this part a polygonous skin would have existed, which carried four low, blunt, spinelike or knoblike dermal ossifications arranged in a row across the tail. The median pair of these ossifications is evidently the continuation of the double median row of ossifications of the lumbar shield, while the lateral pair is the continuation of the lateral rows. After this rather rigid segment follows a zone of folded granular skin, which is 2 cm long and then follows again a segment of polygonal skin. The second segment is 24 cm long and more than 60 cm broad. It carries, as the foregoing segment, again four dermal ossifications. These are circular plates, each with a stout, large and blunt knob in the middle. The median ossifications are much nearer to each other than on the foregoing segment. Their tops are only 15 cm wide apart. The tops of the lateral ossifications are, on each side, 16.5 cm further off. The height of the central knob on each of these plates is about 5.5 cm.

A second narrow zone of granular skin separates the second rigid segment from the third. The latter is but 20 cm long. This one has also several badly preserved dermal ossifications. Then follows the beforelast segment of granular skin that is preserved. On the last rigid segment only two large dermal ossifications are present. They are (as shown in textfigure 13) two rather high and comparatively slender spines (Plate VI fig. 1), which have a somewhat compressed cross-section and arise rather abruptly from a wide conical base of oval section. These two caudal spines are directed obliquely upwards

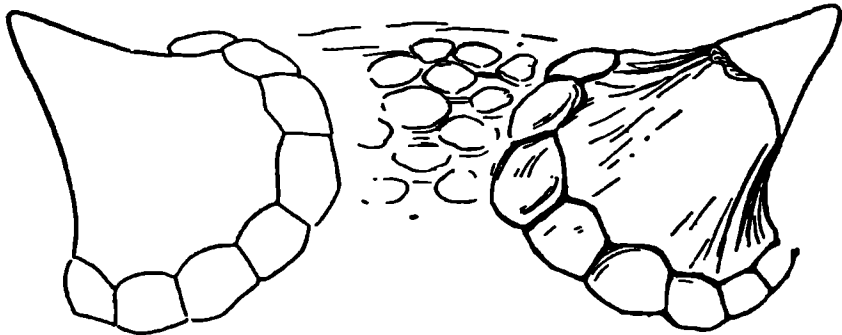


Fig. 13. Distal end of the caudal armour in *Scolosaurus*.

and outwards. Their basis is 16.5 cm long, their height was probably more than 11 cm. The augmentation of the size of the dermal spines in *Scolosaurus* towards the end of the tail is a very remarkable feature. Together with the segmented nature of this organ it reminds one very strongly to the tail of some of the pliocene gigantic South-American sloths.

The entire breadth of the distal part of the tail of *Scolosaurus* is not surely known, because the tail is somewhat flattened out by pressure so that the skin extends further than the lateral spines, but judging from the dimensions that can be measured on the beforelast segment, the transverse diameter of the tail may probably have been something over 60 cm. Its dorso-ventral diameter was probably somewhat less. Curiously enough, on the side of the tail the polygons show an other type of sculpture than on the back of the animal. They are smaller than the others and the furrows between them are crossed by small elongated pits, which stand at right angles to the margins of the polygons. A photograph of such a region is given on Plate VII fig. 3.

Scolosaurus is the single hitherto known Dinosaur in which the dermal covering of the anterior extremity is preserved in situ. Consisting in some part of crested, roof-shaped plates (fig. 14) that to some extent overlay each other, the dermal armour of this part recalls, at least to some degree, the plated elbow armour of mediaeval knights.

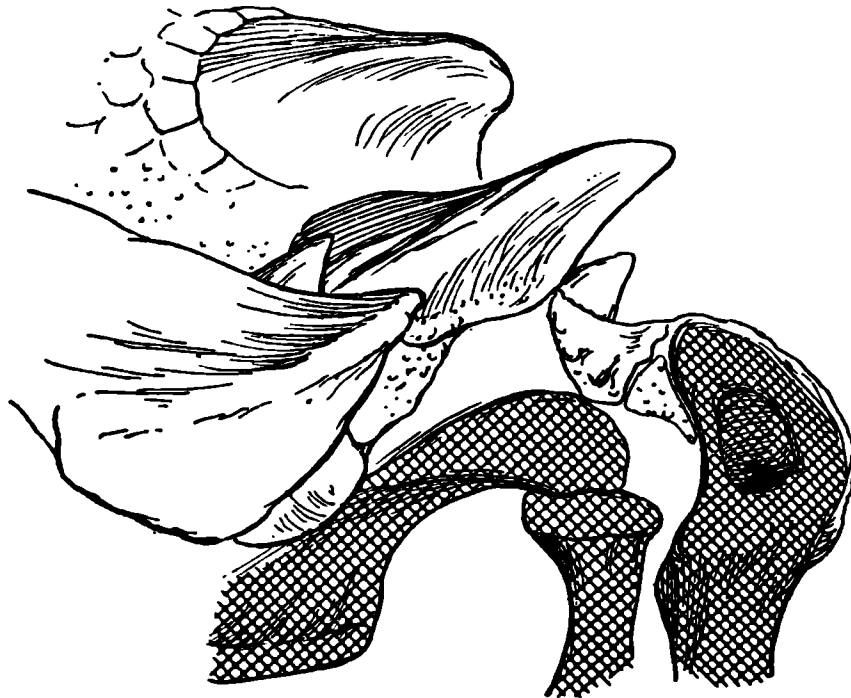


Fig. 14. Anterior extremity of *Scolosaurus* and its dermal armour.

The first element of the dermal cover of the upper arm of *Scolosaurus* is a small but very sharp and slender spine of polygonal cross-section. It is 10 cm high. This spine is placed in a modified type of granulated skin. In this skin the bony ossicles are not, as on the rest of the body, nodules, but flat circular rosettes with strongly corrugated edges. The diameter of these rosettes is somewhat less than 1 cm.

Next to this spine and beyond the modified granular skin follows a large plate of bone bearing a symmetrical spine 8 cm high (Plate VII h. sp.). The base of this plate has an irregular and asymmetrical outline. The one border has the shape of a quarter of an ellipse, the two other borders are straight. They are of unequal length and abut against each other in an angle of about 135 degrees. The greatest length of this basal part is 23 cm, its transverse diameter 13.5. Near the longer of the straight margins and parallel to it rises a crest that culminates in the spine already mentioned. Under the crest the base of the plate is deeply excavated and this gives the plate an asymmetrical roof-like transverse section. This plate overlaps in an imbricating manner the following dermal ossifications and between these two plates some granular skin can be detected, containing very small bony nodules. This skin forms a fold under the roof-shaped part of the larger, more proximal dermal bone. The third dermal bone of the upper arm is a small, sharp spine recalling the first piece. It is embedded in very coarse

granular skin and is followed by a crested piece of elliptical outline, which is 13 cm long, 11.5 cm wide and 4.5 cm high. The summit of the crest is on this piece at the distal end.

The following pieces, that formerly covered the elbow, are all displaced and therefore their position can not be fixed. One of these bones is an elongated piece bearing a blunt cone, an other is a plate having an elongated keel, while in some other pieces that probably covered the lower arm, not even the shape can be made out clearly, for they are all muddled together. In contrast to the blunt cones of the back, the elements of the dermal armour of the upper arm are very conspicuous for their sharpness.

B) RECONSTRUCTION AND SYSTEMATIC POSITION.

Reconstruction. For the reconstruction of *Scolosaurus* two sorts of indications are available. Some of the points, on which the reconstruction is based, can be derived from the actual preservation of the specimen, others from the study of the anatomical details.

As already mentioned at the beginning of the description, *Scolosaurus* was found laying on its back with the coracoidea and the hind limb pressed on the vertebral column. This indicates, that the skeleton was evidently exposed to some force, which thrust some bones downward, but this seems only to have been the weight of the bones themselves. Any further pressure, that would have been brought to work against the whole skeleton to such an extent as to flatten the body, would first of all have pressed the forearm down and besides it would have left very clear traces on the disposition of the folds of the dorsal skin. Apart from the fact that the neural spines of the vertebrae project slightly from under the skin (Plate VII fig. 1 n. sp.) and that the part of the one shoulder-blade is slightly displaced, the skin does not show any trace of the body of *Scolosaurus* having been flattened out after the death of the animal to any greater extent.

In this regard it is of course of great importance that on the back not even the slightest trace of a post mortem longitudinal folding can be observed, whereas such a folding would have invariably set in, if the cross-section of the body of *Scolosaurus* would have been markedly flattened out after death. Already this obliges one to reconstruct *Scolosaurus* with a flat and broad body, for at present the specimen shows this shape. For the reconstruction of the cross-section of the neck of *Scolosaurus* one is guided by the relief of the nuchal plates. These are transversely remarkably flat bones, but nevertheless they indicate a neck that was more rounded than the body. The tail seems to have been round.

As has already been mentioned, several anatomical observations show how the limbs were placed. The horizontal position of the humerus and of the femur having already been dealt with, only the general dimensions of the new reptile have yet to be discussed. The height of the animal between the shoulder-blades can not have been more than 90 cm, because the glenoidal fossae were scarcely more than 44 cm above the ground. The inner and upper ends of the humera could not have been more than 5.6 cm above their outer and lower ends and these again stood, as shown by the length of the forearm, but 34—35 cm above the ground. The elbows were about 132 cm apart. Behind the elbows the outline of the body must have bulged out fairly strongly, because the middle of the body and the sacrum is at present 170 cm broad. Contrarily to what is generally assumed, the hind part of the body

did not stand higher above the ground than the front part. This is not only proved by the position of the femur but also by the fact that the impression of the skin does not show the slightest trace of the part between the shoulder-blades and the lumbar shield having been longitudinally either concave or convex. The cranio-caudal median line of the lumbar shield is perfectly straight up to its anterior margin and this indicates in a conclusive manner that the longitudinal section of the body further in front was also practically straight. For the middle of the sacral region in *Scolosaurus* a maximal height of 100 cm can be assumed. The knees must have been 60 cm above the ground, for this is the total height of the tibia and metatarsus. Probably the knees stood 120 cm far apart. The neck which stretched in front of the unyieldish body was flexible but thick. It carried probably a comparatively large head, which is supposed to have been much the same as in *Panoplosaurus*. The tail was thick and clumsy. Towards its end it was armed with projecting spines and its end was, as generally in such cases, most probably blunt. On account of the large size of the posterior spines it does not seem very likely that it carried a club as in *Dyoplosaurus*. Also in some of the extinct gigantic South-American sloths the tail is short and stout, while in comparatively closely allied genera it finishes in an elongated club.

The reconstruction of *Scolosaurus* as deduced from these observations and given in Plate VIII differs markedly from all the reconstructions hitherto given of allied animals. In a certain sense it seems to corroborate the general ideas expressed by J. WALTHER¹⁾ in his reconstruction of *Polacanthus*, but the essential difference between his reconstruction and the new one is, that the knees are placed in a mammal or bird-like manner in the reconstruction of *Scolosaurus* and in a reptilian manner in the case of *Polacanthus*.

Of course it remains a puzzle how an animal as flat as *Scolosaurus* came to lay after its death upon its back. One must either suppose that this was due to some accident, in the course of which the animal rolled down from some higher place and perished by being incapable of regaining its normal position somewhat like a turtle, or that it was turned upon its back during a fierce struggle. In the latter case it evidently perished because its adversary got at its unprotected belly. This is perhaps even the reason why the skin of the belly is so badly preserved. That the belly was opened before the animal got buried by sand, can be deduced from the leaf alluded to at the beginning of this note.

Naturally the correct reconstruction of *Scolosaurus* has some bearing on the reconstruction of *Polacanthus*. First of all it has to be emphasized, that the limb-bones of *Polacanthus* have to be placed somewhat as in *Scolosaurus*, secondly it is likely that the dermal spines of the left side of the reconstructed *Polacanthus* probably belong to the right side and those of the right to the left. Whereas at present the concave flank of each spine is turned obliquely inward, after such a change it comes to be situated below as in *Scolosaurus*. Apart from this by such a change the spines are no more turned upward as at present but outward, so that they come to have the same position as the lateral elements of the nuchal plates of *Scolosaurus*. Allowing for such a change of course the circular flat dermal plates of *Polacanthus*, which at present could be placed nowhere, can now form two median rows of dorsal dermal ossifications.

Altogether *Scolosaurus* and probably also *Polacanthus* must have had the appearance of a gigantic *Molochus* or *Phrynosoma*.

¹⁾ J. WALTHER: A föld és az élet története. Budapest, 1911.

