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Geology

NEW SERIES, NO. 32

Pachypleurosaurs (Reptilia: Sauropterygia) from the Lower Muschelkalk, and a Review of the Pachypleurosauroidea

Olivier Rieppel
Lin Kebang

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Pachypleurosaurs (Reptilia: Sauropterygia) from the Lower Muschelkalk, and a Review of the Pachypleurosauroidea

Olivier Rieppel Lin Kebang

Abstract

The type material of all pachypleurosaurs from the lower Muschelkalk is redescribed and pachypleurosaur systematics are reviewed. Three species of lower Muschelkalk pachypleurosaurs are recognized, *Anarosaurus pumilio* Dames, *Anarosaurus heterodontus* n. sp., and *Dactylosaurus gracilis* Gürich. A cladistic analysis based on 50 characters shows *Keichousaurus* to be the sister-taxon to all other pachypleurosaurs; *Dactylosaurus* is the sister-taxon to *Anarosaurus* plus the *Serpianosaurus*–*Neusticosaurus* clade; *Anarosaurus* is the sister-taxon to the *Serpianosaurus*–*Neusticosaurus* clade; *Serpianosaurus mirigiolensis* is the sister-taxon to *Neusticosaurus*. The genus *Neusticosaurus* includes four species, *N. edwardsii*, *N. peyeri*, *N. pusillus*, and *N. toeplitzchi*. The stratigraphic and biogeographic relations of pachypleurosaurs indicate that pachypleurosaurs reached the European epicontinental sea (Muschelkalk Basin) by invasion from the east in Anisian times, and that a faunal interchange was possible between the Muschelkalk Basin and the southern Alpine intraplateau basin facies at least during late Anisian and Ladinian times.

Zusammenfassung

Das Typusmaterial aller Pachypleurosaurier aus dem unteren Muschelkalk wird neu beschrieben. Drei Arten von Pachypleurosauriern lassen sich im unteren Muschelkalk feststellen: *Anarosaurus pumilio* Dames, *Anarosaurus heterodontus* n. sp., und *Dactylosaurus gracilis* Gürich. Eine kladistische Analyse weist *Keichousaurus* als Schwestergruppe aller anderen Pachypleurosaurier aus; *Dactylosaurus* ist die Schwestergruppe von *Anarosaurus* und der *Serpianosaurus*–*Neusticosaurus*-Linie; *Anarosaurus* ist die Schwestergruppe der *Serpianosaurus*–*Neusticosaurus*-Linie; *Serpianosaurus mirigiolensis* ist die Schwestergruppe von *Neusticosaurus*. Die Gattung *Neusticosaurus* umfasst vier Arten: *N. edwardsii*, *N. peyeri*, *N. pusillus*, und *N. toeplitzchi*. Stratigraphische und biogeographische Beziehungen zeigen, dass die Pachypleurosaurier das Germanische Becken von Osten her kommend im Unteren Anis erreichten. Zwischen der Germanischen und der Alpenen Trias fand zumindest während dem späten Anis und dem Ladin ein Faunenaustausch statt.

Introduction

The Pachypleurosauroidea (Pachypleurosauridae) constitute a monophyletic clade of the sauropterygian radiation (Rieppel, 1987, 1989; Storrs, 1991; Sues, 1987) that first appears in the lowermost Muschelkalk (lower Anisian) of Upper Si-

lesia (*Dactylosaurus gracilis*, Gürich, 1884) and in the lower Middle Triassic of China (Young, 1958, 1965). The clade has not been recorded beyond the upper Ladinian (upper Middle Triassic), perhaps lower Carnian (lower Upper Triassic), deposits in the southern Alps (Ca' del Frate, Italy: Tintori et al., 1985). Pachypleurosaurian anatomy

is well known for the Middle Triassic taxa abundantly represented in uppermost Anisian and lower Ladinian deposits at Monte San Giorgio, Switzerland (genera *Neusticosaurus* and *Serpianosaurus*: Carroll & Gaskill, 1985; Rieppel, 1989; Sander, 1989), but the interrelationships of pachypleurosaur in general still remain poorly understood. This results from the relatively poor knowledge of earlier representatives of the clade. Of these, only a guttapercha cast of the holotype of *Dactylosaurus schroederi* Nopcsa (1928) from the Muschelkalk of Gross-Stein, Upper Silesia, has recently been restudied (Sues & Carroll, 1985; *Dactylosaurus schroederi* Nopcsa is considered a junior synonym of *Dactylosaurus gracilis* Gürich: see below). A second pachypleurosaur from the lower middle Muschelkalk, *Anarosaurus pumilio* Dames, 1890, from Remkersleben in Saxony, has not been restudied since Arthaber's (1924) and Nopcsa's (1928) contradictory comments on its morphology (a reconstruction of the skull was published by Carroll, 1981, Fig. 32a).

Since the early original description of pachypleurosaurid taxa from the lower Muschelkalk (lower to middle Anisian), new material has accumulated in various museum collections, the identification of which remains problematic until the diagnoses of the originally described taxa are refined. It is the purpose of this paper to pull together all available information on the original type material of pachypleurosaur from the lower Muschelkalk. A redescription of the original type material will also provide the basis for a review of pachypleurosaur interrelationships and the reconstruction of their evolutionary and paleobiogeographic history.

Systematic Paleontology

Sauropterygia Owen, 1860

Pachypleurosauoidea Huene, 1956

Pachypleurosauridae Nopcsa, 1928

DEFINITION—A monophyletic group including the common ancestor of *Anarosaurus*, *Dactylosaurus*, *Keichousaurus*, and all of its descendants.

DIAGNOSIS—Small to medium-sized Sauropterygia with the preorbital region of the skull longer than the postorbital region; frontal with concave lateral edge, entering the dorsal margin of the orbit; broad parietal skull table; mandibular artic-

ulation at level with occipital condyle; quadrate with concave posterior margin; ectopterygoid absent; trough on dorsal surface of retroarticular process present; anterior teeth not strongly procumbent; posterior process on interclavicle rudimentary or absent; radius slightly longer than ulna; iliac blade absent (i.e., reduced to narrow dorsal process).

DISTRIBUTION—Middle Triassic of China and Europe (Tethyan Province).

Anarosaurus Dames, 1890

TYPE SPECIES—*Anarosaurus pumilio* Dames, 1890.

GENERIC DIAGNOSIS—A small pachypleurosaur with a spatulate expansion of the tooth crown; a high dorsal vertebral count (25 or 26); an open obturator foramen in the pubis; pubis with a distinct anteroventral spine; and a distinctly elongated femur (femur length/standard length = 1.55).

DISTRIBUTION—Lower and middle Muschelkalk, central Europe.

