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A NEW FIND OF  
GERROTHORAX RHAETICUS NILSSON  
A PLAGIOSAURID FROM THE  
RHAETIC OF SCANIA

BY

TAGE NILSSON

WITH 3 PLATES AND 13 FIGURES IN THE TEXT

LUND  
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## Introduction.

Recent investigations have shown that the fauna of the coal-bearing Rhaetic strata of North-West Scania comprises a species of a Stegocephalian. This has been referred to as *Gerrothorax rhaeticus* NILSSON (1934, 1937) and clearly belongs to the family *Plagiosauridae*, a group which has been made the type family of a separate order of Triassic Stegocephalians, *Plagiosauria*, distinguished from the Labyrinthodonts (cf. NILSSON 1939, p. 24). As a whole the Plagiosaurids form a strange group, which is as yet but insufficiently known. Therefore all new finds that can contribute to our knowledge of these animals are welcome.

During a visit in the summer 1942 to the coal-mine at Bjuv, the locality of the earlier finds of Stegocephalian remains, I was informed by Mr. WALLERIUS MÅNSSON, an overseer of the mine, that new remnants of a large fossil had been uncovered about a month earlier. On close inspection they were found to belong to the same form of Stegocephalians as those previously found. At the time of my visit the remains were still kept in a passage down in the mine together with a lot of non-fossiliferous slabs. Five slabs with remains of the fossil could be sorted out. Without doubt more remains had originally been present, probably the whole animal, but most of the fossil had evidently been destroyed by the blasting that uncovered the remnants. The preserved fragments had been observed and brought together by Mr. MÅNSSON, a man with an open eye for fossils, immediately after the blasting. According to his own statement he sought in vain for other fossiliferous slabs.

The new find was acquired by the Palaeozoological Department of the Swedish Museum of Natural History, Stockholm, where it has been given the museum number B. 18 a—e. It was immediately cleaned by myself, but the further study of it had to be put off until now on account of intervening work.

The new remains are almost entirely postcranial. They belong to some extent to parts of the body already known through the earlier finds. New very important information has been gained, however, especially as regards the hind leg and the anterior and posterior parts of the body.

The photographs for this paper have been taken by Mr. G. AHL. The retouch work as well as the drawing of most of the text-figures have been performed by Mr. S. EKBLOM.

## Description of the New Material.

Order *Plagiosauria* (JAEKEL 1913; emend. NILSSON 1939).

Family *Plagiosauridae* JAEKEL (1913; emend. ABEL 1919).

Genus *Gerrothorax* NILSSON (1934).

### *Gerrothorax rhaeticus* NILSSON.

(Figs. 2—13; pls. I—III.)

1934 *Gerrothorax rhaeticus* NILSSON (1934, pp. 428—442, figs. 2—3).

1937 *Gerrothorax rhaeticus* NILSSON (1937, pp. 15—53, figs. 2, 3, 5, 9—11; pls. I—IV).

**Material.** The previously described finds are the following:

1) *Holotype* (coll. 1933; preserved in the Geological-Mineralogical Institute of the University of Lund; NILSSON 1934, 1937): the posterior part of the dermal shoulder-girdle, the anterior and middle parts of the gastral skeleton and corresponding parts of the axial skeleton, ribs, and dorsal scale-armour;

2) *B. 2—4* (coll. 1885; preserved in the Palaeozoological Department of the Swedish Museum of Natural History, Stockholm; NILSSON 1937): a fragment of the posterior part of the skull.

The new find, *B. 18 a—e* (coll. 1942; kept in the Swedish Museum of Natural History) is preserved on five slabs of rock. Three of these slabs (»dorsal slabs»), *B. 18 a—c* (pl. I; pl. II, fig. 1; pl. III, fig. 2), contain essentially dorsal parts of the fossil, the other two (»ventral slabs»), *B. 18 d—e* (pl. II, fig. 2; pl. III, fig. 1), mainly ventral parts.

The following parts are preserved in spec. *B. 18*: insignificant fragments of the most posterior part of the skull; parts of the hyobranchial skeleton; a number of presacral and anterior caudal vertebrae and ribs; the most anterior part (and an insignificant fragment of the posterior part) of the dermal shoulder-girdle; fragments of the pelvis; large parts of the hind legs; fragments of the middle and posterior part of the gastral skeleton; parts of the remaining dermal scale-armour from the middle and posterior part of the trunk and the anterior part of the caudal region.

Slabs *B. 18 c* and *a* are partly counter-slabs to *B. 18 d* and *e* respectively. *B. 18 a* and *e* in the main show parts of the sacral and anterior caudal regions, *B. 18 c* and *d* parts of the posterior part of the trunk. As slab *B. 18 d* has a small posterior surface fitting in with a corresponding surface on *B. 18 e*, the original mutual position of the four slabs *B. 18 a, c—e* could be firmly established (fig. 2). Slab *B. 18 b* exhibits *i. a.* the posterior part of the skull and the foremost part of the dermal shoulder-girdle. Thus there must be a considerable gap in the preserved material between slabs *B. 18 b* and *c*. As the latter slab, *B. 18 c*, in its most anterior part has some

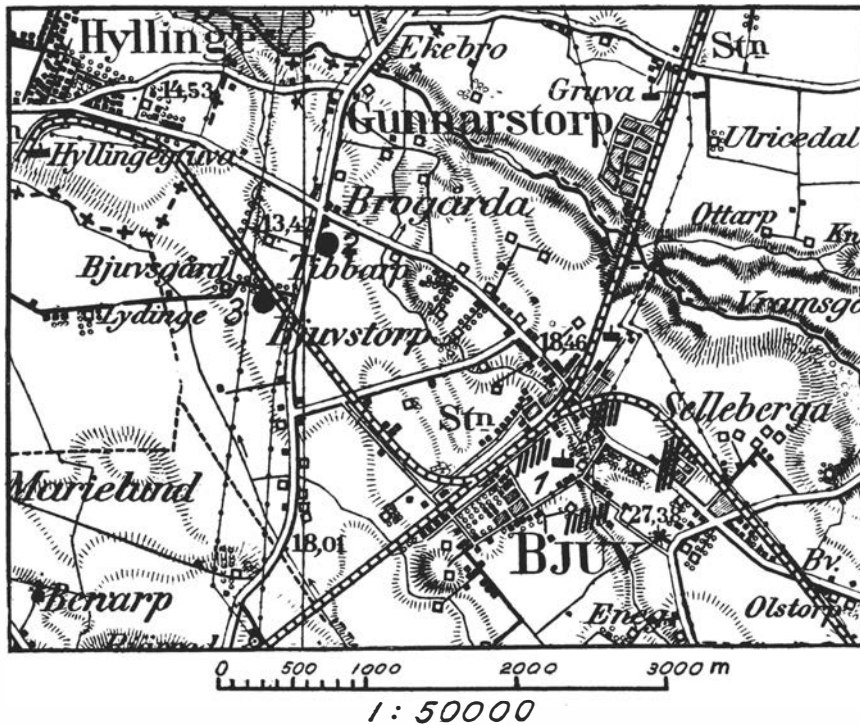


Fig. 1. Map showing the find localities of *Gerrothorax rhaeticus* NILSS. 1, B. 2—4; 2, holotype; 3, B. 18. The exact find place of B. 2—4, which was brought into light in 1885, is unknown, but the areas of mining for the year 1885 are marked by shading, according to information kindly furnished by Mr. W. MÅNSSON.

remains of the hindmost part of the right clavicle, the size of the gap could be approximately estimated with the aid of a restoration of the dermal shoulder-girdle (figs. 2, 5).

The restorations of the general shape of the body and the organization of the animal are largely founded on spec. B. 18. In applicable parts also the holotype has been used. The outlines of the skull have been completed with the aid of spec. B. 2—4 and the skull of the German species *Gerrothorax pulcherrimus* (cf. NILSSON 1937, fig. 14); the shape of the humerus is indicated after the conditions in *Plagiosaurus depressus* (cf. NILSSON 1939). The position of certain skeletal elements, which had evidently been displaced during fossilization, has been corrected. *I. a.* the dermal shoulder-girdle was evidently fairly far displaced in a posterior direction. In connection with that the gastral skeleton was torn into rags for a good distance behind the dermal shoulder-girdle.

**Geological horizon and locality** (cf. fig. 1). The first find, B. 2—4, was made at Bjuv in the »plant-bearing bed 3» of NATHORST, a bed of argilliferous schistose sandstone separated from the underlying »Lower Coal Measure» by argillaceous

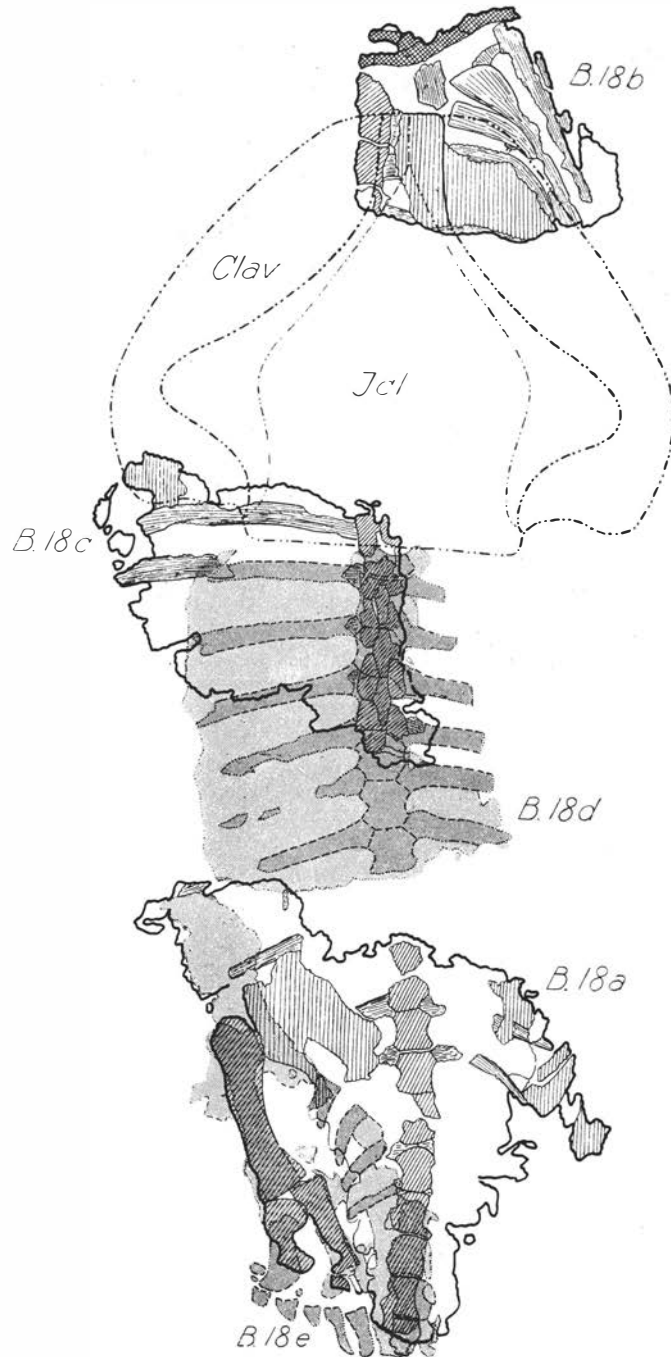


Fig. 2. *Gerrothorax rhaeticus* NILSS. Sketch showing the orientation and mutual original position of the fossil remains exhibited on the slabs B.18a—e. Remains shown on the slabs containing chiefly dorsal parts of the fossil («dorsal slabs») are marked by shading with (crossed or uncrossed) lines and circumscribed by a thick line, remains shown on «ventral slabs» are denoted by two different screen tones and circumscribed by a thin dotted line.  $\times 0,3$ .

strata with an average thickness of about 45 cm (NILSSON 1937, pp. 8 f.). The holotype was also found at Bjuv in a grey, argilliferous sandstone about 40 cm above the same coal measure. The last find, B. 18, was made not far from the find locality of the holotype<sup>1</sup> in a similar rock about 60 cm above the »Lower Coal Measure». According to the discoverer, Mr W. MÅNSSON, the find horizon was visible for a long distance as a thin, 1—2 cm thick, argillaceous layer.

All three finds were thus made in practically exactly the same local horizon, 40—60 cm above the »Lower Coal Measure».<sup>2</sup> The said horizon belongs to the middle part of the Rhaetic layers in Scania, *i. e.* to the middle part of the zone with *Lepidopteris ottonis*, according to the delimitation of the zones in the Rhaetic-Liassic by HARRIS (cf. NILSSON 1937, pp. 9—11).

### 1. Skull.

(Figs. 2, 4; pl. II, fig. 1.)

On spec. B. 18 but insignificant fragments of the most posterior part of the skull are present. They have been interpreted as remnants of the exoccipital (*Eo*), supraoccipital (*So*), basioccipital (*Bo*), postparietal (parieto-extrascapular SÄVE-SÖDERBERGH; *Ppar*), and, with some doubt, entopterygoid (*Enpt?*). The foramen magnum (*f.m*) and foramen vagi (*f.vag*) are also shown.

### 2. Visceral skeleton.

(Figs. 3, 4; pl. II, fig. 1.)

