

# GEOLOGICAL AND PALEONTOLOGICAL PAPERS

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## REVIEW OF THE REPTILIA OF THE TRIASSIC

BY

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IN TÜBINGEN

WITH 78 TEXT-FIGURES AND 9 PLATES

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## FOREWORD

The following compilation of Triassic reptiles arose as a by-product of the revision of the Dinosauria of the European Triassic. It was naturally necessary for me to learn about all the contemporaneous reptilian fauna. And indeed I went beyond Europe and brought the rest of the world into the range of my investigations, as far as was possible using the literature and friendly cooperation, especially of the American workers. I think I have seen most of the specimens in question that are preserved in the European collections. To this end I visited the following collections:

Anabach, Basel, Bayreuth (Kreismuseum and private collection of Herr STRUNZ), Berlin, Breslau, Bristol, Crailsheim (hon. BLEZINGER), Edinburgh (Museum of Science and Arts and Geological Survey), Elgin, Freiburg im Breisgau, Göttingen, Halle am Saale, London (British Museum, Jermyn Street Museum, and private collection of Prof. SEELEY), Milan, Munich, Oxford, Paris (Muséum d'Histoire naturelle and École des Mines), Poligny, Strassburg, Stuttgart, Tübingen, Vienna (Geological and Palaeontological Institute of the University, Hofmuseum and Imperial Geological Institute), Warsaw.

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I have attempted to assemble as much material as possible but I realize that there is still much omitted. It was not my aim to attain absolute completeness nor to treat all the usable data exhaustively, but I am satisfied to show at least to some extent the wealth and diversity of the reptilian fauna of the Triassic. Therefore I also tried to illustrate this by as large a number of figures as possible, many of which are copies, partly to save the reader numerous references. Many well-known facts are repeated, other new ones are produced in addition, which is in keeping with the character of such a compilation that, in a way, attempts to combine the results of previous studies in this field.

All parts of the work are not dealt with in the same way, thus e.g. the section on the Dinosauria is made very short, although most new facts could have been stated here. But since I will publish a larger monograph on this subject in the near future, I will not anticipate it.

In many respects it was not possible for me to keep to the often far too schematic classification of paleontological textbooks. This will perhaps be most striking in the "Rhynchocephalia." The Anomodontia are also interpreted in bounds rather different from usual. The thorny question of the relation between the Anomodontia and the Monotremata, or Mammalia in general, is not referred to at all, since I have not come to any satisfactory original opinion concerning it.

In the following, a number of new names are introduced, which are in part based on poor remains. This is only a last resort since it is more convenient to use names in discussion than to describe the piece each time.

Tübingen, 11th May 1902.

Friedrich von Huene.

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## A. INTRODUCTION

The reptilian fauna of the Triassic claims great interest since it includes nearly the oldest representatives of this vertebrate class and yet consists of very different elements. The attractiveness of this picture is increased further by the fact that the extremely diverse and well-known reptilian fauna of the Jurassic and Cretaceous is derived from that small vestige only by a comparatively limited evolutionary change. The distance to the Permian is much larger, since many orders had still not appeared there in the Triassic. The Permian characters are still recognizable and the Jurassic ones are already present.

When all the data are gathered, it is very surprising how many reptiles are included in the Triassic fauna; it is sufficient to quote the number of 153 genera (excluding synonyms). All orders represented in the Jurassic are already present and in addition there are the remarkable Anomodontia and the very interesting group Parasuchia standing between Crocodilia and Dinosauria. The Stegocephalia also play an important role, successors from the Permian which are almost entirely absent in the Jurassic (1). On the other hand, in the upper Mesozoic the first small mammals and the birds appear. The many small anomodonts of the South African Triassic and Central Europe (*Microlestes*, etc.) may well have recalled the former in appearance and mode of life.

We are in rather a good position to form an idea of the higher vertebrate fauna of the Triassic. Neither the dry land nor the water were more sparsely populated than at present in the regions which man has not yet devastated by his cultural efforts. Certainly today there are animals living so entirely differently that it is difficult to form a graphic conception of this fauna. We shall certainly find some creatures that, by our knowledge of recent animal populations of the earth, could appear to us as old friends by their external morphology. A number of large and small crocodile-like animals and some rare turtles belong here. But now a multitude of more or less strange forms follow, some downright fantastic. In the coastal seas the rapacious Nothosauria, etc. in all possible sizes swim with paddling movements; the long swan-neck gave them quite a strange appearance. These are reproduced on a larger scale in the contemporaneous Plesiosauria; the body short, squat, broad, flat; on it a short thick tail and a neck as long as the thorax and tail together; the small head armed with pointed long teeth, the four adapted paddle-like limbs, long, broad and pointed at the end. Likewise in the salt water some Ichthyosauria moved, forerunners of the fish-like reptiles which populated the sea in large herds in the succeeding Liassic period. In the fresh water and its surroundings lived the very numerous crocodiles, among which the long-snouted forms, such as *Mystriosuchus* in particular, were predestined to grub for food in the mud like the present-day gavia. These crocodiles attract attention by their strong and sometimes beautifully decorated armor. The peculiar Stegocephalia mostly stayed in swamps and near water. They are generally ranked with the Amphibia which include today the insignificant frogs and salamanders. But these strongly armed monsters equipped with formidable teeth are very different from them; the head alone in many was almost 1 m long. Also the Pterosauria, which can be compared with the remotely related bats, are not quite absent from the Triassic.

The two groups remaining are the most extensive and important, namely Dinosauria and Anomodontia. They populated especially the land. Dinosauria (i.e. in this case, Theropoda), whose length varies from 2 to about 10 m, had a heavy, large body, long neck and tail, very strong,

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(1) Found in the English Lias and Dogger (see below).

large hind legs and small, but muscular forelimbs which were probably used occasionally for locomotion and support of the body, but mainly for the seizing and holding fast of prey. The extremely small head must also have given these strange beasts a highly peculiar appearance. More than 20 different genera of dinosaurs compete in the strangeness of their body structure. Some of them are distinguished by an extremely long, flexible neck and tail (*Tanystrophaeus*); its belly was greatly distended and supported by bones (pubis); thus when it lowered itself it could rest on the ground and then be used as a support.

Anomodontia is composed of animals very different in appearance. Their size ranges from that of an ox to that of a mouse. In general they are stoutly built, have a large head, short neck and relatively long legs. Their teeth sometimes recall reptiles, sometimes mammals. According to their mode of life and appearance, we find among them large carnivores, small insectivores, fat rodents and stout herbivores, even the turtle-like Placodontia number in their ranks. They populated particularly the great continents, grown over with the *Glossopteris* flora with their rivers and lakes as well as the salt water of the coast.

After we have briefly compiled information on the extent of the Triassic Reptilia, it will be of value to discuss the most important data and points of comparison of the particular groups, in order to combine the results for an overall view.

## B. THE EIGHT REPTILE ORDERS, WITH DISCUSSION OF INTERESTING AND NEW FORMS AS AN APPENDIX TO EACH SECTION

### 1. "RHYNCHOCEPHALIA"

In textbooks Rhynchocephalia are placed at the head of Reptilia. The order Rhynchocephalia will include, by common characters:

- 1) Proganosauria (essentially *Palaeohatteria* and *Proterosaurus*),
- 2) Mesosauria,
- 3) *Rhynchosaurus* and *Hyperodapedon*,
- 4) *Telerpeton*,
- 5) Pleurosauridae (i.e. the elongated Jurassic forms *Homoeosaurus*, *Pleurosaurus*, *Sapheosaurus*, *Sauranodon*, etc.),
- 6) *Champsosaurus*, and
- 7) *Hatteria*.

The differences between Proterosauridae and the genera of the Upper Jurassic or Rhynchosauridae and *Hatteria* are obvious. I think it is practical henceforth to detach Proganosauria as a separate group, for they have closer relation with Crocodylia and Dinosauria and with many Anomodontia and in several points with Stegocephalia (cf. e.g. pelvis). This may be dealt with in more detail elsewhere. *Rhynchosaurus* and *Hyperodapedon*, the Rhynchosauridae, are a very specialized group which deviates widely from Proganosauria. Their dentition is highly adapted to a specific way of life and recalls to some extent Endothiodontidae. The structure of the premaxilla nearly makes these forms degenerate. *Rhynchosaurus* recalls *Ornithosuchus* somewhat in the form of the head, thus a parasuchian; also its scapula is very crocodile- or dinosaur-like. But otherwise, particularly in *Hyperodapedon*, there is much similarity with therosuchian Anomodontia. The long transverse processes of the caudal vertebrae are not unlike those of

*Pareiasaurus*. According to R. BURCKHARDT (1), both these genera are most closely related to the Endothiodontidae, which in their turn occupy a rather isolated position among Therosuchia. The vertebrae of Rhynchosauridae should be opisthocoelous, as well as the several Proganosauria. They have less in common with true Rhynchocephalia of the Mesozoic and the present day and are definitely to be separated from them.

The Mesosauria, which likewise often figure as Rhynchocephalia, occupy a most interesting central position between Anomodontia and Sauropterygia (particularly Plesiosauria). The whole structure recalls the latter very much. The distally expanded humerus shows an entepicondyloid foramen, like Nothosauria. The limbs are still developed as walking feet. The lower leg recalls *Archegosaurus* in that tibia and fibula diverge strongly and are curved outward as in the former. Astragalus and intermedium are fused, the calcaneum is separate; if one thinks this is also fused, the first tarsal row would resemble *Pareiasaurus* and *Sclerosaurus* most; the outline is the same. (On Mesosauria, cf. the sections on Anomodontia and Sauropterygia.) Further connections exist with Proganosauria, but those to Anomodontia and particularly Sauropterygia are so great that one is best to regard them as South African and American forerunners or representatives of the latter in the Triassic.

Finally, *Telerpeton* from Elgin still remains as a Triassic rhynchocephalian. It has absolutely nothing to do with Rhynchosauridae and Mesosauridae. However, as far as is known, it seems that true Rhynchocephalia of the Mesozoic and kionocrane Lacertilia stand closer. A glance at the pelvis and the posterior half of the skull, particularly the quadrate, suffices to produce this impression. *Telerpeton* is very lacertilian-like. But the pelvis also rather recalls *Eryops*. It is not at all impossible that a direct connection exists between the temnospondylous Stegocephalia and *Telerpeton* and from here to Mesozoic Plesiosauridae, etc. and *Hatteria*.

The important studies of OSAWA, SCHAUNSLAND, and HOWES, among others, have shown that even *Hatteria* of the present day is closely related to Lacertilia. Without wishing to repeat the arguments of the authors named, I might only call attention to the great differences between *Hatteria* on the one hand and Proganosauria and Rhynchosauria on the other. The nearly dogmatized isolation of "Rhynchocephalia" is severely shaken by this. Also, it is not admissible to judge a whole host of fossil reptiles by the present-day *Hatteria*, for this has recently been claimed, from a zoological point of view, as a highly specialized lacertilian.

#### PROTEROSAURUS-LIKE REPTILE FROM THE BUNTER SANDSTONE

In the collection of the Geological Institute at Halle is found a large slab from the *Cheirotherium* Beds of the Middle Bunter Sandstone of Bernburg, which contains a confused jumble of poorly preserved bone remains. The hon. VON FRITSCH called my attention to it very kindly with the comment that it was probably a proterosaurid. This view seems most likely to me although I do not venture to maintain it with absolute certainty. I refer to the interesting occurrence here only for the sake of the completeness of the review of the Triassic.

The elongated caudal vertebrae, the short and high dorsal vertebrae, the femur and the abdominal ribs seem to me to indicate a proterosaurid. Five cervical vertebrae are preserved in connection and two isolated; in a length of ca. 4 cm they reach a height of ca. 2 cm; the zygapophyses are strongly developed, and the spinous process is broad and low. One of the caudal vertebrae recalls the 4th cervical vertebra of *Proterosaurus speneri* which SEELEY figured (1). The

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(1) *Geol. Mag.*, 1900, vol. VII, pp. 486-492.

(1) *Phil. Trans. Roy. Soc. London*, vol. 178, 1887, p. 208.

dorsal vertebrae have distally thickened spinous processes. The four connected dorsal vertebrae are 2.5 cm long and 4-5 cm high; the centrum itself is only ca. 1.5 cm high. An upper arch shows a long, thick spinous process, and an articular surface displays a deepened facet. The numerous dorsal ribs are single-headed with a thickened and particularly high proximal end that possesses a trace of doubleness. Angularly curved abdominal ribs of varying structure are scattered over the whole slab; between them lie peculiar structures that I take for cervical ribs. The broad, straight femur is quite reminiscent of *Proterosaurus*. Pubis and scapula are not unlike many Sauropterygia. It is not my intention to describe this unique find or to name the animal (2). I specify it only as a proterosaurid.

## 2. ICHTHYOPTERYGIA

In connection with "Rhynchocephalia" a few words will be said on Ichthyopterygia. In the Triassic they still play quite a subordinate but nevertheless very interesting role, for this later so important group appeared for the first time here. Certainly the Triassic Ichthyosauria do not indicate as much of the phylogeny of that class as one might hope. BAUR first called attention to the fact that radius and ulna in the skeleton from the Raibl beds of Besano, which he separated as *Mixosaurus*, are still clearly elongated bones and readily distinguishable from the carpals. This was the first confirmation of the natural postulate, that the Ichthyosauria must have come from land reptiles; from which ones is certainly the important question, and we are still unfortunately not certain on this. Tibia and fibula are elongated just like the forearm bones. The main difference, however, from Liassic Ichthyosauria lies in the shoulder girdle (3).

Unfortunately it is still not possible to say anything at present on the phylogeny of Ichthyosauria. The general plan of the head agrees, as Rhynchocephalia. The pineal foramen in both lies in the posterior half of the frontals and not in the parietals as in most Reptilia.

The Ichthyosauria appear for the first time in the Wellenkalk. They are found particularly frequently in western Württemberg, less often in north Germany (e.g. at Querfurt, north of the Harz). Several of the smaller vertebrae recall *Mixosaurus* very much; other larger ones certainly differ. It is not impossible that the latter belong to *Shastasaurus*. Here I reckon particularly an upper arch of a dorsal vertebra from the Wellenkalk of Freudenstadt, which is found in the Tübingen Museum. The spinous processes of *Mixosaurus* are long and slim but *Shastasaurus* has thick, short spinous processes with weakly developed zygapophyses, as also the upper arch in question from Freudenstadt. The Tübingen collection possesses from the same locality and stratum a well-preserved episternum, which is far broader than that of a Liassic *Ichthyosaurus* and itself broader than that of *Mixosaurus*. The humerus, which E. FRAAS figured in his time (1), and because of which he placed the Swabian species in *Mixosaurus*, is interpreted incorrectly; according to FRAAS it should possess two articular surfaces separated by an interspace at the distal end, which indicates an elongated radius and ulna. But now the humerus of *Mixosaurus* has, in spite of the fact that these bones are noticeably elongated, two distal articular surfaces meeting each other roof-like exactly. If one examines the Tübingen humerus, the surface interpreted as an articular facet is doubtfully a fracture surface, while the interspace is a part of the articular surface pushing closely into the other. But a definite conclusion on *Mixosaurus* or *Ichthyosaurus* cannot be

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(2) In a more detailed treatment, many interesting facts would no doubt emerge.

(3) More exact explanations of these and other points is awaited in a description of the Mixosauria by Prof. REPOSSI of Milan, due to appear soon.

(1) Die Ichthyosaurier der süddeutschen Trias- und Jurasblagerungen. Tübingen, 1891, pl. 3, fig. 5.

drawn from this for they are both the same in this point. Several *Ichthyosaurus* vertebrae have been found also in the Lower Muschelkalk at Halle am Saale, among others a small lower jaw which is very like that of *Mixosaurus*. Larger *Ichthyosaurus* vertebrae occur in between in the Schaumkalk of Freiburg am Unstrut (Middle Muschelkalk); four of these are found in the Geological Museum at Halle.

In the collection of the Imperial Geological Institute of Vienna are three *Ichthyosaurus* vertebrae (?*Shastasaurus*) from Grossreifling, Styria from the Reifling Limestone. Since the large skeleton which was destroyed by the burning of the monastery Admont comes from the same locality (also because of the handed-down drawing (VON ARTHABER, *Beitr. z. Pal. Österr.-Ung.*, Bd. 10, p. 108)), we can probably assume that this also belonged to an *Ichthyosaurus* and not a *Capitosaurus*. The block with a 4-foot long head was found in 1843 by Prof. FRANGER. H. von MEYER, who only knew it from a sketch and oral description, compared it with *Ichthyosaurus platyodon* (1). At Ettersburg, near Weimar, *Ichthyosaurus* vertebrae have been found in the Upper Muschelkalk, which are now preserved in the Mineralogical Museum at Jena (2).

The Ichthyosauria from the Raibl Beds of Besano have already been mentioned. *Shastasaurus pacificus* MERRIAM is found in the Upper Triassic of Shasta County, California, and in the Upper Triassic of Spitzbergen (*Shastasaurus polaris* and *Mixosaurus nordenskjöldi* HULKE sp. 1873). In the Rhaetic, *Ichthyosaurus* remains are frequent; I mention centra from the Swabian bonebed, vertebrae and skeletal bones from the Rhaetic of Autun, France (*Rhachitrema pellati* SAUVAGE is an upper arch of an ichthyosaur, moreover *I. rhaeticus* and *I. carinatus* SVGE. also occur there) and numerous vertebrae from the Rhaetic of Aust Cliff, near Bristol; a giant snout fragment also comes from there (size of *I. platyodon* and *I. trigonodon*), preserved in the Bristol Museum. From the Kössen Beds of the Schlemmer Mountains in Achenerthal, H. von MEYER knew of two *Ichthyosaurus* vertebrae (3).

### 3. ANOMODONTIA (AND STEGOCEPHALIA)

The order of Anomodontia (= Theromorpha) includes a large number of different forms, some of quite peculiar appearance. Many of them attained considerable size. Beside great specialization is found extreme primitiveness.

Most genera are chiefly based on characters of the skull, and here again the greatest authority on South African Anomodontia, H. G. SEELEY, places the greatest value on the development of the palate. He divides the order (4) into two groups, differing rather from COPE and ZITTEL; the first group, Therosuchia, embraces ZITTEL's Theriodontia and Pareiasauria, the second, Therochelonina, contains Dicynodontia, and thus R. OWEN's "Anomodontia". SEELEY also thinks it probable that Mesosauria (*Mesosaurus* and *Saurosternum*), which were placed in "Rhynchocephalia" by ZITTEL, should form a third suborder; in any case, however, *Mesosaurus* is closely related to Endothidontia, which could rather be brought into relationship with Proganosauria. All Anomodontia (as also Sauropterygia and Chelonina) have only a single pair of temporal fossae, but *Palaeohatteria* and Rhynchosauria have two. However *Proterosaurus*, which was placed in Proganosauria by ZITTEL, ought likewise to possess only a single pair of temporal

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(1) *N. Jahrb. f. Min.*, 1847, p. 190 and 191.

(2) *N. Jahrb. f. Min.*, 1856, p. 825.

(3) *N. Jahrb. f. Min.*, 1856, p. 824 and 825.

(4) SEELEY, On the Theriodontia. *Phil. Trans. Roy. Soc. London*, vol. 185, 1894, p. 1013 pp.

fossae, according to SEELEY's studies and reconstruction. Only in *Galesaurus*, a theriodont, is the temporal fossa nearly split in two by a piece of bone reaching in from far in front (?postorbital). Palatal dentition which, already as such, recalls Stegocephalia and Rhynchosauria, is found in Pareiasauria and Endothiodontia. The palate of Theriodontia (Lycosauria, Cynodontia and Gomphodontia) strongly resembles *Hatteria* by the narrow pterygoid, curved characteristically outward. In front lie broad palatines that run backward and downward into a transverse process ("palato-transversal" SEELEY); between pterygoid and palatine lies an unpaired palatal opening as in *Hatteria*. In Pareiasauria also the unpaired palatal opening is found far back between pterygoid and palatine. The toothed palatines have a great extent; in the middle in front the vomers, which likewise bear teeth, participate in the formation of the palate; long lateral processes of the pterygoid are connected with the quadrate, the basisphenoid is very short. In the massive skull of *Endothiodon* the unpaired palatal opening also lies behind the main part of the toothed palatine; the latter do not meet in the midline, the channel is closed only further forward by the toothless vomer. The region of the intermaxilla is marked by a deep pit between the two long canine teeth. I lack more exact information on *Tapinocephalus* (Dinocephalia), SEELEY says: "Palato-nares placed far forward". Further information on the palate is hard to determine. From OWEN's figure of a complete skull, one might think that an unpaired palatal opening lies between the palatines close behind the vomer. The posterior part of the palate is not preserved. As far as can be recognized on R. OWEN's figure of *Gorgonops*, the pterygoids are delicately built, narrow bones and are strongly curved outward so that large openings remain free below the orbit. The palatines are likewise narrow and terminate close to the maxillae, they only meet in the posterior part; the narrow vomers follow anteriorly (including probably a narrow process of the palatines), on both sides of which the inner nasal openings lie separate; anteriorly they are not bordered by bone, no intermaxilla appears to be present at all, and so a hard palate roof is not present anterior to the middle. Just as in *Gorgonops* also, the position of the inner nasal openings is on both sides of the vomers in *Deuterosaurus*, terminated laterally by palatine and maxilla and anteriorly by the intermaxilla. The whole palate is bony; pterygoid, ectopterygoid [transversal], jugal, maxilla, intermaxilla, vomer, and palatine participate in its formation (presphenoid not preserved). The whole palate is very like that of Nothosauria, as SEELEY correctly emphasized. In *Deuterosaurus* the palate compares best with Dicyodontia. The short sphenoid is surrounded by the pterygoid, which sends the ectopterygoid far anteriorly, and has a pointed process medially that entirely or nearly reaches the vomer. On both sides of this process and the posterior part of the vomer are found the inner nasal openings, which are bordered laterally by ectopterygoid and palatine; anteriorly the intermaxilla occupies quite a large pit. *Ptychognathus*, which belongs in this group, differs somewhat in that the nasal openings are only separated by the vomer, and a high bulge surrounds the sides and dorsal wall of the same (pterygoid and ectopterygoid). The palatines recede almost completely.

The palate of Anomodontia can scarcely be compared with Stegocephalia, not even *Pareiasaurus*, which however recalls this ancient animal group in many parts. But the sculpture of the covering bones of the skull, their dermal plate-like form, the nearly complete roofing over of the temporal fossa; all these are conditions which, are found again very similarly in *Cyclotosaurus*, *Mastodonsaurus*, and other Triassic Labyrinthodontia. The small frontals which surround the orbits not at all or only in short stretches, are common to Theriodontia, like e.g. *Procolophon*, etc., Temnospondyli (e.g., *Actinodon*) and other Stegocephalia. The supratemporal also in *Pareiasaurus* and *Mastodonsaurus* is present in the same way. In Anomodontia all transitions are present from a single occipital condyle to the two-headed one of Stegocephalia, i.e. the so-called amphibian type. The three-part condyle forms the transition step, e.g. *Dicyodon*. In general no absolutely certain

characteristic for the separation of older Amphibia and Reptilia is known to me. Amnion and allantois naturally cannot be considered here, for it is a question of fossils. Who can prove that the differences accepted as sweeping by zoologists in this point are not later acquisitions of one branch of a common stem? It might almost seem as if in reality the great difference held by us between Amphibia and Reptilia did not exist yet then (1).

The primitive structure of the shoulder girdle in *Pareiasaurus* is also stegocephalian-like. It can be compared particularly well with the Permian temnospondylous *Eryops*. In *Pareiasaurus* this consists of episternum, clavicle, cleithrum, scapula, coracoid, and procoracoid. The Triassic *Mastodonsaurus* is also very similar. The intercentrum of the vertebrae, the more or less deeply amphicoelous articular surfaces of the centra, whose bodies and the thick, mostly single-headed ribs are characteristics that *mutatis mutandis* very much recall many Permian and Triassic Stegocephalia. In *Pareiasaurus* the centra are even perforated by a nerve cord as in *Eryops*. The noteworthy distal expansion of the posterior dorsal ribs of *Cynosuchus* recalls a similar feature of the ribs of *Archegosaurus*. Also the long, distally expanded sacral ribs and the narrow ilium with expansion at the acetabular and upper end is just as in *Dicynodon*, *Mastodonsaurus*, *Eryops*, *Chelonia* and Proganosauria. The ilium of several other Anomodontia, like *Cynosuchus*, *Pareiasaurus*, etc. likewise recall this type, although the upper end of the ilium is rather broader by the large number of sacral vertebrae. The ilium of Nothosauria and Placodontia is also similar. Several Nothosauria certainly have a short, thick ilium that recalls *Pareiasaurus bombidens* more.

The femur and tibia of *Pareiasaurus* also have great similarity with temnospondylous Stegocephalia like *Eryops* and *Actinodon*. In the femur both have in common the huge, plate-like development of the greater trochanter that projects far over the tiny femoral head which is little more than a small wart; *Deuterosaurus* and *Rhopalodon* are the same. The backward, deeply bilobed proximal articular surface of the tibia of *Pareiasaurus* and *Eryops* is strikingly similar.

In most Anomodontia the ischium is larger than the pubis. Frequently both are fused almost completely, and both participate in the formation of the close acetabulum. The obturator foramen is most obvious.

Placodontia claim a particular interest since they are brought into a clearer light now by a find of skeletal bones and dermal armor described by Prof. O. JAEKEL (1). For a long time SEELEY has connected them with Anomodontia, and specifically with Deuterosauridae from the skull proportions. The new find from the Raibl Beds of Vesprum on the Plattensee has now aroused all possible interest as we gather from JAEKEL's preliminary description. The entire back (in *Placochelys*) is armored, the armor consists of small polygonal plates with elevated midpoints, between which are scattered larger and higher plates. *Psephoderma alpinum*, *P. anglicum*, and *Psephosaurus suevicus* are therefore, as I see it, no more than the dorsal armor of Placodontia. Further, it emerges with certainty from the seldom-preserved cervical and dorsal vertebrae that *Tanystrophaeus* has nothing to do with Placodontia, as has been suggested already. The ribs have a triangular cross-section with a flat side above. Abdominal ribs are present. Further an almost circular pubis is present. Most skeletal bones of this new find are similar to *Nothosaurus* to such

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(1) cf. CREDNER, Eotetrapoda.

(1) Közlöny földtani. 1902. *N. Jahrb. f. Min. etc.* 1902, I, p. 127 pp. Prof. JAEKEL was kind enough to show me the specimen in Berlin in detail last November, for which I thank him sincerely.

an extent that, if found isolated, they would have been assigned, in our hitherto inadequate knowledge, without thought to Nothosauria (2).