Anarosaurus pumilio Dames, 1890

- 1890 *Anarosaurus pumilio*, Dames, p. 74, Pl. 1, text figs. 1, 2.
- 1899 *Anarosaurus pumilio*, Schrammen, p. 408, Pl. 25, Fig. 8.
- 1910 *Anarosaurus pumilio*, Jaekel, pp. 325, 335, text fig. 1.
- 1924 *Anarosaurus pumilio*, Arthaber, pp. 480–483, text figs. 12a, b, 13.
- 1928 *Anarosaurus pumilio*, Nopcsa, pp. 30–31, 43, Pl. 4, Figs. 1, 2.
- 1935 *Anarosaurus pumilio*, Zangerl, pp. 64–65, 68.
- 1959 *Anarosaurus pumilio*, Kuhn-Schnyder, p. 652.
- 1981 *Anarosaurus pumilio*, Carroll, text fig. 32a.
- 1985 *Anarosaurus pumilio*, Sues and Carroll, p. 1349.
- 1987 *Anarosaurus pumilio*, Rieppel, pp. 1110, 1115–1116.
- 1993 *Anarosaurus pumilio*, Rieppel, p. 10.

HOLOTYPE—The holotype was originally housed at the Institut und Museum für Geologie und Paläontologie, Georg-August-Universität, Göttingen, but can no longer be located today (lost or

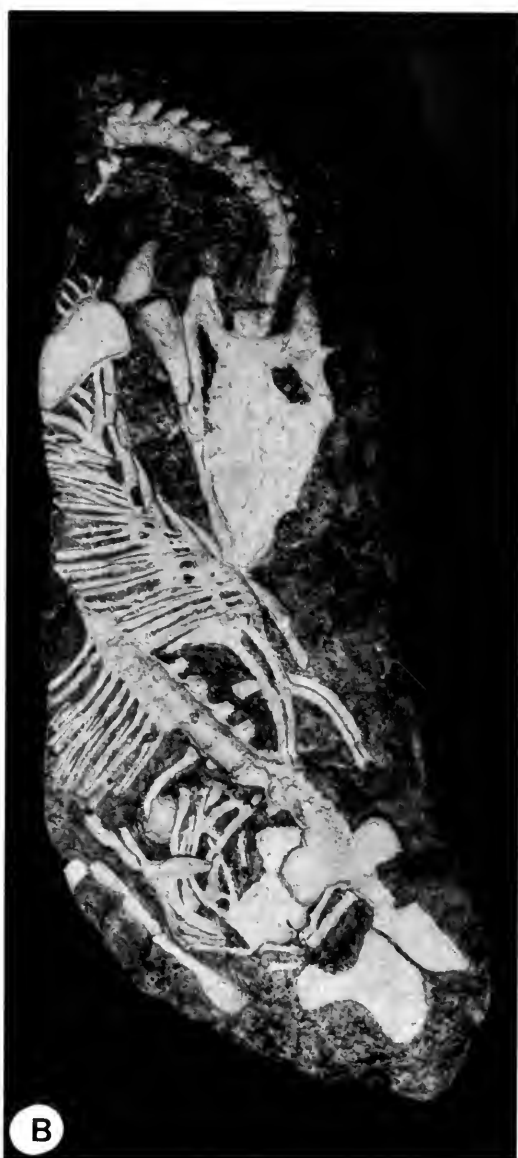


FIG. 1. Casts of the holotype of *Anarosaurus pumilio* Dames, deposited by Nopcea in the British Museum (Natural History). A, Dorsal view (BMNH R-5691); B, ventral view (BMNH R-5866). Scale bar = 20 mm.

destroyed during World War II; H. Jahnke, in litt. 1991). Two casts are available at this institution (Orig. Nr. 409-1). The specimen came from the *orbicularis* beds near Remkersleben, approximately 15 km west of Magdeburg. The *orbicularis* beds were assigned to the top of the lower Muschelkalk by Dames (1890), but are now considered the base of the middle Muschelkalk (Hagdorn, 1991).

Arthaber (1924) describes a guttapercha cast of

the holotype in the Natural History Museum, Humboldt University, Berlin (MB R. 57.1-3, dorsal view; MB R. 58, ventral view), deposited by Jaekel (1910) after further preparation of the holotype.

Additional casts (Fig. 1) were deposited by Nopcea in the British Museum (Natural History) (BMNH R-5691, dorsal view; BMNH R-5866, ventral view). Other casts are kept at the Institut für Geowissenschaften, Martin-Luther-Universität,

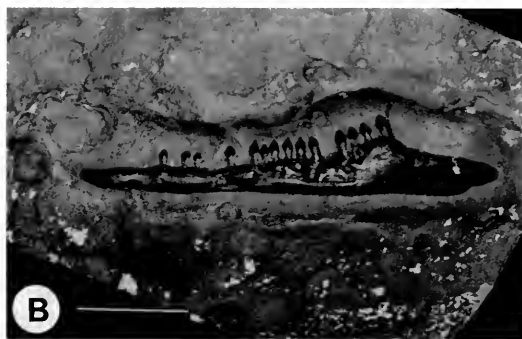
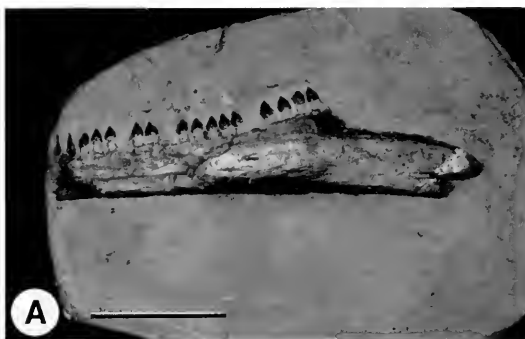


FIG. 2. *Charitosaurus tschudii* Meyer. A, Cast of the Esperstädt specimen (original of Meyer, 1851, Pl. 31, Fig. 22; MB R. 62); B, cast of the Querfurt specimen (original of Meyer, 1851, Pl. 31, Fig. 23; MB R. 61). Scale bar = 20 mm.

Halle (M4/12, skull only), and at the Staatliches Museum für Naturkunde, Stuttgart (SMNS 59073).

DIAGNOSIS—Same as for genus, but about half the size of *Anarosaurus heterodontus*, homodont dentition with eight teeth in premaxilla, and a weak sculpturing of dermal skull bones.

LOCUS TYPICUS—*Orbicularis* beds (middle Muschelkalk) of Remkersleben, 15 km west of Magdeburg, Germany.

DISTRIBUTION—Lower middle Muschelkalk, Anisian, Europe.

COMMENTS—*Anarosaurus pumilio* was originally described by Dames (1890). Schrammen (1899) found *Anarosaurus* to be closely comparable to *Cymatosaurus*, perhaps because of the spatulate expansion of the tooth crown. Jaekel (1910) reconstructed the skull of *Anarosaurus* after further preparation of the holotype, and used *Anarosaurus* (as well as *Simosaurus*) in support of his argument that sauropterygians are a subgroup of the Diapsida. Arthaber (1924) criticized Jaekel's (1910) reconstruction of the skull, and presented new vertebral counts in his redescription of *Anarosaurus*. He also noted the similarity of the pubis of *Anarosaurus* to other, isolated elements from the lower Muschelkalk referred to "*Macrotrachelii*" by H.v. Meyer (1847–1855). Nopcsa (1928) rejected Arthaber's (1924) vertebral counts in *Anarosaurus*, and compared the taxon to *Dactylosaurus*. He considered the skull to be very similar in both genera, but found differences in the postcranial skeleton to support the generic distinction of the two taxa.