Surprisingly enough remains of visceral arches, forming a well developed hyobranchial skeleton, are preserved. The remains above all comprise a series of long, curved bars (*Kbr*), lying close to each other on the left side of the foremost presacral vertebrae, immediately behind the remnants of the skull. At first the bars were assumed to be cervical ribs; their nature of visceral arches is clear, however, from the following facts. Antero-medially to their proximal ends there are fragments of other bones, which were evidently connected to the bars in some way. The foremost of these lie in front of the first vertebra. Immediately behind the bars in question is a true rib (*C*). This has the same straight shape as the more posterior ribs and is entirely different from the above-mentioned bars. That we are concerned with branchial arches is also borne out by the fact that narrow, 1.5—2 mm long denticles (*dt*) are found in close connection with the bars. They seem to be situated in pairs on separate small laminous ossifications lying close to the inner (postero-medial) face of the bars. The denticles are narrow, conical, and acute, and quite different from the tubercles of the dermal bone covering.

<sup>1</sup> »Ort nr 3, linjebrott nr 29», according to the designations on the map of the mine.

<sup>2</sup> The bed referred to appears to be the most important vertebrate-yielding horizon of the Rhaetic of North-West Scania. In the last decades it has thus yielded a number of beautiful, as yet undescribed ganoid fishes (cf. also ERDMANN 1911—15, p. 363).

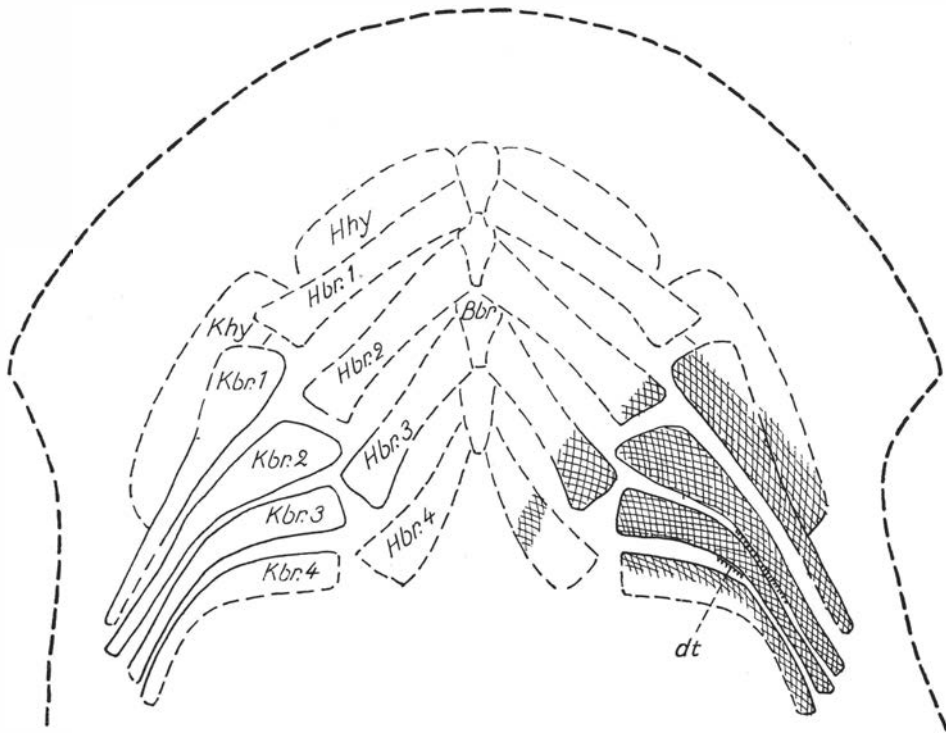


Fig. 3. *Gerrothorax rhaeticus* NILSS. Restoration of the hyobranchial skeleton. The denticles (*dt*) on the keratobranchials only partly indicated. Ventral view. After spec. B.18 b.  $\times 1/2$ .  
Explanation of lettering pp. 41 f.

Thus no confusion with such structures is possible. The denticles are comparable to those found on the tooth-bearing plates covering the branchial arches of certain fishes (cf. HOLMGREN & STENSIÖ 1936, pp. 393, 474, 493) and to the denticles marking the position of the cartilaginous branchial arches in the larvae of fossil Amphibians (*Branchiosaurus* and allied forms; CREDNER 1886, pp. 599—606; FRITSCH 1879—83, pp. 77, 81; THEVENIN 1906, p. 8; BULMAN & WHITTARD 1926, pp. 543—545). It may also be noticed that, according to STADTMÜLLER (1926 a, pp. 155—163; 1926 b, pp. 382—399), the filter processes of the hyobranchial apparatus of recent Urodeles are the homologues of tooth rudiments.

The curved bars described above (*Kbr*) may correspond to the structures termed keratobranchials in recent Amphibians. Antero-laterally and in part dorsally to the foremost keratobranchial there is a fragment of a substitution bone which seems to terminate backwards a good distance in front of the posterior ends of the keratobranchials. Very likely it is a remnant of a keratohyal (*Khy*). Postero-medially to this bone there are four keratobranchials, which may accordingly be referred to as the first, second, third, and fourth keratobranchial (*Kbr. 1—4*). Thus the same number of keratobranchials are present as are developed in



the larvae of most recent Amphibians including the neotenic *Siren lacertina* (cf. STADTMÜLLER 1936, pp. 657—687).<sup>1</sup> All keratobranchials are fairly long bones, the longest attaining a length of about 9 cm. They have a strongly broadened, more or less claviform ventro-medial end; the remaining, longer part is compressed, uniformly narrow, and directed postero-laterally and dorsally. The first keratobranchial is almost straight, the second and in particular the third and fourth keratobranchials are strongly curved, the concavity facing postero-medially and dorsally.

The elements situated antero-medially to the keratobranchials must represent the postero-lateral ends of hypobranchials (*Hbr*). More or less large fragments are present of the second, third, and probably also of a fourth hypobranchial (*Hbr*. 2—4). The preserved parts are fairly broad. At least the second and third hypobranchial were directed antero-medially. In the living animal the first hypobranchial and the hypohyal were probably also ossified. The ventral parts of the hyoid and branchial arches may be assumed to have been connected by copulae (basibranchials and ? basihyal), very much as shown in the restoration fig. 3.

If the above identifications are correct, the present form has one or two more hypobranchials than recent Amphibians. In larval *Urodela* only the first and second hypobranchials are developed, in larval *Anura* the continuous so-called hypobranchial plate is assumed to be formed chiefly by the first hypobranchial,<sup>2</sup> in larval *Gymnophiona* the hypobranchial components probably enter in the formation of the first three continuous branchial arches (STADTMÜLLER 1936, pp. 657—687). The number of hypobranchials in Rhipidistid Crossopterygians is unknown (HOLMGREN & STENSIÖ 1936, p. 355).

Upon examining to what extent structures corresponding to the above described hypobranchial apparatus are known in other Stegocephalians, we find that the larvae of *Branchiosaurus* and allied forms had four branchial arches (keratobranchials), as a rule in a cartilaginous state (CREDNER 1886, pp. 604 f.; BULMAN & WHITTARD 1926, pp. 543 ff.; cf. also above); according to CREDNER they had at least one hypobranchial (ossified), probably the first. At least two branchial arches were present in the larvae of *Melanerpeton* (FRITSCH 1879—83, p. 98). v. MEYER (1857, pp. 107 f.) is of the opinion that certain small elongate laminae arranged in arches on each side behind the skull in *Archegosaurus* represent remnants of (an uncertain number of) ossified branchial arches. They are present also in small mature individuals but have not been found in large specimens; according to v. MEYER they probably no longer bore any gills. *Platyceps wilkinsoni* from the Triassic of New South Wales, a form regarded as a larva of a Brachyopid, has branchial arches of such an appearance that external gills must be assumed to have been present, according to WATSON (1926, p. 199). *Tungussogyrinus bergi*, a larva of a Stegocephalian from the Permian of Siberia, exhibits three pairs of carbonified structures interpreted as external gills by BYSTROW (1939, pp. 139 f., fig. 8).

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<sup>1</sup> The Rhipidistid Crossopterygians have also a fifth keratobranchial (WATSON 1926, p. 250).

<sup>2</sup> Possibly also the second hypobranchial enters in its formation (cf. GAUPP 1905, pp. 740 f.).

In all these cases we are concerned with the hyobranchial skeleton (and gills) in larval forms or in a state of strong reduction in adults. The hyobranchial apparatus of *Gerrothorax* agrees with that of the larval *Branchiosaurus*, the best known of the forms just referred to, as regards the number of keratobranchials. In *Gerrothorax*, however, the keratobranchials are strongly ossified, in *Branchiosaurus* they are as a rule cartilaginous. In addition *Gerrothorax* has a greater number of ossified hypobranchials than *Branchiosaurus*.

Apparently a few Stegocephalians had well developed branchial arches and functioning gills also in the mature stage. They were thus in this respect comparable to the perennibranchiate Urodeles and, quite as these, they are regarded to be neotenic by several authors. The neotenic Stegocephalians known so far are:

1) *Lysorophus tricarinatus* of the Permian and *Cocytinus gyrinoides* of the Carboniferous of North America, two representatives of the order *Adelospondyli*, a group possibly related to the Urodeles (WILLISTON 1912, p. 661; FINNEY 1912, p. 666; SOLLAS 1920, pp. 513—516; ROMER 1930, pp. 82 f.; STEEN 1930, pp. 883 f.; BYSTROW 1938, pp. 274 f.; etc.);

2) *Dvinosaurus primus*, rhachitomous Labyrinthodont of the Upper Permian of North Russia (AMALITZKY 1921; 1924, p. 60; EFREMOV 1931, pp. 62—67; SUSHKIN 1936, pp. 62—66; BYSTROW 1938, pp. 250—256, 276).

In *Lysorophus* a keratohyal, a hypohyal, three keratobranchials,<sup>1</sup> three hypobranchials,<sup>1</sup> and parts of the fourth branchial arch and the basibranchials are found ossified, *Cocytinus* probably exhibits a keratohyal, a hypohyal, four keratobranchials, and two or three hypobranchials. In *Dvinosaurus* a keratohyal, a hypohyal, four keratobranchials, and two hypobranchials are met with.

In addition to the forms mentioned, *Trimerorhachis* is also claimed to be perennibranchiate by WILLISTON (1916, p. 297). His interpretation of a certain fragment belonging to that genus as being »an unusually large hyoid or epibranchial bone» has been questioned, but seems to be verified by new finds by CASE (1935, p. 251).

If the interpretation of the conditions in *Gerrothorax* given above is correct, the hyobranchial skeleton of this genus comprises remnants of a third and fourth ossified hypobranchial, structures not preserved in *Dvinosaurus*; in *Lysorophus* and *Cocytinus* at least the fourth hypobranchial is unknown or uncertain (*Lysorophus*). The anterior part of the hyobranchial apparatus could not be studied in *Gerrothorax*, it is true, but it was certainly present in an ossified state. *Gerrothorax* thus exhibits the most complete ossified hyobranchial apparatus known as yet in Amphibians.

The existence of such a well developed visceral skeleton in a doubtless adult individual involves that we are forced to assume gill-breathing to have

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<sup>1</sup> By SOLLAS and certain other authors the elements of *Lysorophus* and other fossil forms here termed keratobranchials and hypobranchials are referred to as epibranchials and keratobranchials respectively.

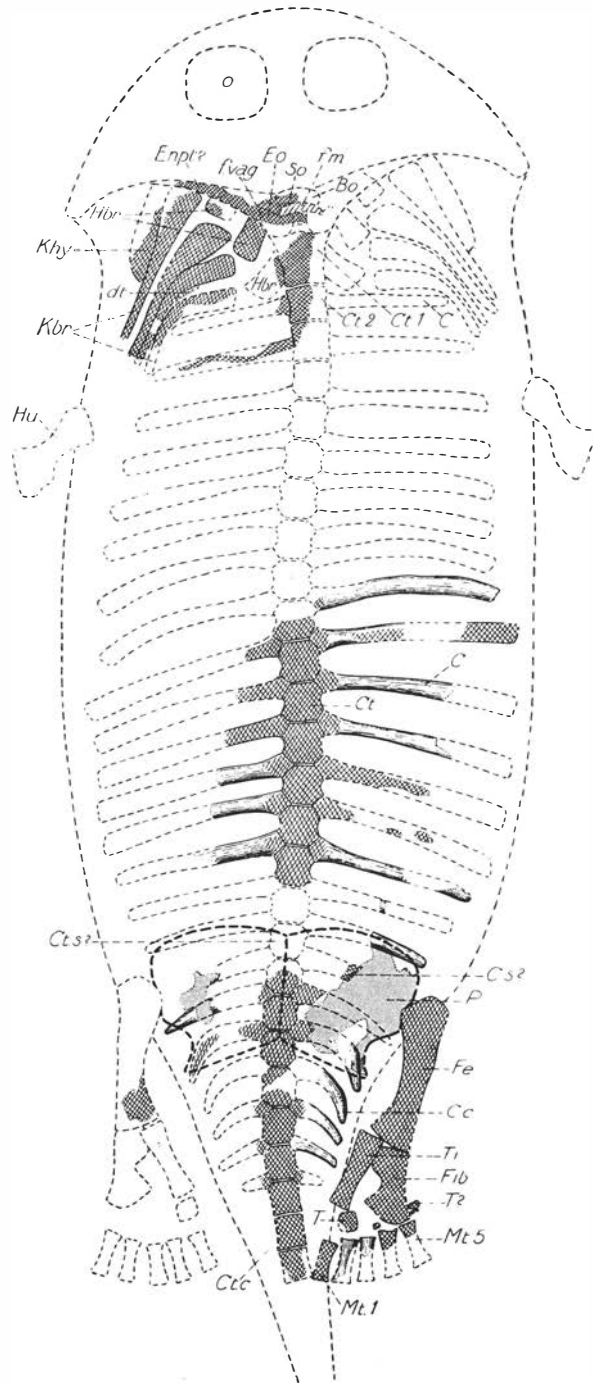


Fig. 4. *Gerrothorax rhaeticus* NILSS. Restoration of the vertebral column (neural arches omitted), ribs, pelvis, hind legs, branchial arches, and general shape of the body. Of the pelvis the ventral outlines are shown (preserved parts marked with a screen tone). Dorsal view. Mainly after spec. B.18; in agreement with the following figures, the outlines of the skull are restored after spec. B.2—4 and the German species *G. pulcherrimus*, the humerus after *Plagiosaurus depressus*.  $\times 1/4$ . Explanation of lettering pp. 41 f.

persisted also in the mature stage in *Gerrothorax*. In *Dvinosaurus* this could be proved by finds of grooves for gill arteries on the branchial arches. In *Gerrothorax* the state of preservation of the parts in question prevents a close investigation of these matters. On the postero-medial face of the keratohyal and the third keratobranchial there are possibly traces of such grooves.