The skull of *Placochelys* has decorations like *Miolania* on the occiput. The skulls of *Placodus* and *Cyamodus*, known for a long time (which I learned about in Bayreuth, Munich, and London), seem to me to indicate without doubt close connection with certain Anomodontia. It was the occiput in particular that gave me this idea. The basioccipital with the two lobe-shaped downward processes, to which the extraordinarily short basisphenoid is connected, is as in *Rhopalodon* and *Dicynodon*. The internal border of the foramen magnum is formed by the exoccipitals which extend far horizontally toward the side and nearly reach the quadrate; they participate in the formation of the condyle. In *Rhopalodon* it is almost exactly the same. The exoccipitals of *Dicynodon* are much broader. The supraoccipital of *Placodus* is small and roof-shaped, in *Rhopalodon* broad and extended horizontally, in *Dicynodon* broad and high. *Rhopalodon* possesses a large interparietal, which still inserts a little between the parietals, exactly as in *Placodus*, only it reaches the upper surface of the skull roof; the parietals begin only near the middle of the temporal fossa. The interparietal is also present in *Dicynodon*. In these genera the squamosals also participate in the dorsal wall of the skull. The opisthotics are not separated by a suture. The pterygoids, whose posterior wings are turned over high upward, are likewise visible with a large surface posteriorly in *Placodus* and this is not the case in *Dicynodon*. Thus in the formation of the occiput there is perfect agreement between *Placodus* and *Rhopalodon*. The skull roof and sides may also be compared. Both genera have very small frontals and parietals and huge prefrontals in common. But the palate of *Placodus*, *Rhopalodon*, and *Dicynodon* is entirely different. The vomer does not generally occur in *Placodus*; palatine, maxilla and premaxilla, which are all provided with the well-known large pavement or incisor teeth, have a considerable extent. The pterygoid and ectopterygoid recede almost entirely. But this difference may be explained by the special development and function of the teeth. Only an unpaired inner nasal opening is present, which is bordered by palatine, maxilla and premaxilla. As in all Anomodontia only a single temporal fossa is present. From what has been said I think it is obvious that Placodontia are members of Anomodontia. SEELEY even viewed them directly as a subdivision of Deuterosauria. The pavement dentition and dorsal armor, otherwise unknown in Anomodontia, are no grounds against this view, for they connect directly with the way of life and give Placodontia the stamp of highly specialized forms; indeed the tooth loss indicates senility of the premaxilla (probably covered with a horny beak) in *Placochelys*. It is probably likely that Placodontia is related to *Deuterosaurus* and *Rhopalodon*, but the differences not only in the skull but also in the skeleton are, however, again so large that this is not positively certain. Nevertheless I can find nothing in the skeleton that contradicts such a direct relationship. In any case Placodontia is very much adapted to water or coastal living, which is already indicated by the dentition. If JAEKEL held Placodontia for the ancestors of Chelonia, I cannot agree with him. Against it is firstly the structure of the palate, then the presence of the interparietal and perhaps also that of the abdominal ribs. Also the geological occurrence deserves sufficient assessment. *Chelyzoon* from the Muschelkalk and *Proganochelys* from the Upper Keuper are the oldest Chelonia, but Placodontia are found from the Lower Muschelkalk (of Upper Silesia (1)) to the Rhaetic (Schönthal, Upper

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(2) This also goes for the ilium, although JAEKEL says that it differs somewhat from that of Nothosauria, for he only seems to be thinking of the broad ilium of many Nothosauria, but not of the rod-shaped, curved one cf. *Nothosaurus strunzi* and other species.

(1) Already *Cyamodus taraowitzensis* from the Lower Muschelkalk possesses attachments for the spines of the occiput, which are so very much developed in *Placochelys*.

Bavaria, Lombardy, Somerset); thus fully developed Chelonia (cryptodire and pleurodire, see below) already appear long before the extinction of Placodontia, indeed even nearly contemporaneous with them. I hold Placodontia for an aberrant branch of land-living Anomodontia (perhaps Deuterosauridae) adapted to water life which became extinct at the end of the Triassic. The similarity of the limbs of *Placodus* and *Nothosaurus* seems to me to arise from the fact that Nothosauridae also arises from Anomodontia, even if from elsewhere (see below) and have also adapted to water life, only to a much greater extent and by other means.

Placodontia, which is distributed over nearly the entire European Triassic, also seems to have a representative in South Africa in the small *Eunotosaurus africanus* SEELEY. SEELEY compares it with *Mesosaurus* (2); certainly the thick ribs recall it, however they are strongly expanded on the dorsal side. But in particular the extraordinarily elongated dorsal vertebrae make close relationship with Sauropterygia impossible. The long vertebrae with low spinous process (see Fig. 20, dorsal side, the two most anterior vertebrae), the low cross-section of the centra in comparison to the thick ribs which first bend wing-like upward (see Fig. 20, dorsal side, 6<sup>th</sup> vertebra from front) to above the spinous process and then curve downward in the sides with a broad, smooth dorsal surface, recall *Placodus* very much as I have figured it on Pl. V, fig. 1 and 2. The pubis (see Fig. 20, ventral side) corresponds entirely with that of *Placochelys* which Prof. JAEKEL showed me in Berlin. Despite the lack of skull and limbs it is very likely that *Eunotosaurus* is a South African placodont.

Anomodontia must have been an extraordinarily plastic order, for its characteristic features embrace so many different animal forms, many very generalized, others highly specialized. They give the impression of uniting Stegocephalia and highly organized Reptilia more directly and promptly than occurs in other (genetic) lines. The Anomodontia cut off, as one might say, a detour. FÜRBRINGER expresses himself very aptly when he says that high specialization is built up on a very primitive base within Anomodontia.

Firstly, under the names *Trochanterium* and *Eurycervix*, remains will be described that could be placed in Stegocephalia rather than Anomodontia.

*TROCHANTERIUM GAUDRYI* n. gen., n. sp.

(Name referring to high greater trochanter) Pl. VI, Fig. 2.

H. von MEYER in his "Fauna der Vorwelt," Pl. 65, fig. 8, figured a bone not clear at the time. It comes from the Upper Muschelkalk of Bischmisheim near Saarbrücken. Now that similar ones have been described by OWEN, SEELEY, and GAUDRY, we can easily get onto the right track.

It is a small but very massively built right femur. The greater trochanter is developed thickly fan-shaped and rises far above the femoral head, which projects upward in direct continuation of the diaphysis as a small spine, so that a small pit remains between it and the root of the greater trochanter. On the lateral side the greater trochanter is thicker than on the median; the whole fan curves a little outward. The diaphysis is short and very thick; it is thicker on the median side than the lateral; three edges arise from this, the two median ones are straight, the lateral curved strongly outward. The distal end is again thickened and bears the two condyles, of which the median one projects more strongly and further than the lateral. Thus the end seems obliquely cut off.

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(2) *Quart. Journ.*, 1892, p. 584.

The construction of the femur indicates a stocky animal with relatively short limbs. The distal end in particular shows that tibia and fibula must have stood far apart, which again requires a very muscular lower leg.

Similar femora are frequently present, in *Pareiasaurus*, *Deuterosaurus* ("Dinosaurus"), *Rhopalodon*, *Eryops*, *Actinodon*, etc. But only in these is found a related group (Temnospondyli, Pareiasauridae, Deuterosauridae) which also has many other things in common. In the former view, the similarity with *Actinodon* and *Pareiasaurus* is greatest. The formation of the femoral head is perhaps most similar to *Deuterosaurus*, but here as in the others named the greater trochanter is much higher and narrower and the femoral head is still insignificant and moved more toward the side. The femur of *Actinodon* is unfortunately not known from the posterior side, however it is not so broad and strongly built as in *Trochanterium*. For a deuterosaurid the latter is again too stocky. In *Pareiasaurus* and *Eryops* the condyles are formed entirely differently; thus it cannot have belonged to any of them. It agrees best with built; but whether it was a true temnospondyl naturally cannot be decided with certainty. It is also possible that it is a transitional form between Stegocephalia and Pareiasauridae. This is one of the few remains of land reptiles from the German Muschelkalk.

In GAUDRY's honor, *Trochanterium* may bear his name, which the knowledge of *Actinodon* has made so highly deserved.

*EURYCERVIX POSTUMUS* n. gen., n. sp.

Pl. IX, Fig. 2.

In the collection of the honorable BLEZINGER of Crailsheim are found several very noteworthy ribs. They come from the Upper Muschelkalk bonebed of the Oelmühle, near Crailsheim. There are two rather complete specimens and four fragments. The form is very noteworthy; it recalls broad, double-bladed paddles, strongly constricted in the middle, at the same time thickened toward one side; both ends expanded flat and turned a little toward each other. The expanded part has a thickened and a thin edge; the thick edge lies on one side diagonally opposite to that of the other end; therefore also the thickening in the constricted middle runs rather obliquely to the longitudinal axis. Proximal and distal ends are difficult to distinguish. The Geological Collection at Breslau possesses a piece of a similar, almost equally large cervical rib; it comes from the *Dadocrinus* horizon of the Lower Muschelkalk of Gogolin, Upper Silesia.

The smaller *Discosaurus* from the Plauen Valley near Dresden (1) has almost exactly similar cervical ribs, but similar ones also in *Melanerpeton*, *Brachiosaurus*, *Sclerocephalus*; further *Archegosaurus*, *Actinodon*, etc. Also the dorsal ribs of *Cynosuchus* have a certain similarity.

The agreement of these cervical ribs with those of the named temnospondylous Stegocephalia is so striking that there is no doubt that we also have here remains of a gigantic ancestor of the group. The whole animal must have been 2.5-3 m long, if one takes into consideration the proportions of the ribs at hand to those of the 1 m long *Sclerocephalus*.

It is not impossible that that form of the tibia belongs to the same genus which is found fairly frequently in the Schaumkalk of Freiburg am Unstrut and occasionally also in the Lettenkohle of Hoheneck. It is characterized by a high, straight, and strongly marked crest. The distal end

shows two articular facets meeting roof-like. The proximal end, seen from above, is long, broader backward and divided in two. The shaft is considerably narrower in the middle than at the ends. I

figure here (Pl. V, fig. 1) a particularly fine example from the Upper Muschelkalk of Steinbiedersdorf, Lorraine, which belongs to the Strassburg Collection; a sketch should illustrate a piece from the Schaumkalk of Freiburg am Unstrut in the Halle Collection.

The similarity with the tibia of *Sclerocephalus labyrinthicus* CREDN. is striking. Despite small differences in the individuals, the overall structure is exactly the same (1).

Since both the cervical ribs and the tibia recall *Sclerocephalus*, it is suggested that they belong to the same or a very similar genus.

Here I also rank a fibula from the Schaumkalk of Freiburg am Unstrut, which, from its entire structure, agrees very well with the described type of the tibia. Probably it belongs to the same genus.

#### *CRUROSAURUS PROBLEMATICUS* n. gen., n. sp.

From the Schaumkalk of the Middle Muschelkalk of Freiburg am Unstrut there is in the Geological Collection at Halle am Saale a strange bone that, at first glance, resembles an ulna, but must rather be a femur.

A few sketches of the bone may suffice to give an idea of its structure. I refrain from a detailed description. It is important to me in general to show what kind of interesting things occur in the Muschelkalk.

In the interpretation of the bone as a femur, the plate-like forward-reaching part must be the greater trochanter and the ascending triangular part the femoral head. The upper leg of *Trochanterium* is indeed almost built on a similar principle. In the Freiburg piece both condyles are very strong at the distal end.

The structure of the bone seems to me to indicate the order Anomodontia (cf. about this, the statements on *Trochanterium*), more cannot be said in advance, for the find is completely isolated.

#### NEW OBSERVATIONS ON *SCLEROSAURUS ARMATUS* H. von MEYER

1857 FISCHER, Über *Sc. armatus* H. v. M. N. *Jahrb. f. Min. etc.*, p. 136-140, pl. 3 and 1 text-fig.

1859 H. v. MEYER. *Palaeontographica* VII, 35-40, pl. 6.

= *Labyrinthodon rütimeyeri* WIEDERSHEIM.

1878 WIEDERSHEIM, *Labyrinthodon rütimeyeri*, Ein Beitrag zur Anatomie von Gesamtskelet und Gehirn der triadischen Labyrinthodonten. *Abh. Schweiz. pal. Ges.* Bd. 5.

= *Aristodesmus rütimeyeri* (WIEDERSHEIM sp.) SEELEY

1895 SEELEY, On an anomodont reptile from the Bunter Sandstone near Basel. *Proc. Roy. Soc.* 59, 167-169.

1900 SEELEY, *Aristodesmus rütimeyeri* (WIEDERSHEIM). *Quart. Jour.* 56, 620-645.

#### Pl. I-III and IV, fig. 5.

The two valuable slabs of stone from the Main Bunter Sandstone of Riehen near Basel that bear the impression of the well-known fossil (1), which were lately described in detail by SEELEY (*loc. cit.*) and placed in the correct light, were recently very kindly sent to me from the Museum at Basel. WIEDERSHEIM had described the animal only from the negative, in the course of which

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(1) Whose identity with *Sclerosaurus armatus* H. v. M. 1859 (1857) has hitherto remained unnoticed.

several quite disturbing errors crept in. SEELEY made casts of separate parts and was thus in a position to judge the systematic position correctly. When I was fortunate enough to see the rubber casts in Prof. SEELEY's house last summer, I decided at once to attempt a complete cast, if permitted. This permission was granted with great kindness in January 1902 for which I thank most sincerely the Museum Commission at Basel and especially Dr. STEHLIN.

The cast was made by TH. TRAA of Stuttgart, the very skilled plaster cast maker, in the Geological Institute, Tübingen. Since the work was some of the most difficult of its kind, it will be in order to say a few words on the technical execution. Firstly the sandstone was hardened with ether copal resin and then coated with white shellac (which could be removed with alcohol). He used as a casting medium a mixture in approximately equal parts by volume of "brown hare lime" (of Paris (1)) and glycerine. This mixture has a strong enough bond and is nevertheless so soft and plastic that there is no risk of breaking some of the brittle sandstone. Also the deepest hollows could be molded using it; but where he broke the gelatine he later made a special cast in which was previously fixed an unravelled cord that he attached carefully with a heated knife. The greatest difficulty was converting the gelatine positive into one of plaster, since a gelatine mold was impossible because of the hot molding. Thus a negative of (red-colored) plaster had to be made and (white) plaster poured into it. Now the positive was in plaster but could not be withdrawn like the first plaster form and the red negative had to be dissected carefully using a needle, which took many days. This form was hardened with linseed oil and reproduced by the well-known methods (2).

The casts produced by this method not only give an idea of the habitus of the complete skeleton, which could already be recognized with care from the negative (originally) but they have also produced some real surprises. Above all, the skull has a bizarre appearance because of the huge skull spines which are similar to those of *Elginia* and the North Russian *Pareiasauria*.

The purpose of these lines is not entirely to replace SEELEY's excellent description by a new one but mainly to indicate the further important discoveries made possible for the first time by the complete casts.

Of the skull, the lower jaw is preserved complete; also present are the inner surface of the skull roof, the right maxilla, the two posterior angles of the skull and parts of the occiput. That originally the complete skull roof was present in the block of stone is to be gathered regrettably from the following words by WIEDERSHEIM (*loc. cit.*): "When the slab of stone first came into my hands, there was visible on one of the slabs, PL. I, only the roof of the oral cavity or, more exactly, only the dorsal half of the cast of the oral cavity, once full of sand. But soon I noticed, by examination with very flexible probes, that I could reach from different openings into one enlarged cavity that extended along the entire dorsal surface of the mass of stone, interpreted by me earlier as a skull. I did not hesitate to take chisel and hammer in my hand and not rest until the entire upper surface was freed from the stone core. Yet I did not conceal from myself the fact that by this procedure possible fossils of the skull bones in the covering mass of stone, which I was reducing to chips by hammer blows, must have disappeared along with the matrix. Thus I can say nothing of their possible existence, only a repeated examination of the chipped fragments showed me that the bones, if they had left behind fossils, bore no sculpture of the kind borne by most labyrinthodont skulls but must have been perfectly flat...In the middle of the posterior region, 1.5 cm from the occipital edge, one sees a round, bud-shaped elevation. It was originally much longer than it appears in the figure, for we have before us the only point by which the upper surface of the

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(1) To be obtained from the firm Faulstich, München.

(2) The casts can be bought new from B. Sturtz of Bonn am Rhine.

internal cast was suspended by a well-shaped small column surrounded by the casing of stone. There can be no doubt that we have here the place where sediment intruded into the parietal foramen from above and later hardened; it was blocked by it and I could conclude, from the original height of the stone plug before it fell under the chisel, the huge thickness of the parietal in the immediate surroundings of the parietal foramen.” It is much to be regretted that such an effort was made with this valuable object in the endeavor to find an endocranial cast! WIEDERSHEIM has indeed claimed the inner impression of the skull cap for this (3)! The different openings through which he reached with flexible probes into an extensive cavity will probably have been the head spines which covered the whole skull, like *Elginia*. The cavity was the space that formerly received the bones of the skull roof. The position of the parietal foramen is hardly recognizable any longer in the present condition of the fossil. Only with the help of WIEDERSHEIM’s figure can they be found, and it is reproduced as a photographed cast on Pl. IV, fig. 5. The considerable diameter of the foramen agrees well with *Procolophon* (*Pareiasaurus* much smaller); many short-snouted dicynodonts are also similar.

Of the spines present the large 4.5 cm long ones go out from the squamosal, the deeper-placed second largest ones from the quadrate, and the two which are found above it take their origin from the supratemporal (posteriorly) and the quadratojugal (anteriorly), just as in *Elginia*. The squamosal spine is actually only 2.5 cm long, but it stands on a 2 cm high base that is isolated by a rim. It is analogous to the horn structure of mammals. Of recent lizard heads one can best compare *Phrynosuchus* in a sense; it only has dermal spines that are not connected with the skull bones, but in *Phrynosoma* not only the occiput but almost the whole body is covered with such spines.

The whole skull of *Sclerosaurus* must have been much flatter than that of *Elginia*, as already shown by the relatively closer arrangement of the skull outgrowths. The quadrate spine on the right is preserved on slab II, the other on slab I. The distance from the point of one to the point of the other measures 10 cm.

The occiput is quite well preserved only strongly displaced. The basioccipital with the large spherical condyle which, with the basisphenoid and the left exoccipital and half the supraoccipital together with the base of the left squamosal spine, is reversed so that dorsal and ventral and anterior and posterior are exchanged, however right and left remain correct. The right quadrate with the posterior edge of the right pterygoid and perhaps part of the right exoccipital are still found in their natural positions. If these bones are brought into their natural connection—as I have done with a gelatine cast—it arises that the dorsal wall of the skull sloped very obliquely from posterodorsal to anteroventral. The strong condyle represents quite a uniform hemisphere as in *Pareiasaurus* and *Elginia*. The exoccipital is directed laterally and downward. The border of the foramen magnum is unfortunately missing, however the place is clearly recognizable. I hold the flat bone piece which has lain above the left lower jaw ramus for the left supraoccipital. Below the occipital condyle, the basisphenoid extends anteriorly (here posteriorly), medially it shows a very deep groove, so that it has a U-shaped cross-section. This is also the case in *Pareiasaurus* and *Elginia*, but in particular exactly the same in *Procolophon*. In the continuation of the groove anteriorly, the posterior unpaired palatal opening might follow. But here the suture between basisphenoid and pterygoid is lost. On the right side one sees that the pterygoid sends a wing far posteriorly that curves dorsally on the posterior edge of the skull and reaches the quadrate. Unfortunately the largest part of the palate is missing.

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(3) For the endocranial cast he takes (*loc. cit.*) the whole surface from the occiput to the point of the snout, whereby e.g. the impression of the orbits will represent the large cerebral hemispheres.

What SEELEY believed was the palate is no more than the skull roof from the inside. One sees the large orbits which are directed dorsally as in *Procolophon*, and not laterally as in *Elginia*. Between them remains only the narrow 12 mm bar that is formed from the frontals. Also the roof of the broad snout is clearly recognizable. If one knows where to look, one thinks one can recognize the sutures between frontals and nasals. The snout terminates broadly in front. No nasal openings are present up to there; thus they must lie terminally and be placed vertically as in *Procolophon*. The right maxilla is for the most part preserved, it bears seven blunt, conical teeth that do not differ essentially from those of the lower jaw. In the posterior half, the rather broad attachment for the ectopterygoid is to be seen. On the maxilla, the jugal and quadratojugal terminate backward, both of which however only show the underside. Below the snout are still stuck four intermaxillary teeth which are rather sharper than the others. From WIEDERSHEIM's evidence (*loc. cit.*), the dorsal surface of the skull does not seem to have possessed the pitted sculpture of *Elginia* and *Pareiasaurus*, thus it also seems to have been like *Procolophon* with the exception of the spines.

The lower jaw, which is very like that of *Pareiasaurus*, still bears three teeth on the left and six on the right. They are ca. 4 mm high, conical, and with rather blunt points. The second most anterior tooth of the right mandible is flattened above. In the middle of each lower jaw *Pareiasaurus* has thick, downward-directed pegs; *Procolophon* and *Sclerosaurus* lack these.

The skull of *Sclerosaurus* is on the whole most similar to that of *Procolophon*, only exactly twice as large. It is however more strongly flattened, and indeed to the same extent as in *Pareiasaurus*; *Elginia* is much higher, and both certainly preserve the same habitus by means of the head spines. In *Procolophon* the appendages of two spine zones on the skull are noticeable, namely on the squamosal and on the quadrate. The so-called Permian Pareiasauria from North Russia have several rows of small spines on the skull roof; the postorbital region up to the quadrate is lobe-like, drawn deep down, and bears large spines (quadratojugal, jugal, etc.) (1). Of reptiles that show similar bone growths on the skull, but have absolutely nothing to do with *Sclerosaurus*, we may name the placodonts *Placochelys* and to a lesser degree *Cyamodus*, both also from the Triassic, further the Cretaceous Sauropoda, *Triceratops* and *Agathaumas*, and the Miocene chelonian *Miolania*.

The skull of *Sclerosaurus* is broader than long. The measurements follow:

|   |           |
|---|-----------|
| Length of the midline   | 8 cm      |
| Breadth from point of one quadrate to the other                             | 10 cm     |
| Ditto, with subtraction of spines   | 8.5 cm    |
| Approximate height of occiput   | 3-4 cm    |
| Height of snout   | 1.5-2 cm  |
| From anterior edge of orbit to snout point                                  | 3 cm      |
| Transverse diameter of orbit  | 12.5 cm   |
| Length of the same  | over 3 cm |
| Length of left lower jaw ramus from medial edge of symphysis to the angular | 6 cm      |
| Length of right lower jaw ramus in middle above                             | 1 cm      |
| Length of left lower jaw ramus in posterior third                           | 3 cm      |

SEELEY has described the skeleton of *Sclerosaurus* so thoroughly that little more can be added.

In the vertebral column I count 18 presacral, three sacral, and 13 (+ 2 gaps = 15) caudal vertebrae, thus altogether 34 (36), which are clearly visible; but there are still 3-4 indistinct impressions at the end of the tail. I do not understand how WIEDERSHEIM and SEELEY counted 22 presacral vertebrae. A part of the cervical vertebrae is covered by the displaced portion of the skull on one side and by the shoulder girdle on the other. Of the visible vertebrae, at most the four most anterior can be ranked in the neck; therefore perhaps 2-4 short cervical vertebrae are inaccessible. Then there would be 14 dorsal and 6-8 cervical vertebrae. However the border between cervical and dorsal vertebrae cannot be identified with certainty, for the vertebrae appear so similar to each other. Only a slimming of the spinous process and a narrowing of the diapophysis occurs toward the front. Also the ribs cannot as otherwise be used as a criterion because the neck bears long ribs that do not really differ from the dorsal ribs, as e.g. in *Palaeohatteria*. Also in *Pareiasaurus* there is no clear separation between cervical and dorsal ribs; SEELEY counts ten cervical and eight dorsal vertebrae, the reverse seems more plausible to me (I have seen the original), but I dare not say anything on it with certainty. In *Procolophon* (1) there are 17 presacral vertebrae, including gaps for two vertebrae; I do not think many more were there. *Sclerosaurus* may have had 20-22 presacral vertebrae.

SEELEY has observed that the ventral side of the centra is always rather shorter than the dorsal side and from this concludes on the presence of intercentra. In fact this is also to be observed in the present cast between the 10<sup>th</sup> and 11<sup>th</sup> dorsal vertebrae. The centra are literally hourglass-shaped, in that the hollow cones almost entirely meet in the middle. On the ventral side they all have a sharp edge; their cross-section is triangular. The most posterior dorsal vertebrae become broad and thick. The upper arches of the dorsal vertebrae all have a long spinous process, particularly strongly flattened and expanded distally, which recalls *Pareiasaurus* very much. In the cervical vertebrae it is longer and slimmer than in the dorsals, both in *Sclerosaurus* and *Pareiasaurus*. The diapophysis is extraordinarily strong, broad, and long with double strutting on the underside, particularly in the posterior part of the dorsal vertebral column. Also the pre- and postzygapophyses stand very far laterally, which *Sclerosaurus* has in common *Pareiasaurus* and even more with *Procolophon*. In several places one seldom sees more clearly how the zygapophyses naturally fit into each other. A broad horizontal plate extends between the postzygapophyses. The ribs are single-headed with very high, vertically placed proximal ends.

The last dorsal vertebra has a 10 cm long transverse process, and the first sacral vertebra has one 20 cm long that thickens strongly at the distal end. It is only visible from the abdominal side (slab I). The second sacral rib is only imperfectly recognizable. The third has a length of 16 mm, but is much thinner than the first; it is a little thickened at the distal end and curves somewhat anteriorly. *Procolophon* likewise has three sacral ribs, which are greatly thickened at the distal end; the middle seems to be the weakest. The most anterior sacral rib of *Procolophon* likewise curves anteriorly, but is not stronger than the following caudal ribs and in this differs very much from the three sacral ribs. *Pareiasaurus* has four sacral ribs, but the fourth differs from the preceding in that it stands out from the axis of the vertebral column at a right angle, while the three others bend significantly posteriorly. In *Sclerosaurus* the vertebra following the third sacral vertebra has such a short centrum that it should not be regarded as the fourth sacral. A fragment of the right rib of this first caudal vertebra lies on the right pubis, from which is to be seen not only its considerable length but also its anterior curvature just like the first caudal rib in *Procolophon* and the fourth sacral rib in *Pareiasaurus*.

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(1) *Phil. Trans. Roy. Soc. London*, 183, pl. 23, fig. 3, 1892.

The 13 visible (+ 2 gaps = 15) caudal vertebrae are shorter and become continually shorter especially posteriorly, they decrease rapidly in size. It did not have more than 18 altogether. They are distinguished by the thin transverse processes that project far, as also in *Pareiasaurus* and *Procolophon*. 17-18 caudal vertebrae are visible in *Procolophon* and some still seem to be missing at the end; *Pareiasaurus* has 18-19 of them.

The shoulder girdle consists of the interclavicle, clavicle, procoracoid, and scapula. The piece of bone on slab I on the left beside the episternum seems to be a broken-off piece of the episternum. (The bone lying in front between the two lower jaw rami is the point of the broken-off right pterygoid piercing through from slab II.) The episternum and also coracoid and procoracoid have the greatest resemblance to these same bones in *Procolophon*. Both together are much larger than the scapula. The figures are clearer than a long description. These five bones (slab I) still lie in natural association. The right scapula is overturned so that the contact surfaces of the scapula and coracoid are rather displaced. On slab II the scapula is seen from lateral view, the coracoid from medial view. The scapula is very like that of *Pareiasaurus*, only the acromion here lies further posteriorly. On SEELEY's illustration the latter does not stand out much. The clavicle articulates on the acromion as a broad, rather curved bone. The extremely broad and strongly built humerus recalls *Pareiasaurus* very much. For the arm, I refer to SEELEY's description, only I might reverse the interpretation of the radius and ulna for the following reasons: the radius is round and proportionally thicker at the distal end than the proximal, this latter does not project on the other side of the humerus as SEELEY figures, by which the appearance of undue length (olecranon on SEELEY's "ulna") is made greater, but terminates under the distal blade of the humerus. The ulna is a flat, broad bone without an olecranon, and the proximal end is broader than the distal. The oblique joint surface at the articulation of the distal end of the ulna with the radius, characteristic of many reptiles, is visible; also the sharp edge of the articular surface is characteristic of the distal end of the radius. The position of the humerus also seems to me to justify this interpretation of the bones; as can be best seen on slab I, it must be rotated by 90° about the longitudinal axis to arrive at its natural position, and if radius and ulna change over by this, the radius keeps its rightful lateral position, the ulna the medial position.