Among the recent lizards all four excessively spiny genera *Molochus*, *Phrynosoma*, *Zonurus* and *Uromastix* live in desert or semidesert regions, in which the vegetation offers but scanty shelter. The flat body-shape of these spiny creatures is an adaptation to the life in an open country, where these animals flatten down to escape attention. When discovered, they defend themselves with their spines. On account of *Scolosaurus* having a similar body, one may presume, that *Scolosaurus* lived in the same sort of environment as *Phrynosoma* and *Molochus*, but naturally in accordance to its size its enemies also were larger. *Molochus*, *Phrynosoma* and *Zonurus* are insectivorous and only *Uromastix* is herbivorous. The osseous palate of the insectivorous lizards is not much modified by the nature of their food, but nevertheless the outline of the premaxillary is always rounded.

Both in *Euoplosaurus* and in *Struthiosaurus* the quadrate is remarkably feeble and this was probably also the case in *Panoplosaurus*. This indicates that in all those fossil spiny reptiles, that are somehow related to *Scolosaurus*, a great pressure was never brought to bear against the quadrate, therefore one must conclude that their food must have been rather soft. The teeth of these animals are frequently more or less reduced, the food they took was therefore not even cut to pieces. The claws of *Scolosaurus* show no special fossorial adaptation, the food of *Scolosaurus* was therefore not dug up out of the ground, thus *Scolosaurus* evidently did not live on subterranean bulbs. It did not live in a marshy country, therefore soft aquatic plants are also excluded as food, hard desert plants are naturally still more excluded and even succulent desert plants could not be dissected. Surely its immobility prevented *Scolosaurus* from procuring its food by running to and fro and all this limits the nature of its food to a great extent. The result is that insects are the single sort of food that has seriously to be considered.

As many recent deserticolous reptiles are insectivorous, one may suppose that the same was also the case in *Scolosaurus*. The insects that abound nowadays in deserts are *Coleoptera*, *Orthoptera* and *Neuroptera*. All these groups are known from precretaceous times. Especially *Orthoptera* occur in arid regions occasionally in tremendous swarms and they supply sometimes great quantities of food. All this agrees with the supposition that *Scolosaurus* was insectivorous, but the comparatively rare occurrence of swarms of *Orthoptera* nevertheless necessitates one to try to fix to a certain extent, how much food *Scolosaurus* may have consumed.

According to the data given by DÖDERLEIN¹⁾, a *Lacerta*, weighing 24—30 gramms, consumed in nine months 500 gramms of worms, that is about 13 gramms a week. The ratio of the weight of the body to the weekly amount of food is 100:4.3. It is, as DÖDERLEIN emphasizes, eight to ten times more than a mammal (*Sorex*) would have eaten in the same time. An Anaconda (*Eunectes*), weighing 75 kilogramms, took in five years twentyfive times food, devouring each time an animal weighing 7 kilogramms. This gives an average of 0.5 kilogramms per week. The ratio of the body-weight to the average weekly food was thus in this case 100:0.9.

Miss J. PROCTER was so kind to have different reptiles and their food weighed in the Zoological Garden at London. The data given are the following:

¹⁾ DÖDERLEIN, L.: Betrachtungen über die Entwicklung der Nahrungsaufnahme bei Wirbeltieren. Zoologica. Heft 71. Stuttgart 1921.

N a m e:	Weight of the animal:	Nature of food:	Weight of food per week:	Ratio of weight of body to weight of weekly food:
<i>Python reticularus</i> (summer diet)	3488 gr	rabbits	673 gr	100 : 19
<i>Python reticularus</i> (winter diet)	3488 "	rabbits	337 "	100 : 10
<i>Python regius</i>	673 "	rats	63 "	100 : 10
<i>Coluber obsoletus</i>	1025 "	mice	47	100 : 5
<i>Amphibolurus barbatus</i>	203 "	mealworms	76 "	100 : 37
<i>Trachysaurus rugosus</i>	266 "	banana	94 "	100 : 35
<i>Chameleon senegalensis</i>	78 "	insects	94 "	100 : 120
<i>Chameleon dilepis</i>	31 "	insects	46 "	100 : 148
<i>Sphenodon punctatus</i>	213 "	worms	141 "	100 : 65
<i>Alligator mississippiensis</i>	454 "	meat	187 "	100 : 41

To these important contributions Miss PROCTER adds the following remarks: „These statistics, although accurate so far as they go, are entirely arbitrary. A *Python* weighing 7 lbs. 10 oz. eats a rabbit weighing 1 1/2 lbs., but a *Python* whose weight is estimated at 40 lbs. would not get more than two rabbits to say 3 to 4 lbs. Pythons weighing certainly over 50 lbs. get one or two lbs. fowls. Each reptile frequently „goes off the feed“ (as the Keepers say) completely. Fasts varying from 3 or 4 weeks up to a year or eighteen months in the case of big Pythons. On the other hand some reptiles would, if allowed to, go on until further orders, especially Crocodiles. The feeding question is entirely elastic.“

All these data together show that the heavier reptiles eat comparatively less food than the lighter ones. In reptiles having a body-weight over a thousand gramms, but under five thousand gramms, the food-ratio varies irregularly between 100:5 and 100:19. In reptiles weighing between two hundred and five hundred gramms the ratio varies just as irregularly from 100:35 to 100:63, in those finally which weigh less than one hundred gramms it rises from 100:43 to 100:148.

Engineer GEORGE SZEBENY in Budapest was so kind to calculate the approximate bodyweight of *Scolosaurus*. Basing his calculation on the dimensions of the reconstruction, he arrived to about 1700 cube-decimeters of living matter, corresponding to a body-weight of 1800 to 2000 kilogramms.

Taking that *Scolosaurus* consumed every week relatively as much food as the lizard mentioned by DODERLEIN, it would have consumed about 860 kilogramms of food a week, but if it did not eat relatively more than the *Python* mentioned by the same author, than it may have lived on 18 kilogramms. Because of *Scolosaurus* having been a huge, slow and sluggish animal, that lived in a warm climate, it quite probably consumed very little food.

These data tend to show that it may quite well have depended, as far as its foodsupply was concerned, on small desert animals and especially on the temporary occurrence of „locusts.“ As BUXTON¹⁾ has shown, on the northern hemisphere in many deserts in recent times the occurrence of *Orthoptera* shows two maxima: a principal one between March and July and a second one of less importance in October. This shows that even in a semi-desert region a coldblooded animal feeding on *Orthoptera* and capable of enduring long fasts, might find food all the year round.

¹⁾ BUXTON P. A.: Animal life in Deserts, a study of the fauna in relation to the environment. London, 1923.

One large grasshopper weighs about 2 grammes, so *Scolosaurus* could have lived on even less than 7000 grasshoppers and beetles a week.

Perhaps the dependency of *Scolosaurus* on the occasional insect-swarms of a dry climate contributed to some extent to its extinction, as it is well known that the proliferation of *Orthoptera* and other insects strongly depends on climatic conditions and evidences of a fairly strong climatic change to the worse at the end of the Cretaceous are quite abundant.

S y s t e m a t i c p o s i t i o n . As has already become evident in the course of the description, *Scolosaurus* differs quite markedly from the *Ceratopsidae* and the *Stegosauridae* and recalls those but incompletely known *Thyreophora*, in which the whole body is more or less covered by dermal ossifications.

These genera can provisionally be put together in three groups:

I.

Struthiosaurus (Turonian) (IX 828)
Tröodon (Belly River) (IX 340)
Stegoceras (Judith River) (IX 571)
Acanthopholis (Chalk) (IX 837)
Hylaeosaurus (Wealden) (IX 917)

II.

Ankylosaurus (Edmonton) (IX 91)
Palaeoscincus (Judith River) (IX 756)
Hierosaurus (Niobrara) (IX 1094)
Stegopelta (Benton) (IX 780)
Nodosaurus (Benton) (IX 631)
Polacanthus (Wealden) (IX 818)
Hoplitosaurus (Dakota) (IX 318)

III.

Panoplosaurus (Belly River) (IX 574)
Dyoplosaurus (Belly River) (IX 927)
Polacanthoides (Wealden)

The genera enumerated in the first column have all a remarkably small skull and cervical vertebrae decreasing forward rapidly in size. As far back as 1902 the genera comprised in this list have been grouped together as *Acanthopholidae*. In having relatively large cervical vertebrae, *Scolosaurus* is easily separated from this group.

The second and third column contains animals having a relatively large skull and accordingly also large cervical vertebrae. In the first of these latter groups (group II) the skull is relatively large and covered with numerous osseous bones (*Ankylosaurus*, *Palaeoscincus*), in the third group it is covered only with few bones (*Panoplosaurus*, *Dyoplosaurus*). When few skull-plates are present, correspondingly the number of nuchal plates is smaller.

Polacanthus, in which the skull is unknown, is separated from the first group on account of the large axis, described by SEELEY (IX 1000) and now supposed to belong to *Polacanthus*. *Hoplitosaurus* is placed into the second column on account of its great resemblance to *Polacanthus*. Of course there is yet no evidence as to whether *Polacanthus* and *Hoplitosaurus* belong into the second or third group. *Polacanthoides* resembles, as has already been pointed out, strongly to *Scolosaurus*, there-

fore it has to be entered into the same group as the latter. *Hierosaurus* and *Stegopelta* have nuchal plates, they must therefore be separated from *Struthiosaurus*, finally *Dyoplosaurus* has a skull recalling the one in *Panoplosaurus* and consequently these two must be placed together.

On account of its whole structure and especially on account of the large cervical vertebrae *Scolosaurus* can only be compared with the *Thyreophora* of the second and third column.

From *Ankylosaurus* the genus *Scolosaurus* can easily be distinguished by the shape of the glenoidal cavity, besides *Ankylosaurus* does not seem to have had dermal spines but only plates.

Palaeoscincus differs from *Scolosaurus* by the greater number of nuchal plates and by the lateral nuchal bones being armed with spines and not with crests.

On account of the fragmentary nature of its remains *Hierosaurus* is rather difficult to compare with *Scolosaurus*, luckily however in *Hierosaurus* a caudal dermal ring is preserved, while such rings do not occur in *Scolosaurus*.

Stegopelta resembles in so far *Scolosaurus* as also in this genus a median nuchal plate is present, that bears a Y-shaped furrow, in spite of this it can however easily be distinguished from *Scolosaurus* by the union of its dermal lumbar ossifications with the pelvis.

Polacanthus and *Hoplitosaurus* have gigantic asymmetrical dorsal spines, that are replaced in *Scolosaurus* to a good extent by flat dermal plates.

Of all better known American and European heavily armoured Dinosaurs *Panoplosaurus* comes nearest to *Scolosaurus*. It recalls the new Canadian fossil by the general nature of the nuchal plates and the acromion of the scapula, though each of the nuchal plates bears in *Panoplosaurus* a strong longitudinal keel, that is missing in *Scolosaurus*. The shape of the glenoidal cavity is also rather different and finally the proportion of the humerus to the tibia differs in the two genera.

In spite of its very similar caudal vertebrae *Dyoplosaurus* can easily be distinguished from *Scolosaurus* by the ornamentation of its tail.

Polacanthoides is rather similar in structure but the great difference of its geological age warrants a generic difference.

The outcome of these comparisons with various *Thyreophora* is that *Scolosaurus* is a genus of its own. Its characteristic features, by which it can be classed as a member of the *Ankylosauridae* and can at the same time be distinguished from the other members of this family, are:

Comparatively large cervical vertebrae, a scapula slightly longer than the humerus and bearing an acromion (?), a cranio-caudally elongated glenoidal cavity. Humerus a trifle longer than tibia and twice as long than radius. Ratio of humerus to femur 2 : 3. Dermal armour of neck consisting of two pairs of tuberculated nuchal plates and crested lateral plates. Back and tail segmented. On the anterior median region of the back a double row of blunt median spines and laterally crested plates. Further behind everywhere round disc-shaped dermal plates. The tail carrying two rows of spines diminishing backwards in number, but increasing in size. The humerus protected by imbricated dermal bones carrying alternatively pointed spines and sharp crests. Locality of the type specimen: Dead Lodge Canyon, Red Deer River, Alberta, Canada.

VII. ON THE CLASSIFICATION OF THE *CROCODILIA*.

The classification of the *Crocodylia* has been dealt with by various authors. HUXLEY (X 376) was the first, who pointed out that, during the evolution of *Crocodylia*, before all other things the shape of the vertebrae and of the choanae change. He accordingly separated a suborder *Mesosuchia* from a suborder *Eusuchia*. Into the first suborder were entered, without hesitation, *Steneosaurus*, *Pelagosaurus*, *Teleosaurus*, *Teleidosaurus* and *Metriorhynchus*, and with a query *Goniopholis*. The genera *Thoracosaurus*, *Holops* and *Gavialis* were placed among the Eusuchians.

In a most important paper, published in the *Geological Magazine* in 1887 LYDEKKER (X 470) distinguished three families. Family 1. *Teleosauridae* with the subfamilies *Teleosaurinae* and *Metriorhynchinae*; Family 2. *Goniopholidae* with the subfamilies *Petrosuchinae*, *Goniopholidinae* and *Bernissartinae*; Family 3. *Crocodylidae* with a longirostral and brevirostral section.