### 3. Axial skeleton and ribs.

(Figs. 4, 5; pls. I—III.)

**Axial skeleton.** Spec. B. 18 exhibits remnants of the centra<sup>1</sup> of ten presacral vertebrae (*Ct*), among others the three foremost (*Ct. 1, 2*), and nine postsacral or caudal vertebrae (*Ct.c*).<sup>2</sup> A large part of the neural arches (*Neu*) are also shown. The number of presacral vertebrae may be estimated at about 17. One sacral vertebra (*Ct.s*) was probably present.

The presacral vertebrae fundamentally agree with those previously described (NILSSON 1937, pp. 16—18, 58—63). As these they consist of comparatively small and elongate centra and free and low neural arches, situated »intervertebrally» and showing almost equal articular facets for two consecutive centra. Just as the whole individual B. 18 is somewhat smaller than the holotype, the vertebrae are also a little smaller in the present material. They have the same proportions, however, as in the holotype. The length of the second presacral centrum is 19 mm; the length of the centra situated farther posteriorly in the trunk is about 20—22 mm, the breadth of their middle part about 18—19 mm.

The first presacral centrum (*Ct.1*) lies immediately behind the remains of the exoccipital. It is much longer (29 mm) and more heavily built than the other centra. Certain differences as regards its spongiosa and the shape of its lateral outlines, which seem to be a little projecting in the middle part, indicate that it is probably formed by two centra fused to each other. — The neural arches connected with the foremost centra could not be studied in detail on account of the deficiency of the material. It could be proved, however, that a free neural arch was present in a normal, »intervertebral» position between the first and second presacral centra.

The length of the caudal centra is about 18—19 mm; the foremost of those centra are 16—17 mm broad, farther posteriorly they become somewhat narrower. The neural arches connected with the caudal centra could not be studied more extensively. They occupied an »intervertebral» position, however, as is indicated at least in the foremost caudal vertebrae. Haemal arches or haemapophyses (*haem*), previously unknown in Plagiosaurids, have been observed at least on the sixth to eighth caudal centra (fig. 5; pl. II, fig. 2). These have been somewhat

<sup>1</sup> In the following the term »centrum» is used in a general significance, without considering whether the structure in question is an intercentrum (hypocentrum) or a pleurocentrum (true centrum).

<sup>2</sup> In the previously described material ten middle presacral vertebrae were preserved.

rotated in the fossil, so that the haemal arches come into view on the left side. The haemal arches are uniformly low (about 6—7 mm high), but very elongate structures, forming outgrowths from the entire length of the ventral face of the centra. The two halves of each haemal arch are fused to each other in the mid ventral line, giving rise to a closed caudal canal (*cau.c*). The ventral part of the haemal arch is truncated, forming a fairly broad, almost flat ventral face. No haemal spine is developed.

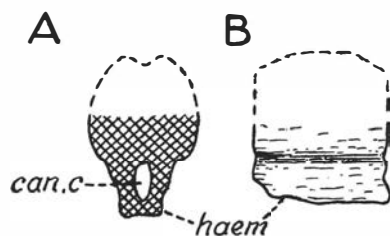


Fig. 5. *Gerrothorax rhaeticus* NILSS. Restoration of a middle caudal vertebra (about no. 7). A, in cross-section; B, in lateral view (anterior end to the left). B. 18 e. Nat. size. Explanation of lettering p. 42.

**Ribs.** In the most anterior part of the body there are remains of two ribs. They are joined to the second and third vertebrae and appear to be almost straight, just as are the ribs situated more posteriorly in the trunk. All told, fragments of 11 pairs of presacral ribs are preserved (*C*). They closely agree with those described in the holotype (NILSSON 1937, pp. 20—23). As these they have no distal, wing-like extensions, as they have in many Stegocephalians. The entire length of four ribs from the middle part of the trunk could be exactly measured (cf. fig. 4). The longest of them is about 11 cm long. The ribs become distinctly shorter more posteriorly in the trunk. The last presacral rib is thus about 7 cm. As a rule the presacral ribs have truncated distal ends, with rough terminal faces evidently covered with cartilage in life.

There is only one fragment of a rib in such a position that it may be a sacral rib (*C.s?*). It has a considerable length, however, being at least half as long as the adjoining ribs.

Behind the supposed sacral rib there are remains of at least five or six pairs of caudal ribs (*C.c*). They gradually diminish in length backwards, the fifth caudal rib being only about 3 cm long. The first and fifth are fairly straight, the other three, in particular the second and third, are strongly curved, their distal ends being directed almost straight posteriorly. The three foremost caudal ribs have rounded, tapering distal ends, the fourth and fifth are more uniformly broad with truncated and smooth distal ends. Evidently the distal ends of the caudal ribs were never covered with cartilage.

As they do in the holotype, almost all the ribs articulate »intervertebrally» with two consecutive centra. The articular facets for each of the two fore-

most presacral ribs are restricted, however, to one single centrum. This must have had an appearance greatly resembling the Plagiosaurid centrum figured by PIVETEAU (1928, pl. V, fig. 9).

#### 4. Pectoral and pelvic girdles.

**Dermal shoulder-girdle** (figs. 6, 11; pl. II, fig. 1; pl. III, fig. 2). As was stated above (pp. 4 f.), the dermal shoulder-girdle could be approximately restored. This was done by combining the parts preserved in spec. B. 18 and the holotype (cf. NILSSON 1937, pp. 23—31).<sup>1</sup>

The new facts presented by spec. B. 18 refer to the anterior parts of the interclavicle and left clavicle. The foremost part of the interclavicle (*Icl*) is a thin (about 1—2 mm thick) lamina, the dorsal and ventral faces of which are largely smooth. Its anterior end is truncated. In a restored state this anterior part must be fairly long and narrow, probably more elongate, more uniformly broad, and better set off than the same part in *Gerrothorax pulcherrimus* (v. HUENE 1922, pl. II, figs. 1, 2) and, particularly, *Plagiosaurus depressus* (NILSSON 1937, fig. 7; KUHN 1939 a, pl. 18, fig. 1). It corresponds to the so-called anterior process of the interclavicle in a great many other Stegocephalians (cf. NILSSON 1943, pp. 228—235).

The ventral face of the anterior part of the interclavicle must have been largely covered by the two clavicles (*Clav*). These must have met each other, forming a fairly long median suture. The nature of the anterior margin of the interclavicle indicates that the clavicles probably did not extend forwards in front of the anterior end of that bone. In dorsal (internal) view the two clavicles must, therefore, have been widely separated from each other anteriorly by the interclavicle.

**Pelvis** (*P*; fig. 4; pl. I). Owing to the fragile nature of the substitution bones in the fossil, only fragments of the ventral, pubo-ischiadic part of the pelvis are preserved. Its lateral outlines are partly intact. The pubo-ischiadic part of the pelvis seems to be remarkably short and broad. Owing to the material's poor state of preservation, no sutures, either median or transverse, could be discerned. Therefore, it must remain undecided whether the pubis and ischium were separate elements or fused to each other. In any case it should be noticed that the pubis was an ossified element.

#### 5. Free extremities.

**Fore leg.** Of this the present specimen exhibits no parts. The humerus (*Hu*) may be supposed, however, to be a comparatively weak bone, agreeing with that in *Plagiosaurus depressus* (NILSSON 1939, pp. 12—15). As regards the function of the fore legs cf. below (p. 19).

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<sup>1</sup> As regards the orientation of the different elements of the dermal shoulder-girdle cf. also NILSSON (1939, p. 5).

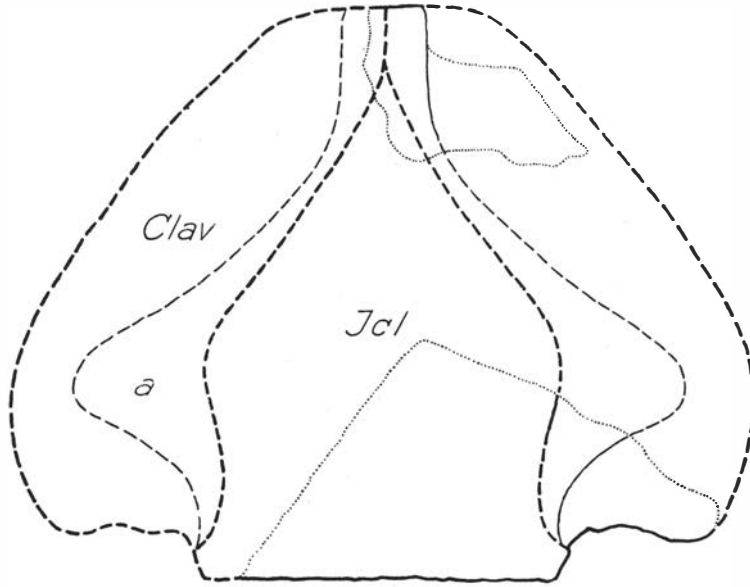


Fig. 6. *Gerrothorax rhaeticus* NILSS. Restoration of the dermal shoulder-girdle. Ventral view. The fine, partly broken line indicates the internal (dorsal) boundary between clavicles and interclavicle. The extension of the actually known parts marked with dotted lines. The anterior part restored after spec. B. 18 b, the posterior part after the holotype.  $\times \frac{2}{5}$  (B. 18). Explanation of lettering pp. 41 f.

**Hind leg** (figs. 4, 7, 11; pl. I; pl. II, fig. 2). Several elements of the right hind leg are preserved in juxtaposition with each other and with the pelvis; in addition there are also one or two small fragments of the left hind leg (*Fe*, ?X) in a position exactly corresponding to that of the right one. Thus we may be justified in assuming the natural position of the hind legs to be shown in the fossil.

In its entirety the hind leg is approximately straight and directed backwards almost horizontally along the tail. Its longest part is the femur, which is nearly double the length of the crural bones. The breadth of the hind leg increases considerably and uniformly in a distal direction. The hind leg is turned so as to show the extensor face mainly in a ventral position, the preaxial (tibial) side facing medially and the postaxial (fibular) side laterally.

The femur (*Fe*) is a moderately long and slender bone. Its extensor face, which is generally referred to as the dorsal (or superior) face, by certain authors (CASE, GREGORY, SUSHKIN, etc.), however, as the anterior face, is directed ventro-laterally in the present fossil. This condition is evidently connected with the posterior direction of the bone. During the locomotion of a lower Tetrapod the femur is normally rotated to a certain extent. According to ROMER (1922, p. 581) the main movement of the femur »is one down and back from an anterior and dorsal position, coupled with rotation (clockwise as seen in the right leg from the side view)«. In the present fossil a rotation of somewhat more than  $90^\circ$  must be inferred.

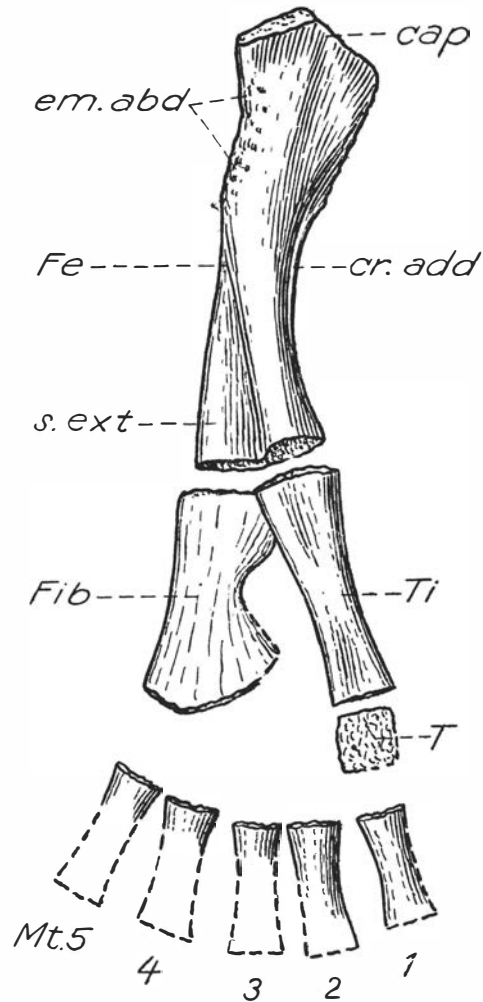


Fig. 7. *Gerrothorax rhaeticus* NILSS. Restoration of the extensor aspect of the right hind leg. Partly based on information gained by a negative-preparation of the parts shown in pl. II, fig. 2. B.18.  $\times \frac{3}{4}$ . Explanation of lettering pp. 41 f.