Two rows of carpals are present. In the proximal row they consist of an ulnare and a radiale; of the four carpals of the distal row C. I lies on Mtc. I and II, C. II on Mtc. II and III, C. III on Mtc. IV, and C. V nearby, presumably on the missing Mtc. V. A pisiform still lies above it. Thus there are seven bones in all. The numbering of the digits of the manus must also be modified in accordance with the position of the radius and ulna. I can only see four digits remaining (cf. SEELEY, *loc. cit.*); the fifth, in any case present, is not visible. The first digit lies nearest the lower jaw, the fourth furthest away. As one sees on slab I, the first digit has two phalanges; the others each have three.

The pelvic girdle with both hind limbs is especially beautifully preserved. They come into view only on slab II. The right ilium is found in natural position and shows the lateral side; the left is overturned; one sees the attachment place of the sacral ribs. For a more accurate description refer to SEELEY. The left ilium is still in natural contact with the ischium and pubis: little else is to be seen of the latter. The ilium and ischium take a peculiar intermediate position between *Pareiasaurus* on the one hand and *Dicynodon* on the other. The femur is certainly built after the type of *Pareiasaurus*, but much slimmer. The tibia strikingly recalls *Eryops*, which in this and many other points resembles *Pareiasaurus*. The fibula is flat, rather broad, and strongly curved, as in Proganosauria and Archegosauria. The tarsals of the second row are not fossilized. The astragalus and calcaneum are represented by a single large, triangular bone with clearly separated

articular surfaces for the tibia and fibula, exactly as also in *Pareiasaurus*. Five digits are present. Metatarsals I and II are compact and short, the others slimmer. There are two phalanges in the first digit, three in the second, three in the third, and four in the fourth; only the metatarsal of the fifth is there.

As for the dermal armor, SEELEY has already “seen two or three rows of small irregular scutes which lie between the ribs” (1). The complete cast has also provided more clarity on this point. Six longitudinal rows of armor plates extend from the sacrum to the beginning of the neck. On both sides of the spinous process, corresponding to the number of vertebrae, is a thick, oval bone plate generally 12 but up to 20 mm long, and ca. 7 mm broad; each of them bears a longitudinal ridge and has pitted sculpture on both sides of it. All these plates are directed obliquely posteriorly and extend from the spinous process always above the postzygapophyses. The next row consists of rather smaller, rounded plates with the same sculpture; they alternate with the former and are thus found between the ribs. The third row of pairs is quite incomplete and consists of small ossifications, which however also show the pitted sculpture. Behind the sacrum the armament abruptly ceases and decreases gradually toward the neck. Also the flattened dorsally and greatly expanded spinous processes of the dorsal vertebrae have shown the sculpture of the armor plates.

Now for the first time, after having discussed the two most important pieces, the statement made above, that *Aristodesmus* and *Sclerosaurus* are identical, should be proved. The original of *Sclerosaurus* comes from the Upper (green) Bunter Sandstone of Warmbach near Rheinfelden, thus also from the region of Basel (found 1856). 11 dorsal vertebrae and 12 (left) ribs as well as parts of the ischium and pubis are preserved on the one (lower) slab. The second slab, fitting on it, shows the dorsal armor from the inside; the eight split vertebrae, whose upper arches and sometimes the neural canal are visible, as well as the pubis, show surprising similarity with the piece from Riehen; the zygapophyses project far laterally; the horizontal plates between the postzygapophyses and the spinous processes are built exactly the same, as are the ribs. The femora are to be seen from the ventral side; thus they form a good supplement to the block from Riehen which only shows the dorsal side of both femora. As might be expected from the structure of the rest of the skeleton, the femur is formed exactly after the type of *Rhopalodon* and *Pareiasaurus*, only rather slimmer. The fragments of the pelvis may be identified by their structure. The dorsal armor is preserved better *in situ* than in the Riehen block. One recognizes (from the ventral side (2)) the elongated large side plates, on which lie one or two rows of smaller plates in the middle and upper region of the back. In about the eighth dorsal vertebra (reckoned from the rear) the median plates divide into three separate plates. Nothing clear is preserved of such median plates in the Riehen block.

Of the armored reptiles, apart from Chelonia and Parasuchia of course, there have been known hitherto in the European Triassic only Placodontia and *Rhynchosaurus*; to these is added a find from the Wellenkalk of Gogolin (see below), which Dr. W. VOLTZE has just described, and *Sclerocephalus* from Warmbach and Riehen. Armored Anomodontia are unknown from South Africa; *Pareiasaurus* (*bombidens*, *baini*, etc.) certainly possesses the same thickened spinous processes but no armor. On the other hand, the Permo-Triassic Pareiasauria from the Suchona, which Prof. AMALITZKY has discovered, are strongly armored on the back and sides, and to increase the resemblance with *Sclerosaurus* further, the skull is also furnished with strong spines and outgrowths.

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(1) WIEDERSHEIM says, *loc. cit.*: “Finally I will still say that no trace whatever of dermal armor is preserved.”

(2) However in some scales a little of the upper side is still recognizable; it is covered with irregular pits as in the piece from Riehen.

Whether *Sclerosaurus* is related to *Sphenosaurus* H. v. M. from the Bohemian Permian sandstone, and to *Parasaurus geimitzi* H. v. M. from the Kupferschiefer of Thuringia, as von MEYER suggested (*loc. cit.*, 1859), cannot be established for the present.

*Procolophon*, *Sclerosaurus*, and *Elginia* form a closely related group that is most nearly related to Pareiasauria. That *Procolophon* is the most primitive representative of Procolophonia arises from the absence of the bizarre head spines. Which of the two families is more primitive cannot easily be said even if the Pareiasauria most resemble Stegocephalia by their skull sculpture.

#### VERTEBRA OF *PLACODUS GIGAS*

Pl. V, Fig. 1 and 2.

A piece of rib of *Placochelys* agrees completely with the ribs found on two vertebrae from Bayreuth and Göttingen, and thus I must hold these are also those of a placodont. Prof. JAEKEL, to whom I sent a drawing of the Göttingen vertebra, writes to me saying that he also agrees with me. The centrum is rather elongated and narrows ventrally in cross-section; constricted in the middle and almost boat-shaped, it recalls the "thecal" thoracic vertebrae of *Placochelys*. The articular surfaces are only hollowed a little. In the centrum, a separate long canal of 4-5 mm diameter and round cross-section passes under the neural canal. It recalls the deep openings on the articular surfaces of the vertebrae of *Pareiasaurus* and *Tapinocephalus*, only they are separated there by a thin septum, which cannot be established here without a longitudinal section. This feature also points very much to the anomodont nature of the Placodontia. The neural canal is proportionately large and deep. Ribs and transverse process are completely ossified so that a suture can no longer be recognized. The ribs are triangular in cross-section with one flat side below. The lower edge thickens proximally to a broad scar, below which the neurocentral suture is still recognizable. The transverse process or the rib bends first rather dorsally, then runs for a bit horizontally and bends in a broad curve again ventrally. The sharper edge of the rib lies on the posterior side, and the rather more rounded one on the anterior side of the dorsal surface. The spinous process is low and narrow but strong and directed posteriorly. It rises no higher than the highest arch of the rib so that thus the dorsal armor shown by JAEKEL lies quite close above it.

Because *Placodus gigas* certainly chiefly occurs in the German main Muschelkalk, it is likely that both the vertebrae belong to this species.

#### *PSEPHODERMA* AND *PSEPHOSAURUS*

The discovery of JAEKEL's *Placochelys* with complete dorsal armor now at last allocates the isolated pieces and armor plates described as *Psephoderma* and *Psephosaurus* to their correct place; formerly traces in them were thought to be sometimes nothosaurian, sometimes chelonian. They belong to *Placodus*. Just as the skull of *Placochelys* is more strongly sculptured than that of *Placodus*, so also are the armor plates of the former high and pyramidal, but those of the latter are almost entirely flat. However the outline is exactly the same, and also the central elevation is more or less recognizable. Also the arrangement of the few larger plates between numerous smaller ones is exactly the same in both. In *Psephoderma alpinum* only small plates of the same size are preserved, but *P. anglicum* and especially *Psephosaurus suevicus* correspond completely to *Placochelys*. It might in fact be a question of different species or even genera of Placodontia.

*Psephosaurus suevicus* (1) is found at its best in the Upper Leettenkohle of Hoheneck near Ludwigsburg, and *Psephoderma alpinum* in the Upper Bavarian Dachsteinkalk. The small plates as from Hoheneck are also found isolated in the Rhaetic of Aust Cliff near Bristol, such as *Psephoderma anglicum* H. v. M. (2), and in the *Zanclodon* Bed of Schönthal near Basel (see Pl. V, fig. 3) together with *Capitosaurus*, *Belodon*, and *Gresslyosaurus*. Such plates are also found in the Rhaetic of Lombardy (3).

*ANOMOSAURUS* gen. nov.

Pl. IV, fig. 3 and 4; Pl. VI, fig. 4; Pl. VII, fig. 6.

Among large suites of nothosaurid bones a number of vertebrae have been found that differ immediately by their very deeply amphicoelous articular surfaces.

These vertebrae differ among themselves in several points, but besides the deeply amphicoelous articular facets all have a long spinous process and hyposphene; they would probably represent different species of one genus.

They are relatively most frequent in the Schaumkalk (Middle Muschelkalk) of Freiburg am Unstrut (province of Saxony). I have seen seven specimens of them in the University Collection at Halle, one from the region of Quedlinburg and eight from Altenberg near Naumberg. Such ones also occur in the Lower Muschelkalk at Gogolin and Naklo in Upper Silesia and at Sulzbad, Upper Alsace. Then four such vertebrae from the Upper Muschelkalk are present, two of which come from Bayreuth, one from Neckarvaihingen, Württemberg, and one from Mühlhausen, Thuringia.

The vertebrae from the Lower Muschelkalk of Gogolin (*Dadocrinus* horizon, 3 m above the Röth) are so like the better-preserved ones from the Saxon Schaumkalk that I only describe the last one in more detail but draw attention to several smaller differences.

The centrum is rather longer or as long as high. The articular facets converge rather posteriorly and are so deeply amphicoelous that the hollow cones nearly meet. The deepest point of the latter clearly lies considerably below the median longitudinal axis. In most vertebrae the neural canal is very high but narrow, sometimes wider above, sometimes below. Therefore the upper arch ventral to the diapophysis in many vertebrae has a larger diameter than the centrum. Characteristic of the upper arch are the long transverse processes, thickened at the distal end. In most vertebrae the spinous process is high and narrow, its base is moved a little posteriorly; however in some it is short and quite thick; it is probably a question of different species, or sometimes of different sections of the dorsal vertebral column. The pre- and postzygapophyses are moderately oblique to flat and are strongly developed. In some the postzygapophyses have clear longitudinal grooves and a lateral curving of the lateral edge for firmer control of the joint. A triangular pit is found in the middle behind the prezygapophyses anterior to the base of the spinous process. A very strong hyposphene is always present ventral to the postzygapophyses; it reaches deep down and becomes very broad ventrally. Seen in posterior view, it is almost an equilateral triangle with the point directed dorsally. The vertebrae from Freiburg and Querfurt from the Schaumkalk vary in overall height from 6-12 cm; the larger are more frequent. The pieces from Gogolin are only 6-8 cm high. The transverse processes are hollow in both, as one occasionally

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(1) E. FRAAS, Die schwäbischen Trias-Saurier, Stuttgart, 1896, 13, 14.

(2) *Palaeontographica*, 1867, vol. 15, 261 pp., pl. 40.

(3) I have seen such ones in the Museo Civico, Milan, but without precise details of the localities.

sees on fracture surfaces. The transverse process is allusively doubly strutted from below, most clearly in the pieces from Gogolin.

Before me lie four considerably larger vertebrae from the Upper Muschelkalk. The quite thick centra are rather longer than high. The edge of the articular surfaces is tilted over considerably toward the sides. The articular surfaces themselves are deeply amphicoelous; both hollow cones meet in the middle and probably communicate by a small hole. Dorsal to the centrum the upper arch is very high. The border between both is recognizable as a clear suture. The posterior opening of the neural canal is about 2.5 cm high and 1.5 cm broad in a vertebral length of 3.2-2.4 cm. The centrum from Neckarvaihingen has a breadth of 3.5 cm posteriorly; but the dorsal surface of the transverse process is 7.8 cm above the ventral, and the spinous process measures a further 6 cm, thus giving a total height of 13.5 cm. In one of the vertebrae from Bayreuth the transverse process is 6.5 cm long. The transverse process is flat dorsally, begins very thick and broad with only a trace of two- or three-fold strutting from below (this is rather different in the four vertebrae), then becomes thinner again with an approximately triangular cross-section, but thickly club-shaped at the distal end. The spinous process, which is preserved only in one vertebra from Bayreuth and that from Neckarvaihingen, projects vertically upward; one is rather thickened at the distal end. Both display a narrow, projecting longitudinal ledge on the dorsal side of the spinous process, as is found in *Nothosaurus* and *Pareiasaurus*. At the root of the spinous process and between the postzygapophyses lies a deep, flat-bottomed cavity. The postzygapophyses in the different vertebrae project laterally in different positions corresponding to their position in the skeleton, however not to any extent, and all ascend more or less outward. In the middle ventral to them an extraordinarily strongly developed hyposphene is formed. This projects as far posteriorly as the postzygapophyses and has articular surfaces that clearly converge dorsally, as is the case in *Zanclodon* and related Triassic Dinosauria in the posterior dorsal vertebrae. The prezygapophyses are not preserved but it is easy to decide their structure from the form of the postzygapophyses.

Because of their deeply amphicoelous articular surfaces and the hyposphene, these vertebrae give a strange impression, especially in the German Muschelkalk together with innumerable Nothosauridae. However such vertebrae could not belong to a sauropterygian.

Vertebrae of *Pareiasaurus*, *Propappus*, *Tapinocephalus*, *Loxomma* (Permian) have in the middle of the barely concave articular surface a deep hole that almost or completely passes through. The dorsal vertebrae of *Dicynodon*, *Embolophorus*, *Dimetrodon*, and *Inostrancevia* (1) however have an hourglass shape in longitudinal section, exactly like the vertebrae in question, only the vertebrae of *Dicynodon* are shorter than those of the others named. The underside of the centrum from Mühlhausen, Thuringia, has almost exactly the same cross-section as a series of Anomodontia (*Pareiasaurus*, *Tapinocephalus*, *Dicynodon*, *Sclerosaurus*); the centrum is rather constricted in the middle, wedge-shaped ventrally, rather flattened right below, and again constricted laterally above the middle.

A hyposphene is known to me only from Dinosauria, *Embolophorus*, and *Inostrancevia* (2). But the former have two-headed ribs and cannot be considered here. Thus the hyposphene seems to indicate Anomodontia. Other characteristics also lead to the same conclusion.

Because the vertebrae are found in the marine main Muschelkalk, it is very likely, even if by no means necessary, that they belong to a swimming animal or a land animal that was also able

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(1) *Inostrancevia* AMALITZKY ms. is a lycosaur that was discovered in the great excavation in the Suchena in the area of the Dvina River, North Russia, in supposedly Permian beds. Prof. AMALITZKY had the kindness to show me his still-undescribed treasures in Warsaw.

(2) Whether *Dimetrodon* possesses a hyposphene could not be recognized definitely in the material available to me.

to swim. Anomodontia are in general land animals, however Placodontia have gone into the water; also close relations or descendants of the Anomodontia, the Sauropterygia and Chelonia, have adapted themselves entirely or partly to water life. The hyposphene might suggest that the vertebrae in question belong to Anomodontia adapted to a swimming way of life. This serves in all events for firmer articulation of the vertebral column and (considering the extraordinary length of the hyposphene: 1 cm in a vertebral length of 3.5 cm) especially prevents great lateral bending of the body—this is not required for swimming. In Triassic Dinosauria the hyposphene is only noticeable on the dorsal vertebrae whose articular facets are developed as saddle-shaped; both features indicate that vertical movement in raising the body or in bending down to the ground proceeded on the short forelimbs. In Dinosauria the structure of the hyposphene in any case connects with the way of life; it is as in *Anomosaurus*. That lateral bending was otherwise possible here is shown by the deep pits between postzygapophyses and hyposphene on the medial edge, whose purpose was to allow the medial edge of the prezygapophysis freedom to move right and left. In any case the hyposphene is a characteristic of secondary adaptation. The strengthening of the vertebral column for greater elasticity in a swimming way of life is always achieved in separate cases in the most economical way with the available means (e.g. ligaments, intercalary cartilage, zygapophyses, etc.). Two *Nothosaurus* vertebrae from Bayreuth (Tübingen Collection) illustrate best how the hyposphene may have arisen in this case. In Nothosauria the long neck certainly requires strong connection, particularly of the posterior vertebrae. The edges of the posterior opening of the neural canal and the medial edges of the postzygapophyses meet in a point and form an expansion there that perhaps already functioned as a hyposphene, so to speak.

A piece of skeleton in Breslau (from Gogolin), which will be described in detail by Dr. VOLTZ, shows vertebrae that are similar to those here, ribs that send a strange flat process posteriorly, a limb, a circular pubis, and thick abdominal ribs, as well as several small, thick dermal ossifications in connection.

It would be interesting to learn whether a relationship exists between *Anomosaurus* and Placodontia. In favor of this are the long diapophyses, the form of the prezygapophyses, abdominal ribs, pubis, and dermal ossifications; against are the high spinous processes, the shortness of the dorsal centra, and the occurrence in the main Muschelkalk together with entirely differently built vertebrae, which at any rate belong to *Placodus* (see above).

I think there is no doubt that these vertebrae belong to an anomodont. This occurrence, hitherto not appreciated or ignored, shows again the extraordinary plasticity of this noteworthy reptile group.

#### *CTENOSAURUS KOENENI* n. gen. n. sp.

A very noteworthy find has been made in the uppermost part of the middle Bunter Sandstone east of Reinhausen near Göttingen. There are four large slabs that contain dorsal vertebrae with enormous spinous processes and ribs. Such a vertebra with a spinous process is ca. 60 cm high, as I estimate from a four-times reduced photograph that the hon. VON KOENEN was kind enough to send to me. A simple outline sketch may be helpful. All the bones are flattened and the preservation is not very good. Thus e.g. the spinous processes seem to be flat from their base onward, but it cannot be said with certainty whether they originally had a round cross-section; in the upper half they are in any case flat and rather expanded. They are curved and bent rather

posteriorly. The centra are nearly twice as long as they are high. The upper arch joins onto the anterior part of the centrum, but reaches the postzygapophysis far posteriorly.

I know of nothing better with which to compare these vertebrae than the Permian Clepsydripidae from Texas and Bohemia. The outline of the centrum recalls *Naosaurus* and *Dimetrodon* most, the structure of the upper arch recalls *Naosaurus*, *Dimetrodon*, and *Embolophorus*. But of these three, *Dimetrodon* has the greatest similarity. Whether the centra are amphicoelous as in Clepsydripidae is impossible to determine. Also the abnormal development of the spinous process is most to be expected in Clepsydripidae; I need only recall *Naosaurus* and *Dimetrodon*. For all that, I think it is more than likely that *Ctenosaurus* is a last straggler of the Clepsydripidae, hitherto only known from the Permian. Such an occurrence is very interesting for the completion of the Triassic land fauna.

#### 4. SAUROPTERYGIA

Sauropterygia play a leading role in the marine Triassic, particularly in that of Germany, both in wealth of individuals and of forms. Sauropterygia are characterized by their high degree of adaptation to the swimming way of life. Many forms are more or less specialized, e.g. *Lariosaurus* is taken to be adapted or at least gives the impression of being adapted to the swimming life up to a certain point. One need only consider the flat humerus, the flat broad forearm and lower leg bones, the plate-shaped development of the carpals and tarsals, and the similarity of the fore- and hind limbs. The long neck with the fairly large head in proportion to the short limbs is sufficient to show that the animal was adapted, in the first place, for swimming, even if the structure of the feet with digits suggests that it may have moved on dry land. Nevertheless *Lariosaurus* is one of the most primitive representatives of Sauropterygia. In a Liassic *Plesiosaurus* this neck is very much longer, the body shorter, and the pectoral and pelvic girdles have become true pieces of armor, particularly on the ventral side. The limbs are changed into *Ichthyosaurus*-like fins; the forearm and lower leg bones can scarcely be distinguished from the other foot bones. In the Upper Jurassic and in Cretaceous this specialization goes even further. It is clear that we have here a succession of animals more and more adapted to swimming; the earliest limbs clearly show that they are derived from land animals, but the source is not immediately obvious. ZITTEL contented himself with a general remark on the resemblance to Rhynchocephalia.

Sauropterygia are divided into three (1) families: Nothosauria, Plesiosauria, and *Pistosaurus*, which are all already found in the Triassic; the first and last exclusively, the Plesiosauria which continue up to the Upper Cretaceous only at its beginning and as a great rarity. Nothosauria are the rulers of the seas of the Triassic. They are very important because of their frequent occurrence, particularly in the German Triassic. Most genera and species are based on isolated skulls. Larger parts of the skeleton are seldom found in articulation. Thus there is often doubt as to which skull the widely differing skeletal parts belong. A monographic revision of the extensive material, scattered over all of Germany, is an urgent requirement, but can only be undertaken when all the specimens have been examined.

Some Plesiosauria already appear in the Muschelkalk and Keuper. Several of these occurrences will be described briefly below. *Pachypleura* and *Neusticosaurus* lean toward Plesiosauria by the structure of the humerus.

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(1) See below on Mesosauria.

*Pistosaurus* is known from a single skull which has strikingly small nasal openings lying far back. *Pistosaurus* can be compared best with *Cymatosaurus* and is in any case descended from it.

It is not the purpose of these short lines to throw light on the evolution of the genera and species, but I may go into the genetic relations of Sauropterygia a little.

Let us consider Anomodontia. The skull of Sauropterygia, and especially Nothosauria, is quite different in its appearance from the forms of Anomodontia. The elongated structure and uniform dentition indicate strong adaptations to water life. Both groups are alike in that they have only *one* temporal fossa, and indeed it is homologous to the upper one of other reptiles. The position of the outer nasal openings is again similar to *Dicynodon*; they are divided externally by the premaxilla and are found between the snout point and the orbits. The inner nasal openings lie paired in the anterior half of the whole bony palate, and in both groups they are separated by the vomer, which participates in the formation of the palate roof in rather small circles. The rudimentary palatal dentition mentioned by BOULENGER on the pterygoid of *Lariosaurus* is very interesting and extremely important in phylogeny; it recalls Thecodontia. The occiput presents many points of comparison despite many differences. Let us take a *Nothosaurus* (*Cymatosaurus*) from the Berlin Museum (after KOKEN (1)) and a *Ptychognathus* figured by R. OWEN. In *Nothosaurus* the exoccipitals play quite a small part in the occipital condyle, in *Ptychognathus* considerably more; on the other hand in *Dicynodon feliceps* just as in *Nothosaurus*. The two diverging processes of the basisphenoid are found in *Ptychognathus* and the other Anomodontia and are present likewise, however directed more horizontally and less projecting. Laterally below is the pterygoid which is already to be seen to rise not so high in Anomodontia. Both the exoccipitals, which surround the greatest part of the foramen magnum, have in *Ptychognathus* a large broad continuation upward and a rather narrower one downward; the opisthotic appears between them with a small outer surface, it borders part of the canalis ossis quadrati. In *Nothosaurus* the opisthotic is much larger and the upper continuation of the exoccipital is less developed. In *Ptychognathus* the supraoccipital not seem to reach above the foramen magnum; also in *Nothosaurus* it is pressed into a small upward point by the exoccipital. The quadrate in *Nothosaurus* is much broader and projects more laterally than in *Ptychognathus*. The median ridge of the supraoccipital in *Nothosaurus* is only hinted at in *Gorgonops torvus* (2), and otherwise it is normally missing in Anomodontia. But the lower position of the supraoccipital below the parietal corresponds exactly to the characteristics of all Anomodontia.

The skull of *Deuterosaurus* and *Rhopalodon* may be compared in many respects even better with *Nothosaurus* than with that of Anomodontia. The palatines close the largest part of the palate. The inner nasal openings are completely in front of them and are separated by the vomer. Behind, the pterygoid reaches the skull base rather higher than in Anomodontia. The supraoccipital meets the foramen magnum. Above it an interparietal with ridges inserts. By the indicated points of comparison, of which SEELEY has already mentioned several, I might only say that the principle of the skull structure is not so entirely different as it might seem at first.

The vertebrae of *Nothosaurus* are platycoelous or slightly amphicoelous and without tendon remains; in Therochelonina and Theriosuchia they are deeply amphicoelous; in Pareiasauria a tendon canal persists on both sides reaching deep into the centrum. Intercentra in *Nothosaurus* are only present on the atlas, while they have a greater distribution in Anomodontia. The length and height of the vertebrae are not very different. The structure of the upper arch is most like that of

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(1) *Zeitschr. d. deutsch. geol. Gesellschaft*, 1893, 352.

(2) R. OWEN, *Descr. and Illustr. Catalogue of the fossil Reptilia in South Africa in the Collection of the British Museum*, 1876, pl. 21, fig. 1; pl. 22, fig. 4.

*Rhopalodon* and *Deuterosaurus*; the strong, short diapophysis even recalls *Pareiasaurus*. In *Nothosaurus* the cervical ribs are two-headed, the dorsal ribs single-headed, the proximal ends thick and rather S-shaped. This is the case in Anomodontia and Pareiasauria. The greatest difference lies in the amphicoelous nature of the centra in Anomodontia as compared to Nothosauria. It is quite conceivable that this was lost in the latter by extreme adaptation to water life. The number of sacral vertebrae—two in *Nothosaurus*, three in *Anarosaurus*—is the same as in Deuterosauridae. The arrangement of the sacral ribs is even strikingly similar, as the figures show.

The similarity of the ilium of *Nothosaurus* (two forms) with the several Pareiasauria and Anomodontia is to be seen particularly if one considers that *Nothosaurus* has only two sacral vertebrae instead of 6-8; thus the proximal end does not need the expansion. The distal part with the large, closed acetabulum in both recalls each other greatly. Ischium and pubis of *Cynognathus crateronotus* SEELEY (1) agree strikingly with younger Sauropterygia, many Plesiosauria, but Nothosauria can also be compared with this.

The femur of Deuterosauridae is very like that of Pareiasauria, Theriodontia, and Clepsydripidae (*Dimetrodon*). On the other hand, the femur of *Dicynodon* may be placed alongside of that *Nothosaurus*, because it comes between both.

Shoulder girdle and forelimb are once again adapted to water life in *Nothosaurus*. In the former, therefore, all the bones are fused and only separated by sutures, to provide more strength. I dare express no opinion as to whether the distal spine-like process of the scapula of *Nothosaurus* may be compared with the meso-scapula SEELEY (= epiclavicle = cleithrum) of *Pareiasaurus* and the thick short part of the scapula with the disc-shaped scapula of *Mastodonsaurus* (which has much in common with *Pareiasaurus*). In any case the clavicle of *Mastodonsaurus* shows great similarity with that of *Nothosaurus*. But above all there is great agreement with *Pareiasaurus*, but at first glance one is struck by the curved clavicles with the small episternum fused in between them. SEELEY in particular draws attention repeatedly to the necessary previous existence of a cartilaginous procoracoid. The scapula has three articular surfaces, of which one receives the humerus and one the coracoid. There is no bone for the third. The coracoid has a notch on the articular surface for the scapula, and medially nearby an apparently useless process follows. The cartilaginous coracoid must have sat here; then the supracoracoid foramen would grow out from the notch, giving the third articular surface a purpose.