In 1887 KOKEN (X 409) thought it necessary to unite the longirostral Crocodiles into one group and the brevirostral ones in another. Among the longirostral mesozoic Crocodiles he distinguished three subfamilies, for which *Teleosaurus*, *Metriorhynchus* and *Teleidosaurus* may be considered as types. *Macrorhynchus* is considered as representative of a separate family, that includes also *Tomistoma*. He criticised LYDEKKER's classification and later on united the *Crocodylidae* with the *Bernissartinae*, the *Alligatoridae* he put together with the *Goniopholidae* and the *Macrorhynchidae* with the *Teleosauridae*. He thus formed three independent phyla, one of which was traced back to the Jurassic (X 410).

For the subsequent period ZITTEL's textbook is of first rate importance. In the first edition of ZITTEL's *Handbuch der Palaeontologie* (X 838) the *Crocodylia* were divided into two sections. For one section the name *Longirostres*, for the other the name *Brevirostres* was accepted. The longirostral section was made to include the families *Teleosauridae*, *Metriorhynchidae*, *Macrorhynchidae*, *Rhynchosuchidae* and *Gavialidae*, in the brevirostral section the *Atoposauridae*, *Goniopholidae*, *Alligatoridae* and *Crocodylidae* were put together. In 1919 O. ABEL (X 3) tried to improve the classification given by ZITTEL by laying no more stress on the development of the snout and therefore he distinguished the families *Teleosauridae*, *Geosauridae*, *Pholidosauridae*, *Atoposauridae*, *Crocodylidae* and *Gavialidae*. The genera *Goniopholis* and *Notosuchus* were included in the *Pholidosauridae*, *Lybicosuchus* and *Hylaeochampsia* in the *Crocodylidae*. As the following investigation will show, ABEL's trial was a failure.

In the last edition of ZITTEL's „Grundzüge“ BROILI (X 839) stuck essentially to the classification of the first edition, the terms *Longirostres* and *Brevirostres* were however omitted. BROILI dropped the family *Alligatoridae*, but he accepted for the genera *Congosaurus*, *Dyrosaurus* and *Libycosuchus* separate families. It is thus evident, that there exists a rather marked discrepancy between the classifications used by ABEL and by BROILI. In my book on the families of reptiles (X 588) I separated the *Teleosauridae* and *Geosauridae* from other *Crocodylia* and used for the rest of the Crocodiles the vague terms *Amphicoelidae* and *Procoelidae*; the classification of the rest was considered unsatisfactory.

Owing to the fact that lately my attention had been attracted by the importance of some points in the skeletal structure of the *Crocodylia* that had previously escaped general notice, a revision of the classification seemed possible.

The true Crocodiles are a quadrupedal suborder of the archosaurian reptiles. Together with the *Procrocodiloidea* they form the order *Crocodilia*.

The suborder *Crocodiloidea* comprises animals with conical teeth, a quadrate strongly rotated backward, a comparatively short neck and dorsal ribs articulating with two heads on the neural arch. Clavicularae are absent, a separate prepubis is always present and the tail is long and gradually passes into the body. The carpal bones are modified.

In a classification that is based only on the length of the snout one might distinguish in this group longirostral, brachyrostral and semi-longirostral forms; basing a classification on the shape of the centra of the vertebrae one would come to a division into an amphicoelous and into a procoelous group. In a poorly preserved longirostral fossil Crocodile from Nigeria the vertebrae are concave in front and very slightly convex behind (X 591). A classification that is only based on the position of the choanae would lead to the recognition of eusuchian and mesosuchian types. In the *Eusuchia* the vertebrae are procoelous, while they are amphicoelous in the *Mesosuchia*. Taking the relation of the nasals to the nares as a basis of classification, one comes to recognise one group in which the nasals divide the nares, a second group, in which they just only touch the nares, a third group, in which the nasals are already excluded from the nares, but retain the contact with the premaxillaries, and finally a fourth group, in which the nasals are not even in contact with the premaxillaries. As comparisons of different species in the genus *Crocodylus* show, such a classification is quite unnatural, for these changes are to a great extent only in correlation with the length of the snout. This holds also good for nearly all the other characters mentioned above, for also these are only signs of adaptation. In spite of such characters not being of great systematic value, nevertheless they were till now extensively used in the classification of the *Crocodilia*.

The development of the ventral armour, the presence of a prelacrymal fossa, the relationship of the parietal to the postfrontal, the relationship of the splenial to the symphysis and finally the development of the postorbital bar have all been more or less ignored in the systematic classification of the *Crocodiloidea*. DOLLO (X 209, 213) was, as far as I am aware, the only author who laid stress on some of these points.

The following classification of the *Crocodilia* is based on the relation of the splenial to the symphysis, the development of the jugal part of the postorbital bar, the relation of the parietal to the postfrontal, the presence of a perforation on the mandible and on the development of the ventral armour. Besides these characters there have been considered: the position of the choanae, the development of the nares, the presence of a prelacrymal fossa, the length of the muzzle, the type of the vertebral articulation and the peg on the dorsal dermal plates. A great many of these characters are not in correlation with each other, therefore it is possible to corroborate conclusions.

It seems as if it were possible to distinguish six families of *Crocodiloidea*. These are:

- | | |
|-----------------------------|---------------------------|
| 1. <i>Atoposauridae</i> , | 4. <i>Teleosauridae</i> , |
| 2. <i>Notosuchidae</i> , | 5. <i>Goniopholidae</i> , |
| 3. <i>Stomatosuchidae</i> , | 6. <i>Crocodylidae</i> . |

The distinct nature of the first four families will become clear by their definition, but the distinctness of the *Crocodylidae* and *Goniopholidae* may be questioned. The possibility has to be consi-

dered, that the animals included in the two last units might be grouped in a longirostral and in a brevirostral family. This would lead to the establishment of the longirostral family *Gavialidae* and the brevirostral family *Crocodylidae*. The value of such a classification will be discussed later on. For nearly each subfamily of these groups, on Plate IX the sketch of a typical member is given. Owing to the lack of space, figures of a representative of the *Stomatosuchidae* and of the *Hyposaurinae* had to be omitted, but on account of the bad preservation of the skulls of both types this omission is of minor importance.

1. *Atoposauridae*. The exclusively jurassic forms (X 456, 540, 795) belonging to this distinct group, are small, lizard-shaped, brevirostral reptiles, in which the nares are separated by the premaxillaries and the nasal bones. They differ from the *Procrocodiloidea* by the position of the postorbital bar and the flattened head. The postorbital bar is in a lower niveau than the other arches. The superior temporal fossae are small, the mandible has no perforation or only a very small one. The vertebrae are amphicoelous; the extremities are long, the dorsal armour is narrow, the ventral armour is wanting. This group comprises the genera *Alligatorium*, *Alligatorellus* and *Atoposaurus* (Fig. 1). According to BAUR (II 35), *Atoposaurus* differs from all other Crocodiles by having an ectepicondylar foramen. There exists a good amount of general resemblance between the *Atoposauridae* and the short-snouted *Goniopholidae*, but the feeble development of the dermal armour of the *Atoposauridae*, that recalls the feeble dermal armour of the *Procrocodiloidea*, enables one to distinguish the two units very sharply.

2. *Notosuchidae*. The *Notosuchidae* are strongly brevirostral Crocodiles of the upper Cretaceous (X 171, XIII 301), in which the orbits are very large and the quadrate is only slightly rotated backward. Both characters give the skull somewhat the same outline as that of a very young *Alligator*. The postfrontal touches the parietal, so that the frontal is excluded from the superior temporal fossa. These temporal fossae are small. The postorbital bar is depressed. The mandible has a very large perforation, the splenial enters into the symphysis, the vertebrae are amphicoelous. There exists no dermal armour. From the *Procrocodiloidea* this family is separated by the development of the postorbital bar and the carpals.

In this family the presence of a prelacrymal fossa, the structure of the nares and the arrangement of the openings of the palate separate the *Notosuchinae* from the *Lybicosuchinae*. In the *Notosuchinae*, that include the genera *Notosuchus* (fig. 2) and *Cynodontosuchus*, the nares are terminal and confluent, a prelacrymal fossa is present and the palate shows the normal type. In the *Lybicosuchinae*, that are established on the single genus *Lybicosuchus* (fig. 3), the nares are lateral and separated in the median line, the prelacrymal fossa is wanting and the palate shows a peculiar modification.

From the *Atoposauridae* the *Notosuchidae* can easily be distinguished by the outline of the skull, the large perforation of the mandible and the lack of a dermal armour. From the *Goniopholidae* they differ by the parietal touching the postfrontal, the large orbits and the large perforation of the mandible.

3. *Stomatosuchidae*. An investigation of the type of this group¹⁾ hitherto only represented by one genus, revealed some characters originally not recognised by Prof. STROMER (XIII 289). The skull is broad and flat, the upper temporal fossae are behind the fronto-parietal suture and nearly closed. The

¹⁾ NOPCSA FR. : Neue Beobachtungen an *Stomatosuchus*. Centralbl. f. Min. Geol. u. Palaeontol. Abt. B. Stuttgart, 1926.

large orbits are on the top of the skull and directed upwards. The part of the skull in front of the orbits is enormously elongated, but rounded in front. The quadrate has a curious shape and is rather strongly rotated backwards. The mandible is edentulous and was flexible in its anterior half, so that it was capable of forming, as in Pelicans, a huge pouch. There is no mandibular foramen but posteriorly the lower border of the mandible has a peculiar, wing-like expansion that served as surface of attachment for those muscles that held the pouch. The symphysis is very feeble. The vertebrae are procoelous. A dermal armour seems to have existed.

The weak symphysis, the thinness of the anterior part of the mandible, its wing-like process, the lack of mandibular teeth and the great elongation of the facial part of the skull, at once distinguish this group from all other Crocodiles. The trend of evolution of this group of gigantic Crocodiles is unparalleled among reptiles.

4. *Teleosauridae*. The majority of *Teleosauridae* occurs from the Lias to the Lower Cretaceous (X 21, 213), one type persisted, however, in Africa till to the Eocene (X 777). The *Teleosauridae* are longirostral Crocodiles with large superior temporal openings, which are to a large extent bordered by the frontals. In the armoured types the postorbital bar is on the same level as the other arches of the skull, in the unarmoured ones it is depressed. The splenial enters into the symphysis, the vertebrae are always amphicoelous or concave in front and flat behind.

According to the development of the dermal armour, the size of the prefrontal, the presence or absence of a prelacrymal fossa and the presence or absence of a mandibular perforation, three subfamilies may be distinguished. In the *Teleosaurinae*, that consist of the genera *Mycterosuchus*, *Pelagosaurus*, *Steneosaurus* (fig. 4), *Teleidosaurus* and *Teleosaurus*, the prefrontals are yet small, the postorbital bar is not depressed, prelacrymal fossae and mandibular perforations are present and the dermal plates of the dorsal armour have a characteristic peg. The ventral armour consists more or less of polygonal plates. This subfamily differs from the longirostral *Pholidosaurinae*, to be dealt with later on, by the position of the postorbital bar, by the size of the temporal fossae and by the presence of a prelacrymal fossa.

In the subfamily *Dyrosaurinae*, with the single genus *Dyrosaurus* (fig. 5), the prefrontals are likewise small, the postorbital bar is likewise not depressed, but the prelacrymal fossae are absent and a dermal armour is present. The mandibular perforation is very small. The histology of the bones is similar to that in *Teleosaurus*.

The third subfamily, *Geosaurinae*, comprises the genera *Dacosaurus*, *Geosaurus*, *Metriorhynchus* (fig. 6), *Neustosaurus* and *Enaliosuchus*. It is characterised by the large size of the prefrontals, by the depressed position of the postorbital bar, by the lack of a dermal armour and the specialisation of the extremities and of the tail. In *Geosaurus* the secondary Haversian systems are much more numerous than in the true *Teleosauridae*. The extremities of the *Geosaurinae* are webbed and more or less converted to paddles, the tail bore a caudal fin. The lack of a well marked preorbital fossa, of a mandibular perforation and of a dermal armour brings this subfamily somewhat near to the *Dyrosaurinae*.

With exception of the displacement of the postorbital bar, that has been developed independently in different families of Crocodiles, all the gradual changes that are observable between the *Teleosaurinae*, *Dyrosaurinae* and *Geosaurinae* are such as would be acquired by an adaptation to aquatic life,

it may however be mentioned, that the aquatic specialisation of the *Geosaurinae* is so great as to justify, to a certain extent, the creation of a special family *Geosauridae*. This family would have the same relation to the *Teleosauridae* as the *Mososauridae* to the *Platynotidae*.