In 1958, Huene described a second species, "*Anarosaurus*" *multidentatus*, from the lower Anisian of the Lechtaler Alps, Austria. The specimen consists of a lower jaw characterized by an elongate

symphysis and a heterodont dentition. In a recent redescription of the holotype, the species has been referred to the genus *Cymatosaurus* (Rieppel, 1995).

In 1838, Meyer reported the collection of two lower jaw fragments (left dentaries), one from the Saurierkalk (lower middle Muschelkalk) of Esperstädt, the other from the *orbicularis* beds (lower middle Muschelkalk) of Querfurt. The original of the Esperstädt specimen was kept in Dresden, that from Querfurt was kept in Jena. Both specimens are now lost, but casts of both specimens are preserved in the Staatliches Museum für Naturkunde in Stuttgart (SMNS 80082–83), and in the Humboldt Museum in Berlin (MB R. 61–62) (Fig. 2). The specimens first reported in 1838 were redescribed as lower jaws of fishes by Meyer (1851), who renamed them *Charitodon tschudii*. *Charitodon* (*Charitosaurus*) *tschudii* resembles *Anarosaurus* in tooth structure, with a constricted base and an expanded crown, but the tooth crown of *Anarosaurus* is more distinctly lanceolate than the rather bulbous tooth crown of *Charitosaurus*. At the present time, *Charitosaurus tschudii* must remain a nomen dubium.

MORPHOLOGICAL DESCRIPTION—The holotype of *Anarosaurus pumilio* is known from casts only. The original specimen consisted of part (dorsal view) and counterpart (ventral view). The Institute and Museum of Geology and Paleontology in Göttingen holds two casts of the dorsal view that differ in size; measurements of limb bones taken from one cast (Gö 409-1b) being consistently smaller than those taken from the other (Gö 409-1a). Other casts kept at the natural history museums in Berlin, London, and Stuttgart (see above) yield different values again, indicating the limited ac-

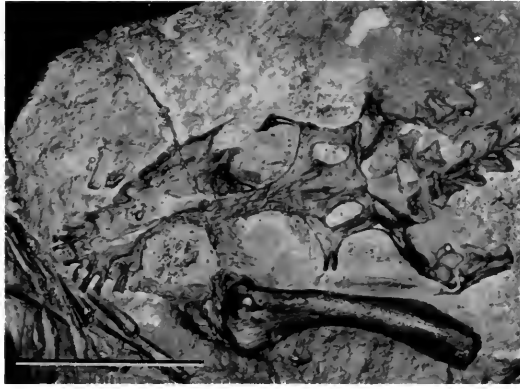


FIG. 3. Cast of the skull of *Anarosaurus pumilio* Dames (holotype) (Institut für Geowissenschaften, Martin-Luther-Universität, Halle, M4/12). Scale bar = 20 mm.

curacy of those casts. Unless noted otherwise, the measurements given below are from the Göttingen cast, Gö 409-1a.

The skull (Figs. 3, 4) is incompletely preserved, partially crushed, and (or) destroyed by preparation. In dorsal view, both premaxillae, the right maxilla, right prefrontal, and most of the skull table are well exposed. The distance from the tip of the snout to the posterior margin of the skull table (as preserved) is 34.5 mm, the distance from the tip of the snout to the posterior margin of the supraoccipital (as preserved) is 38 mm. The longitudinal diameter of the (right) orbit is 13 mm, the longitudinal diameter of the upper temporal fossa is 5 mm (right) and 4.5 mm (left), respectively.

The premaxilla forms the anterior and antero-

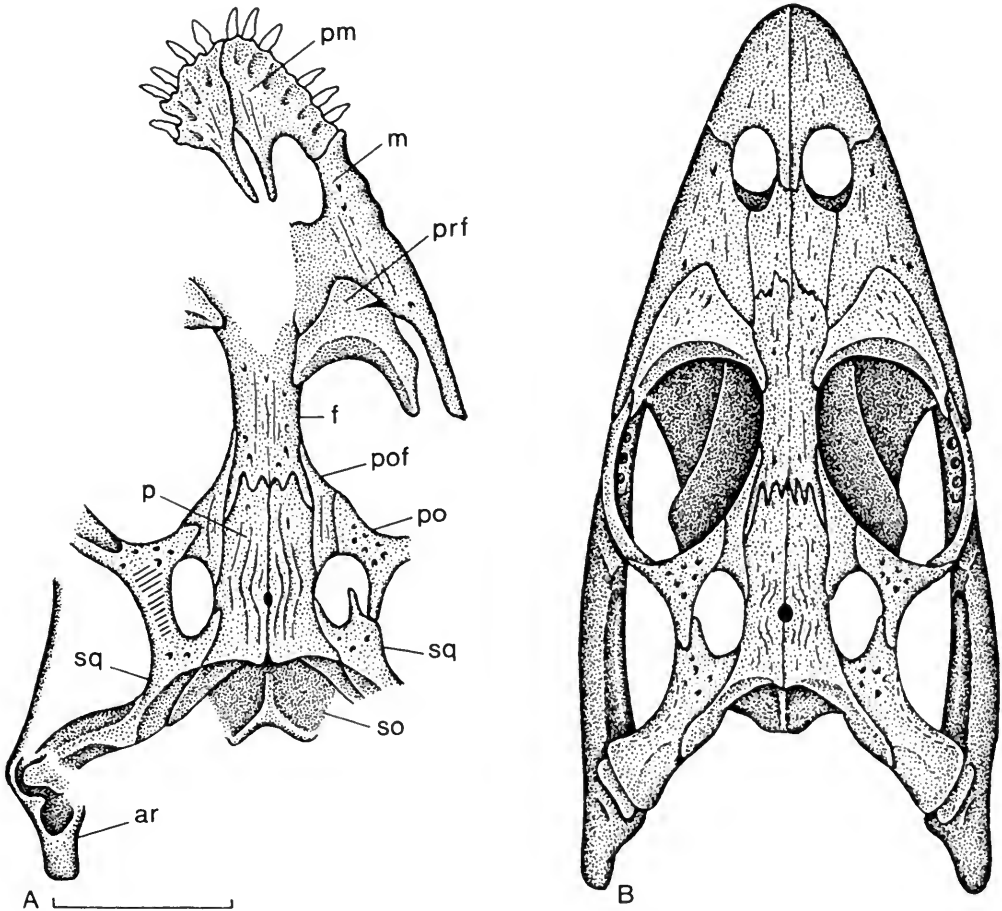


FIG. 4. Skull of *Anarosaurus pumilio* Dames (holotype). A, Drawing of the cast kept at the Institut und Museum für Geologie und Paläontologie, Georg-August-Universität, Göttingen, Orig. Nr. 409-1); B, reconstruction of the skull in dorsal view. Scale bar = 10 mm. Abbreviations: ar, articular; f, frontal; m, maxilla; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; so, supraoccipital; sq, squamosal.