If such a procoracoid is present now, this gives another point of comparison with Anomodontia, because it does not occur as a separate bone in other groups of animals (it is recognized with certainty in Chelonia, but they also fuse in *Palaeohatteria*, Crocodilia, and Dinosauria).

The distal part of the humerus of *Nothosaurus* has an entepicondyle reminiscent of *Dicynodon*, *Deuterosaurus*, etc., with a matching foramen and an ectepicondyle with an ectepicondylar sulcus (rarely foramen). Again this may only be compared with Anomodontia.

The distal part of both limb pairs is very greatly modified (only well known in *Lariosaurus* and *Nothosaurus*). In Liassic Sauropterygia (*Plesiosaurus*) the forearm or lower leg bones have become similar to the carpals and tarsals and to an even greater degree in Upper Jurassic representatives.

Now, as far as Plesiosauria are concerned, one must not think that in general they follow the Nothosauria in time without a contemporaneous occurrence of both. Nothosauridae certainly never extended into the Liassic, but Plesiosauridae probably extended into the Triassic. *Plesiosaurus* is

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(1) *Phil. Trans. Roy. Soc. London*, 186, 1895, fig. 20, p. 115.

not uncommon in the English Rhaetic (Aust Cliff near Bristol). *Termatosaurus albertii* PLIEN. from the Swabian Rhaetic is a true plesiosaur. Several vertebrae of a *Plesiosaurus* from the Rhaetic bonebed of Bebenhausen are found in the Tübingen collection. *Plesiosaurus bibractensis* SAUVAGE and *Plesiosaurus costatus* OWEN from the Rhaetic of Autun also belong there. In the *Zanclodon* Beds of Schönthal near Basel, extraordinarily large *Plesiosaurus* vertebrae have been found (Fig. 51 and 52, p. 46). The distal end of a humerus from the Rhaetic Keuper is preserved in Göttingen (Fig. 53, p. 47). These are Rhaetic occurrences. But *Plesiosaurus* remains are also found, rarely, in the Upper Muschelkalk; H. von MEYER has already figured some without naming them. Such ones are found in most large collections which possess large series of *Nothosaurus*. Already they occur in the Upper Muschelkalk of Tarnowitz.

From this it seems that Plesiosauria must have evolved early on from a branch of Nothosauria, while others existed and evolved at the same time. These facts will only be observed in more detail in a monographic revision of Nothosauria.

At the beginning of this section attention was drawn to the fact that Sauropterygia are a group that adapt themselves to swimming in ever increasing degrees. But all the parts of the body, even the very primitive limbs, are already not inconsiderably adapted to it. Therefore, in the foregoing the comparison with a doubtless older reptile group is made, and one can only ask whether Sauropterygia are in direct genetic relationship with them or whether they represent an isolated group whose most primitive forms are still unknown. However, properly speaking, this is unlikely. I believe I have assembled sufficient material to show that Nothosauria are more closely related to certain branches of Anomodontia. Close agreements are established with Dicynodontia; but we must remember that these forms are themselves even more specialized. Deuterosauridae and Pareiasauria are primitive, they stand in closer relationship with the foregoing. In this connection it is important to remember that Deuterosauridae are of Permian age but Dicynodontia are of Triassic. However this fact makes the direct descent from the latter well nigh impossible. Therefore I will not be at all surprised if *later* more widely based *studies of Nothosauria prove they are derivatives of Deuterosauridae that have returned to the water* and they thus represent an equivalent branch to Dicynodontia from one stock. This is a point of view that may form the subject of a future monograph on Nothosauria of importance. The presence of a postorbital in some older Nothosauridae, such as *Cymatosaurus* and *Nothosaurus* (*Eurysaurus* (FRECH) *latissimus*), certainly seems to stand the way of the acceptance of this, but Therosuchia also possess one.

## PRESENCE OF PLESIOSAURIA IN THE MUSCHELKALK

As mentioned already, there are found in the German Muschelkalk rare vertebrae of true Plesiosauria which differ only slightly from Nothosauria in some respects. HERMANN von MEYER has already figured a number of these in his "Fauna der Vorwelt"; they are mainly as follows: pl. 25, fig. 3; pl. 52, fig. 3, 7, 12; pl. 53, fig. 2-8; pl. 57, fig. 3, 4, 6.

Such vertebrae from the Upper Muschelkalk of Bayreuth lie before me. The cervical vertebrae are keeled along the middle with the characteristic foramina; the dorsal vertebrae are rounded and smooth. Once again I figure a posterior cervical centrum and a complete anterior cervical vertebra from Bayreuth (pl. VIII, fig. 4 and pl. V, fig. 5). Pl. V, fig. 5 represents an anterior cervical vertebra from Bayreuth. In the latter the high formation of the upper arch falls between the diapophysis and the zygapophyses, which are strongly developed. The spinal process

is narrow and short. Another cervical vertebra from the lower bonebed of the Lettenkohle of Biebersfeld (pl. V, fig. 4) shows the two characteristic foramina very strongly marked on the underside. The upper arch is missing, thus a further two pairs of smaller foramina are visible from the base of the neural canal. The other pair lies right in front on the edge of the articular surface; each of the two openings is very elongate. The posterior pair is  $\frac{2}{5}$  of the length of the vertebra (= 10 mm of 25) distant from the rear edge. The base of the neural canal is much broader toward the rear than the front.

The *Plesiosaurus* vertebrae from the Muschelkalk may first of all be combined as

*Plesiosaurus priscus*

indeed it is suggested that they are distributed over more than one species (Tarnowitz!).

PECULIAR SACRAL VERTEBRAE FROM THE MUSCHELKALK

Pl. VI, fig. 6.

Further a sacral vertebra from Bayreuth (Tübingen Collection) is very interesting. The sacral rib is preserved complete and is remarkable for its shortness, compared with *Nothosaurus*; measured from the root, it is exactly as long as the centrum, namely 3.5 mm. The centrum is strongly keeled on the underside and has a small foramen on one side of the keel, it is obliterated on the other side. The sacral rib is directed backward and somewhat outward; it is thickened at the distal end and has along the upper front edge a wing-like process that makes it seem twisted. Nothing is preserved of the upper arch. The quite flat neural canal is broader behind than in front. It is not quite certain whether this vertebra belongs to a plesiosaur. It cannot be a nothosaurid for these never have keeled centra; however it could be dinosaurian. In support of the latter hypothesis are, excluding the keel, the length of the centrum and the twisted sacral rib. But against this and in favor of Plesiosauridae are: on the underside a small foramen is found on one side of the keel, it is obliterated on the other side; the lower attachment of the sacral rib is more characteristic of Sauropterygia, as is the fact that the sacral rib curves downward, however the bending backward is strange for them. But chiefly opposed to the Dinosauria seems to be the structure of the neural canal as well as the beginning of the upper arch, which indicate its very short cramped structure, the rounded upper surface of the sacral rib, and the lack of a distal extension of the surface (thickening is not enough). Apart from the length of the sacral rib all these indicate Plesiosauridae; e.g. *Plesiosaurus conybeari* OWEN from the Lower Lias has short thick sacral ribs, of which I was able to convince myself from an example in the Bristol Museum. If all previous explanations of the origin of Sauropterygia are established, it would be conceivable that we have here a primitive plesiosaur, which still possessed a strong ilium (with corresponding strengthening of the sacral rib) and walking feet. The keeled centrum also agrees with this. From this hypothesis, expressed with all due reserve, whose correctness must first be proved by further finds, perhaps we have here a case of a transitional form between Anomodontia and *Plesiosaurus*.

PLESIOSAURUS FROM THE UPPER KEUPER AND RHAETIC

Numerous finds of *Plesiosaurus* are known from the Rhaetic, particularly frequent from the region of Bristol and Gloucester in England; also from the Rhaetic of Autun, from where SAUVAGE (1) listed two species, namely cervical vertebrae of *Plesiosaurus costatus* OWEN and dorsal vertebrae of *Plesiosaurus bibractensis*, a species named by him. A number of vertebrae of *Plesiosaurus rugosus* OWEN in the Tübingen Collection have been found in the bonebed of Bebenhausen. *Termatosaurus albertii* QUENST. is also a true *Plesiosaurus*; there are cervical vertebrae of a probable English species.

In the Museum at Basel are found the largest *Plesiosaurus* vertebrae that I have seen (see text-fig. 51 and 52). They come from the *Zanclodon* beds of Schönthal and were found together with *Gresslyosaurus ingens* RÜTIM., an extraordinarily large *Belodon*, and remains of *Mastodonsaurus*. A dorsal centrum is 8.5 cm long and broad, and 8 cm high. One sees the characteristic cross (spinal cord and diapophysis attachment) on the upper side. The articular facets of the centrum are almost entirely flat, for the rest I refer to the figure. Another vertebra from the border region between neck and back still has most of the upper arch. The centrum is 5.5 cm long, 6-7 cm broad, and just as high. In cross-section it is wedge-shaped below and rather flattened in the middle. The indicated double rib attachment is very broad and strong. The parapophysis lies about at the level of the centrum. The neural canal is large and wide. Very large and strong postzygapophyses are found above it. When further vertebral remains are considered, there is a left pre- and postzygapophysis, which indicates a short but very high upper arch, probably of a cervical vertebra. The form recalls to some extent the also very high cervical vertebrae from the Muschelkalk of Bayreuth (see pl. V, fig 5); only there the zygapophyses are longer and less strong. A small caudal vertebra (one of the very last, very small) is also present from Schönthal. In the same place were found several long, conical, rather curved teeth circular in cross-section and over 5 cm long, which could also probably belong to this *Plesiosaurus*.

In the Geological Collection at Göttingen University is found the distal end of a humerus of *Plesiosaurus* from the Rhaetic Keuper of the Little Hagen near Göttingen (see text-fig. 53). The piece preserved indicates quite a slim bone. One longitudinal contour goes at almost a right angle from the end surface, the other is curved toward the midline, this is the posteriorly directed edge. The muscle attachments are strongly marked. The piece is 8 cm long and 12 cm broad. No one doubts that this humerus belongs to a *Plesiosaurus* and not perhaps to an *Ichthyosaurus*.

*DOLIOVERTEBRA FRITSCHI* n. gen. et sp.  
(*dolium* = barrel)

The Geological Collection at Halle am Saale possesses a very fine sacrum consisting of three vertebrae, from the Schaumkalk of Freiburg am Unstrut, a sketch of which I reproduce here. The centra are strangely barrel-shaped, with narrow raised edges and flat articular surfaces. The upper arch is bulky and recalls in this way the pygmy Sauropterygia of the Lower Muschelkalk of Silesia and Saxony. The barrel-shaped centra are most like those of *Proneusticosaurus* VOLZ (ms.). The spinal process is not high but so broad that they all three meet. The transverse process is short and very thick. Separated by a clear suture, a long, hollow sacral rib, triangular in cross-section, terminates on it. The flat sides of the sacral ribs curve upward and possess a roughly plate-shaped horizontal expansion in the middle. The sacral ribs stick out at a right angle; only the distal ends curve rather downward. The first and third sacral ribs bend toward the second, which is also

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(1) *Ann. des Sc. géol.* 1882, 14, art. no. 3, 1-44, pl. 6-9.

the shortest, so that a semi-circular contact surface for the ilium results from it. To judge from the form of the vertebra, I suppose the animal was related to *Neusticosaurus* and *Proneusticosaurus*.

## 5. TESTUDINATA

Only little is known about Chelonia from the Triassic. From the Upper Keuper of Württemberg there are two specimens of *Psammochelys keuperina* QUENST. (= *Proganochelys quenstedti* BAUR): armor and dorsal vertebrae as well as the negative of the scapula described. The vertebrae described by H. von MEYER as *Chelytherium obscurum* from the same bed and locality also seem to belong to *Psammochelys*. According to BAUR and FRAAS it is a true pleurodire. It is striking, almost astonishing, that such a highly developed type still appears as the oldest known chelonian. It is obvious that this cannot in reality be the oldest chelonian. Moreover, I believe I can now mention cryptodire Chelonia from the Upper Muschelkalk (see below). Without, however, wishing to give an opinion on the difficult question of the position of the Dermatochelidae, I might try to consider more closely the connections of the Chelonia with other reptile orders, on the basis of general chelonian features.

Comment is repeatedly made on the noteworthy resemblance of the external appearance of the skulls of a chelonian and *Oudenodon*. Both are highly adapted toothless forms, which on its own makes a direct connection very unlikely. According to SEELEY, *Oudenodon* is certainly found in the oldest of the five divisions of the Karroo. For all that, it is of value to examine carefully the skull of Chelonia and several Anomodontia. The views of the occiput of *Euclastes* (Eocene), *Dicynodon* (which agrees almost completely with *Oudenodon*), *Placodus*, *Nothosaurus*, and finally *Pareiasaurus* are very instructive. *Euclastes*, *Dicynodon*, and *Placodus* have a three-part condyle, the form of the exoccipital is very similar to these and *Nothosaurus*, above it the opisthotic likewise. The parietals follow directly on the supraoccipital only in *Nothosaurus* and Chelonia; in *Dicynodon* and *Placodus* interparietals intercede. The pterygoid is only visible from behind in *Nothosaurus*, *Placodus*, and *Pareiasaurus*. The skull of *Kistecephalus* agrees in all essential points with *Dicynodon*. I have appended here the posterior view of the skull of *Pareiasaurus* in order to show the similar hollowing out of the parietals here and in Chelonia. Chelonia have a posteriorly open temporal fossa, but it can be entirely covered by the parietal, squamosal, and postfrontal, as is the case in e.g. *Euclastes* and *Rhinochelys*. However only a single pair of temporal fossae exists in Anomodontia. As in *Dicynodon*, *Oudenodon*, and *Ptychognathus*, the frontals are comparatively small and only play a small part in the bordering of the orbit. The same is the case in Theriodontia and particularly in many Stegocephalia; I recall only the temnospondylous *Actinodon*. Chelonia lack a postorbital as do most of Nothosauria (except *Cymatosaurus* and *Eurysaurus*) and Dicynodontia (Therochelonia SEELEY), while other Anomodontia (= Therosuchia SEELEY) including *Placodus* have one. Therefore in Chelonia the postfrontal is developed very large. As in many Anomodontia, however not in *Dicynodon*, the nasal opening is single, not paired; in *Kistecephalus arctatum* OWEN (1) both nasal openings have become a single, spectacle-shaped opening by a narrow lateral connection. The palate is also built on one and the same plan in Chelonia and Dicynodontia. If we next compare *Euclastes* with *Dicynodon* and *Oudenodon*, we see in both a short presphenoid, beside it the narrow, curved pterygoid, elongated forward and backward, close in front of the unpaired nasal opening, which is bordered laterally by the palatine and vomer; the premaxilla follows in front as a continuation of the vomer. In other Chelonia, like

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(1) R. OWEN, *Descr. and Illustr. Catalogue*, etc. (*loc. cit.*), 1876, pl. 65, fig. 5.

*Chelydona* or *Emys*, all this is much more broadened, by which the physical appearance is changed; also the nasal opening is divided in two by the vomer and an opening has appeared between the palatine and pterygoid; however the general structure remains the same.

Different analogies and homologies may also be found in the skeleton. The more or less wedge-shaped centra in cross-section are still preserved in the anterior half of the tail; in Dicynodontia in the dorsal and caudal region; the structure of the ilium, e.g. in *Chelydra* and *Dicynodon*, is similar (so also in Sauropterygia). The proximal end of the chelonian femur is comparable only with the Therochelonian, and not with the Therosuchia, in that a large femoral head sits in the acetabulum and the greater and lesser trochanters project in front like wings and produce a deep pit between themselves and the head. We find a similar situation in *Dicynodon (orientalis* LYD.). However, in the Therosuchia, like *Pareiasaurus*, *Rhopalodon*, *Cynosuchus*, etc., the greater trochanter is developed shield-like and the femoral head sits like a small wart on the lower end of the greater trochanter, by which a similar structure is obvious upon consideration of the head. Thus the fossa in the connected skeleton of the Therosuchia is to be seen from the dorsal and lateral sides of the animal, in the Therochelonian (and in *Hatteria*) from the ventral side. The femur of *Nothosaurus* has a triangular end surface at the proximal end which corresponds to the head and both trochanters; however the great development of these three parts does not occur, they have become rudimentary to some extent by the swimming way of life; therefore it cannot be decided from which of the two types of femur it is derived. The chelonian humerus has an entepicondyloid fossa at the distal end and often an ectepicondyloid foramen (radial nerve canal), which both occur as foramina in Anomodontia and Rhynchocephalia. The structure of the primary shoulder girdle also agrees in its elements (namely scapula, coracoid, and procoracoid) with Anomodontia and Rhynchocephalia (according to FÜRBRINGER, DOLLO, and HUXLEY; contrary to BAUR).

The numerous analogies between Chelonia and Nothosauria are often pointed out. But since both appear simultaneously the descent of one from the other is impossible. It is conceivable rather that both had a joint ancestor. There are so many points of agreement and similarity with Dicynodontia that this connection seems very likely. Chelonia and *Hatteria* certainly have some points in common, in particular similar ischium, pubis, and ilium, the number of two sacral vertebrae, and the proximal end of the femur; but the similarity with the Dicynodontia outweighs this, however distant. Indeed I will not even maintain a direct descent of Chelonia from Dicynodontia, as already said, but I cannot entirely agree with the arguments put forward by FÜRBRINGER (1) for the other side.

As already stated and proved, I do not believe that Placodontia are primitive Chelonia, but that they also branched from Anomodontia, but that they are now more connected with Deuterosauridae, while Chelonia has nothing to do with Deuterosauridae.

*CHELYZOOON LATUM* n. gen. et sp.

Pl. VII, fig. 2

Among a large number of vertebrae from the main Muschelkalk of Laineck near Bayreuth, in the Palaeontological Museum at Munich, a cervical vertebra attracted my attention and I took it for chelonian. Already the fact that it is procoelous isolates it completely from all known Triassic vertebrae. The centrum, 5.8 cm long, is strongly keeled on the underside, as in many Chelonia, and in the middle and below it is extremely strongly constricted. The height of the centrum is 3 cm.

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(1) *Jen. Zeitschr., N. F.*, vol. 27, 1900, 633 pp.

The posterior, roughly heart-shaped articular surface is convex and only 2.5 cm broad; the anterior, 3.5 cm broad, is round and clearly concave. The actual spinal process is unfortunately broken off, yet the part still present seems to indicate a low, ledge-shaped spinal process. The prezygapophyses are placed flat, are strikingly strong and broad; their outer edges stand 4 cm apart. Below them are found even more strikingly, broad projecting parapophyses with downward-directed articular surfaces. Diapophyses are absent or are fused with the parapophyses. The postzygapophyses are unfortunately not preserved. The points of the parapophyses stand 5 cm apart. In favor of the chelonian nature are the procoelousness, the keeled centrum, and the development of the prezygapophyses and parapophyses.

The cervical vertebrae of *Chelydra* and *Macroclermys* agree strikingly with that described here. There the anterior articular surface is also very broad. The prezygapophyses are developed similarly, and the articular surfaces are bordered behind in exactly the same way. The parapophysis, found right in front, projecting strongly with a downward-directed surface, is present similarly in both. However no articular surfaces for the cervical ribs are present. A similar development of the parapophyses (or ? diapophyses) is generally characteristic of chelonian cervical vertebrae. Therefore it seems that the affiliation of these vertebrae to Chelonia is justified, and I believe it is most likely they are to be ranked with Cryptodira because of their resemblance to *Chelydra*. This is a fact of great importance for the phylogeny of Chelonia, because hitherto only the pleurodire *Psammochelys* was known from much younger beds of the Triassic. The Cryptodira, specifically *Sphargis*-like forms, have been regarded as the most primitive Chelonia by several people. The occurrence of *Chelyzoon* in the Muschelkalk is indeed no positive evidence for the opinion just mentioned, but it shows that forms from this relationship group were present already in the Middle Triassic, and also that at that time, or rather later in the Keuper, Cryptodira and Pleurodira already existed as separate related suborders. Here it may be enough merely to establish this.

*CHELYZOON BLEZINGERI* n. sp.

Pl. VII, fig. 1

Another similar cervical vertebra belongs to the Natural History Cabinet, Stuttgart (No 8728). It was collected in the upper Muschelkalk bonebed of Crailsheim by BLEZINGER. This vertebra is the largest and best preserved. It differs from the previous one by its greater length but it is built almost the same. The differences listed, together with the younger age, make another species of the same genus likely.

The centrum, 9 cm long and 3 cm high, makes the earlier interpretation (on the label) as *Tanystrophaeus* seem understandable. The posterior articular surface is narrow, heart-shaped and convex; unfortunately the anterior is missing. The underside of the centrum is keeled. In the middle of the side a high edge runs the length from behind to the parapophysis. The parapophysis projects, in chelonian fashion, from the side with a downward-directed surface. The very strong prezygapophysis is found above it with a small, round, clearly bordered articular surface. The postzygapophyses are also quite massive. The articular surfaces are only slightly curved, almost horizontal. The spinal process rises 2 cm above the postzygapophyses; its base is just less than 5 cm long. This vertebra differs from the previous ones by relatively greater length, broader prezygapophyses with smaller articular surfaces and stronger but lower lying side keels.

These two vertebrae, which were found in different horizons of the Muschelkalk in Swabia and Bavaria, indicate a wide distribution of marine Chelonia. It is striking that they have hitherto been so completely ignored, although these vertebrae are very like those of the living species.

#### ON *ARCTOSAURUS OSBORNI* ADAMS

I think that the single cervical vertebra of *Arctosaurus osborni* ADAMS (1) also belongs here. Whether it is also procoelous cannot be definitely seen from the figure, but it is possible. It is keeled below; the far-projecting prezygapophysis bears the characteristic small round articular surface, which is present in *Arctosaurus* and *Chelyzoon* on the edge running anteriorly from the postzygapophysis; the diapophyses are unfortunately not preserved; in front below the prezygapophysis is a fracture place, on which the parapophysis clearly sat. The entire vertebra recalls *Chelyzoon blezingeri* and *Chelyzoon latum* very much, but it is considerably shorter than these. The separate generic name is justified for the present by this and other small differences. *Arctosaurus* figured previously among the Dinosauria, but with which it had little more in common than the keeled underside (of the cervical vertebra). In particular such a bordered small, round articular surface on the prezygapophysis, as *Arctosaurus* and *Chelyzoon* and the Chelydridae in general possess, never occurs. Also the Dinosauria, with the exception of *Tanystropheus*, never lack the diapophysis.

#### VERTEBRA FROM THE RHAETIC

Pl. VII, fig. 5

Finally I may mention a vertebra from the Rhaetic of Schösslesmühle near Steinbronn (Tübingen Collection), whose figure is almost unrecognizable in QUENSTEDT's "Jura" pl. 2, fig. 3. It is a rather elongated, weakly procoelous vertebra. The anterior articular surface is oval and barely noticeably deepened, while the posterior is clearly convex, very narrow below and broader above. The centrum is noticeably constricted in the middle and sharpened downward, but is truncated again on the outermost edges by a horizontal surface that is broader anteriorly than posteriorly and clearly shows the three parallel keels there. The spinal process curves posteriorly rather flat. The postzygapophyses are broken off as is the anterior part of the prezygapophyses; the neural canal is high, the attachment of the diapophyses is strikingly high and narrow and is found right in the middle of the length of the vertebra. In order to classify such a caudal vertebra, one must consider Dinosauria, Crocodilia, and Chelonia; other reptile groups cannot come into question. Crocodilian caudal vertebrae are usually rounded; in them and the Dinosauria, the root of the diapophysis is horizontal and not extended vertically; but both these points are possible in the Chelonia, which have procoelous articular facets, which is also a feature characteristic of Chelonia. Therefore this vertebra is probably chelonian. Yet I will not attempt to assign it to a particular family.

#### CHELONIAN REMAINS FROM BUSENDORF

Pl. VII, figs. 3 and 4

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(1) *Proc. Roy. Irish Academy*, ser. 2, II, 1875, 177 ff.

In the Geological Collection of Alsace-Lorraine at Strassburg are two pieces from the Upper Muschelkalk of Busendorf, Lorraine (collected by Prof. BENECKE in 1879). One of them most resembles the free rib end of *Thalassemys*, the other may be best compared with an armor fragment of the same genus. The rib end shows on the upper side wavy longitudinal grooves lying close together. It is 2 cm broad and still has the natural sharpened end. The fragment is 3 cm long. The broken-off edge begins the granulated sculpture that distinguishes the piece of armor. The granulation is very like that of *Thalassemys*. On the underside, the ribs and armor piece are smooth. The rib has a strong longitudinal keel and is in general flat. Also the armor piece shows an overall gradual thickening in one direction on the posterior side, and thus could well be a costal plate.

FEMUR inc. sed.  
Pl. VIII, figs. 1 and 3

In his "Fauna der Vorwelt", H. von MEYER has figured (pl. 65, figs. 5-7, p. 79) a left femur of curious shape, which comes from the Upper Muschelkalk of Bischmishein near Saarbruck. It belongs to the Strassburg National Collection. Three similar femora have been found in the same beds at Laineck near Bayreuth and are in the regional museum there; one of them is very much slimmer than the others, two are lefts and one is a right femur. The shaft is considerably S-shaped, in the distal half it is quite flat and thickened at the proximal end. The femoral head stands right-angled inward. The greater trochanter rises above the femoral head as a direct continuation of the shaft. The lesser trochanter is merely a reinforcement of the greater trochanter. The muscle scars are very clearly marked, particularly that of Mm. vastus medius and gastrocnemius. In a specimen from Bayreuth the epiphyses are missing, by which the proximal end retained the triangular appearance, as in *Nothosaurus*.

I know of such femora in no other reptile orders than Chelonia, although they do not fully agree with any known chelonian (1). The lesser and greater trochanters in particular are developed differently. However, I think that this structure of the femur indicates a transitional form between many anomodont types and the true Chelonia. The similarity with the femur of *Dicynodon orientalis* LYD. is very great, but the proportions of the femoral head and greater trochanter recall also the primitive anomodont forms such as *Pareiasaurus*. When both the trochanters divide and move away from each other laterally, as a result of greater adaptation to chelonian life, the perfect chelonian femur exists, which could be connected to the limitation of movement by the armor plates.

The cervical vertebrae and the rib and armor fragments indicate the same group of Chelonia, the size is also in agreement; considering the rarity of Chelonia in the Triassic, these remains could perhaps belong to the same genus. It is also suggested that the femora belong to it.

HUMERUS inc. sed.  
Pl. V, fig. 6

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(1) The femur of *Thalassochelys caretta* is relatively the most similar, which struck me in a specimen in the Vienna Hofmuseum.

An extremely peculiar humerus has been found in the area museum, Bayreuth, which comes from the main Muschelkalk there. Although its affiliations have not been determined, I have figured it because it is without doubt of great interest and perhaps thereby others will be put on the right track.