The whole extensor face of the femur is known in detail, most of the flexor face is not accessible, however, for a close investigation. Both ends of the femur (and the other bones of the hind leg) have rough faces and must have been covered by cartilage. The caput femoris (*cap*) is strongly developed and rounded; its articular face seems to have extended fairly far down the bone on the tibial side, *i. e.* on the medial face of the bone in its actual position in the fossil. As usual in lower Tetrapods there is no collum. The shaft of the bone is fairly elongate and curved in a characteristic way; in consequence the tibial side is markedly concave. On the distal extremity of the bone the tibial and fibular condylar faces are indistinctly



separated from each other. From about the middle of the extensor face a deep and straight extensor groove (sulcus extensorius, *s.ext*; = bicipital fossa, anterior intercondyloid fossa, and fossa tendinalis of authors) runs obliquely across that face to the distal extremity between the fibular and tibial condyles. The groove in question appears to be considerably more elongate than in other Stegocephalians (ROMER 1922, pl. 46, *Eryops*; STEEN 1934, fig. 19, *Calligenethlon*; BYSTROW & EFREMOV 1940, fig. 54, *Benthosuchus*; WATSON 1919, fig. 8, *Lydekkerina*; CASE 1935, fig. 27, *Trimororhachis*; WILLISTON 1910, pl. 13, fig. 2, *Cacops*; CASE 1931, fig. 9; 1932, fig. 36, *Buettneria*; SUSHKIN 1936, fig. 18; BYSTROW 1938, fig. 28, *Dvinosaurus*). On the fibular side of the groove the distal extremity of the femur seems to be fairly thin, on the tibial side, on the other hand, it is thick and rounded in section. The fibular side of the extensor face proximally exhibits two rugosities. These must have served for the insertion of m. pubo-ischio-femoralis internus, one of the most prominent of the abductor muscles of the femur (cf. ROMER 1922, pp. 565 f., pl. 46). The rugosities will be referred to as the eminentiae abductorii (*em.abd*). Similar structures are found at least in *Eryops* among other Stegocephalians and in certain reptiles (*l. c.*).

A fairly low, but distinct adductor ridge, crista adductoria (*cr.add*; crista aspera femoris BYSTROW) is present on the flexor face of the femur. It takes its origin somewhat above the middle of the bone; thence it runs downwards, fading out on the tibial side of the distal extremity. The adductor ridge is very much lower than the corresponding structure in the majority of Stegocephalians (CASE 1911, figs. 32, 33, *Eryops*; WILLISTON 1909, fig. 5; OLSON 1941, fig. 12, *Trematops*, *Acheloma*; BYSTROW & EFREMOV 1940, figs. 54, 83, *Benthosuchus*; WILLISTON 1910, pl. 13, figs. 3—5, *Cacops*).<sup>1</sup> Proximally to the origin of the ridge there is indicated the presence of a large, only slightly raised and rough area, once covered with cartilage.

The tibia (*Ti*) is a straight bone with the proximal extremity somewhat more expanded than the distal one. The extensor and flexor faces of the shaft are fairly broad; in axial view the shaft seems to be thin, particularly as compared with the proximal end of the bone. On the extensor face of the proximal extremity there are indicated a shallow depression and a low, rounded »cnemial ridge», situated on the preaxial side of the depression. On the flexor face of the same extremity is a fairly strong groove. This begins abruptly some distance below the upper end of the bone, continuing to and fading out towards its lower end.

The fibula (*Fib*) is a flat bone with very broad extremities. Its postaxial boundary is slightly concave, the preaxial one is strongly concave.

For the most part the tarsals (*T*) seem to have been cartilaginous. One element was largely ossified, however, another had a diminutive osseous core. They have probably been displaced somewhat during the fossilization. Outside the lower end of the fibula there are remains of two bones (*T* ?), one proximal, which certainly is a displaced tarsal, and one distal, which has the appearance of being the most

<sup>1</sup> In *Dvinosaurus* the adductor crista is low (BYSTROW 1938, fig. 28).

proximal end of a (6th!) metatarsal (or a phalanx); it may perhaps be most naturally interpreted as part of another tarsal bone.

The proximal ends of five undoubted metatarsals (*Mt. 1--5*) are present. They have all approximately the same breadth. No phalanges are preserved. Judging from the metatarsals, the pes must have been markedly broad.

The hind leg of the Plagiosaurians was previously almost unknown. Apart from the problematic structure assumed by PIVETEAU (1928, p. 7; pl. V, fig. 32) to be the proximal extremity of a femur of *Plagiosaurus sp.*, a number of isolated bones, supposed to represent a tibia, metatarsals, and phalanges, etc., are recorded by KUHN (1939 a, pp. 274 f.; pl. 20, figs. 7, 8; pl. 21, fig. 5; pl. 23, fig. 1) from Halberstadt. They are referred to *Gerrothorax pulcherrimus* (FRAAS) by that author, but they much more probably belong to *Plagiosaurus depressus* JAEKEL. According to KUHN the said remains indicate a remarkably slender structure of the Plagiosaurid legs.

The knowledge of the Plagiosaurid hind leg gained by the study of the present material is much more complete.

Viewed in its entirety, the hind leg of *Gerrothorax* is a unique structure among Stegocephalians. The characteristically curved, fairly elongate femur, with its low adductor ridge, very long extensor groove, well developed eminentiae abductoriae, and probably preaxially directed proximal articular face, is well distinguished from the femora of all other Stegocephalians so far known. Further, the posterior direction of the whole hind leg and the uniform and unusually strong widening of its distal parts are unparalleled among Stegocephalians.

Evidently the particular structure of the hind legs must primarily be seen in relation to the function. Their posterior direction was probably a permanent character. This condition and the strong, fin-like, distal widening of the hind legs give them a striking resemblance to those of recent seals (*Phocidae*). In these the two posterior extremities together form a sort of a complex »caudal fin», the tail being reduced. Evidently the hind legs in *Gerrothorax* had a similar function. The tail of this form was still fairly strong, however, though probably fairly short and not flattened from the sides (cf. below p. 26). We must infer that the principal locomotory organ of this animal was composed of the two hind legs and the tail, together functioning as a »caudal fin». There are also other fundamental differences between the hind legs of *Gerrothorax* and those of a recent seal. In the latter the femur is short and stands out from the body, the crural bones being very elongate and lying parallel to the body, while in *Gerrothorax* the femur is a long bone and the whole leg directed backwards. Further, in a recent seal the first and fifth toes are especially strong and elongate, while in *Gerrothorax* those toes were certainly not particularly strengthened.

According to KUHN (1939 a, p. 275) the slenderness of the Plagiosaurid legs is one of a series of features which make him inclined to assume a particularly close relationship between the Plagiosaurids and the Anurans. As is now clear, the similarity mentioned is not very profound. The slenderness of the legs is due to

entirely different causes in the two groups. In frogs the hind legs are used for swimming in a duck-like way and for jumping, in the Plagiosaurids for swimming, the hind legs functioning as part of a »caudal fin».

The fore legs of the Plagiosaurids are largely unknown. Apart from a radius, only the humerus is described (in *Plagiosaurus depressus*). It is fairly small and distinguished from all other Stegocephalian humeri by several characters. At the time of its description the differences were very difficult to explain (NILSSON 1939, pp. 30—32). As a result of an analysis of its muscle insertions, I concluded in the cited work that the body of the animal could not very well have been pulled forwards by the action of the fore legs. I tried to reconcile the difficulties by suggesting the possibility that the animal shoved itself forwards with stretched fore legs. The result gained above that the Plagiosaurids swam with the aid of the hind legs throws new light on the structure of the fore legs. They probably had a function to some extent resembling that of the paired fins of fishes and fore legs of seals.

## 6. Dermal scale-armour.

(Figs. 8—13; pls. I—III.)

In 1922 v. HUENE for the first time described a well developed dermal scale-armour in a Plagiosaurid, *Gerrothorax* (»*Plagiosaurus*») *pulcherrimus* (v. HUENE 1922, p. 438, pl. I). Already JAEKEL (1913, p. 208), however, inferred that such an armour existed in *Plagiosaurus depressus*. In the holotype of *Gerrothorax rhaeticus* the structure particularly of the ventral part of the Plagiosaurid dermal armour could be more closely studied (NILSSON 1934; 1937, pp. 32—41; pls. I, II; pl. III, fig. 4). That revealed the presence of a complex, well delimited gastral skeleton, comprising also so-called abdominal ribs. Abdominal ribs similar to those found in reptiles were previously not known with certainty to have existed in an Amphibian (cf. however v. HUENE 1922, pp. 437 f.). The specimen now described aptly completes the earlier results, thus contributing to a better knowledge of the remarkable dermal scale-armour of the Plagiosaurids. A synoptical account of the dermal armour of the present species is given below.

**Gastral skeleton** (figs. 8—11; pl. I; pl. II, fig. 2; pl. III, fig. 1). Through the find of spec. B. 18 the size and posterior extension of the gastral skeleton could be established. It occupies almost the whole breadth of the ventral face of the trunk between the dermal shoulder-girdle and the hind legs. Its lateral boundaries are very well defined; anteriorly the lateral margin is slightly concave, posteriorly it is convex. As a whole the gastral skeleton distinctly broadens backwards. It is mainly composed of two elements:

1) a pavement of dermal scales, closed on its ventral side; these scales will be called gastral scales (*G.sc*); they have a tubercular ornament on their superficial (ventral) face and narrow overlapping areas arranged in an irregular way;

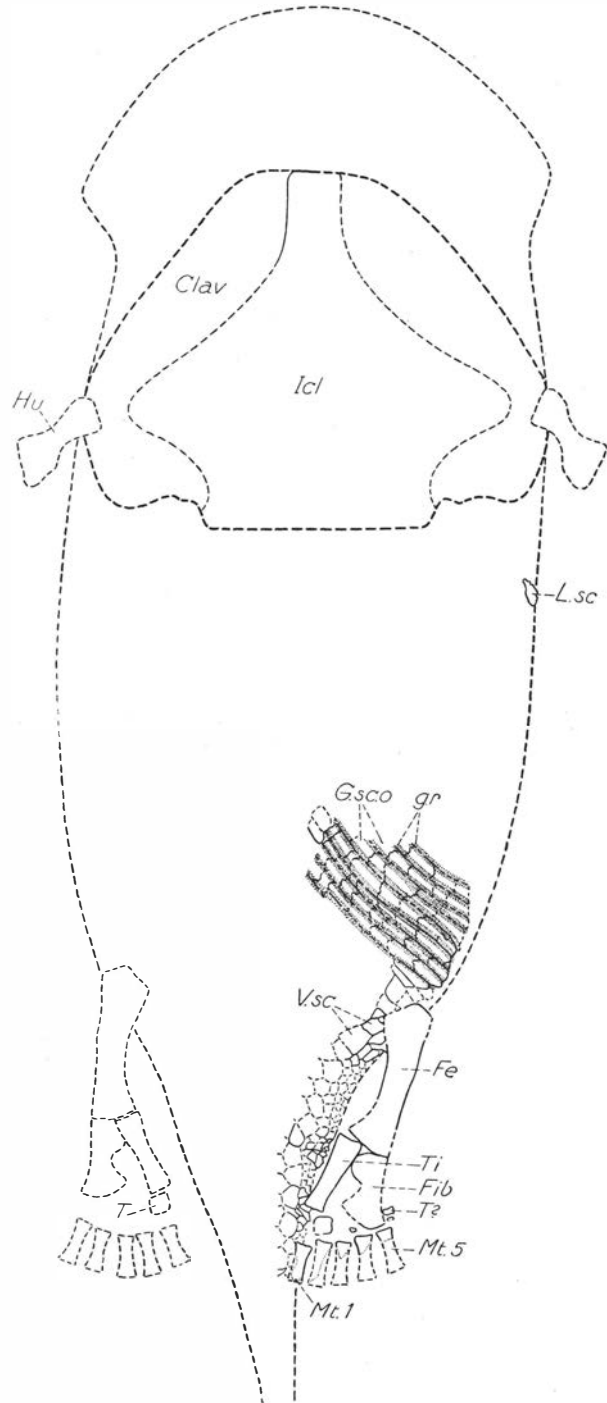


Fig. 8. *Gerrothorax rhaeticus* NILSS. Restoration of the parts of the ventral scale-armour shown in spec. B. 18. Dorsal view. Dotted areas in the gastral skeleton denote grooves for the gastral ribs.  $\times 1/4$ . Explanation of lettering pp. 41 f.

2) so-called abdominal ribs, lying in dorsal grooves formed by the gastral scales; in the following these ribs are referred to as gastral ribs (*Gr*).