The crocodylian ancestors of the primitive liassic *Teleosaurinae* are still unknown, because they cannot be sought for among any of the known *Crocodylia*, for they are distinguished from all Crocodiles by the exceedingly primitive structure of the postorbital arch. Such a primitive postorbital arch is not even met with among the primitive *Atoposauridae*. The *Geosaurinae* became extinct without leaving descendants.

The recent Crocodiles and the most of the fossil ones enter into none of the four families hitherto defined. They evidently form units of their own.

The length of the snout or the relation of the nasal bones to the nares enables one to distinguish among them brevirostral and longirostral types. The structure of the choanae and of the vertebral articulation leads to the establishment of a longirostral and brevirostral „mesosuchian“, and a longirostral and brevirostral „eusuchian“ group. In most of these „Mesosuchians“ the ventral armour is polygonal, it is however arranged in transverse rows and imbricated in all the „Eusuchians.“ Exceptionally it is imbricated also in some „Mesosuchians.“ In all the longirostral and in some brevirostral types the splenial enters into the symphysis, but it is excluded from the symphysis in some younger brevirostral types, that show eusuchian vertebrae and choanae.

The decision as to the nature of all the characters just mentioned, that are partly correlated with each other, is given by the bordering of the temporal fossae. This character, first emphasized by TROEDSSON, is not in correlation with the nature of the vertebral articulation, nor with the relation of the splenial to the symphysis. It gives therefore a good basis to control the conclusions arrived at by the study of all other parts.

In all *Procrocodyloidea*, in the *Atoposauridae*, in all *Teleosauridae*, in all other „Mesosuchians“, whether longirostral or brevirostral, and in two eusuchian genera, *Thoracosaurus*¹⁾ and *Leidyosuchus*, (X 306) the frontal partakes in the bordering of the upper temporal fossa, and the postfrontals and parietals do not touch each other. Contrarily to this, in the *Notosuchidae* and in the majority of the Eusuchians the parietals and the postfrontals touch each other and, consequently, the frontals are excluded from the temporal fossae.

This shows, as far as the longirostral types are concerned, that these probably derived from longirostral but mesosuchian types and that *Thoracosaurus* represents the intermediate stage. For the brevirostral types such a transition, indicated in *Leidyosuchus*, can be proved as well. This consideration would lead to the establishment of the families *Crocodylidae* and *Gavialidae* and the time will probably come, when the *Crocodylidae* will have to be grouped in this manner, provisionally however it is considered best to classify all the Crocodiles not pertaining to the *Atoposauridae*, *Notosuchidae*, *Teleosauridae* or *Stomatosuchidae* only according to their degree of specialisation and not according to their phylogenetic relation. This leads to the establishment of the families *Goniopholidae* and *Crocodylidae*.

¹⁾ TROEDSSON, G. T. On Crocodylian remains from the Danian in Sweden; Lunds Univers, Arskrift N. F, Avd. 2 Vol. XX, Lund, 1924.

5. *Goniopholidae*. The *Goniopholidae* (X 22, 299, 358, 409, 807, 817) are nearly all cretaceous, but one genus (*Congosaurus*, X 213) occurs also in the Eocene. In this family the frontals always border the temporal fossa, the postorbital bar is depressed, the nares are confluent, the choanae are in front of the pterygoids, the splenial enters into the symphysis, the mandible generally shows a very small perforation, the vertebrae are amphicoelous and the bony plates of dorsal dermal armour have a characteristic peg. The longirostral members of this group are distinguished from the longirostral armoured *Teleosauridae* by the development of their postorbital bar.

Among the *Goniopholidae* five subfamilies can be distinguished; three subfamilies, the *Pholidosaurinae*, the *Hyposaurinae* and the *Congosaurinae* are longirostral, two subfamilies, the *Goniopholinae* and *Bernissartinae* are brevirostral.

The *Goniopholinae* comprise the genera *Amphicotylus*, *Bottosaurus*, *Coelosuchus*, *Doratodon*¹⁾ and *Goniopholis* (Plate IX Fig. 7). They differ from the *Bernissartinae*, that include the genera *Bernissartia*, *Nannosuchus* and *Theriosuchus*, by the presence of a sometimes large prelacrymal fossa and the development of a more or less polygonal ventral armour. From the *Atoposauridae* they are separated by the presence of a ventral armour and the structure of the nares. Probably the *Goniopholidae* are descendants of some *Atoposauridae*, in which the dermal armour was gradually ameliorated, till it reached the imbricated state visible in the *Bernissartinae*. In the *Bernissartinae* the ventral armour is arranged in transverse rows and a prelacrymal fossa is wanting.

Much the same differences, as those that separate the *Goniopholinae* from the *Bernissartinae*, separate the longirostral *Congosaurinae* from the likewise longirostral *Pholidosaurinae*. The *Pholidosaurinae* and *Congosaurinae* are otherwise very similar, but in the *Pholidosaurinae* the ventral armour again consists more or less of polygonal plates, while it consists of bones arranged in transverse rows in the *Congosaurinae*. In accordance with this definition, *Crocodylimus*, *Machimosaurus*, *Petrosuchus*, *Pholidosaurus* (Plate IX Fig. 8.) and *Teleorhinus* have to be classed as *Pholidosaurinae*, *Congosaurus* is the only known member of the *Congosaurinae*.

Hyposaurus can probably be considered as the representative of a special subfamily that is essentially built on the Pholidosaurian plan, but differs from the *Pholidosaurinae* by the quite remarkable size of the upper temporal fossae (XIII 291). In this respect *Hyposaurus* recalls the *Teleosauridae*, it differs however from the *Teleosaurinae* and *Dyrosaurinae* by the depressed postorbital bar and from the *Geosaurinae* by its armour and by the feeble development of the prefrontals.

6. *Crocodylidae*. This family comprises all living Crocodiles and reaches back to the upper Cretaceous (X 22, 306, 410, 434, 554). It is characterised by the backward position of the choanae, the procoelous vertebrae, the confluent nares, the lack of a prelacrymal fossa, the presence of a large mandibular perforation, the lack of a peg on the bony elements of the dorsal armour and the transverse arrangement of the bony elements of the ventral armour. The postorbital bar is always depressed.

At present five subfamilies of *Crocodylidae* can be distinguished. Three subfamilies, the *Thoracosaurinae*, *Gavialinae* and *Hylaeochampsinae* are longirostral, two, the *Leidyosuchinae* and *Crocodylinae* are brevirostral.

¹⁾NOPCSA: Die Reptilien der Gosau in neuer Beleuchtung. Zentralblatt für Mineralogie, Geologie u. Palaeontologie, Abt. B. Stuttgart, 1926.

The *Thoracosaurinae*¹⁾ that comprise the genera *Thoracosaurus* (Plate IX Fig. 9) and *Holops* (X 129), unite to a certain extent the longirostral *Crocodylidae* with the longirostral *Congosaurinae*. Their structure is essentially crocodylian, but they differ in one important character. In all the other procoelous *Crocodylidae* the frontal is excluded from the temporal fossa, in the *Thoracosaurinae* it borders, however, this opening. The ventral armour of the *Thoracosaurinae* likewise recalls the ventral armour of the *Congosaurinae*. The true procoelous longirostral Crocodiles that belong to the subfamily *Gavialinae* are: *Eosuchus*, *Euthecodon*, *Gavialis* (Plate IX. Fig. 10), *Gavialosuchus*, *Gryphosuchus*, *Rhamphosuchus*, *Tomistoma*. In these the frontal is always excluded from the superior temporal opening, so that the parietal touches the prefrontal.

In the same manner as the longirostral *Thoracosaurinae* recall the *Congosaurinae*, so the brevirostral *Leidyosuchinae* recall the *Bernissartinae*, as in the latter the splenial enters into the symphysis, while it is excluded from the symphysis in all other brevirostral *Crocodylidae*.

At present the *Leidyosuchinae* comprise with certainty only the genera *Leidyosuchus* and *Allodaposuchus*²⁾ nov. gen., it is however probable that *Allognathosuchus* and *Heterosuchus* will also turn out to belong to this subfamily. *Allodaposuchus* is therefore of special importance, for its cervical vertebrae show that the differences leading to the genus *Crocodylus* on the one hand and *Alligator* on the other were already established at that stage of evolution, in which the frontals were yet bordered by the supratemporal fossae. Perhaps *Allognathosuchus* is a separate subfamily³⁾.

¹⁾ TROEDSSON: On Crocodylian remains etc. loc. cit.

²⁾ *Allodaposuchus* nov. gen. is closely allied to the genus *Crocodylus*, but differs from *Crocodylus* by the relation of the frontal to the temporal opening.

The generotype of this new genus is the species described and figured in 1915 and is represented by a set of bones from the Danian of Valiora in Transylvania. The remains comprise among others the top of the skull and parts of the atlas and epistropheus. The top of the skull is built as in *Leidyosuchus*, the atlas and the epistropheus as in the *Crocodylinae* allied to *Crocodylus* and not as in *Alligator* and its allies (X 572).

The species itself seems to be, so far as I could gather from both literary data figures and comparisons, identical with the form described by MATHERON under the name of *Crocodylus affuvelensis* (X 498) from the Danian of S. France. The lack of the atlas and of the top of the skull in the remains representing the latter species makes it doubtful whether the identification of the Transylvanian form, figured and mentioned first in 1915 (X 587), with the French form just referred to, is really correct in both the general and specific respect. Obvious congruence of the parts that are to be found in both specimens point towards their being identical, and this is why I hesitate at present to give to the Transylvanian species a new specific name. I refer to it, therefore, under the name of *Allodaposuchus* cf. ? *affuvelensis* MATHERON 1869 (NOPCSA 1928), emphasizing however that if the two forms in question should though prove to be specifically distinct, the generic name *Allodaposuchus* has to be retained for the Transylvanian species which I herewith designate as constituting the generotype. Provided that in future a specific difference should ever be established between the French and the Transylvanian species, I think the latter might be named *Allodaposuchus precedens*. The generic and this specific name seem therefore appropriate because they emphasize the fact, that this „modern“ Crocodylian of the Danian time is a forerunner of that new Asiatic terrestrial fauna of vertebrates that burst upon Europe at the beginning of the Eocene. The possibility of *Allodaposuchus* intermingling with the remnant „Wealden Fauna“ of Europe already in the Danian time was evidently simply due to the fact, that Crocodiles are good swimmers and thus, as always, among the first newcomers on isolated Oceanic islands.

The vexed rules of nomenclature that had to be taken in consideration, when renaming the Transylvanian Crocodile have been dealt with according to the advice given, as in the case of *Deuterosaurus*, by Baron G. FEJÉRVÁRY. This was all the more necessary as even according to his experience, the intricate question how the Transylvanian Crocodile has to be called, is hitherto unique. The term generotype, proposed by DUDICH and others, is employed to replace the former term genotype as used by American and other systematists and opposed to the term genotype as used in heredity research (compare genotype, holotype, etc. on the one hand, genotype and phenotype on the other).

³⁾ ABEL O.: *Allognathosuchus*, ein cheloniphage Nahrungsweise angepasster Krokodyltypus. Pal. Zeitschr. IX. Berlin, 1928.

According to what we know at present, all those brevirostral, procoelous *Crocodylidae*, in which the splenial is excluded from the symphysis and in which the frontal is excluded from the temporal fossa form one rather well defined subfamily. This subfamily must be called *Crocodylinae* and comprises the genera: *Alligator*, *Brachychampsa*, *Caiman*, *Caimanoidea*, *Crocodylus* (Plate IX Fig. 12), *Diplocynodon*, *Dinosuchus*, *Jacara*, *Osteolamus*, *Palimnarchus*, *Thecachampsa*, *Phobosuchus*. Perhaps with the time it will seem advisable to reduce all these names to the generic terms *Crocodylus*, *Alligator*, *Brachychampsa* and *Diplocynodon* and to use all the other names as subgeneric terms. Because of the *Thoracosaurinae* uniting the *Gavialinae* with the *Congosaurinae* and of the *Leidyosuchinae* uniting the *Crocodylinae* with the *Bernissartinae*, the *Crocodylidae* seem polyphyletic.

A genus of uncertain systematic position is the incompletely known *Hylaeochampsa*. It is a longirostral Crocodile with choanae situated far behind, probably procoelous vertebrae and a frontal more or less excluded from the temporal fossa. The palate of this genus shows quite unique features and necessitates its separation from the rest of the *Crocodylidae*, with which it otherwise bears a strong resemblance. An analogous perforation of the ectopterygoid as in *Hylaeochampsa* is to be met with in some *Saurischia* (*Tyrannosaurus*). Provisionally *Hylaeochampsa* (Plate IX Fig. 13) may be placed among the *Goniopholidae* as a representative of a special subfamily *Hylaeochampsinae*, and it may be considered as a forerunner of the *Thoracosaurinae*.