It is 12.5 cm long, the thickened proximal end is smooth, rather flattened, and more strongly curved to one side than the other, as the figure shows best. The shaft is only allusively curved and very thick (2 cm) in an only slightly greater breadth. A plate-like process (?radial process) extends for almost the entire length on the probable lateral side. The median (?) surface of the shaft has an edge on one side; this same side is entirely flat, while the other is greatly curved in cross-section. The distal end shows a clear separation into two condyles. On the lateral (?) side one notices a clear ectepidondyloid foramen. It is probably a right humerus, and then the intercondyloid foramen is on the anterior side. But very little idea can be formed as to the kind of animal which possessed the humerus. However, Pterosauria, Dinosauria, Crocodilia, and Sauropterygia are excluded. The foramen at the distal end is common to Proganosauria, Anomodontia, and Chelonia (also Sauropterygia, but which because of the particular form definitely cannot come into question). No more can be said than that the humerus belonged to a strongly built animal with long limbs. Without in any way being able to prove or advocate the chelonian nature of the animal in question, however I rank the humerus here as an appendix to the Chelonia.

## 6. PARASUCHIA (AND EUSUCHIA AS APPENDIX)

One of the most interesting groups of Triassic reptiles are the Parasuchia and Pseudosuchia, together with the theropod Dinosauria. Although according to the textbooks one belongs to the Crocodilia, the others forming a separate order, they have surprisingly many joint characteristics.

The skull of Parasuchia and Pseudosuchia is known to have many differences in the proportions and in the position of the openings, which is the reason for the separation of these two groups. The Parasuchia have enormously developed premaxillae that produce the crocodile-like long snout. The nasal openings (at least in *Belodon*) lie within the nasals and are bordered by no other bones. They are thus shifted abnormally far backward. This striking fact can probably only be viewed as a secondarily acquired characteristic; digging in the mud with its long snout was thus made very easy for the animal. The Pseudosuchia have a short snout and thus also terminally placed narial openings, in the usual way, which stand laterally and are surrounded by the nasal, maxilla, and premaxilla. The antorbital vacuity lies close behind them. The upper temporal fossae are closed behind (observed in *Aetosaurus*, *Erpetosuchus*, and *Ornithosuchus*), while they are open behind in the Parasuchia (*Belodon* and *Mystriosuchus*), and as a result of this nearly seem to be missing. *Aetosaurus* lacks the lower temporal fossa, *Erpetosuchus* and *Ornithosuchus* have well-developed upper and lower temporal fossae. Thus one sees that these conditions vary a lot. In armored animals, like the Crocodilia, this agrees in any case with the cervical armor on the one hand and with the different jaw length on the other. Therefore the different structure of the temporal fossae agrees in *this* (perhaps single) case with the way of life, for the degree of armament and the jaw length are directly dependent on it. The presence of a postorbital below the small postfrontal is common to both groups. In the previously listed characteristics of the skull, the Triassic theropod Dinosauria stand nearer to the Pseudosuchia (especially *Erpetosuchus* and *Ornithosuchus*) than the Parasuchia. In the position of the cranial nerve exits they even show surprising similarity with *Belodon* and the Eusuchia. The palatal roof shows interesting variety in

the different forms. It is most closed in *Belodon*; the choanae lie far anterior, nearly directly below the external nasal opening; otherwise the palate is entirely closed. In *Ornithosuchus* the choanae are found rather behind the middle of the complete skull length, but the external nasal opening is far anterior so that a long choanal passage, surrounded by the palatine, nasal, and vomer, is necessary. Beside the internal choana opening and anterior to the ectopterygoid lies a rather smaller perforation communicating with the antorbital vacuity. In *Erpetosuchus* the choanae are placed far anterior (nearly meeting the short premaxilla), thus almost directly below the nasal opening. The palatines are long and narrow as also in *Stagonolepis*, whose choanae also lie close below the nasal openings. In *Erpetosuchus* the perforation in front of the ectopterygoid is very small. On the other hand the opening between the ectopterygoid, pterygoid, and jugal is large and present, of course, in all Parasuchia and Eusuchia. With regard to the palate, *Aetosaurus* seems to stand between *Ornithosuchus* and *Erpetosuchus* (only a single imperfect skull is available for this observation). The palate of *Erpetosuchus* is by far the most like that of the Triassic Theropoda (*Zanclodon*); it also has long, narrow palatines, a delicate ectopterygoid, and a broad, posteriorly directed pterygoid.

As for the vertebral column, the numbers of vertebrae in the separate regions (at least in several incomplete specimens of the Pseudosuchia in question) seem to amount to 8-9 cervical, 14-15 dorsal; throughout only two sacral vertebrae are present. These numbers agree with those for the later and Recent Eusuchia almost completely. In any case, the number of cervical and sacral vertebrae is characteristic of the Crocodylia. All Theropoda have at least three sacral vertebrae (as e.g. all Triassic) and 13 cervical vertebrae (*Zanclodontidae*). The vertebrae of Parasuchia are generally also morphologically more crocodile-like than dinosaur-like. The cervical vertebrae of *Stagonolepis* are shorter than tall; those of normal Theropoda are up to three times longer than tall; they are the longest in the whole body; in Parasuchia they are the shortest, therefore the neural arch is also developed entirely differently. The spinal processes on the dorsal vertebrae in the Parasuchia are long, narrow spines, but in the Pseudosuchia they are broad plates, as also in the Theropoda. In the Triassic crocodile groups the strong supports below the diapophyses are missing, whereas they are present in the Theropoda. The long sacral ribs of the Parasuchia and Pseudosuchia, horizontally expanded at the distal end, can never produce such a firm connection with the ilium as do the three extraordinarily strong and complicated sacral ribs of the Theropoda. This again is a purely crocodylian characteristic of the Parasuchia. In *Belodon* the spinal processes of the sacral and lumbar vertebrae are greatly expanded above, so that they have there a horizontal, laterally placed surface. The caudal centra are the most elongated. The Parasuchia first acquire broad spinal processes in the tail. The caudal centra lack the groove on the underside that is so characteristic of the Theropoda.

The ribs of *Belodon* differ from those of true Crocodylia by stronger forking at the proximal end; this is due to the deeper position of the parapophysis. These details agree more with the Dinosauria. The abdominal ribs are also different from those of true Crocodylia.

Both the Parasuchia and Pseudosuchia possess a clavicle and interclavicle, whereas these are generally unknown in the Theropoda and Dinosauria (1). True Crocodylia lack the former, but the interclavicle is all the more strongly developed. Clavicles are known from *Mystriosuchus* and *Aetosaurus*. In *Erpetosuchus* a true acromion is developed on the scapula for articulation with the clavicle. In interclavicle in the same species is distally drawn out into a long spine and proximally expanded. In the other forms from which the interclavicle is known (*Belodon*, *Mystriosuchus*,

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(1) In one of the 29 *Iguanodon* skeletons in Brussels, and elongated ossification is present between the coracoids, which Dr. DOLLO very kindly pointed out to me.

*Stagonolepis*, *Aetosaurus*), the proximal expansion is comparatively smaller, and a considerable swelling follows in front of the pointed distal end.

The scapula and coracoid have been found in *Belodon*, *Mystriosuchus*, *Stagonolepis*, *Aetosaurus*, and *Erpetosuchus*. The scapula has the familiar elongated structure with a broad proximal end, where the disc-shaped, round coracoid with a notch on the side is placed; the latter is most considerable in *Belodon*, it is only arched in *Stagonolepis*, *Aetosaurus*, and *Erpetosuchus*. This is also the form in which the coracoid appears in Triassic Theropoda. The scapula of these is like that of *Belodon*, only even slimmer. The scapula of *Erpetosuchus* differs from the others by its slimmness, stronger curvature, and the already-mentioned clear acromion. In this whole group of forms, the scapula and humerus are about of equal length.

The structure of the humerus varies rather more. The humerus of *Belodon* is expanded at both ends, and constricted in the middle. the strongly upwardly moved radial crest stands at nearly a right angle to the broad surface of the proximal end. The entepicondyle can often be almost confused with that of the former. The shovel-like proximal end of the humerus of *Stagonolepis* is much broader; the crest is placed rather more distally; the epicondyles are not present at the distal end as in *Belodon* (and *Mystriosuchus*). The similarity of the humerus of *Thecodontosaurus* and *Stagonolepis* is strikingly large. In a manner of speaking, this form is also similar to the single humerus from the Rhaetic of Linksfield in Morayshire that SEELEY described as *Saurodesmus*, a crocodile (1). The humerus of *Episcoposaurus horridus* COPE (2), from the New Mexico Triassic, is, like *Belodon*, very broad at both ends, with a strongly developed ectepicondyle, so that the contour of the medial side forms a nearly straight line, that of the lateral an approximately 45° angle. The humerus of *Aetosaurus*, with a rather broad proximal end and narrow distal end, shows great agreement with the Zancloodontidae. The proximal part of the humerus of *Erpetosuchus* is extremely narrow.

The ulna in Parasuchia and Pseudosuchia is quite crocodile-like with its broad and curved proximal part, which possesses an olecranon. The radius is narrow and has a concave proximal articular surface. In Parasuchia (*Belodon*, *Stagonolepis*, *Episcoposaurus*), the ulna is broader than in Pseudosuchia, whose forearm recalls the Theropoda even more, although the latter possess no olecranon.

Quite clear differences between the Parasuchia and Pseudosuchia are shown in the pelvic bones, and here, as usual, the latter approach the Theropoda much more than the Parasuchia. The figures speak better than words. The completely closed, thus crocodile-like, acetabulum in *Belodon* and *Stagonolepis* is characteristic. *Aetosaurus* only exists in poor preservation. In all these forms the main bulk of the ilium is found behind the acetabulum; there the ilium is extended into a long posterior point, just like *Thecodontosaurus*; only *Stagonolepis* is shorter than the others. The ilium of Theropoda is different from the former principally only by the completely open acetabulum.

The ischium is of similar form in all these genera and is very different from that of true Crocodylia. It does not stand transversely as in these, but almost entirely sagittally. Distally it runs into a long, stalk-shaped process; the proximal part is a broad plate that meets the pubis anteriorly and closes the acetabulum ventrally together with this. In the Pseudosuchia the stalk is more slender.

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(1) *Quart. Journ.* 1891, 44, pp.166-170. But in 1894 (*Phil. Trans. Roy. Soc.* 185, p. 711) SEELEY himself expresses the suggestion that it could perhaps even be an anomodont femur built after the type of *Rhopalodon*.

(2) *Proc. Am. Phil. Soc.* XXIV, 1887, p. 214.

The pubis is most interesting. In *Belodon* it is a roundish plate perforated (1) by the obturator foramen; the medial edge is thin, the lateral thick. *Aetosaurus* has a flat plate as a pubis, which articulates on the ilium with a thick stem, the extreme part of which is missing. *Ornithosuchus* has a long, quite theropod-like, plate-shaped pubis, whose thick, narrow proximal end is turned over. The pubis of *Stagonolepis* also seems to be developed dinosaur-like, at least in the proximal parts. HUXLEY has figured a pubis (2) that appears quite crocodile-like, but which lacks the upper end. A piece never figured or mentioned in the literature lies in the collection of the Geological Survey in the Jermyn Street Museum, London, which SEELEY (private communication) holds as definitely the missing proximal part. In any case, Mr. E. T. NEWTON also assured me that the piece belongs to *Stagonolepis*, without however wishing to interpret the bones. I can hardly hold the bones as such for anything else than SEELEY. I figure the pieces here in outline, both of which I have handled, and give in addition a reconstruction according to SEELEY's view (Fig. 73a and b).

The bones of the hind limb, particularly the femur, stand nearer the Crocodylia than the Dinosauria, although both show no great differences. The femur is always clearly S-shaped; it is only entirely straight in *Episcoposaurus* and lacks the fourth trochanter, which is otherwise always present, at least in outlines, and stands above the middle. The distal end of the fibula of *Episcoposaurus* recalls many Theropoda, with a concave and a strongly convex side.

The metatarsals and phalanges of the Parasuchia and Pseudosuchia are developed crocodile-like. In Theropoda they are interesting and important by the different degree of reduction of metatarsals I and V in the separate forms.

The armament of Triassic Crocodylia agrees with Mesozoic Crocodylia in that the back is covered with only two rows of long, decorated plates. *Bernissartia fagesi* DOLLO from the Wealden of Bernissart is the first crocodile that has four rows of dorsal scutes like those now living. The dorsal armor of *Belodon*, *Mystriosuchus*, *Stegomus*, *Stagonolepis*, and *Episcoposaurus* is adorned with two rows of strong dorsal spines; in *Episcoposaurus* they are up to 8.5 cm tall. the abdominal armor of all Parasuchia and Pseudosuchia consists of square scutes; in the best specimens of *Aetosaurus*, *Mystriosuchus*, and in *Dyoplax* one sees a large number of small plates. In block no. XXI of the *Aetosaurus* group, eight rows are recognizable. *Teleosaurus temporalis* E. DESLONGCHAMPS from the Upper Lias has only six rows of abdominal plates. No armor at all is known from Triassic theropod Dinosauria.

From the previous statements, I think it has been shown sufficiently that the Parasuchia and Pseudosuchia belong neither to true Crocodylia nor to Theropoda. However, they perhaps stand rather nearer the Crocodylia than the latter because of:

- 1) the armament.
- 2) the number and particularly the shortness of the cervical vertebrae,
- 3) the missing struts of the diapophyses of the dorsal vertebrae,
- 4) the closed acetabulum,
- 5) the structure of the femur, ulna, and metatarsals.

The form of the coracoid and the structure of the ischium, and to some extent pubis, certainly again indicate the Dinosauria very much.

The Parasuchia and Pseudosuchia on the one hand and the Theropoda on the other seem to me to be parallel branches of one stem, from which one may deduce what one wishes. I will go

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(1) As occurs in Sauropoda.

(2) *Mem. Geol. Surv. Monogr.* III, 1877, pl. 8, fig. 4.

into this question in more detail elsewhere. The one cannot be the progenitor of the other, for they appear simultaneously.

The question now arises as to how the two groups Parasuchia and Pseudosuchia are related to each other. It is to be considered that the latter are less specialized in many respects, although the quite crowded anterior dentition of *Erpetosuchus* does not entirely correspond to this feature. In the Parasuchia which are gavial-like in appearance, the excessive length of the premaxillae as well as the posterior placement of the narial openings is a high-degree specialization that, as far as it concerns the last point, has never been adopted by later true Crocodylia, i.e. the same is achieved there by the posterior placement of the choanae (1). In this the forms classified as Parasuchia prove to be secondarily evolved. For all that, both these groups have so much in common that links them to each other and contrasts them to the Eusuchia and Dinosauria, that it seems proven that this should be expressed in the systematic nomenclature, so that both groups should be placed in a *single suborder*. Because the name *Parasuchia* is the older, the precedence will also belong to it. However, the differences between both groups should not be underestimated in this. They can be distinguished as the *families Belodontia and Pseudosuchia*.

I may now indicate in a few words the enormous *distribution* of the Parasuchia in the uppermost Triassic.

*Belodon* has been made known sufficiently from the Upper Keuper of Swabia and France by H. von MEYER, GÜMBEL, etc.; it also occurs in the Brunswick Rhaetic Keuper. GRESSLY and RÜTIMEYER have collected very fine pelvic bones, teeth, etc. in the Knollenmergel of the uppermost Keuper of Schönthal near Basel. Teeth are known from the Keuper of Warwickshire, Somerset, and Devon in England. LYDEKKER has found *Belodon* in the Indian Maleri Sandstone, and COPE, EMMONS, LEIDY, LEA, etc. have shown teeth, skulls, skeletal parts in great distribution in the North American New Red. *Mystriosuchus* is known from the Swabian Stubensandstein, *Stagonolepis* only from Elgin (Sandstone), *Parasuchus* from the Indian Maleri Sandstone. *Rytiodon* (*Rutiodon*) EMMONS from North Carolina and Connecticut probably stands nearest *Mystriosuchus*; only the upper temporal fenestrae are closed posteriorly by the squamosals, and the quadrate is directed obliquely anteriorly instead of posteriorly. MARSH has named *Stegomus* from a dorsal armament from the Connecticut River Sandstone, which is perhaps identical with *Belodon*. *Sauroidesmus* SEELEY (2) from the Rhaetic of Morayshire is based on a single humerus. *Episcoposaurus* COPE (3) is found in the Triassic of New Mexico. Other isolated occurrences are the finds of *Aëtosaurus* O. FRAAS in the Schilfsandstein, *Dyoplax* O. FRAAS in the Schilfsandstein of Württemberg, and *Ornithosuchus* and *Erpetosuchus* E. T. NEWTON in the Elgin Sandstone.

This otherwise well-known presentation shows the great distribution of Parasuchia in the Upper Triassic. Only *Belodon* can be called really abundant, both in Europe and America, where a

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(1) A very elongated snout also occurs among the "Rhynchocephalia", which on the whole have short skulls, in *Simoedosaurus* GERV. (= *Champsosaurus* COPE) of the Upper Cretaceous and Eocene. Certainly there the narial openings lie in front at the point of the snout as in the gavials. Such elongated snouts are found as phenomena of adaptation mainly in such animals which, living in rivers or swamps, must seek their food deep from the mud. *Belodon* was designed particularly practically for this with its narial openings lying posteriorly. A similar result is attained later in the gavials because the choanae open right behind into the throat, and so they were easily closed by the soft palate found there. In swimming animals like the gavials, and probably also *Simoedosaurus*, the narial openings placed at the tip give a great advantage, in that for breathing the animal did not always need to come right to the surface of the water. *Belodon* may have lived more on dry land.

(2) However, SEELEY has again doubted his own determination (*Phil. Trans. Roy. Soc.*, CLXXXV, 1894, 711).

(3) The remains consist of a splenial, proximal and distal caudal vertebrae, a humerus, two ulnae, parts of the radius, a femur, the proximal end of a tibia, the distal end of a fibula, a calcaneum, and several armor plates.

series of species are distinguished. *Stagonolepis* was certainly only found in the neighborhood of Elgin, but not infrequently there.

## NEW AND MISINTERPRETED PARASUCHIA

I. E. FRAAS in "Festschrift über die Schwäbischen Trias-Saurier" 1896, p. 18, has mentioned a piece of a lower jaw from the Schilfsandstein of Feuerbacher Haide as *Zanclodon arenaceus* n. sp. without however figuring it. He says about it: "there is no doubt about the affiliation to the Dinosauria." It is incomprehensible to me how such an expert on the Triassic Reptilia could say this. In the above sentence I might replace the word "Dinosauria" with "Parasuchia" or "Belodontia". The figure will show anyone that this is a case of *Belodon* or *Mystriosuchus*. On the old label, dated 1869, the piece is also named *Belodon kapffi*. This find is only interesting in that *Belodon* thus dates back in Württemberg to the Lower Keuper.

II. *Rileyia bristolensis* n. gen. et sp. Another find of Parasuchia that I may mention was made as long ago as the 1830s by RILEY and STUTCHBURY in the Magnesian Conglomerate of Bristol, but hitherto not recognized as such.

There are two vertebrae and a humerus which were found among a great mass of *Thecodontosaurus* and *Palaeosaurus* bones and together with them. The humerus was figured by RILEY and STUTCHBURY (1) and has never since been opposed. SEELEY (2) said that at first glance it probably recalls *Belodon*, but since he places the bones reversed, as I attempt here, he comes however to the conclusion that it is a dinosaur humerus, although as he himself says (3), no similar theropod humerus (Saurischia) is known to him. The humerus (No. 95 and 96 in the Bristol Museum) has a length of 17 cm, is 2 cm broad in the middle, and 5.5 cm at both ends. It is very slimly built. The strong distal condyles and particularly the ulnar are striking. The proximal part is unusually narrow, and the radial crest only weakly developed. It seems to me that the bone shows the posterior side and then must be a right humerus, however I cannot maintain this with certainty. Compared with *Belodon*, the median longitudinal side also appears here curved inward; the lateral side is straight. However, the radial crest forms a peculiar acute angle above, and the ectepicondyle is missing, as in all other Parasuchia and the Theropoda. In *Erpetosuchus* the proximal and distal ends are also as broad or narrow as here.

Also the two centra cannot belong to a dinosaur. They were later obtained for the Yale Museum, New Haven, Conn., U.S.A., by exchange. From a photograph taken at natural size, for which I thank Prof. BEECHER, one is 3 cm long and 2.5 cm tall, the other 4.8 cm long and 2.3 cm tall, thus very elongated, more than the caudal vertebrae of *Thecodontosaurus*. In general they are too long, too round in cross-section, and far too constricted in the middle for Dinosauria. The articular surfaces are slightly hollowed. All this indicates Parasuchia. The vertebrae of *Belodon* are not so long, but those of *Stagonolepis* are very similar. since, among the extremely numerous bones of Theropoda, only the humerus and two vertebrae belong to Parasuchia, it is very likely that they come from the same animal; so I combine them both here provisionally under one name. The locality is the dolomite conglomerate (Middle Keuper) of Durdham Down (Redland), near Bristol.

## TRUE (?) CROCODILIA FROM THE LOWER MUSCHELKALK

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(1) *Trans. Geol. Soc. London*, V, 1840, pl. V, fig. 1.

(2) *Quart. Jour.*, 1895, 158.

(3) *Ibidem*.

I) In the Tübingen Collection are two caudal vertebrae from the Wellen dolomite of Merklingen and from Hausen on the Würm. Both lack the neural arch.

The larger specimen from Merklingen (pl. VIII, fig.5), a middle caudal vertebra, is 2.5 cm long, 2.2 cm high, and 2.0 cm broad. On the underside it has a clear groove, and on the posterior edge below, the two attachment surfaces for the haemapophyses. The edge of the rather flat articular surface is upturned and curved, particularly on the posterior side. The neural canal sinks rather deeply into the middle of the centrum and is broader posteriorly than anteriorly.

The second piece is one of the last caudal vertebrae (pl. VIII, fig. 6). It is 1.5 cm long and 7 mm high. It also possesses a groove on the underside. The articular surfaces are slightly hollowed. The sides show indistinct longitudinal ledges, which probably served for the attachment of the strong caudal tendons. The neural canal is quite deeply sunk into the centrum.

I think that such caudal vertebrae seem to agree best with a crocodile, but I cannot prove this.

II) The Geological Collection at Halle possesses a fine large caudal vertebra from the Schaumkalk of Wolfsburg at North Harz. It belongs without doubt to a true crocodile. Despite its length of 4.5 cm, it must come from the posterior half of the tail, for the entire neural arch is so extraordinarily small, one could say rudimentary, and the transverse process is completely missing. Therefore it must have been a huge animal. In the place of a more detailed description I refer to the sketches reproduced here. This isolated find is not sufficient for further conclusions.

#### TRUE CROCODILIA FROM THE UPPER MUSCHELKALK

Several pieces from the Upper Muschelkalk still lie before me which I can only place in the Eusuchia:

I) *Procerosaurus cruralis* n. gen. et sp. (pl. IX, fig.1)

A find that may be of interest is a left femur from the Upper Muschelkalk bonebed of the Oelmühle, Württemberg (1). Unfortunately it lacks the femoral head. The whole piece is rather compressed anteroposteriorly. The fourth trochanter is not developed in this species. The distal condyles are just as in Crocodilia and Theropoda. The preserved length of the bone is 30.5 cm, the breadth in the middle 4 and at the distal end 6 cm; but the compression is to be taken into account in these, for the thickness in the middle is only 1.8 cm. The medial condyle is compressed from the medial side, which causes the great breadth of the distal end. The femur is distinguished in particular by its slim, rather S-shaped structure and the lack of the fourth trochanter. The latter in particular seems to me to prove that it belongs to a dinosaur (2). In the Parasuchia and Crocodilia the fourth trochanter is usually only weakly indicated. An edge is present at the place in question in the Crailsheim piece. The bone is much slimmer than all parasuchian femora. The femur of *Episcoposaurus* is certainly also quite narrow but should be straight. Therefore I hold *Procerosaurus* for a eusuchian. It has the most similarity with a gavial femur.

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(1) I am indebted to the Hon. BLEZINGER of Crailsheim for it.

(2) From COPE's description, which unfortunately lacks figures, some similarity with *Tanystrophaeus longicollis* COPE could exist, in that the proximal end is also strongly curved inward and the fourth trochanter is almost completely missing. But from a cast of the original, for which the Tübingen Collection is indebted to Prof. OSBORN of New York, it is obvious at once that no great similarity exists between the two.

II) *Pectenosaurus strunzi* n. gen. et sp. (pl. VI, fig. 5)

There are two caudal vertebrae that come from the main Muschelkalk of Bayreuth and were collected by STRUNZ. The more complete piece is a vertebra from the middle of the caudal vertebral column, whose neural arch refers it to the Eusuchia. The spinal process lies far back; a narrow lamella is placed on it on the anterior side as in the gavials; its contour is rather curved in the middle where the bone fibers are directed vertically toward the edge, on the posterior side they run more upward and parallel to the spinal process, on the anterior toward the prezygapophysis. For the anterior caudal vertebrae this fact seems to me to indicate similar features to those in *Rhacheosaurus*, *Geosaurus*, or *Gavialis (gangeticus)* in that a spine is found anterior to the spinal process. This is unknown in any Parasuchia. The other vertebra belongs to the same species; its articular facets are almost entirely flat; the centrum is rather flattened on the underside.

III) A left *articular + angular* from Busendorf, Lorraine (pl. VI, fig. 3) has great similarity with that of the gavial; it is certainly not different. The angular is extended longer anteriorly and relatively narrower. The articular surface for the quadrate is inclined more outward than is the case in Recent Crocodilia and seems to indicate a more steeply placed quadrate, also the edge is not so high behind the true articular surface in Recent Crocodilia. The piece shows the contact surface with the splenial and is seen from the lateral side. On the figure, the right side is behind and the left is in front; the most posterior end of the articular is missing.

## 7. DINOSAURIA

The important facts about the Triassic Dinosauria have been mentioned in the foregoing section. Details will be found in a monograph in preparation. The large Dinosauria are confined to the Upper Triassic, the younger Keuper and its equivalents. The huge bones of *Euskelosaurus* are also found in South Africa in the uppermost beds of the Karroo. Smaller forms occur already in the Muschelkalk; they are still undescribed (I refer to the monograph). *Tanystrophaeus*, which stands near the Dinosauria in many points, and which is not yet fully known, is also found in the Lower and Upper Muschelkalk. The Triassic Dinosauria of the entire Earth are divided into about 24 genera that may be grouped in four families.

## 8. PTEROSAURIA

Isolated remains of doubtless Pterosauria have only been found in the very youngest beds of the Triassic. Only a few such occurrences are known to me from the literature.

The first probably flying or fluttering reptile, *Tribelesodon longobardicus*, has been described by BASSANI from the Raibl beds above Besano (*Atti della Soc. Ital.*, vol. 29, 1866, 25-30, without figs.). It is confused by another skeleton mixed up with it. Depending on the interpretation of the bones, it may or may not have possessed flying fingers. I can say nothing certain on the systematic position. A description of this by F. von NOPCSA is awaited soon.

DEFNER and O. FRAAS (1) found poorly preserved flight fingers of a pterosaur named by them *Pterodactylus primus* in the sand marl of the bonebed of the Galgenberg near Malsch (near Wiesloch) in Baden, close above the Rhaetic sandstone.

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(1) *Neues Jahrb. f. Min.*, 1859, 12.

In 1857 OPPEL found three flying finger pieces in the sandstone of the *contorta* zone at Birkengehren near Esslingen. H. von MEYER has described and figured two of them (one is lost) (2). These remains are not enough to support conclusions on the nature of the animal.

ANDLER (3) and H. von MEYER (4) found a split flight finger phalanx, which should be specifically different from that of OPPEL, in the "limestones" of Aichscheiss near Esslingen, which ANDLER assigns to the *angulata* beds and H. von MEYER to the *contorta* beds.

West of Wacht, Somerset, DAWKINS found a hollow *Pterodactylus* bone in the Rhaetic with *Avicula contorta* and *Hypsiprymnopsis* (5).