Immediately behind the interclavicle there are one or two transverse rows of gastral scales (*G.sc.tr*), but no gastral ribs. The dorsal face of the foremost row is covered by the posterior margin of the interclavicle. This anterior part of the gastral skeleton certainly corresponds to the part of the ventral scale-armour described in a number of Palaeozoic Stegocephalians and referred to by German authors as the »Brustflur» (CREDNER 1886, pp. 628 f.; etc.). This is composed of a varying number of scale-rows, running on either side obliquely antero-laterally and forming angles, directed backwards, in the mid ventral line (*Branchiosaurus*,

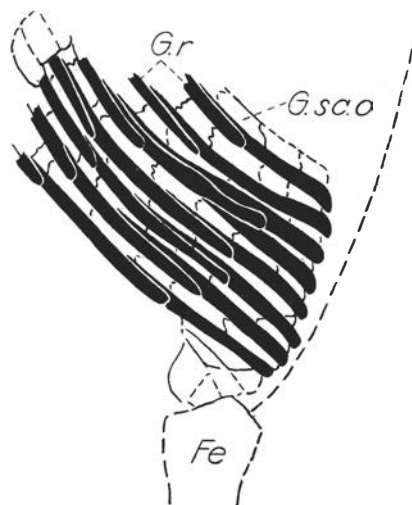


Fig. 9. *Gerrothorax rhaeticus* NILSS. Restoration of the right posterior part of the gastral skeleton of spec. B.18, showing gastral ribs (in black) and oblique rows of gastral scales. Dorsal view.  $\times \frac{1}{2}$ . Explanation of lettering pp. 41 f.

CREDNER 1886; *Cricotus*, CASE 1911, p. 147, pl. 25, fig. 2; *Diplovertebron*, WATSON 1926, p. 241; *Archegosaurus*, v. MEYER 1857, pp. 121 ff.; pl. 17, fig. 1; pl. 18, figs. 1, 2; *Sclerocephalus*, v. AMMON 1889, p. 73, pl. III, fig. 1; BROILI 1926, pp. 215 f., pl. I; *Chelydosaurus*, FRITSCH 1885—89, p. 211, fig. 129; pl. 56, fig. 2; cf. *Actinodon*, BROILI 1927, p. 377).

An antero-lateral area, situated between the main part of the gastral skeleton and the clavicle, is occupied by fairly large, irregularly disposed scales (*G.sc.al*) intimately connected with the gastral skeleton and well delimited in a lateral direction. This area may be considered to constitute an antero-lateral part of the gastral skeleton.

The posterior (main) part of the gastral skeleton, corresponding to the »Bauchflur» of German authors, is composed of about 26 oblique rows of elongate gastral scales (*G.sc.o*) and a corresponding number of gastral ribs on either

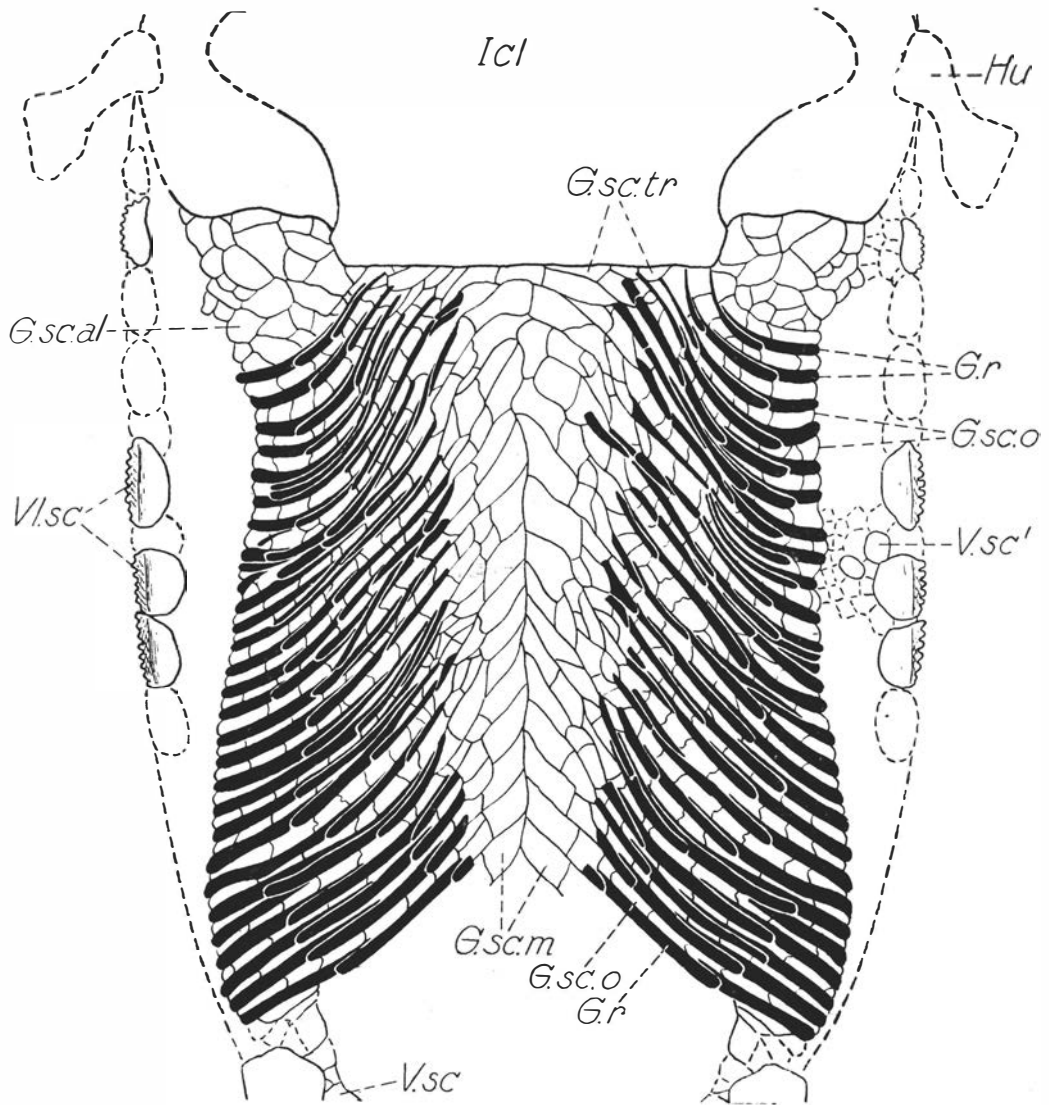


Fig. 10. *Gerrothorax rhaeticus* NILSS. Restoration of the entire gastral skeleton in dorsal (inner) view. Gastral ribs filled black. After spec. B. 18 and the holotype.  $\times 0.42$  (B. 18). Explanation of lettering pp. 41 f. (Cf. fig. 11.)

side. The said rows have an antero-medial direction. The gastral ribs are situated in dorsal grooves formed and delimited by them. The oblique rows mentioned (as well as the gastral ribs) do not reach the mid-ventral line. The rows of the two sides are separated by a number of larger scales (*G.sc.m*), forming two median rows, one on either side of the mid-ventral line. About 16 pairs of such scales seem to be present. Each scale is somewhat elongate; with the corresponding scale on the opposite side it forms an angle with the apex directed forwards.

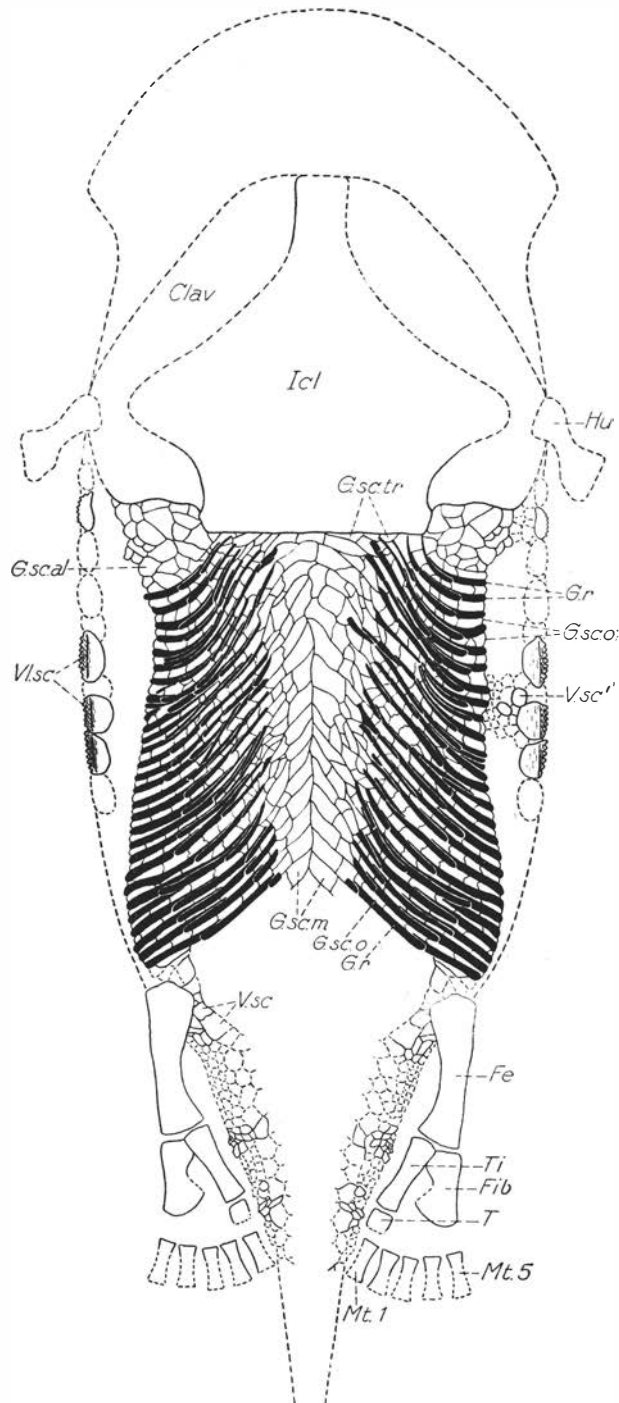


Fig. 11. *Gerrothorax rhaeticus* NILSS. Restoration of the ventral armour (dermal shoulder-girdle, gastral skeleton, etc.) and the general shape of the animal. Dorsal (inner) view. After spec. B. 18 and the holotype.  $\times 1/4$  (B. 18). Explanation of lettering pp. 41 f.

The number of gastral ribs (*G.r*) was about 26 on either side. Each rib is formed of an imbricate bundle of (up to at least 8) very elongate, narrow rods with tapering proximal ends and broader, usually rounded distal ends. These rods have smooth faces against each other and against the adjoining gastral scales. As has previously been elucidated (NILSSON 1937, pp. 37—41), the gastral ribs may be derived from the oblique rows of dermal scales (*G.sc*). Alternating oblique rows are assumed to have been somewhat removed from the surface of the cutis and transformed into rib-like structures. As is also asserted in the cited work, the gastral ribs of the Plagiosaurids and the corresponding, probably homogenetic structures in reptiles must have developed independently of each other.

**Remaining part of the dermal scale-armour** (figs. 8—13; pls. I—III). Apart from the gastral skeleton the dermal scale-armour comprises solely common scales. Their arrangement is not completely known. The individual scales have a very varying size and as a rule an irregularly polygonal shape. Their superficial face is ornamented with tubercles. They are further provided with narrow overlapping areas, arranged in an irregular way.

As a whole the ventral part of the dermal armour has a highly varying structure. Apart from the gastral skeleton described above at least three areas, differing from each other as regards the size and shape of the scales, may be distinguished on either side.

1) A longitudinal row of large ventro-lateral scales or plates (*Vl.sc*) is situated just at the ventro-lateral margin of the trunk. The individual scales are composed of two parts, a broad, horizontal part and a lateral, vertical part, at almost right angles to each other.

2) Between these scales and the gastral skeleton there was evidently a covering of small, or very small, scales (*V.sc'*), forming a highly flexible transition zone between the more rigid parts mentioned.

3) At least laterally the ventral part of the tail was provided with a covering of fairly large scales (*V.sc*), abruptly passing over into a ventro-lateral zone of small, or very small, scales (*Vl.sc'*).