A good deal can already be said about the evolution of the *Crocodylia*. The *Teleosauridae* are evidently a very ancient stock that at a very early date sprang from the *Procrocodyloidea* and developed to some extent on crocodylian lines, but soon adapted strongly to marine life. This group culminated in the *Geosaurinae*. Perhaps the *Hyposaurinae* unite this group with the *Pholidosaurinae*. The crocodylian trend of evolution of the *Teleosauridae* can be discerned in the depression of the postorbital bar, that is found also in all the other *Crocodylia*, but that was evidently acquired independently in different groups.

The recent Crocodiles seem to be the offspring of two different mesozoic phyla, that are traceable to the perhaps diphyletic *Goniopholidae*. The different gaps are bridged over by the longirostral *Congosaurinae* and *Thoracosaurinae* and the brevirostral *Bernissartinae* and *Leidyosuchinae*. The *Goniopholidae* are perhaps again related to the *Atoposauridae*.

The *Notosuchidae* seem to be an aberrant phylum of the *Atoposauridae* or *Goniopholidae* that evidently became more terrestrial than the other *Crocodylia*. By doing so, this phylum lost the dermal armour and retained a rather embryonic skull-shape throughout life. Perhaps even the absence of the dermal armour is only an embryonic trait. The *Stomatosuchidae* may be considered as the descendants of some *Bernissartia*-like form that developed on aberrant lines, but likewise followed the eusuchian trend of evolution.

All these genetical relationships of the different *Crocodylia* are embodied in the adjoining diagram. The chronological sequence corresponds in a rough manner to the hypothetical line of descent. Difficulties arise only with the *Congosaurinae* and the *Dyrosaurinae*, for both these groups occur hitherto only in the Eocene of tropical Africa, while their morphological structure pleads for greater age. Probably both groups are till now only represented by Eocene stragglers of units, that in more ancient times inhabited also other parts of the globe.

Synoptical table of the CROCODILOIDEA

		Longirostral group		Brevirostral group	
Tertiary		CROCODILIDAE	<i>Gavialinae</i>	Crocodylinae	
Upper Cretaceous			<i>Thoracosaurinae</i>	<i>Leidyosuchinae</i>	NOTOSUCHIDAE
Lower Cretaceous		GONIOPHOLIDAE	(<i>Congosaurinae</i>)	<i>Bernissartinae</i>	Lybicosuchinae
			<i>Hylaeochampsinae</i>	<i>Goniopholidae</i>	
Jurassic	TELEOSAURIDAE	GONIOPHOLIDAE	<i>Pholidosaurinae</i>	ATOPOSAURIDAE	
	<i>Geosaurinae</i> (<i>Dyrosaurinae</i>)		<i>Hyposaurinae</i>		
Lias			<i>Teleosaurinae</i>		
Trias	PROCROCODILOIDEA				

In all Crocodiles amphicoelous vertebrae, a splenial entering into the symphysis, a not depressed postorbital bar, the presence of a prelacrymal fossa, separated nares, choanae situated far in front, a

narrow dorsal armour and a polygonal ventral armour or no ventral armour are primitive characters. The large perforation of the mandible and the contact of the parietal with the postfrontal may perhaps likewise be primitive characters for they occur already in the Pseudosuchians, but since these characters are wanting in the older Crocodiles, their turning up in the newer types may as well be cases of reversal.

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Plate I.

Fig. 1. *Deuterosaurus biarmicus*, type specimen from the side ($\frac{1}{3}$ nat. size).

c = canin *de* = dentary *sq* = squamosal

Fig. 2. The same from the other side (same reduction).

c = canin *de* = dentary *ju* = jugal
mo = molar tooth

Fig. 3. The same from in front.

Fig. 4. Newly discovered posterior part of the same piece ($\frac{1}{2}$ nat. size).

art = articular *exo* = exoccipital *ip* = interparietal
co = condyle *for* = foramen quadrati *qu* = quadrate
so = supraoccipital

Fig. 5. The same piece from behind (same reduction; parts lost indicated in outline).

ang = angular *ju* = jugal *qu* = quadrate
art = articular *mx* = maxillary *sq* = squamosal
co = condyle *Orb* = orbit *Te* = temporal opening
de = dentary *qj* = quadratojugal

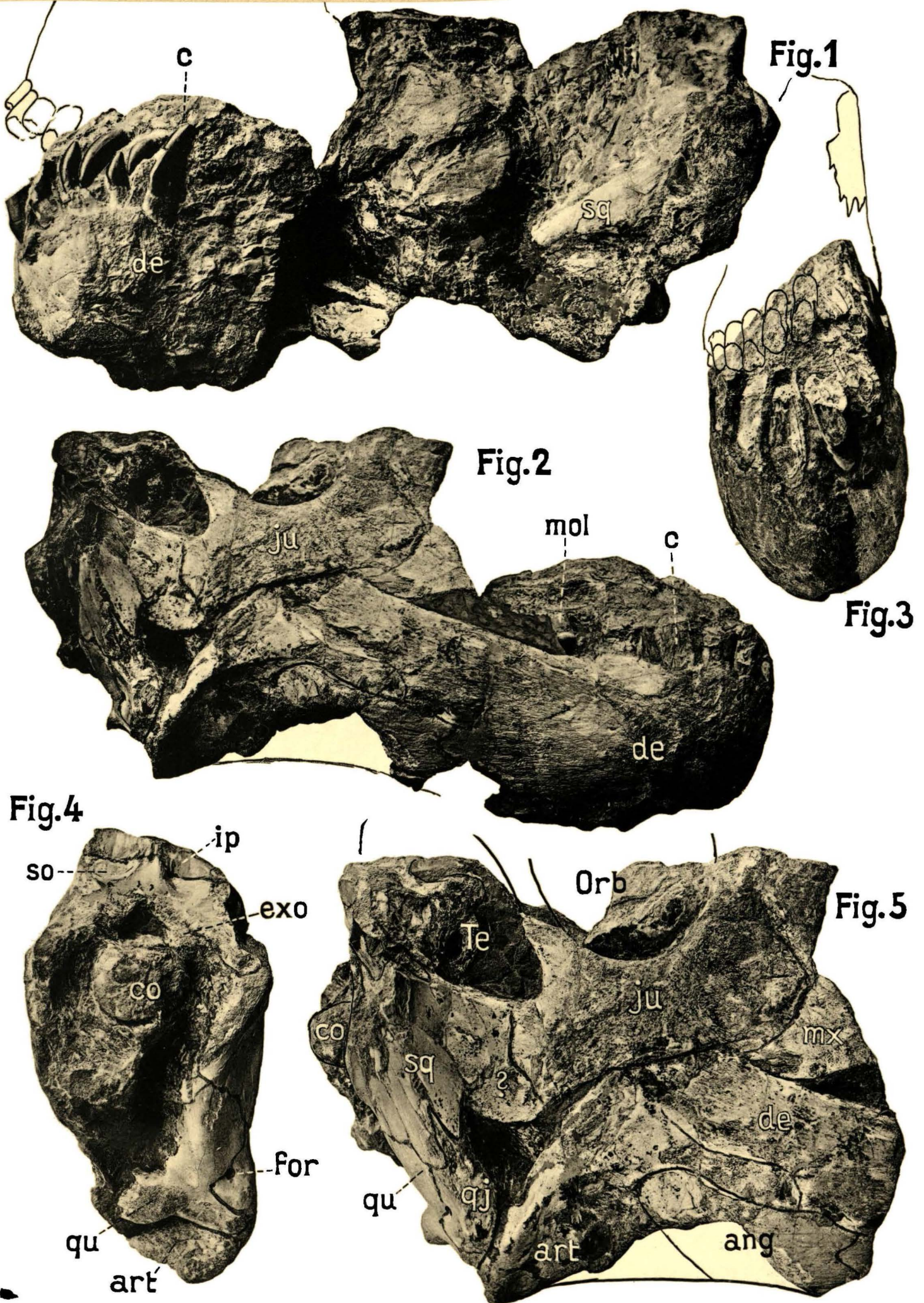


Plate II.

Fig. 1. *Psilotrachelosaurus Töplitschi* nov. gen. et spec. Type specimen viewed from above (twice natural size).

<i>cl</i> = clavicle	<i>co</i> = costoid	<i>cor</i> = coracoid
<i>fe</i> = femur	<i>hu</i> = humerus	<i>isch</i> = ischium
<i>pub</i> = pubis	<i>scap</i> = scapula	<i>vr</i> = ventral ribs

Fig. 2. *Pachypleurosaurus Edwardsi*. Skull of type specimen from above (twice natural size).

fr = frontal

Fig. 3. *Pachypleurosaurus Edwardsi*. Type specimen viewed from above (natural size).

<i>caud</i> = caudal vertebrae	<i>mt</i> = metatarsals	<i>Orb</i> = orbit
	<i>ra</i> = radius	

Fig. 4. Cast of ventral aspect of the scapular arch of the same specimen seen from below (natural size).

<i>cl</i> = clavicle	<i>hu</i> = humerus	<i>icl</i> = interclavicle
	<i>scap</i> = scapula	

Fig. 5. Posterior extremities of the same specimen (twice natural size).

<i>1—3</i> = sacral ribs	<i>fe</i> = femur	<i>il</i> = ilium
	<i>pub</i> = pubis	

Fig. 6. *Palaeohatteria longicauda*. Transverse section of a rib of the type specimen (strongly magnified).

<i>bc</i> = bone cells	<i>Hc</i> = Haversian canals	<i>ex</i> = exterior side
	<i>int</i> = interior side	