GERVAIS (6) also knew a few broken pieces of pterosaurian phalanges from the only slightly younger, certainly Liassic, sandstones of Hettingen, Lorraine.

All these fragments unfortunately throw no new light on the oldest Pterosauria. The only indicate that the adaptation of the forelimbs was already complete.

In the Natural History Cabinet, Stuttgart, I recently discovered the neural arch of a cervical vertebra that could possibly belong to *Pterodactylus* (pl. IX, fig. 3); it comes from the Rhaetic bonebed and bears the figure E.51, but unfortunately no locality description. The Tübingen University Collection has one like it from the Rhaetic sandstone of Schösslesmühle near Steinbronn; it is only 3 mm shorter than the better-preserved Stuttgart specimen. The latter is 28 mm long. The spinal process is broken off, its base is 10 mm long. The zygapophyses are flat, however not quite horizontally placed; the anterior are long and extended forward and rather upward/outward, the posterior corresponding; the articular surface is 8 mm long and 4 mm broad; its outer edges are 13 mm apart, the breadth of the vertebra in the middle measures only 9 mm. Below the prezygapophyses a sharp edge runs downward. The height of the neural arch, which seems to be preserved up to the neurocentral suture, measures 9 mm up to the base of the missing spinal process. The length of the centrum seems to have been 16-17 mm. This vertebra shows great similarity with *Rhamphorhynchus* and *Campylognathus*, the long-tailed forms.

Among the MILLER-ENDLICH material from the Rhaetic bonebed of Bebenhausen, in the Tübingen University Collection, are found two smaller short phalanges that could very probably belonged to the hind limbs or the claw-bearing digits of the manus of a *Pterodactylus*. The larger piece, a fragmentary distal end, measures 4 mm in length, but could have been 1.5-2 cm long when complete.

These remains of cervical vertebrae and phalanges give no information on the phylogeny of the Pterosauria. At most one could regard the cervical vertebrae as further proof that the long-tailed Pterosauria are older than the short-tailed pterodactyls (1). But these remains, even the oldest, leave us quite in the dark as to which reptile order the Pterosauria are derived from.

### C. SYSTEMATIC REVIEW OF THE TRIASSIC REPTILIA

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(2) *Zur Fauna der Vorwelt*, Bd. 3, 1860, 10-89, pl. 8, figs. 9 and 10.

(3) *Neues Jahrb. f. Min.*, 1858, 645.

(4) *Zur Fauna der Vorwelt*, Bd. 3, 1860, 10-89, pl. 8, fig. 11.

(5) *Quart. Journ.*, 20, 1864, 399-409.

(6) *Paléontol. et Zoolog. française*, pl. 51, figs. 14-17.

(1) According to a friendly communication from F. PLIENINGER, all Liassic forms, even those described by QUENSTEDT as *Pterodactylus*, would have been long-tailed.

The Reptilia of the Triassic, as dealt with briefly in the foregoing, present a surprising diversity. All groups of Reptilia are represented already in the Triassic, except for the Ophidia, Pythonomorpha, and true Lacertilia.

In the following I have classified all the genera of Triassic Reptilia in systematic arrangement. The surprisingly high number of 155 arises. Synonyms, as far as possible, are considered; otherwise the number would not increase significantly. It arises from:

|                 |           |
|-----------------|-----------|
| Stegocephalia   | 21 genera |
| Anomodontia     | 64 “      |
| Sauropterygia   | 18 “      |
| Testudinata     | 3 “       |
| Rhynchocephalia | 1 genus   |
| Ichthyopterygia | 3 genera  |
| Proganosauria   | 1 genus   |
| Parasuchia      | 15 genera |
| Eusuchia        | 3 (?) “   |
| Dinosauria      | 24 “      |
| Pterosauria     | 2 (?) “   |

The systematic arrangement differs from ZITTEL and other textbooks. The Stegocephalia are dealt with briefly in the foregoing; I hope to come back to this in more detail on a later occasion. The Temnospondyli seem to me to stand very near the Pareiasauria and through them the Anomodontia in general. It is possible that they are derived from the former. In the classification of the Anomodontia I have followed SEELEY almost entirely, only the Endothiodontia are interpreted as a suborder (instead of family), for they depart further from the Theriodontia, Gorgonopsia, Dinocephalia, etc., than the latter do among themselves. They show agreement with the Rhynchosauria in so many points that the idea of a relationship can hardly be avoided, despite the double temporal fossa of the latter. Therefore they are placed beside each other in the table. Only *Telerpeton* is listed as a “rhynchocephalian”; perhaps it represents a connecting link between certain temnospondylous Stegocephalia and the Pleurosauridae; thus it is excluded from the true Rhynchocephalia. The Rhynchosauria are dealt with in relation to the Endothiodontia, and *Mesosaurus* is placed in the Sauropterygia. The Mesosauria and Plesiosauria are placed side-by-side, because *Mesosaurus-Proneusticosaurus-Plesiosaurus* seems to form a direct line forming the stem of the Sauropterygia; the other line, which develops rapidly into higher forms but remains confused in the Triassic, was *Mesosaurus-Proneusticosaurus-Cymatosaurus*, etc.-*Nothosaurus*; I do not believe that the Plesiosauridae are descended from the Nothosauridae.

## STEGOCEPHALIA

### TEMNOSPONDYLI

|  |                  |                  |
|--|------------------|------------------|
| <i>Eryops</i> COPE                                       | Karoo            | South Africa (1) |
| <i>Eupelor</i> COPE                                      | Upper Triassic   | North America    |
| <i>Pariostegos</i> COPE                                  | “ “              | “ “              |
| <i>Dictyocephalus</i> COPE                               | “ “              | “ “              |
| <i>Petrophryne</i> OWEN<br>(= <i>Micropholis</i> HUXLEY) | Karoo            | South Africa     |
| <i>Xestorhytias</i> HUXLEY                               | Maleri Sandstone | India            |

(1) *E. africanus* LYDD.

\* i.e., systematic position uncertain.

|   |                          |                                   |
|---|--------------------------|-----------------------------------|
| <i>Gondwanosaurus</i> LYDEKKER  | “ “                      | “ “                               |
| <i>Brachyops</i> OWEN   | “ “                      | “ “                               |
| <i>Bothriceps</i> HUXLEY  | Triassic                 | Australia                         |
| <i>Trochanterium</i> v. HUENE   | Upper Muschelkalk        | Lorraine                          |
| <i>Eurycervix</i> v. HUENE  | Lower Muschelkalk        | Upper Silesia                     |
|   | Upper Muschelkalk        | Swabia                            |
| STEREOSPONDYLI  |                          |                                   |
| <i>Trematosaurus</i> BRAUN  | Middle Bunter Sandstone  | central Germany                   |
| <i>Capitosaurus</i> MÜNSTER<br>(= <i>Odontosaurus</i> H. v. MEYER)                                    | Bunter Sandstone-Keuper  | Germany                           |
| <i>Cyclotosaurus</i> E. FRAAS   | Keuper                   | south Germany                     |
| <i>Mastodontosaurus</i> JÄGER   | Bunter Sandstone-Keuper  | Germany, England                  |
| <i>Metopias</i> H. v. MEYER   | Keuper                   | south Germany                     |
| <i>Diadetognathus</i> MIALI   | “                        | England                           |
| <i>Labyrinthodon</i> OWEN   | “                        | “                                 |
| <i>Rhystidosteus</i> OWEN   | Karoo                    | South Africa                      |
| <i>Pachygonia</i> HUXLEY  | Maleri Sandstone         | India                             |
| <i>Gonioglyptus</i> HUXLEY  | “ “                      | “                                 |
| ANOMODONTIA   |                          |                                   |
| THEROSUCHIA   |                          |                                   |
| PAREIASAURIA  |                          |                                   |
| Pareiasauridae  |                          |                                   |
| <i>Pareiasaurus</i> OWEN  | Permo-Triassic           | north Russia                      |
|   | Karoo                    | South Africa                      |
| <i>Anthodon</i> OWEN  | “                        | “ “                               |
| <i>Propappus</i> OWEN   | “                        | “ “                               |
| Procolophonidae   |                          |                                   |
| <i>Procolophon</i> OWEN   | “                        | “ “                               |
| <i>Elginia</i> E. T. NEWTON   | Triassic sandstone       | Elgin                             |
| <i>Sclerosaurus</i> H. v. MEYER<br>(= <i>Labyrinthodon</i> WIEDERSHEIM; = <i>Aristodesmus</i> SEELEY) | Upper Bunter Sandstone   | Basel                             |
| GORGONOPSIA   |                          |                                   |
| <i>Gorgonops</i> OWEN   | Karoo                    | South Africa                      |
| DINOCEPHALIA  |                          |                                   |
| <i>Delphinognathus</i> OWEN   | “                        | “ “                               |
| <i>Tapinocephalus</i> OWEN  | “                        | “ “                               |
| (DEUTEROSAURIA)   |                          |                                   |
| PLACODONTIA   |                          |                                   |
| <i>Placodus</i> AGASSIZ<br>(= <i>Psephoderma</i> H. v. MEYER = <i>Psephosaurus</i> E. FRAAS)          | main Muschelkalk-Rhaetic | Germany, Alps,<br>England, France |
| <i>Pleurodon</i> GÜRICH   | Lower Muschelkalk        | Upper Silesia                     |
| <i>Cyamodus</i> H. v. MEYER   | Lower Muschelkalk        | “ “                               |
|   | Upper Muschelkalk        | Bayreuth                          |
| <i>Placochelys</i> JAEKEL   | Keuper                   | Plattensee                        |
| <i>Eunotosaurus</i> SEELEY  | Karoo                    | South Africa                      |

|  |                          |                        |
|--|--------------------------|------------------------|
| Clepsydropidae   |                          |                        |
| <i>Ctenosaurus</i> v. HUENE                              | Middle Bunter Sandstone  | northwest Germany      |
| THERIODONTIA   |                          |                        |
| Lycosauria   |                          |                        |
| <i>Lycosaurus</i> OWEN                                   | Karoo                    | South Africa           |
| <i>Inostrancevia</i> AMALITZKY                           | Permo-Triassic           | north Russia           |
| <i>Aëlurosaurus</i> OWEN                                 | Karoo                    | South Africa           |
| <i>Cryptodraco</i> OWEN                                  | “                        | “ “                    |
| <i>Pristerognathus</i> OWEN                              | “                        | “ “                    |
| <i>Tigrisuchus</i> OWEN                                  | “                        | “ “                    |
| <i>Theromus</i> * SEELEY                                 | “                        | “ “                    |
| <i>Saurosternus</i> * COPE<br>(= <i>Batrachosaurus</i> ) | “                        | “ “                    |
| <i>Basileosaurus</i> * WIEDERSHEIM                       | Upper Bunter Sandstone   | Basel                  |
| <i>Crurosaurus</i> * v. HUENE                            | Lower Muschelkalk        | prov. Saxony           |
| <i>Actiosaurus</i> * SAUVAGE                             | Rhaetic                  | France                 |
| Cynodontia   |                          |                        |
| <i>Cynognathus</i> OWEN                                  | Karoo                    | South Africa           |
| <i>Galesaurus</i> OWEN                                   | “                        | “ “                    |
| <i>Nythosaurus</i> OWEN                                  | “                        | “ “                    |
| <i>Cynochampsa</i> OWEN                                  | “                        | “ “                    |
| <i>Herpetochirus</i> SEELEY                              | “                        | “ “                    |
| <i>Tribolodon</i> OWEN                                   | “                        | “ “                    |
| <i>Dicranozygoma</i> SEELEY                              | “                        | “ “                    |
| <i>Sceloposaurus</i> OWEN                                | “                        | “ “                    |
| <i>Titanosuchus</i> OWEN                                 | “                        | “ “                    |
| <i>Thrinaxodon</i> SEELEY                                | “                        | “ “                    |
| <i>Phocosaurus</i> * OWEN                                | “                        | “ “                    |
| Gomphodontia   |                          |                        |
| <i>Gomphognathus</i> SEELEY                              | “                        | “ “                    |
| <i>Microgomphodon</i> SEELEY                             | “                        | “ “                    |
| <i>Trirachodon</i> SEELEY                                | “                        | “ “                    |
| <i>Tritylodon</i> SEELEY                                 | “                        | “ “                    |
| <i>Diademodon</i> SEELEY                                 | “                        | “ “                    |
| <i>Theriodesmus</i> SEELEY                               | “                        | “ “                    |
| <i>Microlestes</i> PLIENINGER                            | Middle Keuper<br>Rhaetic | England<br>Württemberg |
| ? <i>Hypsiprymnopsis</i> DAWKINS                         | Middle and Upper Keuper  | England                |
| ? <i>Triglyphus</i> O. FRAAS                             | Rhaetic                  | Württemberg            |
| ENDOTHIODONTIA   |                          |                        |
| <i>Endothiodon</i> OWEN                                  | Karoo                    | South Africa           |
| <i>Esotherodon</i> OWEN                                  | “                        | “ “                    |
| <i>Pristerodon</i> HUXLEY                                | “                        | “ “                    |
| ?Rhynchosauridae   |                          |                        |
| <i>Rhynchosaurus</i> OWEN                                | Middle Keuper            | England                |
| <i>Hyperodapedon</i> HUXLEY                              | Triassic sandstone       | Elgin                  |

|  |  |   |
|--|--|---|
|  | Middle Keuper<br>Maleri Sandstone                                | England<br>India  |
| THEROCHELONIA  |  |   |
| DICYNODONTIA   |  |   |
| Dicynodontidae   |  |   |
| <i>Dicynodon</i> OWEN  |  |   |
| 1) <i>Aulacocephalodon</i> SEELEY                                    | Maleri Sandstone   | India   |
| 2) <i>Rhachiacephalodon</i> SEELEY                                   | Karoo  | South Africa  |
| <i>Ptychognathus</i> OWEN<br>(= <i>Pychosiagma</i> LYDEKKER)         | “  | “ “   |
| <i>Theriognathus</i> OWEN  | “  | “ “   |
| <i>Platypodosaurus</i> OWEN  | “  | “ “   |
| <i>Tropidosteus</i> SEELEY   | “  | “ “   |
| <i>Keirognathus</i> OWEN<br>(= <i>Cirognathus</i> SEELEY)            | “  | “ “   |
| <i>Hyorhynchus</i> SEELEY  | “  | “ “   |
| <i>Eurycarpus</i> SEELEY   | “  | “ “   |
| <i>Gordonia</i> E. T. NEWTON   | Triassic sandstone<br>Permo-Triassic                             | Elgin<br>north Russia   |
| <i>Anomosaurus</i> *   | Lower, Middle, Upper<br>Muschelkalk                              | Germany   |
| Oudenodontidae   |  |   |
| <i>Oudenodon</i> OWEN  |  |   |
| 1) <i>Aulacocephalus</i> SEELEY                                      | Karoo  | South Africa  |
| 2) <i>Rhachicephalus</i> SEELEY                                      | “  | “ “   |
| <i>Geikia</i> E. T. NEWTON   | Triassic sandstone<br>Permo-Triassic                             | Elgin<br>north Russia   |
| KISTECEPHALIA  |  |   |
| <i>Kistecephalus</i> OWEN<br>(= <i>Cistecephalus</i> LYDEKKER)       | Karoo<br>Permo-Triassic  | South Africa<br>north Russia  |
| SAUROPTERYGIA  |  |   |
| MESOSAURIA   |  |   |
| <i>Mesosaurus</i> GERVAIS<br>(= <i>Ditrochosaurus</i> GÜRICH)        | Karoo  | South Africa  |
| Plesiosauridae   |  |   |
| <i>Proneusticosaurus</i> VOLTZ                                       | Lower Muschelkalk  | Upper Silesia   |
| <i>Dactylosaurus</i> GÜRICH  | “ “  | “ “   |
| <i>Anarosaurus</i> DAMES   | “ “  | prov. Saxony  |
| <i>Neusticosaurus</i> SEELEY   | Lettenkohle  | Swabia  |
| <i>Pachypleura</i> CORNALIA  | Raibl beds   | Lombardy  |
| <i>Plesiosaurus</i> CONYBEARE<br>(= <i>Termatosaurus</i> PLIENINGER) | Lower Muschelkalk<br>Upper Muschelkalk<br>Lettenkohle<br>Rhaetic | Upper Silesia<br>Germany<br>south Germany<br>south Germany, France,<br>Switzerland, England |

Pistosauridae

*Pistosaurus* H. v. MEYER

Upper Muschelkalk

Bayreuth

Nothosauridae

*Cymatosaurus* SCHRAMMEN

Lower Muschelkalk

Silesia, Saxony

*Eurysaurus* FRECH

“ “

Silesia

*Nothosaurus* MÜNSTER

Upper Muschelkalk

Germany, Heligoland,

(= *Dracosaurus*)

Lettenkohle

France

Cassian beds

Germany

*Conchiosaurus* H. v. MEYER

Middle Muschelkalk

St. Cassian, Tyrol

*Opiosaurus* H. v. MEYER

Upper Muschelkalk

central Germany

*Lamprosaurus* H. v. MEYER

Lower Muschelkalk

central Germany

*Lariosaurus* CURIONI

Upper Muschelkalk

Silesia

(= *Macromirosaurus* CURIONI)

*Parthanosaurus* SKUPHOS

Raibl beds

Vorarlberg

*Microleptosaurus* SKUPHOS

Partnach beds

“

*Dasygnathus*\* HUXLEY

Triassic sandstone

Elgin

TESTUDINATA

CRYPTODIRA

*Chelyzoon* v. HUENE

Upper Muschelkalk

Bayreuth, Crailsheim

*Arctosaurus* ADAMS

Triassic

Bathurst Island

(Arctic N. America)

PLEURODIRA

*Psammochelys* QUENSTEDT

Middle Keuper

Württemberg

(= *Proganochelys* BAUR; ? = *Chelytherium* H. v. HUENE)

RHYNCHOCEPHALIA

*Telerpeton* MANTELL

Triassic sandstone

Elgin

ICHTHYOPTERYGIA

*Mixosaurus* BAUR

Lower Muschelkalk

Germany, France

Rhaetic

England

Raibl beds

Besano

*Shastasaurus* MERRIAM

(= *Rhachitrema* SAUVAGE)

California,

*Ichthyosaurus* BLAINEVILLE

Upper Triassic

Spitzbergen

PROGANOSAURIA

?*Proterosaurus* H. v. MEYER

Middle Bunter Sandstone

Bernberg

PARASUCHIA

Belodontidae

*Belodon* H. v. MEYER

Lettenkohle

Germany, India,

(= *Phytosaurus* JÄGER;

Keuper

Switzerland,

= *Palaeosaurus* EMMONS;

Rhaetic

North America

|                |  |                           |   |
|----------------|--|---------------------------|---|
|                | = <i>Composaurus</i> LEIDY; = <i>Omosaurus</i> LEIDY; = <i>Eurydorus</i> LEIDY; = <i>Centemodon</i> LEA) |                           |   |
|                | <i>Mystriosuchus</i> E. FRAAS  | Middle Keuper             | south Germany                               |
|                | <i>Stegomus</i> MARSH  | Upper Triassic            | North America                               |
|                | <i>Rhytiodon</i> EMMONS  | “ “                       | “ “   |
|                | <i>Stagonolepis</i> AGASSIZ  | “ “                       | Elgin                                       |
|                | em. HUXLEY   |                           |   |
|                | <i>Sauroidesmus</i> * SEELEY (1)   | Rhaetic                   | Scotland                                    |
|                | <i>Rileya</i> v. HUENE   | Middle Keuper             | England                                     |
|                | <i>Parasuchus</i> HUXLEY   | Maleri Sandstone          | India                                       |
|                | <i>Episcoposaurus</i> COPE   | Upper Triassic            | New Mexico                                  |
| PSEUDOSUCHIA   |  |                           |   |
|                | <i>Aëtosaurus</i> O. FRAAS   | Middle Keuper             | Swabia                                      |
|                | <i>Typothorax</i> COPE ( <i>ex parte</i> )   | Upper Triassic            | New Mexico                                  |
|                | <i>Dyoplax</i> O. FRAAS  | Lower Keuper              | Swabia                                      |
|                | <i>Ornithosuchus</i> E. T. NEWTON  | Triassic sandstone        | Elgin                                       |
|                | <i>Erpetosuchus</i> E. T. NEWTON   | “ “                       | “ “   |
|                | <i>Megalocnemus</i> * BASSANI  | Raibl beds                | Lombardy                                    |
| EUSUCHIA       |  |                           |   |
|                | <i>Procerosaurus</i> v. HUENE  | Upper Muschelkalk         | Swabia                                      |
|                | <i>Pectenosaurus</i> v. HUENE  | “ “                       | Franconia                                   |
|                | Div. gen. indet.   | Lower & Upper Muschelkalk | Swabia, Lorraine                            |
| DINOSAURIA     |  |                           |   |
| THEROPODA      |  |                           |   |
| Zanclodontidae |  |                           |   |
|                | <i>Zanclodon</i> PLIENINGER  | Upper Keuper              | Germany, France,<br>England                 |
|                | (= <i>Smilodon</i> PLIENINGER;<br>= <i>Cladyodon</i> OWEN; = <i>Dimodosaurus</i> PIDANCET & CHOPARD)     |                           |   |
|                | <i>Gresslyosaurus</i> RÜTIMEYER  | Upper Keuper              | Germany, France,<br>Switzerland,<br>England |
|                | (= <i>Avalonia</i> SEELEY;<br>= <i>Picrodon</i> SEELEY)  |                           |   |
|                | <i>Teratosaurus</i> H. v. MEYER  | Middle Keuper             | Swabia, England                             |
|                | <i>Plateosaurus</i> H. v. MEYER  | Upper Keuper              | south Germany                               |
|                | <i>Epicampodon</i> HUXLEY  | Maleri Sandstone          | India                                       |
|                | (= <i>Ankistrodon</i> HUXLEY)  |                           |   |
|                | <i>Bathygnathus</i> LEIDY  | Triassic                  | Prince Edward Island                        |
|                | (? = <i>Teratosaurus</i> H. v. MEYER)  |                           |   |
|                | <i>Euskelosaurus</i> HUXLEY  | Upper Karroo              | South Africa                                |
|                | <i>Orosaurus</i> HUXLEY  | “ “                       | “ “   |
|                | (= <i>Orinosaurus</i> LYDEKKER)  |                           |   |
| Anchisauridae  |  |                           |   |
|                | <i>Anchisaurus</i> MARSH   | Upper Triassic            | Connecticut                                 |

(1) Perhaps *Sauroidesmus* is to be classified beside *Aëtiosaurus* and *Crurosaurus* in the Anomodontia (cf. above in text).

\* i.e., systematic position uncertain.

(= *Amphisaurus* MARSH; = *Megadactylus* HITCHCOCK; = *Clepsysaurus* LEA)

|                                      |                           |                |
|--------------------------------------|---------------------------|----------------|
| <i>Ammosaurus</i> MARSH              | Upper Triassic            | Connecticut    |
| <i>Thecodontosaurus</i> OWEN         | Middle Keuper             | England        |
| <i>Palaeosaurus</i> OWEN             | “ “                       | “              |
| <i>Massospondylus</i> OWEN           | Upper Triassic            | India          |
|                                      | Upper Karroo              | South Africa   |
| <i>Pachyspondylus</i> OWEN           | “ “                       | “ “            |
| <i>Leptospondylus</i> OWEN           | “ “                       | “ “            |
| <i>Hortalotarsus</i> SEELEY          | “ “                       | “ “            |
| <i>Agrosaurus</i> SEELEY             | Upper Triassic            | Australia      |
| <i>Palaeoctomus</i> COPE             | “ “                       | South Carolina |
| <i>Zatomus</i> COPE                  | “ “                       | “ “            |
| <i>Suchoprion</i> COPE               | “ “                       | “ “            |
| two gen. nov.                        | Lower & Upper Muschelkalk | Germany        |
| ?Coeluridae                          |                           |                |
| <i>Tanystrophaeus</i> H. v. MEYER    | Lower & Upper Muschelkalk | “              |
| (= <i>Macroscelosaurus</i> MÜNSTER)  |                           |                |
| <i>Coelophysis</i> COPE              | Upper Triassic            | New Mexico (1) |
| ?Orthopoda                           |                           |                |
| <i>Dystrophaeus</i> COPE             | Triassic                  | Utah, U.S.A.   |
| PTEROSAURIA                          |                           |                |
| “ <i>Pterodactylus</i> ” H. v. MEYER | Rhaetic                   | south Germany, |
| England                              |                           |                |
| ? <i>Tribelesodon</i> BASSANI        | Raibl beds                | Lombardy       |

#### D. DISTRIBUTION AND IMPORTANCE OF THE TRIASSIC REPTILIA

In order to be better able to find our way through the 155 genera of Triassic Reptilia of the whole Earth, and to be better able to judge their faunistic, stratigraphic, and phylogenetic significance, we must once again review the whole host of them.

We confine ourselves first to Europe.

The oldest member of the central European Triassic, the Bunter Sandstone, contains among the scanty organic remains, most of which come from the dry land, several Stegocephalia and Anomodontia. Among the Stegocephalia, the exclusively Permian group of the Phyllospondyli and the mainly Permian group of the Temnospondyli are not represented in the Bunter Sandstone, but Stereospondyli are present. The locality of Bernberg (Middle Bunter Sandstone) in Thuringia is particularly well known for the numerous finds of *Trematosaurus*, which by the form of its head recalls the Permian *Archerosaurus*. *Capitosaurus nasutus* is also found there. Only one proterosaurid comes from Bernberg (see above). In the *Voltzia* Sandstone of Sulzbad, Alsace, a huge skull of a yet-unknown stereospondylous stegocephalian (similar to *Capitosaurus nasutus*) has been found; H. von MEYER's *Odontosaurus* also comes from there (it is no more than a toothed

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(1) This is a new genus standing between *Thecodontosaurus* and *Coelurus*, which has nothing to do with the German *Tanystrophaeus*. Prof. OSBORN was kind enough to send excellent casts of COPE's originals to Tübingen. This genus will be described soon.

jaw fragment from a *Capitosaurus*). Large thoracic armor plates have also been found. Poorly preserved fragments of *Mastodonsaurus* or *Capitosaurus* also occur in the region of Nagold in the Black Forest (2). The main Bunter Sandstone of Riehen near Basel has also yielded dorsal and head plates of *Capitosaurus*. Riehen and Warmbach near Rheinfelden are the only localities in which Anomodontia also occur in good preservation, namely *Sclerosaurus* (= *Aristodesmus*) and *Basileosaurus*. These true, high-limbed therosuchian Anomodontia, with characteristic dermal covering and head spines, are unknown in South Africa, the main home of the Anomodontia, but probably from north Russia and Elgin. The isolated occurrence of a clepsydroid, *Ctenosaurus*, in the Middle Bunter Sandstone of Göttingen, is very noteworthy and peculiar. *Ctenosaurus*, like its other relatives from the Permian (of Texas), is also distinguished by extraordinarily long spinal processes, which probably formed a high crest on the back.