The dorsal part of the dermal armour of the trunk and tail (fig. 12) evidently formed a continuous covering of middle-sized polygonal scales (*D.sc*), arranged in an irregular way and connected with the ventral part of the armour by a covering of lateral scales (*L.sc*). Behind the skull there was probably a zone of smaller dorsal scales. In the holotype particularly large median dorsal plates were observed just above the neural spines, overlapping each other to an unusually large extent (an anterior plate as a rule overlapping the succeeding one). These facts remind of the conditions in the Palaeozoic rhachitinous family *Dissorophidae*. As is well known, the genera of this family, *Dissorophus*, *Cacops*, and *Aspidosaurus*, are characterized by a dorsal median, paired or unpaired row of thick dermal bony plates fixed to the upper ends of the neural spines (cf. CASE 1911). — Immediately antero-laterally to the dermal shoulder-girdle there are remains of two



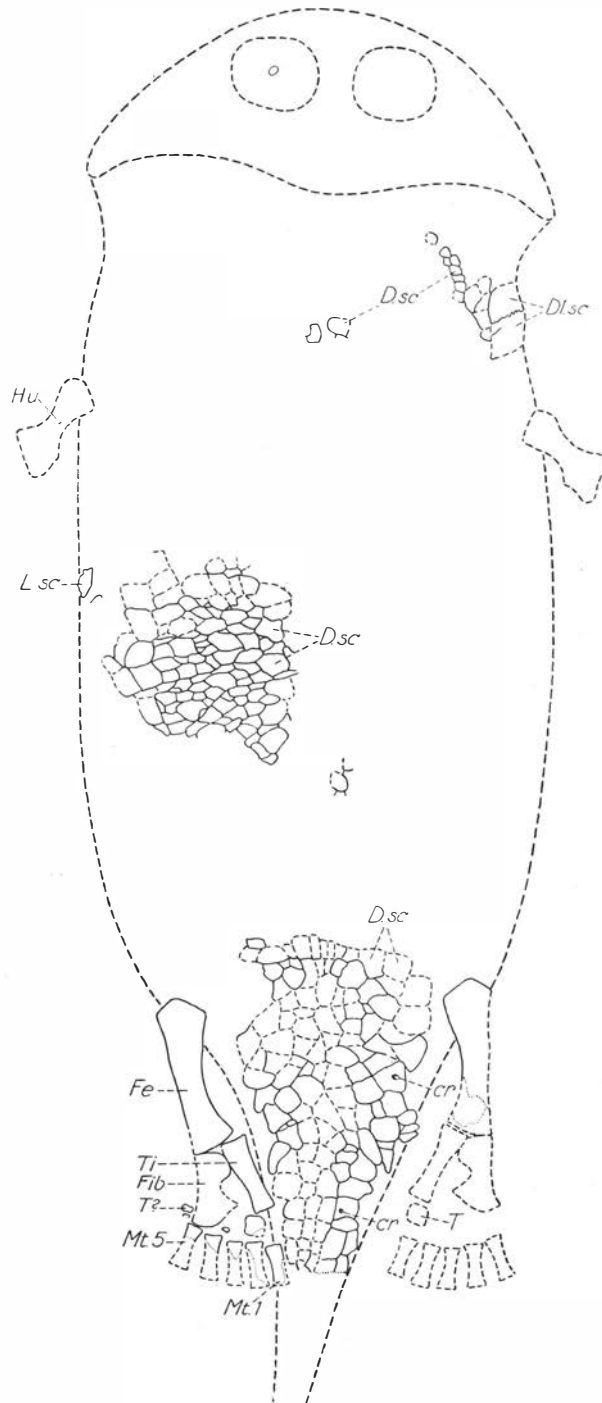


Fig. 12. *Gerrothorax rhaeticus* NILSS. The parts of the dorsal scale-armour shown in spec. B. 18. Ventral view.  $\times 1/4$ . Explanation of lettering pp. 41 f.

fairly large dorso-lateral scales or plates (*Dl.sc*) firmly joined to each other by suture. They were certainly made up of horizontal and lateral parts at about right angles to each other. They show a well marked dorso-lateral edge and were probably situated just in front of the cleithrum.

The arrangement of the scales in the preserved part of the tail shows that it was not flattened from the sides. The dorsal as well as the ventral scales form undisturbed coverings also above and beneath the caudal vertebrae. Thus, no dorsal or ventral caudal fins were developed.

On the deep face of certain lateral scales on the dorsal side of the tail in spec. B. 18 there are observed crater-shaped pits (*cr*), leading into canals probably perforating the scales. They are similar to those found on some lateral dorsal scales of the holotype (NILSSON 1937, pl. II, *k*) and may be supposed to have served either for nerves to lateral line organs or for efferent ducts of poison (venom) glands (cf. ECKER, WIEDERSHEIM & GAUPP 1904, pp. 554 f., 601—605; HERTER 1941, figs. 97, 98, 194).

A continuous dermal armour comparable to that found in the Plagiosaurids is not a unique phenomenon among Stegocephalians. In cf. *Rhinesuchus* (*Myriodon* s. *Uranocentrodon*) *senekalensis* VAN HOEPEN (1915, p. 145) mentions the presence of an evidently continuous dermal armour also on the sides and back of the animal. Similar conditions are found in *Trimerorhachis* (WILLISTON 1916, p. 293; cf. also CASE 1935, p. 269) and cf. *Actinodon* (BROILI 1927, p. 379). In all these cases at least the dorsal and lateral parts of the scale-armour are stated to be feeble, very much feebler than they are in the Plagiosaurids; it is also uncertain whether the scales in question are osseous or merely calcified structures. *Archegosaurus* is also said to have lateral and dorsal scales on the trunk, but according to BROILI (1927) they do not form continuous coverings.

As was mentioned above, there is a very well delimited boundary between the gastral skeleton and the remaining part of the dermal scale-armour in *Gerrothorax*. Probably similar conditions existed also in other Stegocephalians provided with a ventral armour of gastral scales, but owing to bad preservation the boundaries are generally not so distinctly shown as they are in *Gerrothorax*. It is interesting to find that also certain primitive fossil fishes have a flattened ventral area covered with oblique rows of scales directed antero-medially (WESTOLL 1944, figs. 1, 13, 23, 28, *Haplolepididae*; JARVIK 1947, *Osteolepididae*). This ventral scale-covering is laterally well delimited from the scales of the flanks and back by a change in direction of the scale-rows and evidently corresponds to the gastral skeleton of Stegocephalians.<sup>1</sup> The break in the squamation just mentioned extends between the bases of the pectoral and pelvic fins and is supposed by JARVIK (1947; cf. WESTOLL 1944, p. 62) to mark the position of the primitive, paired fin-fold. If this correct, a remainder of the said ancient structure still persists in the Stegocephalians, extending between the fore and hind legs of either side in the lateral boundaries of the gastral skeleton.

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<sup>1</sup> The fishes referred to have nothing equivalent to the anterior part of the gastral skeleton of Stegocephalians, however.

### 7. General remarks.

**Size.** Fig. 13 is an attempt at a restoration of *Gerrothorax rhaeticus*, as it may have appeared in life. Restored in that way, the holotype attained a length of about 97 cm and a maximum breadth of about 31 cm. The corresponding figures for spec. B. 18 will be about 78 and 25 cm. The third specimen, B. 2—4, represents an animal of about the same size as B. 18. Thus the largest individuals of the species probably attained a length of about 1 m.

**Habit.** As was demonstrated above (p. 18), the animal must have swum with the aid of the straight, distally widened hind legs, which were directed backwards, forming a sort of a horizontal »caudal fin» together with the tail (cf. recent seals). The fairly feeble fore legs probably had a function to a certain extent reminding of that of the paired fins of fishes and fore legs of seals.

In its general shape the animal has several features in common with the so-called depressiform adaptation type of ABEL (1912, p. 431). Thus the body was fairly short and broad, with a very short and broad skull. The whole body was well armoured and remarkably depressed in a dorso-ventral direction, which is demonstrated by the shape of the occiput, the very low neural spines, and the low claviculo-cleithral complex (NILSSON 1937; 1939, fig. 1, p. 9). Further the eyes are situated medially on the dorsal side of the skull. All these features make it highly probable that the animal lived benthonic in not too shallow waters. Also the large size of the eyes and the absence of otic notches (cf. below p. 32) may possibly most easily be explained by the same assumption. Presumably the animal as a rule rested motionless on the bottom lurking for prey, the broad gape serving as a trap, and swam only when changing hunting grounds.

The find of well developed branchial arches shows that *Gerrothorax* most probably had functional gills throughout its life (pp. 10—12). Consequently the animal did not need to rise to the water surface for breathing.

As was stated above (p. 5), the find horizon of the fossil remains was referred to by NATHORST (1878, p. 8; cf. 1910, fig. 2, pp. 11 f.) as »the plant-bearing bed 3», a horizon situated immediately above the Lower Coal Measure at Bjuv. At the time of the formation of the coal measure the surroundings were presumably occupied by extensive swamp forests. The nature of the fossil plants in the above-mentioned plant-bearing layer makes it appear probable, according to NATHORST, that they were deposited at the mouth of a river fairly far away from the shore. In view of the state of preservation the Stegocephalian remains cannot have been transported very far after death. On the contrary, they were very probably embedded about at the place of death. Consequently we must imagine *Gerrothorax* to have lived in open water on the bottom of a moderately deep lagoon some distance from the shore. The water in this lagoon was presumably brackish. Salt water at least occasionally flowed in from the sea, judging from sparse finds of marine molluscs in the strata (cf. TROEDSSON 1943, p. 276).

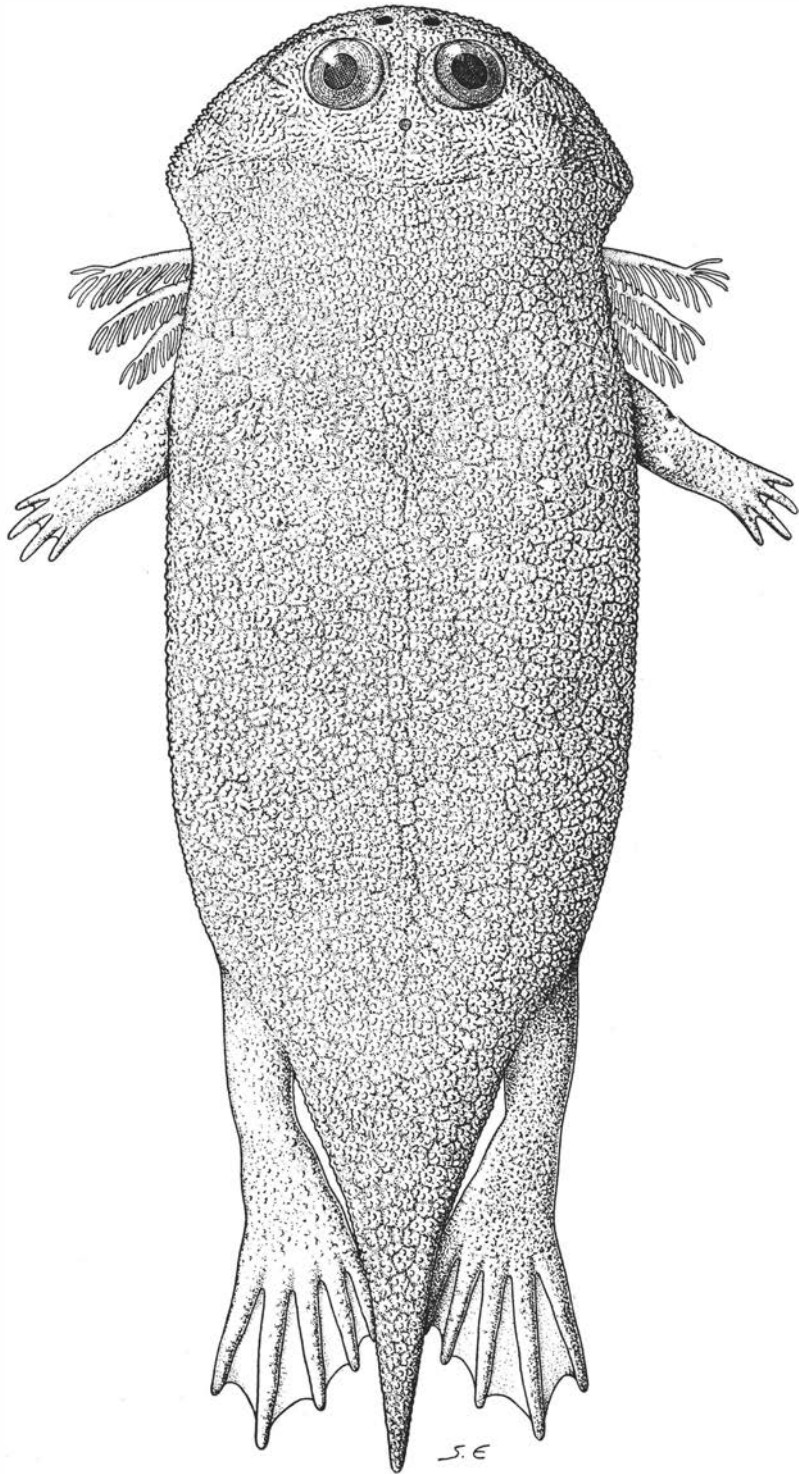


Fig. 13. *Gerrothorax rhaeticus* NILSS. Attempted restoration of the living animal in dorsal view. It should be observed that the number of fingers in the manus, the exact shape of the pes and the fore leg, the length of the tail, and the presence of external gills are merely hypothetical. About  $\frac{1}{3}$  of the natural size of the holotype and  $\frac{1}{4}$  of that of spec. B.18.

## Systematical Position and Affinities of the Plagiosaurids.

**Historical review.** The first scanty finds of Plagiosaurids were referred to by PLIENINGER (1844, p. 67; pl. IX, fig. 8) and v. MEYER (1847—55, p. 92; pl. 63, figs. 1—4) as fragments of Labyrinthodonts (? *Mastodonsaurus*, PLIENINGER). Similar remains were later described by FRAAS (1889) under the name of *Mastodonsaurus granulatus*. More complete material allowed the same author (FRAAS 1896) to erect a new genus, *Plagiosternum*, for the species mentioned. Cranial remains of the form in question were described in detail by FRAAS (1913). Three other genera, *Plagiosaurus*, *Plagiosuchus*, and *Gerrothorax*, closely related to *Plagiosternum* and partly founded on material previously referred to this genus, were erected by JAEKEL (1913), v. HUENE (1922), and NILSSON (1934, 1937).

The most important finds of Brachyopids (*s.s.*), forms generally regarded as allied to the Plagiosaurids (*s.s.*), were described by OWEN (1854, 1855, *Brachyops*) and HUXLEY (1859, *Bothriceps*), further by BROOM (1903) and WATSON (1919; *Batrachosuchus*).