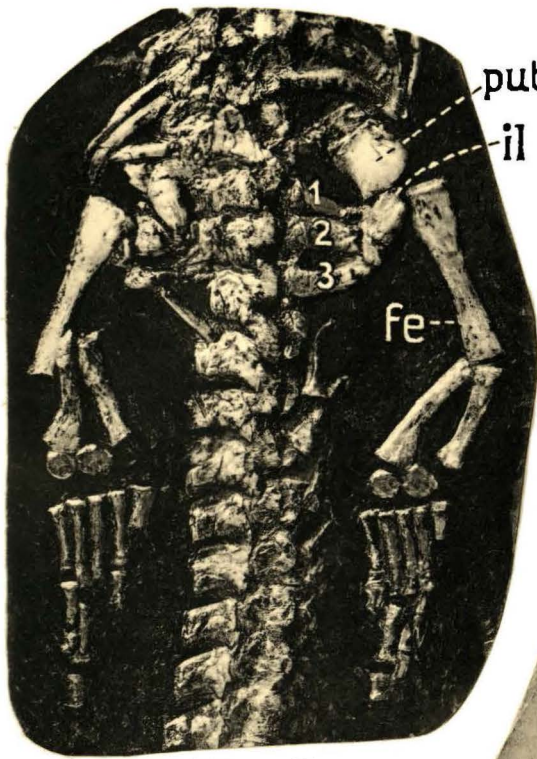


Fig. 5

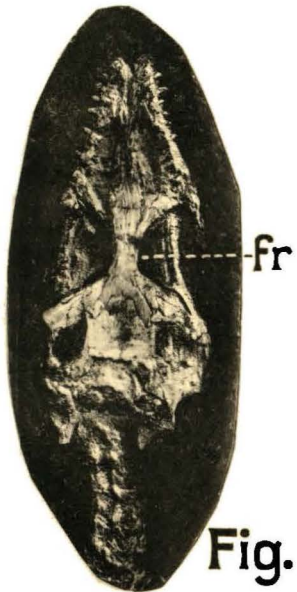


Fig. 2

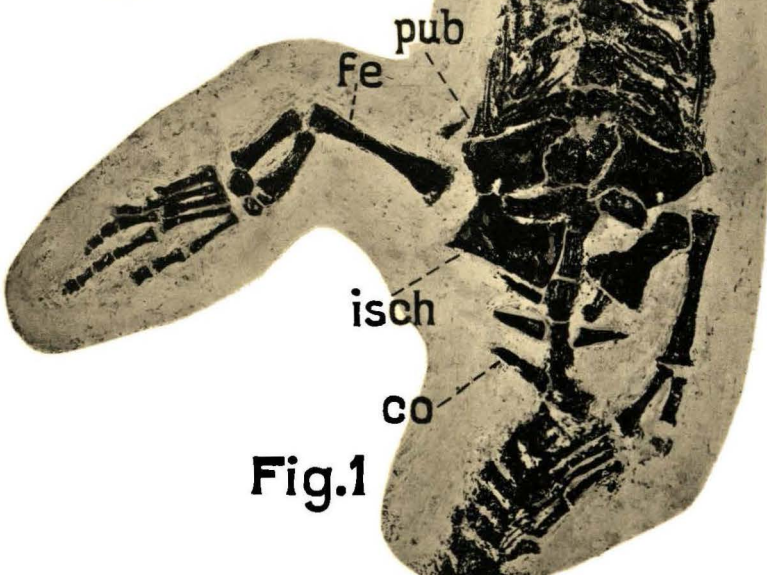


Fig. 1

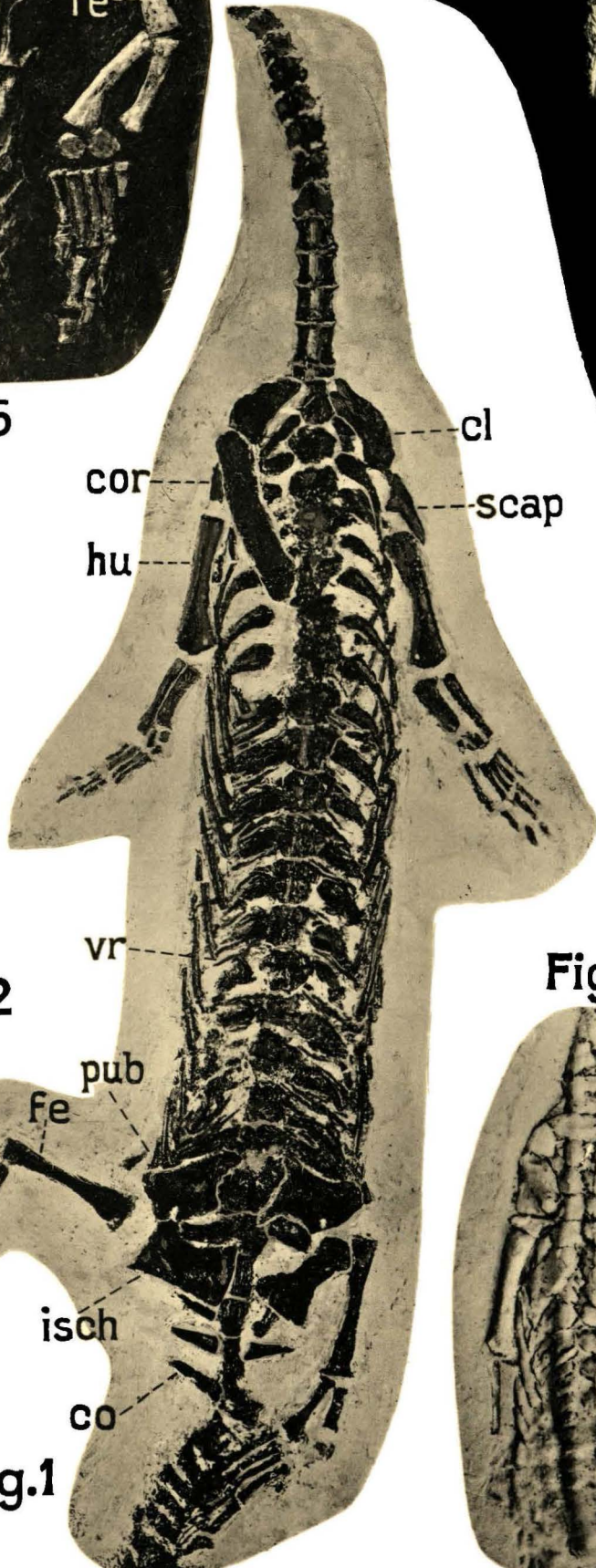


Fig. 3

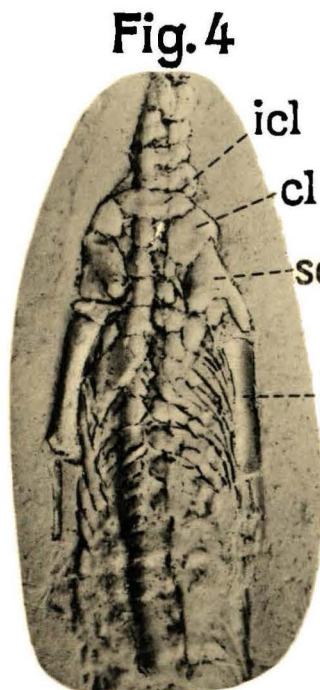


Fig. 4

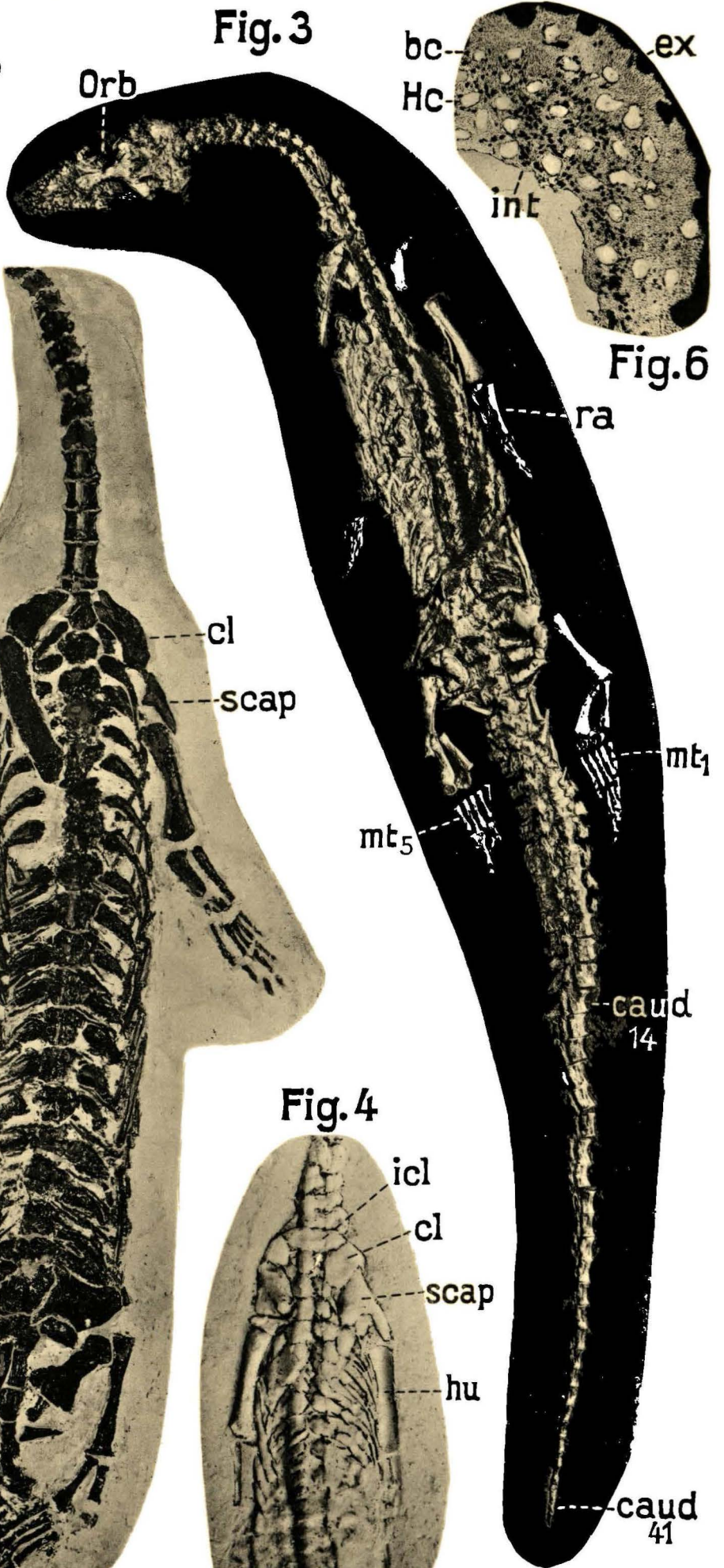
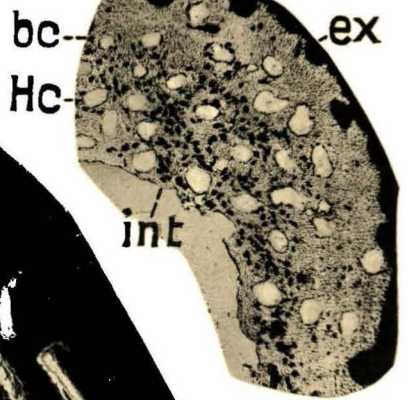


Fig. 6



bc
Hc
int
ex

ra

mt₁

mt₅

caud
14

caud
41

Plate III.

Fig. 1. *Dactylosaurus Schroederi*, nov. spec. Cast of the slab of the type specimen from above (natural size).

cl = clavicle *fe* = femur

Fig. 2. Cast of the counterslab of the same specimen from below (natural size).

co = coracoid *hu* = humerus *is* = ischium
pu = pubis *sc* = scapula

Fig. 3. Cast of the skull of the same specimen from below (twice natural size).

md = mandible *pt* = pterygoid

Fig. 4. Cast of the same skull from above (twice natural size).

md = mandible *fr* = frontal *qu* = quadrate

Fig. 5. Cast of the anterior extremity of the same specimen (twice natural size).

ra = radius

Fig. 6. Cast of the posterior extremity of the same specimen (twice natural size).

fe = femur *pu* = pubis *tib* = tibia



Fig. 2

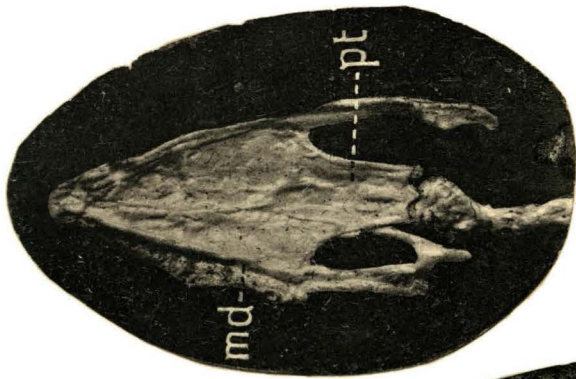


Fig. 3

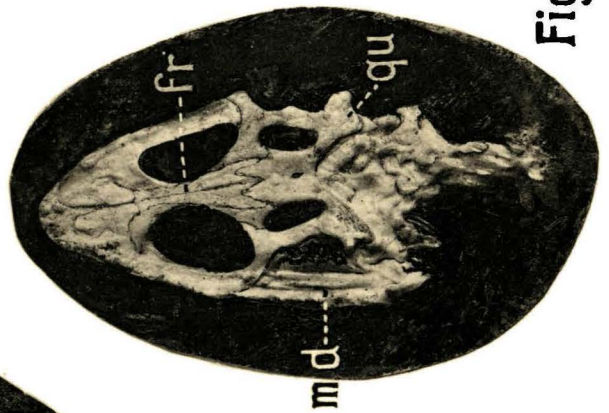


Fig. 4



Fig. 1

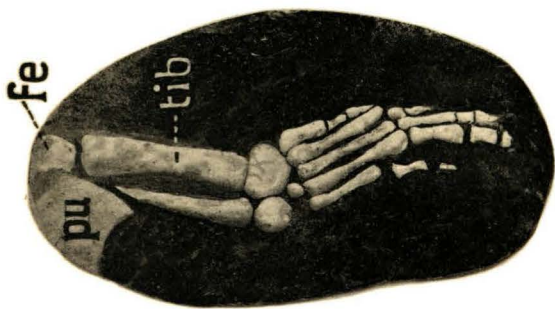


Fig. 6

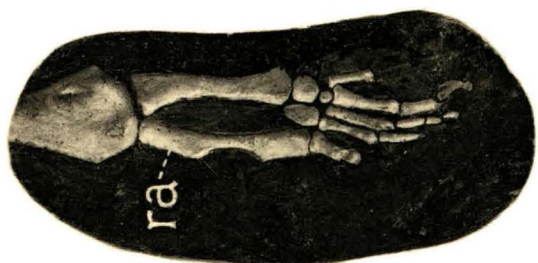


Fig. 5

Plate IV.

Fig. 1. *Anarosaurus pumilo*. Cast of the type specimen from below (natural size).

<i>art</i>	articular	<i>is</i>	= ischium	<i>pu</i>	= pubis
<i>co</i>	= coracoid	<i>p. p.</i>	= prepubic process	<i>qu</i>	= quadrate
<i>fe</i>	femur	<i>pt</i>	= pterygoid	<i>scap</i>	= scapula

Fig. 2. Cast of the counterslab of the same specimen from above (natural size).

<i>art</i>	articular	<i>hu</i>	= humerus	<i>sq</i>	= squamosum
<i>fe</i>	= femur	<i>il</i>	= ilium		

Fig. 3. *Pachypleurosaurus Edwardsi*. Adult Francfort specimen from above (natural size).

<i>cl</i>	= clavicle	<i>is</i>	= ischium	<i>pu</i>	= pubis
		<i>scap</i>	= scapula		

Fig. 4. *Neusticosaurus pusillus*. Skull of the type specimen from below (twice natural size).

<i>ch</i>	= choanae	<i>s. orb.</i>	= suborbital fossa
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Fig. 5. *Proneusticosaurus carinthiacus*. Transverse section of part of a rib (highly magnified).