The great similarity of the head of *Sclerosaurus* with *Elginia* can justify the insertion of the fauna of the Elgin Sandstone in northeast Scotland into the discussion here. The yellow, poorly bedded sandstone of Morayshire apparently lies concordantly upon the upper red and yellowish Old Red. This contact is not exposed directly anywhere (1). The picturesquely wooded hills on the blue Moray Firth have numerous quarries developed. Even from some distance one can recognize the red color below and the yellow above. The quarries in the red sandstone yield numerous Upper Devonian fish, and because of this the entire sandstone complex was originally ranked in the Old Red. No more fish occur in the uppermost Bunter Sandstone, but in the course of time a very peculiar reptile fauna has been collected (already recognized as Triassic by HUXLEY) by HUXLEY, GORDON, GRANT, TRAQUAIR, TAYLOR, etc. Rock type and fauna are not the same in all quarries. The quartz-rich, extremely coarse, nearly conglomeratic sandstone of the southern half has only yielded *Elginia*, *Gordonia*, and *Geikia* (2). The fine sandstone of the region bordering the sea (3) contains very numerous *Stagonolepis*, *Ornithosuchus*, *Erpetosuchus*, *Hyperodapedon*, and *Telerpeton* (also a *Ceratodus* tooth). An arrangement and correlation of the sandstone with the different faunas is not to be observed, for they occur on entirely different hills; both seem to lie concordantly on the Old Red. Without some stratigraphic grounds to refer to, one has gained the impression from paleontological considerations that the sandstone with the *Belodon*-like *Stagonolepis* must be Upper Triassic. *Ornithosuchus* and *Erpetosuchus* are small parasuchian crocodiles which have their nearest relations in *Aëtosaurus* and *Dyoplax* from the Lower and Middle Keuper of Swabia. All other Parasuchia are Upper Triassic. *Hyperodapedon* is also very closely related with *Rhynchosaurus* from the Keuper of Warwickshire. On the other hand, the obviously very close relationship of *Elginia* with *Sclerosaurus* from the Bunter Sandstone could indicate an even greater antiquity. *Gordonia*, a dicynodont, probably stands nearest *Ptychognathus*, and *Geikia* is an ouddenodont. These genera, according to SEELEY, are found in the lowest and middle Karroo of South Africa. *Gordonia* is common in the so-called Permian reptile fauna of north Russia; a skull of *Geikia* was also found there. According to this, the sandstone of Cuttie's Hillock must be placed in the Lower Triassic. But the *Stagonolepis* sandstone can only be Upper Triassic, for the main distribution of the Parasuchia in southern and western England, the whole European continent, North America (Connecticut, South Carolina, New Mexico, etc.), and India is confined to the Upper and uppermost Triassic (Middle and Upper Keuper and Rhaetic).

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(2) See e.g. E. FRAAS, *Jahresh. Ver. f. Naturk. Württemberg*, 57, 1901, 318.

(1) From my own opinion and confirmed by Dr. TRAQUAIR of Edinburgh and Mr. TAYLOR of Elgin.

(2) Locality: Cuttie's Hillock.

(3) Localities: Lossiemouth, Spynie, and Findrassie.

The idea of different ages of the *Elginia* sandstones is suggested on paleontological grounds; I know of no geological grounds in support of this, but certainly none is against it.

The Middle Triassic German formation, the Muschelkalk, contains a whole host of mostly swimming reptiles; however, occasionally true land-dwellers are found. The latter appear again in greater numbers only toward the end of the Triassic in Europe, for the dry land again increased in area for a short time then.

The Lower Muschelkalk at Sulzbad, Alsace, a sandy rock, has yielded a characteristic small fauna in poorly preserved remains. There are several armor plates of Stegocephalia, single-headed ribs that could belong to Sauropterygia or Anomodontia, and a piece of an upper vertebral arch from *Anomosaurus* HUENE (it has a strikingly long shaft, which measures 14 cm from point to point).

In the *Dadocrinus* horizon (3 cm above the Röth) of the Lower Muschelkalk of Upper Silesia, there is a rich fauna in the same place. There, *Capitosaurus silesiacus* KUNISCH is found; a huge cervico-thoracic plate of another stegocephalian was found in the deepest Wellenkalk of the cement works near Halle am Saale; it is 40 cm broad and 30 cm long. It may be the same species at Sulzbad, Gogolin, and Halle. Then vertebrae of *Tanystrophaeus* and two other genera of Dinosauria are to be mentioned from Upper Silesia, of which one survived until the Lettenkohle. *Cyamodus (tarnowitzensis)* GÜRICH is to be interpreted as a coast dweller, which also lived in Silesia in the Lower Muschelkalk. Its pavement dentition enabled it to feed on thick-shelled Mollusca and Crustacea, which only lived in the shallow water and in the proximity of the shore; *Placodus*-like teeth also occur in the Lower Muschelkalk of Halle. Yet other remains, perhaps of land-living reptiles of the anomodont group, have been found in the Lower Muschelkalk of Upper Silesia (Gogolin). In Breslau there is part of a skeleton with walking feet and dermal ossifications. It will be described by Dr. VOLTZ soon.

However, the main bulk of the reptile fauna of the Lower Muschelkalk of Upper Silesia and Saxony consists of Sauropterygia, which were true marine carnivores. The Nothosauridae play the greatest role, some of them very small forms; but already several Plesiosauridae were associated with them. The pygmy forms are *Anarosaurus* (Saxony) and *Dactylosaurus* (Silesia); already *Proneusticosaurus* is rather larger. They stand near the South African *Mesosaurus* and the Permian *Stereosternum* (São Paulo, Brazil) and are, so to speak, direct intermediates to the Plesiosauria. In the area of Jena this fauna begins as early as the Upper Röth. In the south German Lower Muschelkalk this pygmy fauna has still not been found. It is interesting to see that many Sauropterygia, such as *Proneusticosaurus* and *Dactylosaurus*, have limbs in which the reorganization of the walking "foot" to paddles apparently has not yet begun. Already the important genera *Cymatosaurus* and *Eurysaurus* (1) are larger than the oldest Nothosauridae. They are distinguished by the possession of a postorbital, which neither the true Nothosauria of the Upper Muschelkalk nor the Plesiosauria possess. *Cymatosaurus* occurs in the vicinity of Halle even in the lowest Muschelkalk. The structure of the skull (long tapering snout, position of the narial openings, etc.) shows that it, in particular *Cymatosaurus friedericianus* FRITSCH (2), is the forerunner of *Pistosaurus*. Vertebrae of true Plesiosauria also occur in the Lower Muschelkalk of Alt-Tarnowitz. They possess the characteristic foramina on the underside of the vertebrae.

In addition to the sea-dominating Sauropterygia, the Ichthyopterygia also already occur in the Lower Muschelkalk; later, in the Liassic, they followed the long-necked Sauropterygia in supremacy. In the Swabian Wellenkalk the Ichthyosauria (*Ichthyosaurus atavus* QU.) occur as a

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(1) *Cymatosaurus* differs from *Eurysaurus* only by the greater extent of the nasals.

(2) *Abhandl. der Naturf. Ges. zu Halle*, 20, pls. 16 and 17.

large and small species, but which hitherto have not been sufficiently collected and described; it is possible that it is a question of *Shastasaurus* and *Mixosaurus*. An *Ichthyosaurus* (?*Mixosaurus*) also occurs in the Wellenkalk of Querfurt, North Marz, and a lower jaw has been found near the cement works at Halle am Saale that is probably *Mixosaurus*.

The Schaumkalk (upper Lower Muschelkalk) of Freiburg am Unstrut has yielded a rich fauna to the Museum at Halle. The Nothosauridae predominate by far in all possible sizes and forms. Also vertebrae of *Mastodonsaurus* and *Ichthyosaurus* (?*Shastasaurus*) are not absent, and *Placodus* is also present. Then there are the limb bones of temnospondylous Stegocephalia, femora of unknown Anomodontia (*Crurosaurus*), etc. Vertebrae of *Anomosaurus* also occur here, from very different species, in relatively high numbers. Also *Tanystrophaeus*, which is like that from Upper Silesia, has been found, with thin-walled bones like *Coelurus*. Even a true crocodile is already present. These all indicate an extremely rich fauna. The Middle Muschelkalk of Esperstädt near Jena has yielded *Conchiosaurus*, among others.

The reptile fauna of the Upper Muschelkalk is even richer than that of the Lower. The Nothosauria predominate by far in numbers of individuals and species. They are distributed all over the German Triassic province (also in Heligoland), and are found even in the Alpine Muschelkalk (*Lariosaurus* from the Comersee). Numerous genera and species are based on isolated skulls, but in very rare cases the skeleton belonging to it is also known. There seems to me to be two groups among the *Nothosaurus* skeletons; one has a short, thick ilium and blade-like pubis, whereas the other has a rod-shaped, rather curved ilium and a non-stalked pubis. Lunéville and Bayreuth are frequently named as productive localities for Nothosauridae. True *Plesiosaurus* remains are found all over Germany, scattered in the main Muschelkalk, however always as great rarities. I recall once more the sacral vertebra, described above, from Bayreuth. Very fine *Plesiosaurus* and particularly *Nothosaurus* remains are found in the well-known upper bonebed of the Oelmühle near Crailsheim, and in a similar bed near Biebersfeld and Gaildorf, Württemberg, lying only a little higher. As we have seen above, large Ichthyosauria occur in the Alpine Reifling limestone. Further, several chelonian remains (*Chelyzoon*), which have been found in the main Muschelkalk of Laineck near Bayreuth and in the upper bonebed of Crailsheim, give evidence of the diverse population of the sea and its coast. In *Arctosaurus* from Arctic North America, they have a foreign representative. The vertebrae named "*Anomosaurus*", which come from the Upper Muschelkalk of Thuringia (Schlotheim), Bayreuth, and Württemberg (Neckarvaihingen), belong to an unknown anomodont. Teeth and skull remains of Placodontia are well distributed, if not very frequent. They are very common only at Bayreuth, but they are found in the whole extent of the German Muschelkalk. They probably inhabited the coasts and sand banks of the Muschelkalk sea. A small representative of this group, *Eunotosaurus* SEELEY, also occurs in the South African Karroo. Of remains of land animals, poorly defined stegocephalian bones are found at Lunéville and Bayreuth in the main Muschelkalk. At Steinbiedersdorf, Lorraine, Prof. BENECKE discovered a femur, here described as *Trochanterium*, that belongs to a temnospondylous stegocephalian or a *Pareiasaurus*-like anomodont. The famous Crailsheim bonebed has yielded particularly numerous stegocephalian remains. *Capitosaurus* and *Mastodonsaurus* are described in several species from there. *Eurycervix*, based on huge, double-bladed cervical ribs, seems to have been a last large temnospondyl. In the main Muschelkalk of Bayreuth, Göttingen, Lunéville, and the Crailsheim bonebed have been found a number of vertebrae and other bones of small theropod Dinosauria, which very rarely passed from dry land into the marine deposits. These are animals that were about the size of *Anchisaurus*, *Palaeoctomus*, and *Thecodontosaurus*, but which remained far behind the Upper Triassic Theropoda of central Europe and South Africa. Finally, bones of true Crocodylia

(Eusuchia) are already present in the Crailsheim bonebed, and in Lunéville there occur polygonal dermal armor plates with edge serrations, which in the same way belong to the abdominal armor of a crocodile (see above).

More land was already present in the time of the Lettenkohle, particularly in southern Germany. The marshy regions must have been populated then and in the Lower Keuper (Schilfsandstein) by huge crowds of heavily armored Stegocephalia (*Capitosaurus*, *Mastodonsaurus*, *Cyclotosaurus*, *Metopias*). The lower Upper Lettenkohle of Biebersfeld and Gaildorf in Württemberg are good localities. The Upper Lettenkohle of Hoheneck contains only very few Stegocephalia, for it is a more marine and brackish deposit. On the other hand, the Schilfsandstein of the lowest Keuper of the Feuerbacher Haide near Stuttgart is unsurpassed for the host of large and fine stegocephalian remains (1). In the Schilfsandstein of the same locality, a lower jaw of *Belodon* (*arenaceus* E. FRAAS sp.) has been found, as well as a fine specimen of *Dyoplax*, thus two parasuchian crocodiles. We have no traces of Dinosauria from this period in Europe. The coasts and seas were no less richly populated. The Placodontia are still distributed as in the Upper Muschelkalk. Large armor pieces occur at Hoheneck (*Psephosaurus suevicus* E. FRAAS). *Placochelys*, with highly decorated armor and skull, comes from the Lower Keuper of Vesprem on the Plattensee, Hungary. A great wealth of forms of Nothosauridae moved about in great numbers in the German inland sea. Enormous species alternate with very small ones. Of the latter are known in particular the delicate *Neusticosaurus pusillus* of the Upper Lettenkohle of Hoheneck, and *Pachypleurosaurus* from the Lombardy Raibl beds. The Lettenkohle also does not entirely lack large Plesiosaurus (e.g., Biebersfeld near Württemberg). The famous skeletons of *Mixosaurus* also come from northern Italy as well as the first flying reptile, *Tribelesodon longobardicus* BASSANI (and the even better known *Megalocnemis* BASSANI in Sched. Mus. Civico, Milan).

Mostly terrestrial reptiles are preserved from the Middle Keuper. Many remains of *Rhynchosaurus* have been found in Warwickshire and Gloucestershire in western England, which together with *Hyperodapedon* form a separate group. According to R. BURCKHARDT, *Rhynchosaurus* was equipped with a lizard-like armor. Bones and teeth of *Thecodontosaurus* and *Palaeosaurus* also come from the Middle Keuper of the same region (Bristol and Warwickshire). Those small theropod Dinosauria have been found again in the Swabian Stubensandstein. Similar ones occur in North America, South Africa, and Australia. The huge Dinosauria begin with *Teratosaurus* in the Stubensandstein of Württemberg, but they are not yet frequent; they appear there in two forms, one very large and another smaller. Together with them, bones of *Belodon* and *Mystriosuchus* are found in large numbers; they must have lived in whole crowds on the river banks. The most important localities in Württemberg are Messlach, Rübgarten, and Aixheim, but *Belodon* also occurs in the Middle Keuper of France and England. The famous slab with 25 specimens of *Aetosaurus*, a small parasuchian which is very like *Ornithosuchus* from Elgin, comes from Hesslach. Also, several specimens of pleurodire Chelonia (*Proganochelys*) have been found in Swabia, which already display the high development of that reptile group. In Silesia, Plesiosauria (*Terματοςaurus*) occur in the marine or brackish deposits of the Middle Keuper.

The Upper Keuper and Rhaetic display a gigantic fauna of huge reptiles which moved with the strangest structures and gaits on all continents at that time. The Upper Keuper of central Europe, frequently named the *Zanclodon*-bed, is developed here mostly as red or colored inland deposits. In northwest Germany, western France, and western England, the similar rocks of the Rhaetic are most closely associated with these marls. In the Rhaetic, the beginning marine

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(1) A mastodonsaur also occurs in the Grenzdolomit of Backleben near Halle am Saale.

transgression of the approaching Jurassic begins to make itself felt, and so the uppermost Rhaetic beds frequently show a colored jumble of terrestrial and marine fossils. Soon after, the same regions were entirely under the Liassic sea. In *Gresslyosaurus*, the Triassic Dinosauria reach a length of almost 10 m. This largest genus is found in several localities in Württemberg and Franconia, Switzerland near Basel, the Département Jura in France, and Somerset, England (*Avalonia* and *Picrodon* SEELEY). Besides these largest forms, other different ones occur that also reach 6-8 m in length. A large number of individuals is found. Several skeletons were unearthed nearly complete; the finest ones are found in the collections at Tübingen, Stuttgart, and Poligny (France). Also, more teeth of Dinosauria occur in the uppermost Rhaetic bonebed of Württemberg and England, which indicate quite different genera; teeth are even found that recall *Thecodontosaurus* of the Middle Keuper. Phalanges occur in the bonebed of Aust Cliff near Bristol, which MOORE ascribed to the lower Liassic *Scelidosaurus*. Larger bone remains have been discovered in the Rhaetic-Keuper of Wolfenbüttel and Kreuzberg near Göttingen. *Belodon* also occurs in many places that have yielded Dinosauria, but not as frequently as in the Middle Keuper. The largest *Belodon* remains known to me are those from Schönthal near Liestal (the femur is 40 cm long) from the *Zanclodon*-bed. *Belodon* still occurs in the Rhaetic sandstone of Waldhausen near Tübingen, to conclude from an armor plate. Dermal plates of Stegocephalia (1) have been unearthed in the Upper Keuper of Somerset, together with *Avalonia* (*Gresslyosaurus*), and are especially common in Warwickshire (2); armor plates and teeth are frequent in the Rhaetic bonebed of Aust Cliff near Bristol, and the former in the same bed at Schönthal near Basel. *Labyrinthodon supremus* PORLIG comes from the Rhaetic sandstone of Kleinenhagen near Göttingen (Collection at Halle). Moreover it is noted here that the Stegocephalia do not become extinct *before* the beginning of the Liassic, as one frequently reads, but the last representatives are described from the middle Dogger of England. In the Rhaetic the true flying Pterosauria appear for the first time; *Tribelesodon* indeed occurs as early as the Raibl beds, but its systematic position is difficult to determine. Flight fingers and separate vertebrae, which indicate long-tailed Pterosauria, have been found isolated in several localities in Württemberg and England. Flying finger fragments from Hettingen, which GERVAIS described, are already to be ascribed rather to the Liassic. On the sea coasts, Placodontia still lived. Dorsal armor pieces are known as *Psephoderma alpinum* from the Alpine Dachsteinkalk of Upper Bavaria; similar smaller plates have been found in the Rhaetic of Aust Cliff (*Ps. anglicum* H. von MEYER), in the Rhaetic of Schönthal near Basel, and in the Lombardy Rhaetic. Chelonia (a vertebra from the Schlosslesmühle bonebed, Württemberg) also contribute to the enrichment of the coast fauna. In the Rhaetic of Bristol and Warwick, OWEN found peculiar bones and vertebrae (1), which he described as *Labyrinthodon scutulatus*; I suppose that this is why MOORE et al. speak of the presence of *Nothosaurus* in the English Rhaetic, because certain of its limb bones certainly recall femora of *Nothosaurus* to some extent. The vertebrae are not quite unlike caudal vertebrae of Anomodontia. The distribution of sculpture and spinal processes is striking; I cannot say with certainty to which reptile group they belong. As early as 1860, CORNALIA mentioned (2) in the Rhaetic beds of Azzarola, Lombardy, two reptile remains that have some interest, namely a hardly more closely identifiable “lower jaw bone of a crocodile”, and a “median plate of the carapace of a *Cistudo* or *Emys*”. Both as well figured. The latter piece

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(1) In addition to the other genera, also *Diadectognathus* MIALL.

(2) *Trans. Geol. Soc. London*, ser. II, 6. 1844, 545ff.

(1) *Trans. Geol. Soc. London*, ser. II, 6. 1841, 538, pl. 16, figs. 1-5.

(2) CORNALIA, Fossiles de l'Azzarola (Infralias), pp. 35 and 36, pl. 1, figs. 1 and 2; in STOPPANI, *Paléontologie Lombarde*. Milan, 1860-1865.

has clearly serrated side edges and thus could belong to a crocodile or a chelonian, however it is not *Psephoderma*. R. OWEN also described three extremely small vertebrae from Somerset that could probably belong to Chelonia (3); that figured is a cervical, not a dorsal vertebra as OWEN thought. Peculiar bone pegs occur in the Aust Cliff bonebed, which remind me very much of the pegs on the lower jaw of *Pareiasaurus*. But what they really are cannot be said. But in any case small Anomodontia of the group Gomphodontia lived in Europe at this time, I mean *Microlestes*, *Hypsiprymnopsis* (4), and *Triglyphus*. The teeth of *Microlestes* and those of *Diademodon* from the South African Karroo show no important differences at all beyond the size difference. But *Diademodon* belongs in the narrow group of the Gomphodontia, of which the skull and entire skeleton are known; thus the reptilian nature of *Microlestes* cannot be doubted—this has been the view of SEELEY and several other experts for a long time; nevertheless, *Microlestes* is shown in all the textbooks as a multituberculate mammal. The small teeth of *Microlestes* have been found in the Rhaetic bonebed of Degerloch, and more recently in several specimens from Olgahain near Tübingen. However at Holwell, Mendip Hills, near Bristol, MOORE has collected 29 teeth from one quarry over a long time, and DAWKINS has done the same at Watchet. It is very likely that *Triglyphus* (several teeth) from Bebenhausen (Württemberg) is also a gomphodont, for the similarity of the teeth to those of *Tritylodon* is very great, and this has the skull structure of an anomodont from the named group (pre- and postfrontal identified according to R. OWEN and SEELEY). To conclude from the tooth structure, *Microlestes* must have been a very small, probably insectivorous reptile; *Triglyphus* was probably larger (5). From such always isolated finds, one can conclude that the dry land was populated by a fauna that stood in direct connection with that of the beginning of the Triassic and with the contemporaneous ones of South Africa and north Russia. In the uppermost Keuper and Rhaetic, the influx of the Liassic marine transgression sometimes makes itself felt. Thus in the uppermost Keuper of Schönthal near Basel, one finds, between Dinosauria and *Belodon* remains, teeth and vertebrae of *Plesiosaurus*; the vertebrae (see above) reach an unusual size. Also teeth (*Termatosaurus albertii*) and vertebrae of Plesiosauria occur in the Swabian bonebed and the Rhaetic Lissauer breccia of Noczurry and Gattentag and near Lübnitz, Upper Silesia; *Plesiosaurus* (*Termatosaurus*) are also found near Autun and near Göttingen. *Plesiosaurus* is even frequent in the Rhaetic of Aust Cliff. Ichthyosauria also are not infrequent there. Parts of a large lower jaw of *Ichthyosaurus* lie in the Museum at Bristol. *Ichthyosaurus* remains have also been found near Autun, also rarely in the Swabian Rhaetic bonebed.

*Central Europe* was subject to variations during the Triassic. We may find in one and the same locality a continental fauna in older Triassic beds, in younger beds a coastal and marine fauna, and in the youngest again a terrestrial fauna. Therefore it is clear that terrestrial animals could not evolve independently and continually in Central Europe. In order to learn about such a continental fauna, we must turn to South Africa, north Russia, and India.

*South Africa* (i.e., Cape Colony and Boer states) had nearly unbroken continental evolution from the Permian to the Jurassic (*Mesosaurus* beds!). Thus the well-known rich anomodont fauna could be more highly developed there. It has hitherto not been feasible to establish a succession of separate zones for them with sufficient material and thoroughness. SEELEY has indeed tried to divide the Karroo into five geographical and at the same time stratigraphic zones. From the oldest division he named *Pristerodon*, *Oudenodon*, *Anthodon*, and *Mesosaurus*; from the second, *Pareiasaurus* and *Tapinocephalus*; from the third, the cynodonts, *Endothiodon*, *Procolophon*; from

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(3) *Quart. Jour.*, 16, 1880, 492-497.

(4) DAWKINS, Rhaetic beds and white Lias, *Quart. Jour.*, 20, 1864, 41: (3 fig.).

(5) In case *Triglyphus* does not represent the upper jaw teeth of the same reptile.

the fourth, the Theriodontia; and from the fifth, *Euskelosaurus* and *Massospondylus*. However this subdivision is to be accepted with some caution, for it is hardly conceivable that, e.g., *Oudenodon* appears before *Dicynodon*. However, from its paleontological content, zone 5 agrees very well with the uppermost Triassic of Central Europe, England, and North America, which always contain the large Dinosauria.

The Reptilia of the Karroo, as described by R. OWEN, HUXLEY, and SEELEY, stand alone in diversity. There are no fewer than 46 genera of Anomodontia with ca. 120 species. This fact alone is evidence of the long and great evolution.

Most lifestyles of living mammals are represented in those ancient Anomodontia. This is reflected particularly in the teeth and the structure of the limbs. The Pareiasauridae, Gorgonopsia, Dinocephalia, and some of the Dicynodontia are extremely stocky and strongly built. Several Dicynodontia and particularly Theriodontia have a delicate skeleton and must have been agile animals. Several Stegocephalia also lived together with the Anomodontia; of Temnospondyli there are *Petrophryne* OWEN (= *Micropholis* HUXLEY) and a species of *Eryops* (*africanus* LYDEKKER (1)); of Stereospondyli only the genus *Rhystidosteus* is represented. *Petrophryne* is a very ancient form that recalls many Carboniferous genera, and *Eryops* is found elsewhere in the Permian of Texas. Only two genera indicate that they were confined to the water, and at least one even in salt water, namely *Eunotosaurus* SEELEY and *Mesosaurus*. I have (see above) tried to prove that *Eunotosaurus* belong to the Placodontia, and these were probably coastal animals, as one must conclude from their teeth. *Mesosaurus* is a very primitive sauropterygian from the Kimberley shales (= *Mesosaurus* beds), which are of marine origin. It is striking that the whole Karroo lacks Parasuchia and Crocodilia (2).

A partly similar and no less interesting reptile fauna was discovered a few years ago by Prof. AMALITZKY in continental beds of *north Russia* (3). He has ascribed an Upper Permian age to it, however one could perhaps also conclude a Triassic age from the occurrence of the plants *Gangamopteris*, *Glossopteris*, etc. together. Most nearly or quite complete skeletons lie all in one and the same direction in an old river bed, which is now being laboriously uncovered. Pareiasauria are predominant in numbers, then *Gordonia*, a dicynodont, which is already known from Elgin, a skull of *Geikia* (an oudenodont from Elgin); *Inostrancevia* and *Lycosaurus*, two closely related genera, are particularly huge; *Kistecephalus* is also present, and a series of still undetermined skeletons; a single *Deuterosaurus* (4) was also found but it still partly unprepared. Two genera of Stegocephalia are also present, of which one is like *Melanerpeton*. The Pareiasauria, which separate into several species, are distinguished by noteworthy bizarre head-spines, and their entire back is covered with round, sculptured bone plates. In this they differ not a little from the South African ones, and at the same time preserve a truly younger appearance than the latter, because such extreme decorations are not primary but of secondary type. The skeleton mounted in Warsaw

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(1) In the Muséum d'Histoire Naturelle, Paris is found a half vertebra that could belong to a parasuchian or a dinosaur. It bears only the label "*Streptospondylus* Mongolia", thus comes from unknown, probably Triassic or Jurassic beds, of an unnamed locality in Mongolia. In the same museum there is a bone that could be interpreted as a sacral rib of a parasuchian; it was sent to Paris together with the *Euskelosaurus* remains described by FISCHER by Mr. BROWN from South Africa. Thus it is possible that Parasuchia may also occur in the upper Karroo of South Africa.

Lower jaw and rhachitinous vertebrae that R. OWEN previously assigned to *Rhystidosteus*. *Quart. Jour.*, 46, 1890.  
(2) *Pristerodon* HUXLEY is not, as HUXLEY believed, a crocodile, but, according to SEELEY, an anomodont that seems to be very closely related to *Endothiodon*.

(3) Sur les fouilles de 1859 de débris de vertébrés dans les dépôts permien de la Russie du Nord. Varsovie, 1900, 25 pp. and 5 pls. (*Trav. Soc. Imp. Nat. St. Petersburg*, 31; 1, 1900, 201-222).

(4) As opposed to the former (*loc. cit.*) report that *Deuterosaurus* and *Rhopalodon* are very common.

with a high back and rather lower-hanging head looks more natural than the specimens displayed in London. The knobby, spiny appearance of the head gives the impression of a mimicry protection arrangement by matching the stony ground. For this clumsy animal must have been a sluggish herbivore, which certainly must have suffered from the fierce *Inostrancevia* with its long, serrated, *Machairodus*-like fangs (one skull of *Inostrancevia* is 57 cm long). *Pareiasaurus* and *Lycosaurus* are both South African types that do not occur in other Russian (Permo-Triassic) continental deposits, likewise *Kistecephalus*. Only the Procolophonia related to *Pareiasaurus* have already been found beyond South Africa, in Scotland and central Europe (Rheinthal), and both times in armored forms; the skull is equipped with numerous long spines (*Elginia* and *Sclerosaurus*), as is the case in the north Russian Pareiasauria but not in the South African. The Dicynodontia, or rather the Oudenodontia, of north Russia are not identical with the South African and Indian, but with the more closely neighboring fauna of Elgin; in both places there are *Gordonia* and *Geikia*, both with a slender skeletal structure. The Parasuchia are also entirely absent here, for they first appear in the Upper or Middle Triassic.