As regards their systematical position, the first finds of Plagiosaurids and Brachyopids were simply called Labyrinthodonts by their authors. ZITTEL (1887—90, p. 397) grouped the genera *Brachyops* and *Bothriceps* within the *Temnospondyli*, a systematical unit including the rhachitomous and part of the embolomerous Stegocephalians. LYDEKKER (1890, pp. 170 ff.) referred them with hesitation to his family *Dendrerpetidae*, together with *Dendrerpeton* and *Micropholis*, and thus to the suborder *Labyrinthodontia vera*, a group comprising the embolomerous, rhachitomous, and stereospondylous Stegocephalians of authors.

For the genus *Plagiosternum* (including material later referred to *Gerrothorax*) JAEKEL (1911, pp. 109 f.) erected a special systematical unit, the »Nebenordnung» *Plagiosterni*, which he referred to his »Nebenklasse» *Hemispondyla* (otherwise comprising the phyllospondylous, rhachitomous, and stereospondylous Stegocephalians). Two years later the same author classified the genus *Plagiosaurus* (including material later referred to *Plagiosuchus* and *Gerrothorax*, but apparently not *Plagiosternum s.s.*) as the family *Plagiosauridae* in an order of its own, *Plagiosauri* (JAEKEL 1913, p. 209). On account of the »holospondylous» nature of its vertebrae this order was grouped together with the lepospondylous and adelo-spondylous Stegocephalians in the subclass *Microsauria* (class *Miosauria*).

BROOM (1915, pp. 365 f.) erected the family *Brachyopidae* for the genera *Brachyops*, *Bothriceps*, and *Batrachosuchus*. The same forms were grouped among the rhachitomous *Temnospondyli* by BROILI, while the same author placed *Plagiosternum* within the *Stereospondyli* (in ZITTEL 1911, 1918) and *Plagiosaurus*, quoting JAEKEL, in the family *Microsauridae* (subclass *Lepospondyli*; in ZITTEL 1918). — ABEL (1919, pp. 288 ff.) united *Plagiosternum* and *Plagiosaurus* in the family *Plagiosauridae*, which he placed in his order *Rhachitomi*. To this he also referred the mainly »stereospondylous» family *Labyrinthodontidae*.

WATSON (1919, pp. 47 f., 68) was the first to point out the probable affinity between the Brachyopids of BROOM and the forms contemporaneously classified as Plagiosaurids by ABEL. The two groups were regarded by WATSON to belong to one and the same family, *Brachyopidae*, within the »grade» *Stereospondyli*. The Brachyopids are assumed by the same author to have descended from the rhachitinous family *Dvinosauridae*. WATSON'S view was accepted as to matter by v. HUENE (1922, pp. 442 ff.), but as family name he used *Plagiosauridae* instead of *Brachyopidae*, the former name being older than the latter. In the following years the classification of WATSON (partly in the form given it by v. HUENE) became generally used, *i. a.* by BROILI (in ZITTEL 1923, pp. 196 f.), HAUGHTON (1925, pp. 256 f.), PIVETEAU (1928, pp. 7 f.), WOODWARD (in ZITTEL 1932, pp. 217 f.), KUHN (1933, pp. 101 ff.), and ROMER (1933, p. 346; 1945, pp. 590 f.).

SÄVE-SÖDERBERGH (1935, pp. 88, 200) gave another systematic form to the ideas brought forth by WATSON. He grouped the Brachyopids *sensu* WATSON (superfamily *Brachyopoideae*) and Dvinosaurids (*Dvinosauroidae*) together in a suborder *Brachyopoidei* within the order *Labyrinthodontia*. As regards the larger systematical groups he was followed by the present author in 1937 (NILSSON 1937, pp. 54—58); in that work reasons were advanced, however, for dividing the family *Brachyopidae* of WATSON into two separate families, the *Brachyopidae* in the original sense of BROOM, comprising the genera *Brachyops*, *Bothriceps*, and *Batrachosuchus*, and the *Plagiosauridae* (*s. s.*), comprising the genera *Plagiosaurus*, *Gerrothorax*, *Plagiosuchus*, and *Plagiosternum*. KUHN (1939 b, pp. 59—62), instead, widened the family *Plagiosauridae* to comprise also the Dvinosaurids, in addition to the Brachyopids and Plagiosaurids (*s. s.*). These three groups were regarded as subfamilies by KUHN. The family *Plagiosauridae* *sensu* KUHN was referred by him to the suborder *Stereospondyli*, somewhat improperly, however, as it is known that *Dvinosaurus* has vertebrae of the rhachitinous type.

In the same year the present author described in detail the cleithrum of a Plagiosaurid (*Plagiosaurus depressus*; NILSSON 1939, pp. 22—24). It was found to be a singular, very specialized bone, showing certain primitive characters (well developed ornament) not found in Labyrinthodonts combined with the presence of a claviculo-cleithral joint which is specialized more in the direction of the Lepospondyls than in the direction of the Labyrinthodonts.<sup>1</sup> These conditions, added to the unique type of the vertebrae and certain other features, led to the erection of a separate order, *Plagiosauria*, comprising the two families *Plagiosauridae* and *Brachyopidae*. It was systematically placed between the orders *Labyrinthodontia* and *Lepospondyli*, as probably having common roots with them. In the denomination of the new order the old name *Plagiosauri* of JAEKEL (1913) was used, emended as regards form and comprehension. The close relationships between Plagiosaurians and *Dvinosaurus* were also questioned, the detailed structure of this animal having become well known through fresh works by SUSHKIN (1936) and BYSTROW (1938).

<sup>1</sup> As regards the cleithrum of Plagiosaurids cf. also NILSSON (1945).

**Discussion.** In the work just mentioned BYSTROW (1938, pp. 271—286) laid great emphasis upon the neotenic nature of *Dvinosaurus*. Owing to a suppression of metamorphosis, the persistent gill-breathing in the mature age ought to have caused the maintenance of a number of larval characters. As is shown in recent Urodeles, such conditions frequently make the settling of the affinities and systematic position of neotenic forms hazardous. BYSTROW does not deny the relationships between *Dvinosaurus* and the Brachyopids but points out the difficulties caused by the neoteny in the former.

In the present work it is shown that gill-breathing very probably existed also in an adult individual of a Plagiosaurid. This makes it necessary to renew the discussion of the affinities of the Plagiosaurians.

The first question to be elucidated is the extent to which neoteny may have left its marks on such a form as *Gerrothorax*. In the cited work by BYSTROW (1938, pp. 282—289) that author gives reasons for the opinion that neoteny in Stegocephalians is accompanied by a particular kind of dermal bone ornament, consisting merely of radiate, non-reticular ridges. The tubercular ornament of *Gerrothorax* and *Plagiosaurus* is of quite another type. *Plagiosternum*, a genus differing only in details from those forms, shows a fairly normal reticulate ornament (FRAAS 1913, pl. XVII, figs. 1—3), quite as do the Brachyopids (WATSON 1919, pl. I A). Thus the neoteny in *Gerrothorax* (and its relatives) will hardly be reflected in the ornamentation of the dermal bones (cf. also *Trimerorhachis* above p. 10 and CASE 1935, pl. II, fig. 1, etc.).

The parabolic, *Dvinosaurus*-like, larval shape of the skull (cf. BYSTROW 1935, pp. 133 ff.) in the Brachyopids (*s. s.*) is certainly easily reconcilable with an assumption of lifelong gill-breathing. A supposition, however, that the very broad and short shape of the skull in the Plagiosaurids is caused by neoteny implies the hypothesis that the skull of these forms must have undergone first a regressive development from the probably elongate skull of their non-neotenic ancestors to a parabolic, *Dvinosaurus*-like skull, then a progressive development, resulting in the broadening of the larval skull. If correct, such an evolution is antithetic to the original version of DOLLO's well-known law of the irreversibility of evolution. It is well reconcilable, however, with the modified form given to that law by SUSHKIN (1936, pp. 84—87). BYSTROW (1938, pp. 285 f.), on the other hand, speaks decidedly against the assumption of such a restricted reversibility of evolution as is admitted by SUSHKIN; BYSTROW's opinion is possibly correct, but his arguments do not appear to be conclusive.<sup>1</sup>

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<sup>1</sup> There seems to be a peculiar contradiction in the views held by BYSTROW (1938). In his polemics against the opinion of SUSHKIN just referred to he says (*l. c.*, p. 286): »Der *Dvinosaurus* war folglich primitiv in dem Maasse, in welchem diese Primitivität ihm eigen war, ohne dass die Kiemenatmung im erwachsenen Zustande eine Rolle gespielt hätte. Mit anderen Worten, der neotenische Zustand rief nicht mehr Merkmale der Primitivität hervor, als der *Dvinosaurus* ohne Einfluss desselben besessen hätte. Folglich kann die Erhaltung des Atmungstypus der Larve nicht als Ursache eines allgemeinen Regresses der Organisation des *Dvinosaurus*

A series of characters shown in the Plagiosaurians may decidedly be stated not to have been influenced by neoteny. Already *Batrachosuchus*, but in particular the geologically younger Plagiosaurids, exhibit several advanced features, some of them characteristic of all late Stegocephalians (WATSON 1919, pp. 56 f.). It need only be mentioned that the broad connection between the exoccipital and the entopterygoid is a feature common to *Batrachosuchus* and the Plagiosaurids as well as all their Stegocephalian contemporaries.

It may be concluded that the neoteny has left no other certain markings in *Gerrothorax* (and its relatives) but the branchial arches. These are, however, very well developed; the perennibranchiate nature of *Gerrothorax* appears thus to be established. The shape of the skull is the only remaining character of those discussed above which possibly might be influenced by the neoteny, but in the light of the other results gained here also such an assumption seems to be doubtful.

The above conclusions are in good agreement with a statement by NOBLE (1931, pp. 102 f.) that the recent perennibranchiate Urodeles and their relatives show structural changes more or less comparable to those in metamorphosis, but at such »disconnected stages that they cannot be considered metamorphosis». For instance the adult *Siren*, one of the most larval-like of all recent neotenic Urodeles, is said to have the typical metamorphosed structure of the skin.

Now a more detailed comparison between the Plagiosaurians and *Dvinosaurus* may be justified.

Without doubt *Dvinosaurus* to a certain extent shows similarities to the Plagiosaurians. The most important refer to the parabolic skull-shape (cf. in particular the Brachyopids), the large, or fairly large orbits situated anteriorly, the feebly developed or absent otic notches, the presence of well developed branchial arches (cf. *Gerrothorax*), the massive stapes (cf. *Batrachosuchus*), the broad processus cultriformis of the parasphenoid, the heavy, short, and broad quadrate ramus of the entopterygoid, and the presence of an ossified supraoccipital (cf. the Plagiosaurids).<sup>1</sup>

Several of these characters were evidently caused by the shortness of the skull, others are possibly adaptations connected with the life of the animals in not too shallow water (gills, otic notches, stapes; cf. SUSHKIN 1936, p. 82).

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anerkannt werden.» On p. 284 (*l.c.*) he states that »jede neotenische Form ... unbedingt einen kurzen und breiten Schädel besitzen muss». BYSTROW (1935) himself has shown that short and broad skulls must have been characteristic of the ancestors and larvae of all Stegocephalians. Consequently a skull of that shape must be regarded as a primitive character. The supposed non-neotenic ancestors of *Dvinosaurus* possibly had elongate skulls and were thus more advanced than *Dvinosaurus* itself with respect to the shape of the skull. But such a possibility is denied, indirectly, by BYSTROW in the first quotation above.

<sup>1</sup> It should be noticed that the supraoccipital is not ossified in the Brachyopids (*Batrachosuchus*).



The most important differences between *Dvinosaurus* and the Plagiosaurians are enumerated in the following table.<sup>1</sup>

	<i>Dvinosaurus</i>	<i>Plagiosauria</i>
A. Cranial characters		
1) Intertemporal <sup>2</sup>	coalesced with the post-orbital	(absent or) fused with the postfrontal
2) Sulcus jugalis sensorialis	runs through the centre of radiation of the squamosal	runs in the suture between the squamosal and the quadratojugal
3) External nares	removed from each other	close to each other
4) Ornament	without pits and tubercles	with pits or tubercles
5) Lateral outline of the entopterygoid in ventral view	markedly concave	slightly concave to convex
6) Ventral face of the proc. cultriformis	anteriorly with a sagittal crista, posteriorly with a fovea	without crista and fovea
7) Posttemporal fenestra	large	small
8) Trabecula parotica <sup>3</sup>	absent	well developed
9) Lamina ascendens of the entopterygoid	high	very low or absent
10) Ventral outline of the entopterygoid in posterior view	uniformly concave, strongly declining in a lateral direction	distal part abruptly descending
11) Connections of the entopterygoid to the parasphenoid and exoccipital	not existent	well developed
12) Palatal ramus of the entopterygoid	reaching the vomer	far removed from the vomer
13) Interpterygoid fenestra	moderately large	large or very large
14) Occipital condyles	moderately projecting	strongly projecting
15) Parietals	very broad	moderately broad or narrow (at least anteriorly)
16) Postparietals	small	moderately large or large
17) Position of the pineal foramen	in front of the centre of radiation of the parietal	(in or) posteriorly to the centre of radiation of the parietal

<sup>1</sup> As regards the Plagiosaurians all cranial characters referred to in the table are known both in Brachyopids and Plagiosaurids, the postcranial characters, on the other hand, only in the Plagiosaurids.

<sup>2</sup> Dermosphenotic according to SAVE-SÖDERBERGH (1935).

<sup>3</sup> Osseous bar formed by the parotic processes of the tabular and exoccipital (cf. NILSSON 1946, pp. 11, 28).