dorsal margin of the external naris. A slender posterior process entered between the external nares, but its relation to the nasal and frontal remains unknown. The posterior process of the premaxilla does not extend beyond the level of the posterior margin of the external naris. Jaekel (1910) counted four, Arthaber (1924) five premaxillary teeth, numbers that seem to refer to the incompletely preserved left premaxilla. The exact tooth count is difficult to establish on the available casts, but the completely preserved right premaxilla shows a possible maximum of eight teeth or tooth positions. Dames (1890) and Jaekel (1910) showed a characteristic leaflike expansion of the crown of the premaxillary teeth, which cannot be confirmed on the cast kept at the Institute and Museum of Geology and Paleontology in Göttingen; a spatulate expansion of the tooth crown is distinct in one anterior premaxillary tooth in the casts kept at the Staatliches Museum für Naturkunde in Stuttgart as well as in the casts kept at the Natural History Museum in Berlin. The remaining premaxillary teeth are about 3 mm long, slightly recurved, and pointed. The exact structure of the maxilla remains obscure, as does the number of maxillary teeth. Posteriorly, the maxilla forms a short slender process, underlying the prefrontal in the anteroventral margin of the orbit.

The prefrontal is a broad, domed element, as is typical for pachypleurosaurs. It remained broadly separated from the postfrontal along the dorsal margin of the orbit, which is formed by the slightly concave lateral margin of the frontal. The partially fused frontals are long and slender elements, but their anterior portion is missing. Posteriorly, the frontals form an interdigitating suture with the parietals in a rather forward position. Slender posterolateral lappets of the frontals extend backward along the medial side of the postfrontals. The parietals enclose a small parietal foramen that lies midway between the frontoparietal suture and the posterior margin of the parietals. Laterally, the parietal forms the medial margin of the upper temporal fossa. Posteriorly, tapering processes of the parietal extend laterally on to the occiput.

The upper temporal fossa in *Anarosaurus* has rounded contours, and is smaller than the orbit but distinctly larger than the temporal fossa in *Serpianosaurus* and *Neusticosaurus*. The postfrontal forms a considerable portion of the anterior and anteromedial margin of the upper temporal fossa, the triradiate postorbital forms the lateral margin, and the squamosal borders the temporal fossa posteriorly. The upper temporal arch is nar-

row, leaving the cheek deeply "excavated." The ventral process of the left postorbital carries a facet on its anterior margin that received the dorsal end of the jugal. Details of the suspensorium and of the occiput are difficult to ascertain except for the presence of a large supraoccipital with a low sagittal crest.

The palate is difficult to analyze. Little can be seen beyond the general outlines of the major elements and the location of the internal nares (Carroll, 1981). In particular, it is impossible to confirm the presence or absence of the ectopterygoid. A distinct ventral ridge marks the lateral edge of the pterygoid along the anteromedial and medial margin of the subtemporal fossa.

Lateral to the left suspensorium, the articular facet of the lower jaw is preserved in situ, with the retroarticular process extending backward behind the mandibular articulation. A distinct trough can be identified on the dorsal surface of the retroarticular process. The right lower jaw is exposed in ventral view but shows little morphological detail. Its total length, including the retroarticular process, is 47.5 mm.

Posterior to the skull, 16 cervical vertebrae are preserved in articulation. Arthaber (1924) counted 15 cervicals, but obviously omitted counting the poorly exposed atlas. In dorsal view the cervicals show pachyostotic neural arches with a low neural spine; the ventral surface of the centrum is ornamented with paired longitudinal keels. The size of the cervical vertebrae slightly and gradually increases from front to back. The length of the centrum is 4.2 mm in the axis, 4 mm in the 10th cervical, and 4.8 mm in the 16th cervical; the width of the corresponding elements, measured across the zygapophyseal articulations, is 5 mm, 6 mm, and 8 mm, respectively. Three cervical ribs (an incomplete number) can unequivocally be identified, the anteriormost one of which lies adjacent to the 15th cervical vertebra and carries a distinct free anterior process close to its proximal articular head.

Separated from the cervical vertebrae by a gap, a total of 14 dorsal vertebrae (13 complete, 1 incomplete) are preserved in articulation, followed by the first sacral vertebra. The dorsal vertebrae show a weak constriction of the centrum in ventral view. Within the gap between the cervical and dorsal vertebrae series, 10 (left) ribs are exposed, plus the space for one additional rib that was not completely prepared. Following the 16 preserved cervical vertebrae, the contours of four additional elements can be identified (see also Nopcsa, 1928);

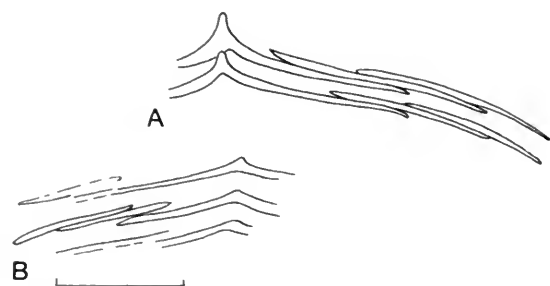


FIG. 5. Gastral ribs of *Anarosaurus pumilio* Dames (holotype) (drawn after SMNS 59073). A, Anterior gastral ribs; B, posterior gastral ribs. Scale bar = 10 mm.

all lie in front of the first exposed (left) rib. With a total of 15 vertebral elements bridging the gap between the preserved series of cervical and dorsal vertebrae, a count of 45 presacral vertebrae results. Dames (1890) counted 43 presacrals, Arthaber (1924) postulated 48 presacrals, and Nopcsa (1928) counted 39–40 presacrals. Since the anteriormost rib exposed within the gap between cervicals and dorsals shows the morphology of a holocephalous dorsal rib without free anterior process, we conclude that *Anarosaurus* had no more than 19–20 cervical vertebrae (in agreement with Nopcsa, 1928) and 25–26 dorsal vertebrae. The standard length was defined as the length of the last four presacral centra (Rieppel, 1989; Sander, 1989), and it is 23 mm (the length of the second but last presacral centrum is 5.5 mm; the standard length is the same in the casts from Göttingen and Berlin, but it is 21.3 mm in the cast from Stuttgart).

The dorsal ribs lack pachyostosis. The gastral ribs are composed of five elements each (Peyer, quoted in Zangerl, 1935), the angled medioventral element bearing a distinct anterior tip at least in the anterior and middle part of the gastral region, and two lateral elements on either side (Fig. 5). The ratio of vertebral elements to gastral ribs is 1:2.

Of the three sacral vertebrae, only the anteriormost is preserved. However, three sacral ribs can clearly be identified, of which the second one (11.5 mm long) is slightly larger than the first one (10.8 mm long), whereas the third one is only incompletely preserved. The sacral ribs are slightly expanded at their proximal end. Nothing is known of the caudal axial skeleton.