The Triassic Maleri Beds of east India have yielded a fauna partly recalling that of South Africa. Particularly numerous Dicynodontia are known from them, which resemble neither those from South Africa, Scotland, nor north Russia. Together with these are found temnospondylous Stegocephalia, such as *Xestorhytias*, *Gondwanosaurus*, and *Brachyops*, and stereospondylous forms such as *Pachygonia* and *Gonioglyptus*. HUXLEY has described a temnospondyl related to these from the Australian Triassic as *Bothriceps*. *Hyperodapedon*, otherwise known only from Elgin and Devon, has also been found in India. Parasuchia and Dinosauria seldom compete with each other. Thus teeth were found in India that have been ascribed to the genera *Epicampodon* and *Massospondylus*. They are without doubt of Upper Triassic age.

In these youngest Triassic beds of South Africa, a considerable dinosaur fauna has also been preserved. *Euskelosaurus* and perhaps also *Orosaurus* are huge *Zanclodon*- and *Gresslyosaurus*-like animals. *Bathygnathus* from the Arctic of North America also belongs to them. However the smaller forms such as *Hortalotarsus*, *Massospondylus*, *Pachyspondylus*, and *Leptospondylus* are partly after the type of *Thecodontosaurus* of Europe, *Agrosaurus* of Australia, and *Anchisaurus* and *Ammosaurus*, *Palaeoctomus* and *Typothorax* (*ex parte*) of North America. Whether *Dystrophaeus* from Utah is really an orthopod, as COPE thinks, could not be previously established. *Tanytrophaeus* COPE from the Triassic of North America is a small anchisaurid or coelurid, whereas *Tanytrophaeus* H. von MEYER from the Muschelkalk and Lettenkohle of Germany seems to have been a dinosaur standing isolated.

The North American Upper Triassic also contains a series of Parasuchia: *Belodon*, *Stegomus*, and *Rhytiodon* are examples. *Eupelor* and *Typothorax* (*ex parte*) are Stegocephalia, and I suppose finally (see above) a cryptodire chelonian in *Arctosaurus*.

The astonishing abundance of Triassic Reptilia that have passed before us just now very briefly are mainly composed of faunas that still have a Paleozoic character. In particular, there are temnospondylous Stegocephalia, Proterosauridae, and Clepsydripidae. Characteristic of the Triassic are the stereospondylous Stegocephalia, the larger part of the Anomodontia, the Nothosauridae (specifically from the German Triassic province), and the Parasuchia (Upper Triassic).

In the following Liassic, the large order Anomodontia is no longer present; the Parasuchia are also absent. Both impart a strange characteristic stamp on the fauna of the Triassic continent. Only a few Stegocephalia prolong a wretched existence into the Dogger. Only the Pterosauria could be said with certain justification to be new for the Liassic and Triassic, although they first

appear at the end of the Triassic. The role of Parasuchia is taken over by the probably more marine Eusuchia, which were also present in the Muschelkalk, but the number of individuals is still very much reduced. The Ichthyosauria and Plesiosauria are not obvious; they are rulers of the sea from now on; probably both these groups were present on the stage of life already in the Muschelkalk, but the Nothosauridae prevailed in numbers then so that the others could not yet evolve. Now the Nothosauridae die out completely. On the threshold of the Jurassic Period, when the ocean moves in and blots out the specific features and living conditions of the German inland sea, the obstacles to free development of the marine reptiles are removed. The terrestrial Dinosauria continue, but we have little knowledge of them from the beginning of the Jurassic.

We see thus that the reptile fauna of the Jurassic, which is almost proverbial for its wealth and variety, had its origins completely in the Triassic; now new order is added to distinguish the Jurassic from the Triassic, but large orders became extinct probably just before the beginning of the Liassic. But the Jurassic brings the remainder received from the Triassic to a new climax, particularly in numbers. I believe that it is sufficiently justified to say that no period of the history of the Earth has possessed such a varied and richly developed fauna (reptile fauna) as the Triassic. Only the Tertiary can compete, in terms of the development of vertebrates, in the field of mammals. But the Reptilia played the role earlier which the mammals have largely taken over later on.

## FIGURE CAPTIONS

Fig. 1. *Stereosternum tumidum* COPE. Permian? Sao Paolo, Brazil. Right pes. F, fibula; T, tibia. After ZITTEL (COPE). Nat. size.

Fig. 2. *Telerpeton elginense* MANTELL. After HUXLEY. a, skull; b, ilium, ischium, pubis; c, scapula with coracoid and procoracoid. Nat. size.

Fig. 3. *Eryops megacephalus* COPE. After BROILI. 1/3 nat. size. Ilium, ischium, pubis with acetabulum.

Fig. 4. *Proterosaurus*-like reptile from the Middle Bunter Sandstone of Bernberg. (Avg. 1/2 nat. size.) Original in the Geol. Museum at Halle am Saale. a, 6 cervical vertebrae and cervical ribs (\* to compare with Fig. 5); b, dorsal vertebrae in lateral view, one articular facet and its profile, and cross-section of an upper arch (?sacral vertebra); c, rib; d, abdominal ribs from different regions; e, scapula (?); f, pubis (?) with obturator incisure; g, femur with nutrient foramen.

Fig. 5. 4th cervical vertebra of *Proterosaurus speneri*. Keupferschiefer of Thuringia. (After SEELEY.) Nat. size (for comparison with the cervical vertebra in Fig. 4a\*).

Fig. 6. “*Ichthyosaurus*”. Caudal vertebra. From the Wellenkalk of Querfurt, Harz. Nat. size. Original in Geol. Museum at Halle am Saale. Anterior, lateral, and dorsal views.

Fig. 7. Episternum of a, *Ichthyosaurus atavus* QU. Wellenkalk of Altbengatett near Calw. Tübingen collection. b, *Mixosaurus cornalianus* BASS. sp. Raibl Beds of Besano. Mus. Civ. Milan. (Drawing very kindly sent by Prof. REPOSSI.) c, *Ichthyosaurus quadrissiscus* QU. Upper Lias, Holzmaden. Tübingen collection. a-c nat. size.

Fig. 8. “*Ichthyosaurus*”. Dorsal vertebra. Schaumkalk of Freiburg am Unstrut. Nat. size. In anterior view, dorsal view, and cross-section. Original in the Geolog. Museum at Halle am Saale.

Fig. 9. *Cynognathus crateronotus* SEELEY. Palate (after SEELEY).

Fig. 10. Palate of *Nothosaurus* (*Cymatosaurus latissimus*) after KOKEN. Nat. size. Lower Muschelkalk.

Fig. 11. Palate of *Deuterosaurus*. Reduced from SEELEY. 1/2 nat. size.

Fig. 12. a, shoulder girdle of *Pareiasaurus baini* (after FÜRBRINGER and SEELEY). Cl, clavicle; Clth, cleithrum (= epiclavicle or mesoscapula SEELEY); Est, episternum; F. gl., glenoid fossa for humerus; F. spc., supracoracoid foramen; I. csc., coracoscapular incisure; Prc., procoracoid; Sc., scapula. b, shoulder girdle of *Eryops* from COPE and BROILI. cl, clavicle; epist, episternum; cor, coracoid; clei, cleithrum. c, episternum and clavicle of *Mastodonsaurus* after E. FRAAS. cl, clavicle; est, episternum.

Fig. 13. Ilium of *Pareiasaurus* after SEELEY.

Fig. 14. Femur of *Propappus* (after SEELEY). Underside.

Fig. 15. Femur of *Eryops megacephalus* COPE. 1/3 nat. size. Permian, Texas. Original in the Palaeont. Museum, Munich.

Fig. 16. Occiput of *Placodus gigas*.

Fig. 17. Occiput of *Dicynodon* after SEELEY. Fm, foramen magnum; Bo, basioccipital; Bs, basisphenoid; Pt, pterygoid; Q, quadrate; Sq, squamosal; Oo, opisthotic; So, supraoccipital; Jp, interparietal; Pa, parietal.

Fig. 18. Palate of *Placodus gigas* M. (from a model). JM, intermaxilla; M, maxilla; N, nasal opening; Pal, palatine; Pt, pterygoid; Tr, ectopterygoid; J, jugal; QJ, quadratojugal; Q, quadrate. 1/2 nat. size.

- Fig. 19. Palate of *Rhopalodon* (after SEELEY). 1.2 nat. size.
- Fig. 20. *Eunotosaurus africanus* SEELEY. d, dorsal side; v, ventral side; p, pubis.
- Fig. 21. *Actinodon fressardi* GAUDRY. Nat. size after GAUDRY. Left femur in dorsal view.
- Fig. 22. *Deuterosaurus* (after SEELEY). 1/2 nat. size. Femur, proximal end. C.f., femoral head.
- Fig. 23. “*Dinosaurus*” EICHW. Nat. size. After SEELEY. Femur from underside.
- Fig. 24. Cervical ribs of *Discosaurus* after CREDNER. Nat. size.
- Fig. 25. Tibia from two sides. Schaumkalk of Freiburg am Unstrut. Nat. size. Original in Haale am Saale University Collection.
- Fig. 26. Tibia of *Sclerocephalus* after CREDNER. Nat. size.
- Fig. 27. Fibula from two sides. Schaumkalk of Freiburg am Unstrut. Nat. size. Original in Haale am Saale University Collection.
- Fig. 28. Fibula of *Sclerocephalus* after CREDNER. 1/2 nat. size.
- Fig. 29. Femur of *Crurosauros problematicus* from two sides. 2/3 nat. size. Schaumkalk of Freiburg am Unstrut. Original in Haale am Saale University Collection.
- Fig. 30. Reconstruction of the palate of *Sclerosaurus armatus* M. 2/3 nat. size.
- Fig. 31. *Procolophon* after SEELEY. Nat. size. a, palate and shoulder girdle; b, skull in dorsal view (squamosal spine!).
- Fig. 32. Vertebral column of *Procolophon* after SEELEY. Nat. size.
- Fig. 33. Reconstruction of *Sclerosaurus armatus* M. 1/2 nat. size. The ribs and limbs of the left side are omitted to simplify the figure.
- Fig. 34. Astragalocalcaneum of *Pareiasaurus*. From the Suchona, North Russia. 2/3 nat. size. Orig. in Warsaw University Collection.
- Fig. 35. *Anomosaurus* sp. Schaumkalk of Freiburg am Unstrut, 2/3 nat. size. Original in the Geological Museum at Haale am Saale (see hyosphene a, b, c).
- Fig. 36. Dorsal centrum of *Pareiasaurus* (after R. OWEN). 1/2 nat. size. Profile of the articular faces dotted.
- Fig. 37. *Dicynodon pardiceps*. South Africa (after R. OWEN). 1/2 nat. size. a, in anterior view; b, longitudinal section.
- Fig. 38. *Embolophorus* from the Catalogue of the Brit. Mus. (LYDEKKER). Permian, Texas (hyosphene!). Nat. size. ptz., postzygapophysis; pt., transverse process.
- Fig. 39. *Inostrancevia annae* AMALITZKY ms. From Suchona, N. Russia. Dorsal vertebra, from right (hyosphene!). 2/3 nat. size. Original, Warsaw University Collection.
- Fig. 40. *Nothosaurus*. Dorsal vertebra from behind. 1/2 nat. size. Upper Muschelkalk from Bayreuth. Trace of hyosphene. Original in Geological Museum, Tübingen.

Fig. 41. *Ctenosaurus koenei* HUENE. ca. 1/8 nat/ size. Middle Bunter Sandstone of Rheinhausen near Göttingen. Original in the Geological Museum at Göttingen.

Fig. 42. a, dorsal vertebra of *Dimetrodon* from the right. Permian, Texas. Profile of the articular surfaces dotted. 2/3 nat. size. Original in the Palaeontological Museum, München. b, dorsal vertebra of *Naosaurus* from the right. Permian, Texas. Profile of articular surfaces dotted. 2/3 nat. size. Original in Palaeont. Mus., München.

Fig. 43. a, *Nothosaurus marchicus* KOKEN. Nat. size. Lower Muschelkalk, Rüdersdorf (after KOKEN); b, *Rhopalodon*. 1/2 nat. size (after SEELEY). P and Pa, parietal; S, temporal fossa; Op, opisthotic; Pt, pterygoid; Ip, interparietal; Sq, squamosal; So, supraoccipital; Exo, exoccipital; Bo, basioccipital; Qu, quadrate; BS, basisphenoid; Fm, foramen magnum; m, jugal; tr, ectopterygoid.

Fig. 44. a, *Nothosaurus (?mirabilis)*. Sacral vertebrae in posterior view. 2/3 nat. size. Upper Muschelkalk. Orig. in private collection of STRUNZ in Bayreuth. b, reconstruction of the first sacral vertebra of *Dicynodon*. 1/2 nat. size, after R. OWEN (*Ill. Cat.*, pl. 36, fig. 1). S. Africa.

Fig. 45. Pelvis of *Cynognathus crateronotus* SEELEY (after SEELEY). obt f, obturator foramen; p, pubis; isch, ischium; ac, acetabulum.

Fig. 46. *Dicynodon orientalis* LYD. after LYDEKKER. a, posterior view; b, anterior view. India.

Fig. 47. *Nothosaurus*. Femur from the ventral (posterior) side (after H. v. MEYER). 1/2 nat. size. Upper Muschelkalk. (For comparison with *Dicynodon orientalis*, cf. Fig. 46a).

Fig. 48. *Nothosaurus* (after H. v. MEYER). 1/4 nat. size. Upper Muschelkalk. Est, episternum; Cl, clavicle.

Fig. 49. *Pareiasaurus baini* SEELEY (after SEELEY). 1/8 nat. size. South Africa. Est, episternum; Cl, clavicle.

Fig. 50. Sacral vertebral in anterior view. Nat. size. Upper Muschelkalk, Bayreuth. Original in Geol. Museum, Tübingen (cf. pl. 6, fig. 6).

Fig. 51. *Plesiosaurus*. Dorsal vertebra. 1/3 nat. size. *Zanclodon* Bed of Schönthal near Liestal. Original in the Museum at Basel. a, dorsal view; b, left lateral view.

Fig. 52. *Plesiosaurus*. Caudal vertebra in anterior view. 2/3 nat. size. *Zanclodon* Bed of Schönthal near Liestal. Orig. in Basel Museum.

Fig. 53. *Plesiosaurus*. Distal end of a humerus. 1/2 nat. size. Rhaetic Keuper of Little Hagen, near Göttingen. Original in Geological Museum, Göttingen.

Fig. 54. *Doliovertebra fritschi* v. M. Sacrum. a, right lateral view; b, posterior view; c, ventral view. 2/3 nat. size. Schaumkalk of Freyburg am Unstrut. Orig. in Geological museum at Halle am Saale.

Fig. 55. *Euclastes*. Occiput, after ZITTEL.

Fig. 56. *Dicynodon*. South Africa. Occiput, after R. OWEN.

Fig. 57. *Pareiasaurus*. Skull in posterior view. Reduced after SEELEY. B.o., basioccipital.

Fig. 58. *Dicynodon*. Skull in ventral view. Restored, reduced after SEELEY.

Fig. 59. *Euclastes*. Palate, after ZITTEL. pm, premaxilla; m, maxilla; v, vomer; pal, palatine; tr, ectopterygoid; pt, pterygoid; j, jugal.

Fig. 60. *Arctosaurus osborni* ADAMS. Nat. size, after ADAMS. Triassic of Bathurst Island, Arctic North America. A, right lateral view; B, dorsal view; C, posterior view; D, anterior view.

- Fig. 61. *Stagonolepis robertsoni* AG. 1/2 nat. size, after HUXLEY. Reconstruction of part of the palate. N, inner and outer nasal openings.
- Fig. 62. *Stagonolepis*. After HUXLEY. 1 and 2, first and second sacral vertebrae, ventral view. Elgin. 1/2 nat. size.
- Fig. 63. *Stagonolepis*. Caudal vertebrae, after HUXLEY. Elgin. 1/2 nat. size.
- Fig. 64. *Erpetosuchus*. Interclavicle, after E. T. NEWTON. Elgin. Nat. size.
- Fig. 65. *Stagonolepis*. Interclavicle. After HUXLEY. Elgin. 1/2 nat. size.
- Fig. 66. *Stagonolepis*. Humerus after HUXLEY. 1/2 nat. size. Elgin. a, proximal end of left humerus in anterior view; b, distal end of left humerus in anterior view.
- Fig. 67. *Stagonolepis*. Ulna, proximal end. Elgin. 1/2 nat. size. Original in Jermyn Street Museum, London.
- Fig. 68. *Aetosaurus*. Right side of pelvis. Nat. size. Il, ilium from no. 22; Is + P, ischium and pubis from no. 6 of the *Aetosaurus* group in the Royal Natural History Cabinet, Stuttgart. Stubensandstein of Neslach.
- Fig. 69. *Ornithosuchus*. Nat. size. After E. T. NEWTON. Elgin. Il, Is, P, right ilium, ischium, and pubis in natural connection.
- Fig. 70. *Belodon*. After H. v. MEYER. 1/3 nat. size. Il, ilium; Is, ischium; P, pubis is twisted, thus is seen from behind. Stubensandstein, Stuttgart.
- Fig. 71. *Thecodontosaurus*. 1/2 nat. size. Middle Keuper of Bristol. Right ilium. Original in the Museum at Bristol.
- Fig. 72. *Stagonolepis*. Il, ilium; Is, ischium. 1/2 nat. size. After HUXLEY. Elgin.
- Fig. 73. *Stagonolepis*. Pubis. 1/2 nat. size. Elgin. a, distal end of right pubis after HUXLEY; b, proximal end of left pubis (?); c, cross-section at the dotted place in b. Original in the Jermyn Street Museum.
- Fig. 74. *Belodon arenaceus* E. FRAAS sp. Schilfsandstein, Feierbache Haide. 1/2 nat. size. Original in the Royal Natural History Cabinet, Stuttgart.
- Fig. 75. *Rileya bristolensis* HUENE. Humerus. Nat. size. Middle Keuper, Bristol. Original in the Bristol Museum.
- Fig. 76. *Rileya bristolensis* n. g., n. sp. Two centra. Nat. size. Middle Keuper of Bristol. Original in the Yale Museum, New Haven, Conn., U.S.A.
- Fig. 77. Caudal vertebrae. Schaumkalk of Wolfsburg in the North Harz. 2/3 nat. size. a, right lateral view; b, posterior view; c, anterior view; d, ventral view. Original in the Geological Museum at Halle in Saale.
- Fig. 78. *Labyrinthodon scutulatus* R. OWEN (copy). From the English Upper Keuper. Nat. size. y enlarged.

#### EXPLANATION OF PLATE I

*Sclerosaurus armatus* H. v. MEYER. Nat. size. Retouched photograph of the plaster cast. Bunter Sandstone of Riehen near Basel.

Sp. Quadr., quadrate spine

S.V. I-III, sacral vertebrae I-III

The other abbreviations are self-explanatory. Posterior view. The armor plates lie on and beside the dorsal vertebrae. The original (negative) is found in the Natural History Museum at Basel.

#### EXPLANATION OF PLATE II

*Sclerosaurus armatus* H. v. MEYER. Nat. size. Unretouched photograph of the plaster cast. Bunter Sandstone of Riehen near Basel.

The abbreviations are self-explanatory. Abdominal view. The original (negative) is found in the Natural History Museum at Basel.

#### EXPLANATION OF PLATE III

*Sclerosaurus armatus* H. v. MEYER's original. Photograph at nat. size. Upper Bunter Sandstone of Warmbach near Rheinfeld (near Basel).

Fig. 1. Dorsal armor seen from the inside. The cranial side lies on the left, the caudal side on the right. Both femora visible from the underside, also fragments of the pelvis.

Fig. 2. Dorsal vertebrae seen from above with ribs or fragments of the pelvis. The cranial side lies on the right, the caudal side on the left.

The piece in Fig. 1 is removed from the piece in Fig. 2. Both belong to the same individual. Original in the Geological Museum at Freyburg im Breisgau.

#### EXPLANATION OF PLATE IV

Fig. 1. Ventral armor plate (?) of a crocodile (?). Nat. size. Upper Muschelkalk, Steinbiedersdorf, Lorraine. (Toothed edge!) Original in the geological area collection at Strassburg.

Fig. 2. Tooth of *Plesiosaurus* (?) sp. Nat. size. Uppermost Keuper, *Zanclodon*-bed. Schönthal near Liestal. Original in the Museum at Basel.

Fig. 3. *Anomosaurus* sp. Nat. size. Lumbar vertebra in posterior view. Upper Muschelkalk. Laineck near Bayreuth. Original in the Geological Museum at Tübingen.

Fig. 4. *Anomosaurus* sp. Nat. size. Dorsal vertebra in posterior view. Upper Muschelkalk. Neckarvaihingen. Original in the Geological Museum at Tübingen.

Fig. 5. *Sclerosaurus armatus* H. v. MEYER. Nat. size. Bunter Sandstone of Riehen near Basel. Photograph of the plaster cast. Right half of skull in ventral view. Original (negative) in the Museum at Basel.

#### EXPLANATION OF PLATE V

Fig. 1. *Placodus gigas* (?) H. v. MEYER. Nat. size. Dorsal vertebra. Upper Muschelkalk, region of Göttingen. a, posterior view; b, anterior view. Original in Geological Museum at Göttingen.

Fig. 2. *Placodus gigas* (?) H. v. MEYER. Nat. size. Dorsal vertebra in right lateral view. Upper Muschelkalk of Laineck near Bayreuth. Original in the Palaeontological Museum at Munich.

Fig. 3. Dermal armor plate of *Placodus* sp. (= *Pseophosaurus* cf. *suevicus* E. FRAAS). Rhaetic bonebed of Schönthal near Liestal. Nat. size. Original in Basel Museum.

Fig. 4. *Plesiosaurus (priscus)* v. HUENE). Nat. size. Cervical vertebra in ventral view. Lettenkohle bonebed of Biebersfeld. Original in Geological Museum, Tübingen.

Fig. 5. *Plesiosaurus (priscus)* v. HUENE). Nat. size. Anterior cervical vertebra. a, left lateral view; b, ventral view. Upper Muschelkalk of Laineck near Bayreuth. Original in the Palaeontological Museum at Munich.

Fig. 6. Humerus, gen. et sp. indet. 2/3 nat. size. Upper Muschelkalk of Laineck near Bayreuth. Original in the district collection at Bayreuth.

#### EXPLANATION OF PLATE VI

- Fig. 1. Tibia, perhaps belonging to *Eurycervix* or a related form. Nat. siz. Upper Muschelkalk of Steinbiedersdorf, Lorraine. Original in the geological area collection, Strassburg.
- Fig. 2. *Trochanterium gaudryi* v. HUENE. Nat. size. Right femur. a, from below; b, from above. Upper Muschelkalk of Bischmisheim, Lorraine. Original the geological collection at Strassburg.
- Fig. 3. Right articular + surangular of a crocodile. Nat. size. Medial view. Upper Muschelkalk of Busendorf, Lorraine. Original the geological area collection, Strassburg.
- Fig. 4. *Anomosaurus* sp. v. HUENE. Nat. size. Dorsal vertebra in posterior view. Upper Muschelkalk of Laineck near Bayreuth. Original in Geological Museum at Tübingen.
- Fig. 5. *Pectenosaurus strunzi* v. HUENE. Nat. size. Middle caudal vertebra. Upper Muschelkalk of Laineck near Bayreuth. Original in Geological Museum at Tübingen.
- Fig. 6. Sacral vertebra of a plesiosaurid(?). Nat. size. Upper Muschelkalk of Laineck near Bayreuth. a, ventral view; b, dorsal view. Original in Tübingen Geological Museum.

#### EXPLANATION OF PLATE VII

- Fig. 1. *Chelyzoon blezingeri* v. HUENE. Nat. size. Cervical vertebra in left lateral view. Upper Muschelkalk bonebed from the Oelmühle near Crailsheim. Original in the Royal Natural History Collection, Stuttgart.
- Fig. 2. *Chelyzoon latum* v. HUENE. Nat. size. Cervical vertebra. Upper Muschelkalk of Laineck near Bayreuth. a, left lateral view; b, ventral view. Original in the Paleontological Museum at Munich.
- Fig. 3. Costal plate of a chelonian reminiscent of *Thalassemys*. Nat. size. a, ventral view; b, dorsal view. Upper Muschelkalk of Busendorf, Lorraine. Original in Geological Museum at Strassburg.
- Fig. 4. Free end of a rib from a chelonian reminiscent of *Thalassemys*. Nat. size. a, dorsal view; b, ventral view. Upper Muschelkalk of Busendorf, Lorraine. Original in Geological Museum at Strassburg.
- Fig. 5. Caudal vertebra of a chelonian(?). Nat. size. Rhaetic bonebed of Schösslesmühle, Württemberg. a, left lateral view; b, profile of anterior articular facet; c, profile of posterior articular facet. Original in Geological Museum, Tübingen.
- Fig. 6. *Anomosaurus* sp. v. HUENE. Nat. size. Dorsal vertebra. Upper Muschelkalk of Schlotheim, Thuringia. a, left lateral view; b, anterior view. Original in Geological Museum, Göttingen.

#### EXPLANATION OF PLATE VIII

- Fig. 1. Left femur, gen. et sp. indet. Nat. size. (Original in H. v. MEYER: *Fauna der Vorwelt*, pl. 65, figs. 5-7.) Upper Muschelkalk of Bischmisheim near Saarbruck. Original in geological area museum, Strassburg.
- Fig. 2. Right femur, gen. et sp. indet. Nat. size. Upper Muschelkalk of Laineck near Bayreuth, Original in area museum, Bayreuth,
- Fig. 3. Left femur, gen. et sp. indet. Nat. size. Upper Muschelkalk of Laineck near Bayreuth, Original in area museum, Bayreuth,
- Fig. 4. *Plesiosaurus priscus* v. HUENE. Nat. size. Cervical vertebra in ventral view. Upper Muschelkalk of Laineck near Bayreuth. Original in Geological Museum, Tübingen.
- Fig. 5. Caudal vertebra of a crocodile. Nat. size. Wellenkalk of Merklingen, Württemberg. a, right lateral view; b, dorsal view. Original in Geological Museum, Tübingen.
- Fig. 6. Caudal vertebra of a crocodile. Nat. size. Wellenkalk of Hausen an der Wurm, Württemberg. a, lateral view; b, dorsal view; c, ventral view. Original in Geological Museum, Tübingen.

#### EXPLANATION OF PLATE IX

- Fig. 1. *Procerosaurus cruralis* v. HUENE. 2/3 nat. size. Left femur in posterior view; the proximal end is missing. Upper Muschelkalk bonebed from the Oelmühle near Crailsheim. Original in private collection of the Hon. BLEZINGER of Crailsheim.
- Fig. 2. *Eurycervix postumus* v. HUENE. Nat. size. Cervical rib. a, dorsal view; b, ventral view. Upper Muschelkalk bonebed from the Oelmühle near Crailsheim. Original in private collection of the Hon. BLEZINGER of Crailsheim.
- Fig. 3. Neural arch of a pterosaurian cervical vertebra. Nat. size. a, dorsal view; b, right lateral view. Rhaetic bonebed of an unknown locality in Württemberg (?Schösslesmühle). Original in Royal Natural History Cabinet, Stuttgart.