	<i>Dvinosaurus</i>	<i>Plagiosauria</i>
B. Postcranial characters		
18) Vertebrae	decidedly rhachitomous; the foremost pleurocentra partly fused to the intercentra and neural arches, these thus situated »vertebrally»	of a unique type; centra elongate, never wedge-shaped, solid; free neural arches in exactly »intervertebral» position
19) Cleithrum (cf. NILSSON 1939, 1945)	simply built; consists of a dorsal part without ornament(?) and a long, narrow processus clavicularis; the lower part of the anterior margin of this process embraced by the groove-shaped processus cleithralis of the clavicle	very complicated; consists of a dorsal and a lateral lamina, ornamented on their outer face, and a medial lamina, provided with a short and broad proc. clavicularis; the lateral face of the proc. cleithralis claviculae joined to the medial face of the proc. clavicularis and the adjoining parts of the medial and dorsal laminae of the cleithrum; a small anterior lateral face of the proc. clavicularis and part of the ventral margin of the lateral lamina of the cleithrum joined to the lateral, vertical lamina of the clavicle
20) Interclavicle (cf. NILSSON 1939, 1943)	with a very short or absent anterior part; anteriorly a deep, narrow incisure, posteriorly a long, narrow processus posterior	with a well developed anterior part; without anterior incisure and posterior process; posterior part very short and broadly truncated
21) Dermal scale-armour	probably absent	very well developed, comprising also gastral ribs and covering the whole trunk and tail
22) Ribs	curved, proximally thickened, distally tapering; indistinctly bicipital	almost straight and uniformly broad, distinctly bicipital
23) Humerus (cf. NILSSON 1939)	of a special type related to that of <i>Eryops</i> ; crista deltopectoralis well developed	deviating from all other types of humeri; crista deltopectoralis merely indicated
24) Hind leg	normal	straight, directed backwards, and functioning as part of a »caudal fin»; femur correspondingly transformed
25) Clavicles	not widened	strongly widened
26) Neural spines	normally high	very low
27) Body-shape	elongate	fairly short and broad

Of the characters enumerated, 1—5 (—7) and 18—22 appear to be the most important, the others representing more insignificant features or such as may be assumed to be primitive in *Dvinosaurus* and advanced in Plagiosaurians.

Such characters as the entirely different relations of the intertemporal, the different directions of specialization of the vertebrae (the conditions in the most anterior vertebrae of *Dvinosaurus* should be particularly noticed), and the very different cleithrum, interclavicle, and ribs must be considered to exclude *Dvinosaurus* at least from the direct ancestry of the Plagiosaurians (cf. NILSSON 1937, p. 55).

The shape of the interclavicle in *Dvinosaurus* is very remarkable. Such a feature as the deep anterior incisure, stated to be present both by SUSHKIN (1936, fig. 10) and BYSTROW (1938, fig. 21), is quite unparalleled among Stegocephalians. The long, narrow posterior process is a character reminding of the reptiles. Apart from *Dvinosaurus* it is found, as far as I know, only in *Melanerpeton*, *Discosauriscus*, *Cacops*, *Hylonomus*, and *Microbrachis* among Stegocephalians (CREDNER 1890, figs. 39, 40; WILLISTON 1910, pl. 11, fig. 1; STEEN 1938, figs. 19, 41).

To a large extent the similarities between *Dvinosaurus* and the Plagiosaurians seem to be fairly superficial. Most probably the Plagiosaurians, therefore, are not more closely related to *Dvinosaurus* than to the other Labyrinthodonts.

An examination of the relations between the Plagiosaurians and the Labyrinthodonts in general discloses that the Plagiosaurians differ from all Labyrinthodonts at least in the characters numbered 5, 9, 10, 14, 18—24.

The nature of the vertebrae and cleithrum is the most significant feature in this connection. As regards the morphological interpretation of the vertebrae of the Plagiosaurids no new points of view have been brought forward since 1937. The reasons given on that occasion (NILSSON 1937, pp. 58—63) for the opinion that the Plagiosaurid vertebrae are possibly not stereospondylous in the current sense of the word, but more probably represent a type of their own, are still valid. — Also as regards the cleithrum my earlier views seem to hold good (NILSSON 1939; cf. also 1945). Accordingly the cleithrum of the Plagiosaurids cannot be derived from any known cleithrum of a Labyrinthodont or a Lepospondyl, though it may be related to the cleithra of both these groups.

The remarkably uniform shape of the ribs in the Plagiosaurids is a character perhaps worthy of special mention in this connection. In the Labyrinthodonts (and also in other Stegocephalians) the ribs are generally curved and frequently provided with widened distal ends and fairly thickened proximal parts; sometimes processus uncinati are developed. Straight and uniformly broad ribs to a certain extent reminding of those in Plagiosaurids are shown in *Micropholis* (BROILI & SCHRÖDER 1937, fig. 6) and *Lydekkerina* (WATSON 1919, fig. 9) among Labyrinthodonts and in *Diplocaulus* (DOUTHITT 1917, figs. 4, 6:6) among Lepospondyls.

Summing up what has been said above, it at present seems most convenient

to maintain the order *Plagiosauria*, comprising the Brachyopids and Plagiosaurids, as was proposed in 1939 (NILSSON 1939, pp. 23 f.). This order shows certain features reminding of the Lepospondyls but probably has more affinities to the Labyrinthodonts. Such a classification has much in common with that proposed by JAEKEL (1913). That author placed the Plagiosaurians nearer to the Lepospondyls than is done here, however.

Below is an attempted diagnosis of the order *Plagiosauria*. It must be kept in mind, however, that all postcranial characters refer to the Plagiosaurids proper, postcranial remains being unknown in Brachyopids. Features referring to the fore and hind legs and the dermal scale-armour have been omitted.

**Diagnosis of the order Plagiosauria:** Large Stegocephalians with a broad or very broad, parabolic, depressed skull. No transverse zones of intense growth on the skull. Large or very large orbits, situated anteriorly on the skull. Otic notches feebly developed or absent. Occipital condyles greatly projecting in a posterior direction. Lateral flange of the entopterygoid abruptly descending. No or only a very low lamina ascendens of the entopterygoid. Lateral outline of the entopterygoid slightly concave to convex, as seen in ventral view. — Vertebrae consisting of solid, never wedge-shaped, elongate centra and free neural arches, articulating between two consecutive centra with two articular faces of approximately equal size. Interclavicle with a very short, broadly truncated posterior part. Cleithrum very complicated, its outer face completely ornamented; large parts of its medial face and only a small part of its lateral face joined to the clavicle. Ribs almost straight and uniformly broad, distinctly bicipital.

### Summary.

New material of *Gerrothorax rhaeticus* NILSSON, comprising essentially postcranial remains, has been described. It comes from exactly the same local horizon in the middle part of the Rhaetic strata at Bjuv in north-western Scania as do the earlier finds (pp. 5 f.). The new results gained from the study of this material may be summarized as follows.

1) The existence of an osseous hyobranchial skeleton, better developed than in any other living or fossil Amphibian, necessitates the assumption that gill-breathing was persistent also in the mature stage of *Gerrothorax* (pp. 7—12).

2) The neural arches occupy an »intervertebral» position also in the foremost presacral and in the caudal vertebrae (p. 12).

3) Certain of the caudal vertebrae are provided with low, very elongate haemal arches, forming outgrowths from the entire length of the ventral face of the centra (pp. 12 f.).

4) In contrast to the presacral ribs the caudal ribs are in part strongly curved (p. 13).

5) The anterior part of the interclavicle and a fragmentary pelvis have been described (p. 14).

6) In the description of the dermal scale-armour certain new details have been given (pp. 19—26). The gastral skeleton of Stegocephalians closely corresponds to a well delimited ventral part of the scale-covering in Crossopterygians and certain other fishes (p. 26).

7) The tail was well developed, but presumably fairly short. It was not flattened from the sides (pp. 18, 26).

8) The femur is well distinguished from that of other Stegocephalians (pp. 15—17).

9) The whole hind leg is almost straight and directed backwards along the anterior part of the tail. It is uniformly and unusually strongly widened in a distal direction. The hind legs of both sides probably served as a sort of »caudal fin» together with the tail (p. 18).

10) *Gerrothorax rhaeticus*, which may have attained a total length of 1 m in large individuals (p. 27), probably lived benthonic in a moderately deep, open, and presumably brackish lagoon some distance from the shore (p. 27).

11) The effect of the neoteny on the structure of the body in *Gerrothorax* and its influence on the problem of the affinities of the Plagiosaurids are discussed (pp. 31 f.).

12) The Plagiosaurians cannot possibly be the direct descendants of *Dvinosaurus*. Most probably they are not more closely related to *Dvinosaurus* than to other Labyrinthodonts (p. 35).

13) The order *Plagiosauria* may conveniently be maintained, comprising the Plagiosaurids and Brachyopids. It shows certain features reminding of the Lepospondyls but probably has more affinities to the Labyrinthodonts (pp. 35 f.).

14) A diagnosis is given of the order *Plagiosauria* (p. 36).

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**Plates.**

The photographs reproduced in the plates have been taken with a ZEISS Tessar objective 1: 4, 5, F. 50 cm. They have been slightly retouched.

**Plate I.***Gerrothorax rhaeticus* NILSS.

Ventral aspect of the dorsal slab B. 18 a, showing posterior parts of the vertebrae and ribs, dorsal scale-armour, and ventral armour of gastral ribs, further parts of the pelvis and hind legs.  $\times \frac{3}{4}$ .

**Plate II.***Gerrothorax rhaeticus* NILSS.

Fig. 1. Ventral aspect of the dorsal slab B. 18 b, showing fragments of the most posterior part of the skull and the most anterior parts of the interclavicle and left clavicle (chiefly seen as casts of their deep faces), remains of the most anterior presacral vertebrae and ribs, and parts of the dorsal scale-armour and the branchial arches.  $\times \frac{3}{4}$ .

Fig. 2. Dorsal aspect of the ventral slab B. 18 e (counterslab to the right part of the dorsal slab B. 18 a, pl. I), showing parts of the caudal vertebrae, right caudal ribs, and right hind legs, also posterior parts of the ventral scale-armour.  $\times \frac{3}{4}$ .

**Plate III.***Gerrothorax rhaeticus* NILSS.

Fig. 1. Dorsal aspect of the ventral slab B. 18 d, showing parts of the posterior presacral vertebrae and ribs and fragments of the middle and posterior parts of the gastral skeleton.  $\times \frac{3}{4}$ .

Fig. 2. Ventral aspect of the dorsal slab B. 18 c (partly counterslab to the ventral slab B. 18 d; cf. the preceding figure), showing fragments of the posterior presacral vertebrae and ribs, a large part of the dorsal scale-armour, and a fragment of the right clavicle.  $\times \frac{3}{4}$ .

## Explanation of lettering used in plates and text-figures.

<i>Bbr</i> , basibranchial (copula)	<i>Fe</i> , femur
<i>Bo</i> , basioccipital	<i>Fib</i> , fibula
<i>C</i> , praesacral rib (costa)	<i>Gr</i> , gastral (abdominal) rib
<i>C.c</i> , caudal rib	<i>G.sc.al</i> , antero-lateral gastral scales
<i>Clav</i> , clavicle	<i>G.sc.m</i> , median gastral scales
<i>C.s</i> , sacral rib	<i>G.sc.o</i> , ordinary gastral scales, arranged in oblique rows
<i>Ct</i> , centrum of a presacral vertebra	<i>G.sc.tr</i> , gastral scales arranged in transverse rows
<i>Ct.1</i> (2), centrum of the first (second) presacral vertebra	<i>Hbr</i> , hypobranchial
<i>Ct.c</i> , centrum of a caudal vertebra	<i>Hbr.1-4</i> , hypobranchial 1—4
<i>Ct.s</i> , centrum of the sacral vertebra	<i>Hhy</i> , hypohyal
<i>Dl.sc</i> , dorso-lateral scales	<i>Hu</i> , humerus
<i>D.sc</i> , dorsal scales	<i>Icl</i> , interclavicle
<i>Enpt</i> , entopterygoid (pterygoid)	<i>Kbr</i> , keratobranchial
<i>Eo</i> , exoccipital	

- Kbr.1—4*, keratobranchial 1—4  
*Khy*, keratohyal  
*L.sc*, lateral scales  
*Mt.1—5*, metatarsal 1—5  
*Neu*, neural arch  
*P*, pubo-ischiadic part of the pelvis  
*Ppar*, postparietal  
*Sc*, scales (in general)  
*So*, supraoccipital  
*T*, tarsal  
*Ti*, tibia  
*Vl.sc*, ventro-lateral scales of the trunk  
*Vl.sc'*, ventro-lateral scales of the tail  
*V.sc*, ventral scales  
*V.sc'*, ventral scales situated between the  
gastral skeleton and the ventro-lateral  
scales
- X*, structure of problematic origin  
*a*, area clavicularis of the interclavicle,  
joined to the area interclavicularis of  
the clavicle  
*can.c*, caudal canal  
*cap*, caput femoris  
*cr*, crater-shaped pit  
*cr.add*, crista adductoria  
*dt*, denticle  
*em.abd*, eminentia abductoria  
*f.m*, foramen magnum occipitale  
*f.vag*, foramen vagi  
*g.r*, groove for gastral rib  
*haem*, haemapophysis  
*o*, orbit  
*s.ext*, sulcus extensorius