<i>car</i>	= cartilaginous bone	<i>l. b</i>	= laminar bone	<i>Hl</i>	= Haversian laminae.
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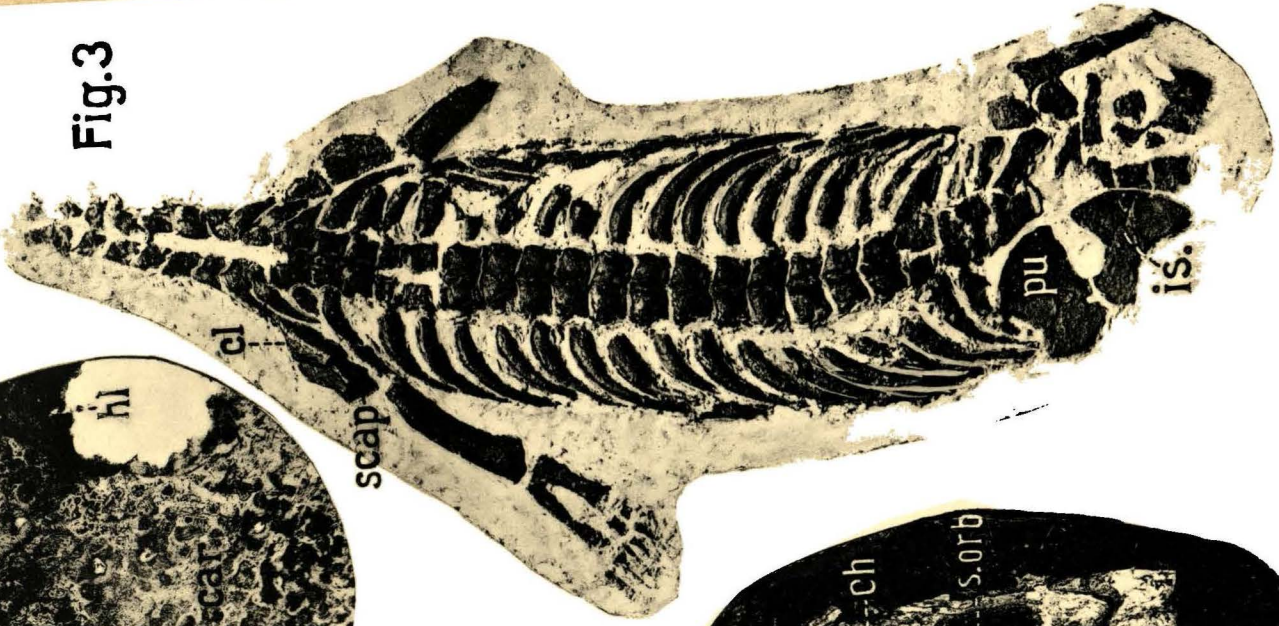


Fig. 3

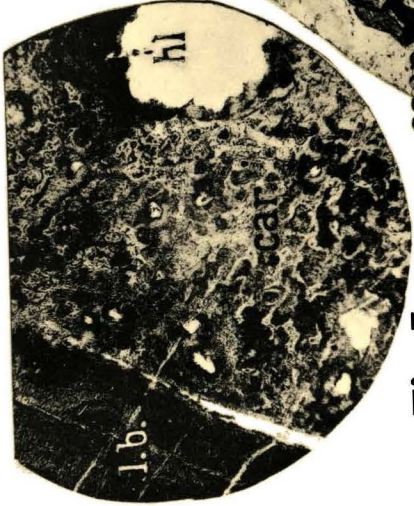


Fig. 5

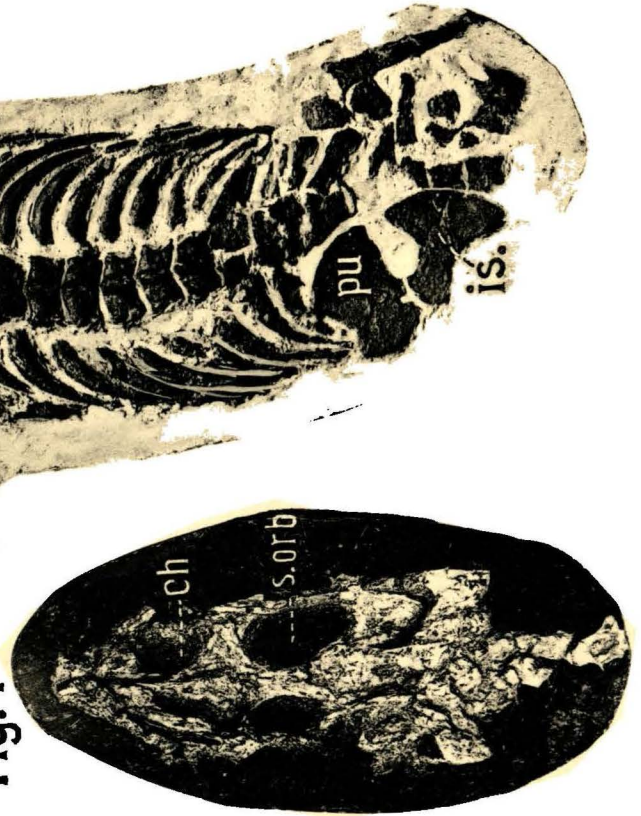


Fig. 4



Fig. 2



Fig. 1

Plate V.

Fig. 1. *Euoplocephalus* sp. Skull from above.

d == dermal plate

Fig. 2. The same specimen from the side.

d == dermal plate

ju == jugal

N == nares

O == orbit

Fig. 3. The same specimen from behind.

art == surface of articulation
of quadrate

co == condyle

d == dermal plate

eo == exoccipital

Fo == foramen magnum

pt == pterygoid

qu == quadrate

so == supraoccipital

Fig. 4. The same specimen from below.

alv == alveolar furrow

art == surface of articulation
of quadrate

bo == basioccipital

Ch == choanae

co == condyle

d == dermal bone

eo == exoccipital

ju == jugal

mx == maxillary

O == orbit

pa == palatine

p == pterygoid

qu == quadrate

sq == squamosal

tr == transversum

vo == vomer

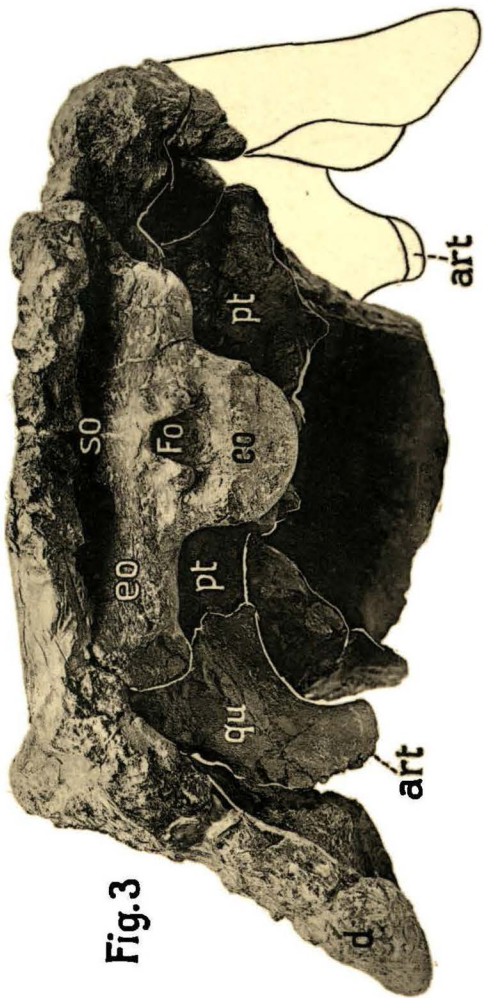
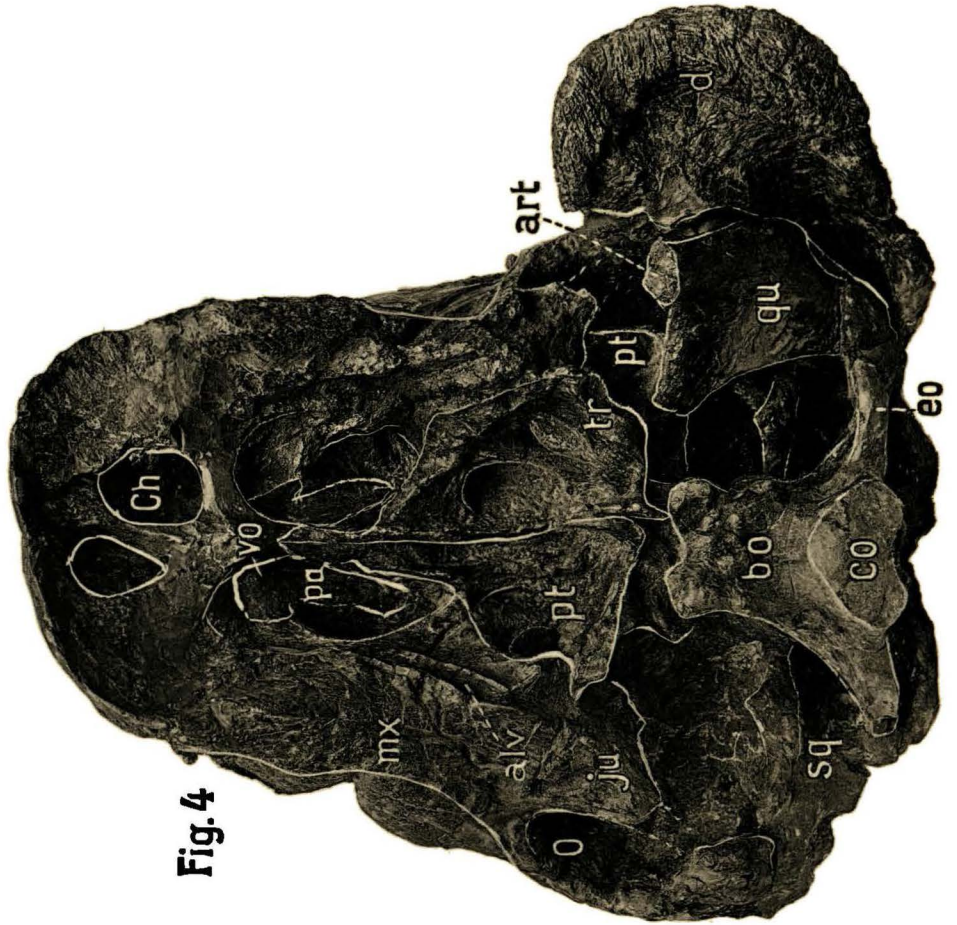


Plate VI.

Fig. 1. *Scolosaurus Cuttleri*. Anterior view of shoulder girdle and anterior limb (10/57 of nat. size).

<i>cerv</i> = cervical vertebrae	<i>co</i> = coracoid	<i>dors</i> = dorsal vertebrae
<i>d. r.</i> = dorsal ribs	<i>hu</i> = humerus	<i>h. sp</i> = humeral dermal spine
<i>ra</i> = radius	<i>ul</i> = ulna	

Fig. 2. Inferior view of the pelvic region of the same specimen (1/8 nat. size).

<i>ac</i> = acetabulum	<i>cd</i> = caudal vertebra	<i>fe</i> = femur
<i>il</i> = ilium	<i>is</i> = ischium	<i>mt</i> = metatarsal
	<i>tib</i> = tibia	

Fig. 3. Inferior view of the tail of the same specimen (the figure joins to fig. 2; 1/8 of nat. size).

<i>cd</i> = caudal vertebrae	<i>ch</i> = chevron bones
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Fig. 4. Dermal scutes on the back of the same specimen near a dorsal spine (nat. size).