The pectoral girdle is poorly preserved and/or exposed, and dermal elements cannot be identified unequivocally. The right scapula is preserved in ventral view, possibly in association with a frag-

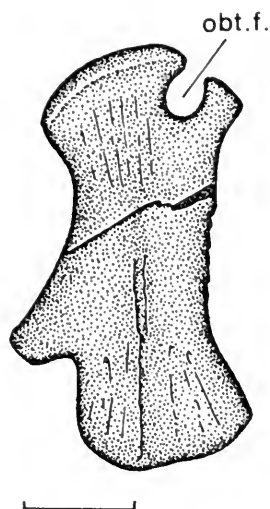


FIG. 6. The pubis of *Anarosaurus pumilio* Dames (holotype). Scale bar = 5 mm. Abbreviation: obt.f., obturator foramen.

mentary clavicle. The right coracoid lacks its distal portion, but shows a rounded proximal head as well as a strongly concave anterior margin opposing the less distinctly concave posterior margin.

Of the pelvic girdle, the ilium is not exposed. The two ischia are preserved in articulation. They show a narrow (“rod-shaped” according to Nopcsa [1928, p. 31]) acetabular portion, strongly convex anterior and posterior margins, and a widely expanded ventral portion with a convex ventral margin. The length of the ischium is 19 mm, its proximal width is 6.5 mm, the minimal width is 4 mm, and the width of the ventral part is 20 mm. The pubis of *Anarosaurus* shows weakly concave anterior and posterior margins. The obturator foramen is not closed, but rather forms an open slit at the posterior margin of the pubis close to the acetabular margin of the bone. The concavity of the central (medial) margin of the pubis results in a distinct spine protruding from the anteroventral edge of the pubis (Fig. 6). A large thyroid fenestra was developed between the pubis and ischium. The length of the pubis is 19.5 mm, its proximal width is 10 mm, its minimal width is 7 mm, the distal width is 9 mm excluding the anteroventral spine, but 13 mm including the latter.

The humerus (Fig. 7A) is the only element of the forelimb that is preserved. The element is slightly curved with a concave medial (preaxial) margin, a well-developed deltopectoral crest, and a broadly expanded distal portion. The entepicondylar foramen is well set off from the distal artic-

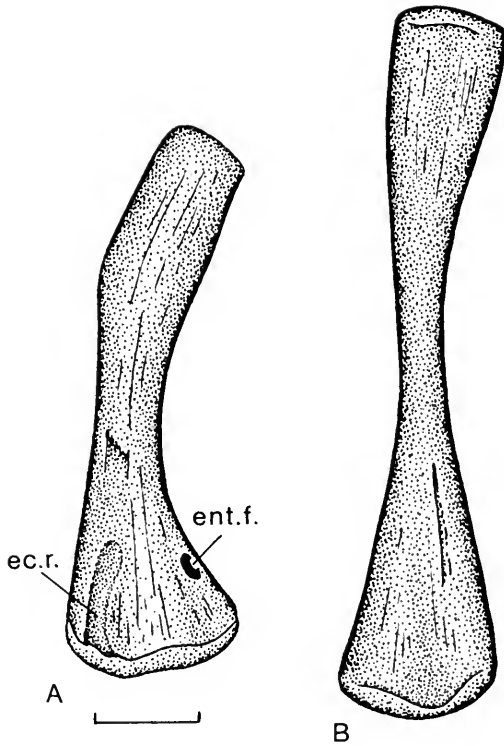


FIG. 7. A, Humerus of *Anarosaurus pumilio* Dames (holotype) (drawn after MB R. 57); B, femur of *Anarosaurus pumilio* (holotype) (drawn after SMNS 59073). Scale bar = 5 mm. Abbreviations: ec.r., ectepicondylar ridge; ent.f., entepicondylar foramen.

ular facet, indicating that the specimen is adult, and a distinct ectepicondylar groove is present. The surface of the bone shows distinct striations radiating toward its proximal and distal ends. These striations are straight rather than vermiculate, more marked, and more widely spaced than the ridges and grooves described on the humerus of *Neuticosaurus* (Sander, 1989), "*Psilotrachelosaurus*"

TABLE 1. Measurements of the humerus of *Anarosaurus pumilio* Dames, in different casts of the holotype.

	Length	Proximal width	Minimal width	Distal width
Gö 409-1a	28.5	5	4	9
Gö 409-1b	25	5	3	8
BMNH 5691	31	6	4	10
MB R-57.1	28	4.7	3.5	9
MB R-57.2	28.3	5.1	3.5	8.9
MB R-57.3	28.4	4.5	3.6	6
SMNS 59073	28.5	5	3.5	8.7

TABLE 2. Measurements of the femur of *Anarosaurus pumilio* Dames, in different casts of the holotype.

	Length	Proximal width	Minimal width	Distal width
Gö 409-1a	35.5	7.5	3	6
Gö 409-1b	32	7	2.5	5
BMNH 5691	40	8	3	6.5
MB R-57.1	36	7.3	3.3	6
MB R-57.2	36	7.1	3.1	5.8
SMNS 59073	35	6.2	2.4	5.6

(Rieppel, 1993), and *Serpianosaurus* (Rieppel, 1989; Sander, 1989). Measurements of the humerus differ on the various casts, as indicated in Table 1.

The femur (Fig. 7B) is the only element of the hindlimb that is preserved. The bone is distinctly elongated, slender, and weakly sigmoidally curved. The surface of the bone shows the same striation on the proximal and distal ends as does the humerus. The measurements of the bone differ in the different casts available, as recorded in Table 2.

Anarosaurus heterodontus n. sp.

HOLOTYPE—Institut für Geowissenschaften, Martin-Luther-Universität, Halle (M4/12): right dentary. Schaumkalk (upper lower Muschelkalk) of Freyburg/Unstrut.

REFERRED MATERIAL—Institut für Geowissenschaften, Martin-Luther-Universität, Halle (M4/12): left premaxilla; Schaumkalk (upper lower Muschelkalk) of Freyburg/Unstrut. Museum Freriks, Winterswijk (#20778): skull; lower Muschelkalk, Winterswijk, Netherlands.

DIAGNOSIS—Same as for genus, but about twice as large as *Anarosaurus pumilio* and characterized by a heterodont dentition, a close approximation of prefrontal and postfrontal along the dorsal margin of the orbit, and a distinct sculpturing of dermal bone surface.

LOCUS TYPICUS—Schaumkalk (upper lower Muschelkalk), Freyburg/Unstrut, Germany.

DISTRIBUTION—Lower Muschelkalk, Anisian, Europe.