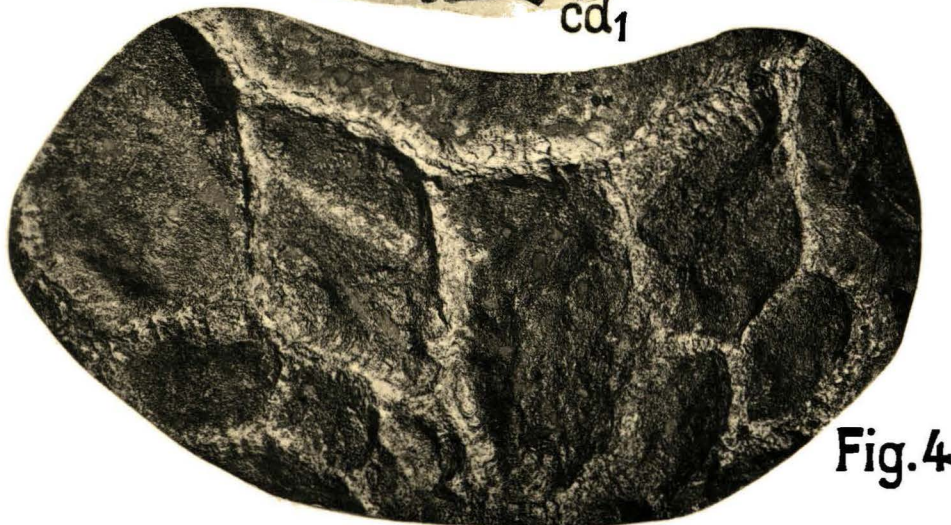
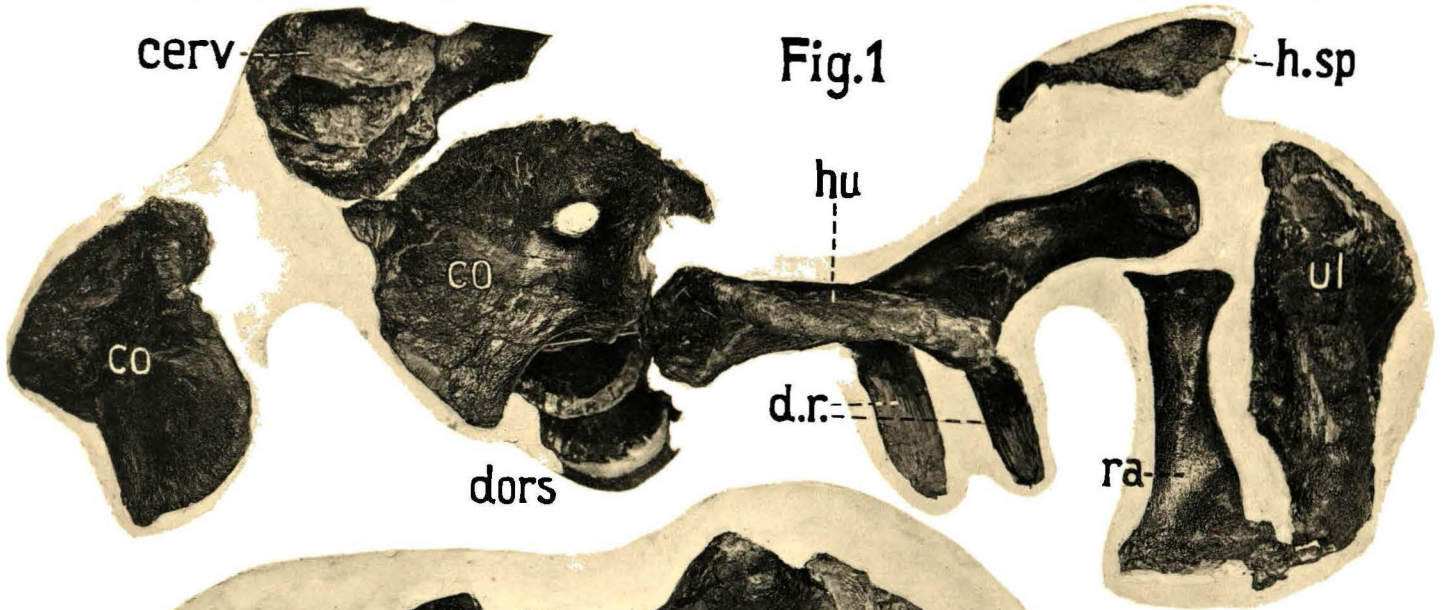


Plate VII.

Fig 1. *Scolosaurus Cuttleri*. Dorsal view (the proportion of the prelumbar part of the photograph to the postlumbar part is 25/225 to 27/225).

<i>dsp</i> = dorsal spines	<i>il</i> = ilium	<i>nu. p</i> = nuchal plates
<i>gsk</i> granular skin	<i>lp</i> lateral plates	<i>s. r.</i> sacral ribs
<i>hsp</i> humeral spine	<i>lr</i> = lumbar rib	<i>tr</i> dorsal rib
	<i>trf</i> = transverse folds	

Fig 2. Dermal scutes of the dorsal side of the tail near a transverse fold (nat. size). The arrow indicates the position of the head.

Fig. 3. Dermal elements of the lateral part of the tail (nat. size).

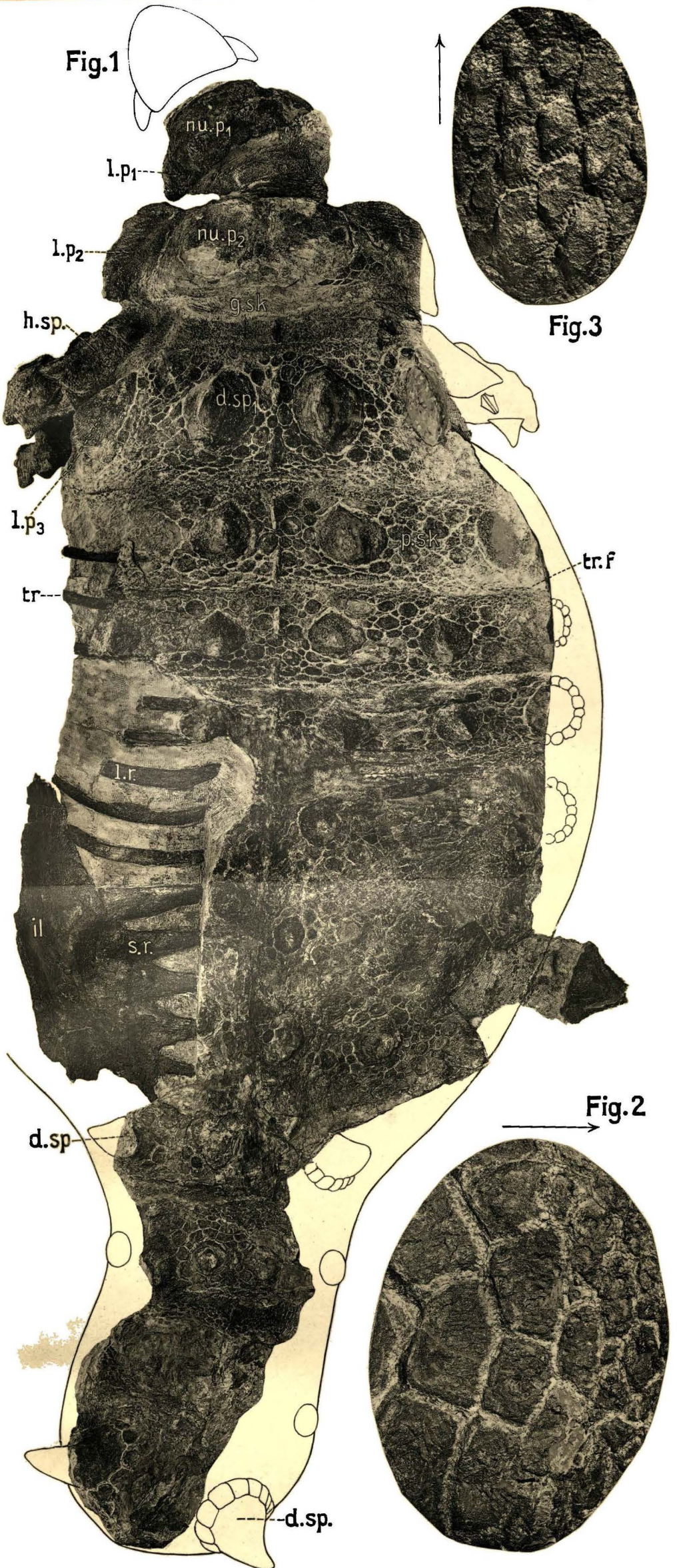


Fig.1

Fig.3

Fig.2

Plate VIII.

Scolosaurus Cutleri. Reconstruction (Published first in „The Illustrated London News“
Sept. 11. 1926 and reproduced here by the courtesy of the Editor).

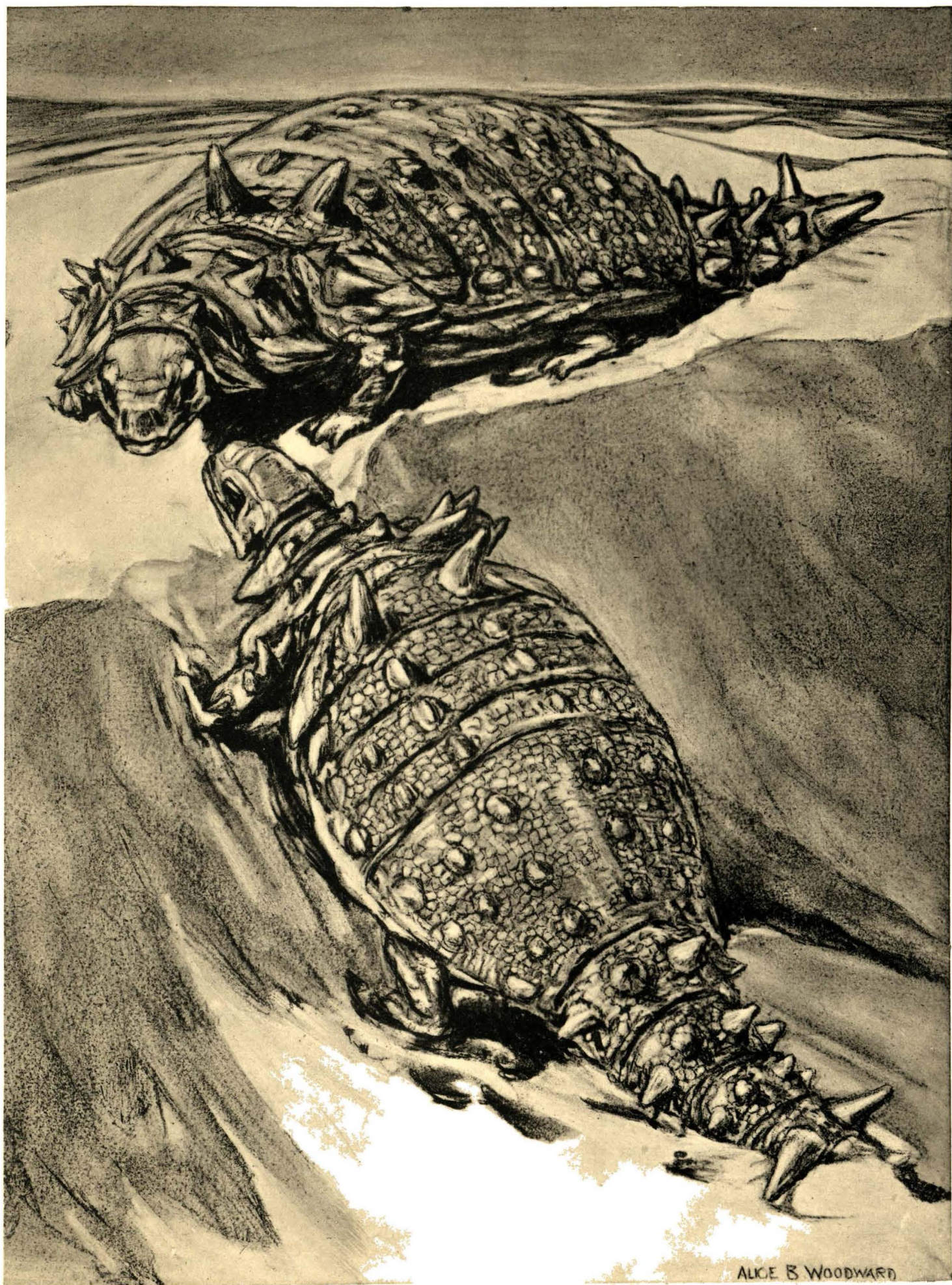


Plate IX.

- | | |
|---|-----------------------------|
| Fig. 1. Skull of <i>Atoposaurus</i> | (<i>Atoposauridae</i>). |
| Fig. 2. Skull of <i>Notosuchus</i> | } (<i>Notosuchidae</i>). |
| Fig. 3. Skull of <i>Lybicosuchus</i> | |
| Fig. 4. Skull of <i>Steneosaurus</i> | } (<i>Teleosauridae</i>). |
| Fig. 5. Skull of <i>Dyrosaurus</i> | |
| Fig. 6. Skull of <i>Metriorhynchus</i> | |
| Fig. 7. Skull of <i>Goniopholis</i> | } (<i>Goniopholidae</i>). |
| Fig. 8. Skull of <i>Pholidosaurus</i> | |
| Fig. 9. Skull of <i>Thoracosaurus</i> | } (<i>Crocodylidae</i>). |
| Fig. 10. Skull of <i>Gavialis</i> | |
| Fig. 11. Skull of <i>Leidyosuchus</i> | |
| Fig. 12. Skull of <i>Crocodylus</i> | |
| Fig. 13. Skull of <i>Hylaeochampsia</i> | (<i>Goniopholidae</i>). |