MORPHOLOGICAL DESCRIPTION—The holotype (Fig. 8) consists of an incomplete right dentary. The total length of the fragment is 67 mm, and therefore represents an animal about twice the size of the holotype of *Anarosaurus pumilio*. The dentary bears a total of 19 preserved teeth, which all

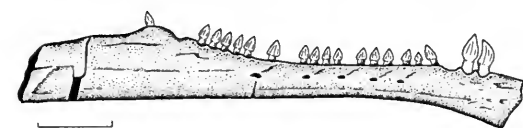
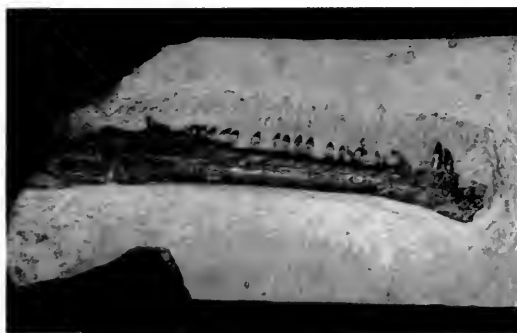


FIG. 8. Holotype of *Anarosaurus heterodontus* n. sp., right dentary (Institut für Geowissenschaften, Martin-Luther-Universität, Halle, M4/12). Scale bar = 10 mm.

share the form diagnostic of the genus *Anarosaurus* (i.e., a constricted tooth base and a lanceolate tooth crown). Of the preserved teeth, the anterior two are distinctly larger (4.5 mm high) than the succeeding teeth (2.5 mm high). Preparation of the dentary from the ventral side revealed a narrow symphysis as is characteristic of pachypleurosaurs. Overall size, tooth morphology, and the increased size of the anterior dentary teeth render the fossil closely similar to a lower jaw reported from the lower Muschelkalk of Winterswijk, erroneously referred to *Cymatosaurus* (Oosterink, 1986, Foto 40).

A perfectly preserved left premaxilla from the Schaumkalk of Freyburg/Unstrut (Fig. 9) has a dentition that matches the morphology diagnostic of *Anarosaurus*. The premaxilla bears five teeth, if a posterolateral trough is interpreted as a facet for the maxilla rather than as part of an alveolus for a sixth tooth. But even with six functional teeth on the premaxilla the number is less than the eight teeth observed on the premaxilla of *Anarosaurus pumilio*. The premaxilla from the Schaumkalk of Freyburg/Unstrut is again about twice the size of the premaxilla in the holotype of *Anarosaurus pumilio*: the distance from the tip of the snout to the anterior margin of the external naris is 25.7 mm in the first, 13.2 mm in the latter.

In terms of size and morphology (five tooth positions), the premaxilla from the Schaumkalk of Freyburg/Unstrut again compares closely to ma-

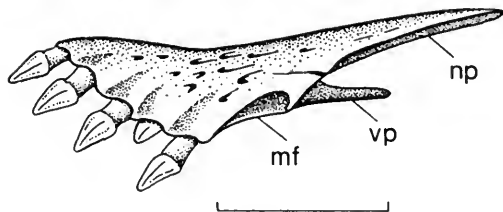


FIG. 9. *Anarosaurus heterodontus* n. sp., left premaxilla (Institut für Geowissenschaften, Martin-Luther-Universität, Halle, M4/12). Scale bar = 10 mm. Abbreviations: mf, maxillary facet; np, nasal process; vp, vomarine process.

terial from the lower Muschelkalk of Winterswijk, which includes a skull deposited in the Museum Freriks, as well as a large amount of undescribed material kept in private collections (Oosterink, 1986, Foto 38). The skull in the Museum Freriks (#20778; Fig. 10) shows a number of characters diagnostic of pachypleurosaurs, such as the relatively short and unconstricted snout, the large prefrontal, the presence of a scleral ring, and the relatively short postorbital portion of the skull, and it shares with other pachypleurosaurs from the lower Muschelkalk the deep embayment of the cheek region and the relatively large upper temporal fossa (as compared to the *Serpianosaurus-Neusticosaurus* clade). Apart from relative size and the heterodont dentition (enlargement of the anterior dentary and premaxillary teeth), the skull differs from the holotype of *Anarosaurus pumilio* by a close approximation of prefrontal and postfrontal, restricting the frontal to a very narrow entry into the dorsal margin of the orbit.

DISCUSSION—The material from the Schaum-

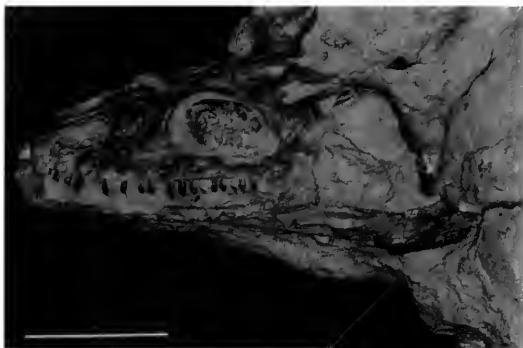


FIG. 10. *Anarosaurus heterodontus* n. sp., skull in left lateral view, from the lower Muschelkalk of Winterswijk (Museum Freriks, #20778). Scale bar = 20 mm.

kalk (upper lower Muschelkalk) of Freyburg/Unstrut and that from the lowermost Muschelkalk of Winterswijk represent a new species of *Anarosaurus* that is geologically somewhat older than *Anarosaurus pumilio* from the lower middle Muschelkalk. Morphological differences include absolute size, the number of premaxillary teeth, the relative size of the anterior dentary and premaxillary teeth, and the configuration of the prefrontal and postfrontal bones. It may be noted that the lower Muschelkalk in the western part of the Germanic basin (Winterswijk) is geologically somewhat younger than the lower Muschelkalk deposits in the eastern part of the basin (Freyburg/Unstrut), which brings the two localities close in geological time.

Using *Captorhinus* (Heaton, 1979) *Petrolacosaurus* (Reisz, 1981), *Claudiosaurus* (Carroll, 1981), and *Youngina* (Gow, 1975) as successive outgroups (Storrs, 1991, 1993a), *Anarosaurus* shows the following plesiomorphic characters: relatively large upper temporal fossae with both the postfrontal and the parietal broadly entering the anterior and anteromedial margin of the fenestra; postorbital distinctly triradiate; humerus retaining an ectepicondylar groove in addition to an entepicondylar foramen, and a well-developed deltopectoral crest; dorsal ribs without pachyostosis; gastral ribs composed of five elements each.

Apomorphic features of *Anarosaurus* include the spatulate expansion of the crown of the teeth, a character discussed and figured in detail by Dames (1890) but which is difficult to ascertain on the basis of the available casts of the holotype of *Anarosaurus pumilio*. The distinction of cervical from dorsal vertebrae is difficult in reptiles in general, a problem aggravated by the fact that the transition

is very poorly preserved in *Anarosaurus*. Nevertheless, a count of 25–26 dorsal vertebrae is most probable, and it is distinctly higher than in all other pachypleurosaurs known.

Both overall size and the position of the entepicondylar foramen at some distance from the distal articular surface of the humerus indicate a mature individual, yet the obturator foramen in the pubis remains widely open. The pubis carries a distinct anteroventral spine resulting from a concavity of its ventral (medial) margin, otherwise known only in *Serpianosaurus* among other pachypleurosaurs (Rieppel, 1989). Isolated elements with an open obturator foramen and an anteroventral spine have also been reported from the base of the middle Muschelkalk (Hagdorn & Simon, 1993), and a concave lower margin of the pubis is a general character for *Simosaurus* and *Nothosaurus* among eusauropterygians.

Carroll and Gaskill (1985, p. 349; see also Kuhn-Schnyder, 1959; Rieppel, 1993) considered the elongated femur diagnostic of *Anarosaurus*. Measurements of the femur differ on different casts, but inspection of Table 2 indicates that 35.75 mm is an average estimate of the length of the femur. Using 23 mm as standard length, the ratio femur length/standard length is 1.55, an exceptionally high value among all other pachypleurosaurs known (Rieppel, 1993), corroborating relative femur length as a diagnostic feature of *Anarosaurus* (Table 3). The corresponding values for other taxa are 0.86 for "*Psilotrachelosaurus*," 0.97–1.2 for *Serpianosaurus* (juveniles and adults, both sexes), 0.91–1.5 for *Neusticosaurus pusillus* (juveniles and adults, both sexes), 0.79–1.06 for *Neusticosaurus peyeri* (juveniles and adults, both sexes), and 0.65–0.96 for *Neusticosaurus edwardsii* (juveniles and adults, both sexes). The distinct striations on the surface of humerus and femur near the proximal and distal heads form another characteristic feature of this genus (sometimes also observed on well-preserved humeri and femora of *Neusticosaurus*: H.-D. Sues, pers. comm.). If these striations are taken as indicators of adult individual age, they document that differences in overall body size and degree of bone sculpturing are not merely ontogenetic variations in *Anarosaurus pumilio* and *Anarosaurus heterodontus*.

***Dactylosaurus* Gürich, 1884**

TYPE SPECIES—*Dactylosaurus gracilis* Gürich, 1884.

GENERIC DIAGNOSIS—A small pachypleurosauroidea with a narrow interorbital bridge formed by the frontals; a close approximation of the postfrontal and prefrontal along the dorsal margin of the orbit due to a long and slender anterior process of the postfrontal (leaving a narrow entry of the frontal in the dorsal margin of the orbit); long but narrow (kidney-shaped) upper temporal fenestrae; no constriction of the dorsal vertebral centra; clavicles with an anterolateral expansion; preaxial margin of the radius with a distinctly concave margin. The humerus is plesiomorphic at the level of the Pachypleurosauroidea but unique within the group by the retention of an entepicondyle distinctly set off from the shaft (in sex *y*).

DISTRIBUTION—Lower Muschelkalk, central Europe.

***Dactylosaurus gracilis* Gürich, 1884**

- 1884 *Dactylosaurus gracilis*, Gürich, p. 125, Pl. 2, Figs. 1, 2.
- 1886 *Dactylosaurus gracilis*, Gürich, pp. 457–458, text fig. 1.
- 1886 *Dactylosaurus gracilis*, Deecke, p. 187.
- 1899 *Dactylosaurus gracilis*, Schrammen, Pl. 25, Fig. 10.
- 1924 *Dactylosaurus gracilis*, Arthaber, pp. 483–484, text fig. 14.
- 1928 *Dactylosaurus schroederi*, Nopcsa, pp. 31–37, Pl. 3, Figs. 1–6.
- 1935 *Dactylosaurus gracilis*, Zangerl, p. 66.
- 1935 *Dactylosaurus schroederi*, Zangerl, p. 67.
- 1959 *Dactylosaurus gracilis*, Kuhn-Schnyder, p. 652.
- 1959 *Dactylosaurus schroederi*, Kuhn-Schnyder, p. 652.
- 1985 *Dactylosaurus gracilis*, Sues and Carroll, pp. 1602, 1608.
- 1985 *Dactylosaurus schroederi*, Sues and Carroll, pp. 1602–1608, text figs. 1–3.
- 1987 *Dactylosaurus gracilis*, Rieppel, pp. 1109–1110.
- 1987 *Dactylosaurus schroederi*, Rieppel, pp. 1109–1110.
- 1993 *Dactylosaurus gracilis*, Rieppel, p. 10.
- 1993 *Dactylosaurus schroederi*, Rieppel, p. 10.

HOLOTYPE—*Dactylosaurus gracilis* was described by Gürich (1884) on the basis of a cast made from a natural mold (Fig. 11) deposited at the Institute of Geological Sciences, University of Wrocław (MGU Wr 3871s). A cast corresponding

TABLE 3. Body proportions in the Pachypleurosauroidea. Abbreviations: fe, femur length; gle-ac, glenoid-acetabulum length; hu, humerus length; stand, standard length (defined as the last four presacral vertebrae).

	<i>Anarosaurus</i>		<i>Dactylosaurus</i>		<i>Serpianosaurus</i>		<i>Neusticosaurus pusillus</i> (Mte. San Giorgio)		<i>Neusticosaurus pusillus</i> (Lettenkeuper)		<i>Neusticosaurus peyeri</i>		<i>Neusticosaurus edwardsii</i>		<i>Neusticosaurus toeplitzi</i>	
	Number of dorsal vertebrae	25–26	19	20–23	22–24	22–24	23–24	19–20	19–20	19–20	19–20	19	19			
Gle-ac: stand		4.38	4.38	3.91–4.80	3.79–5.46	4.21–5.44	3.66–4.58	3.45–4.48	3.66–4.58	3.66–4.58	3.66–4.58	4.66	4.66			
Hu: fe		0.79	0.31	0.75–1.23	0.88–1.15	0.87–1.03	0.90–1.30	0.90–1.30	0.90–1.30	0.90–1.30	0.97	0.97				
Hu: gle-ac		1.24	1.34	0.19–0.36	0.20–0.33	0.18–0.24	0.20–0.33	0.20–0.33	0.20–0.33	0.20–0.33	0.18	0.18				
Hu: stand		1.55	1.55	0.80–1.47	0.95–1.25	0.89–1.25	0.86–1.25	0.86–1.25	0.86–1.25	0.86–1.25	0.83	0.83				
Fe: gle-ac		1.55	1.55	0.21–0.32	0.22–0.30	0.20–0.29	0.20–0.29	0.21–0.25	0.21–0.25	0.21–0.25	0.18	0.18				
Fe: stand		1.55	1.55	0.97–1.20	0.97–1.40	0.91–1.50	0.91–1.50	0.79–1.06	0.79–1.06	0.79–1.06	0.86	0.86				

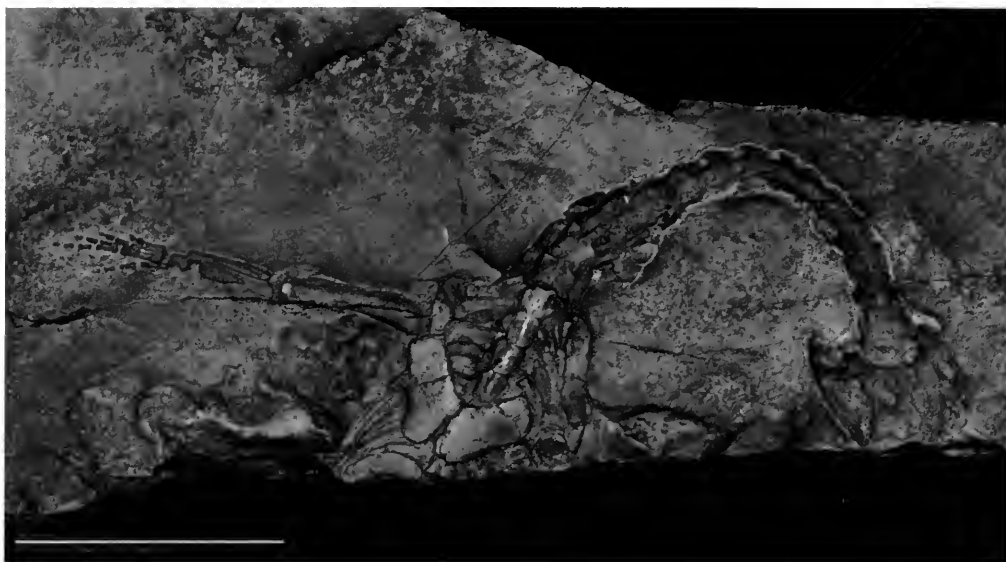


FIG. 11. Holotype of *Dactylosaurus gracilis* Gürich (MGU Wr 3871s). Scale bar = 20 mm.

to the figure given by Gürich (1884, Pl. II, Figs. 1, 2) is kept at the Natural History Museum, Humboldt University, Berlin (MB R. 63). The holotype comes from Michalkowitz, Upper Silesia (now Michalowice, Poland), assigned to the lower Muschelkalk.

The holotype of *Dactylosaurus schroederi* Nopcsa, 1928, was deposited in the collections of the Preussische Geologische Landesanstalt in Berlin (Kuhn, 1934), and now is in the collections of the Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin (uncatalogued) (Fig. 12). A rubber cast of the specimen, described by Sues and Carroll (1985), is kept at the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a.M. (SMF R-4097 a, b). The holotype comes from deposits assigned to the lower Muschelkalk of Gross-Stein, Upper Silesia.

The holotypes of *Dactylosaurus gracilis* as well as *D. schroederi* are both natural molds preserved in yellow matrix. The color of the matrix, as well as the preservation of vertebrate fossils as natural molds, is characteristic of the upper Buntsandstein (Röt) which underlies the lower Gogolin Beds (H. Hagdorn, pers. comm.).

REFERRED MATERIAL—Institut und Museum für Geologie und Paläontologie, University of Tübingen, uncatalogued (Fig. 13), lowermost Muschelkalk of Gogolin (lower Gogolin beds). A poorly preserved specimen represented by barely visible impressions of the skull, cervical and anterior

dorsal region of the vertebral column preserved in dorsal view or as faint impression (of the ventral aspect), right humerus, and left forelimb. The specimen is slightly larger than the one described by Nopcsa (1928).

Nopcsa (1928) and Sues and Carroll (1985) refer to Meyer (1847–1855) who figured humeri closely similar to those of *Dactylosaurus gracilis* from the Muschelkalk (“Saurier-Kalk”) from Jena. Other humeri of this type are known from the lower Muschelkalk of Bobrek near Beuthen (Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, drawer S 45/5 right) (Fig. 14), and from the Muschelkalk of Gogolin (Museum für Naturkunde, Berlin, MB R. 772.1., MB R. 769, and uncatalogued; Institut und Museum für Geologie und Paläontologie, University of Tübingen GPIT 1744/1-10; Rieppel, 1993).

DIAGNOSIS—Same as for genus, of which this is the only known species.

LOCUS TYPICUS—Upper Buntsandstein of Michalowice, Upper Silesia (Gorny Slask, Poland).

DISTRIBUTION—Upper Buntsandstein and lower Muschelkalk, Europe.

COMMENTS—*Dactylosaurus gracilis* is the type species of the genus (Gürich, 1884). The cast available in the Natural History Museum in Berlin is of rather poor quality, and shows little morphological detail. The following description of the specimen is based on a new silicon cast made from

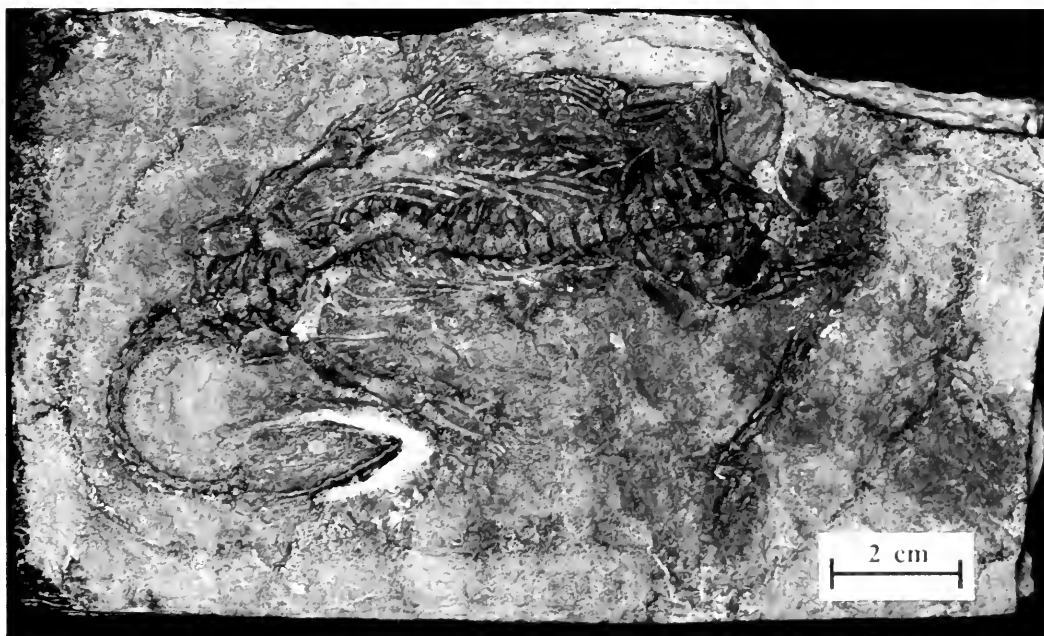


FIG. 12. Holotype of *Dactylosaurus schroederi* Nopcsa (BGR, uncatalogued).

the holotype in 1994. Preserved are the posterior part of the skull, the cervical vertebral column, the pectoral girdle, and the right forelimb, all exposed in dorsal view on the cast.

The posterior part of the skull shows a deeply excavated cheek and relatively large, kidney-shaped upper temporal fossae. Sutures are difficult to

identify except for the posterior end of the post-frontal, which defines the anteromedial margin of the upper temporal fossa. Sixteen cervical vertebrae (including the atlas) are preserved in articulation; an additional vertebra would have been positioned at the level of the clavicles. This count of 17 cervical vertebrae corresponds to the holo-

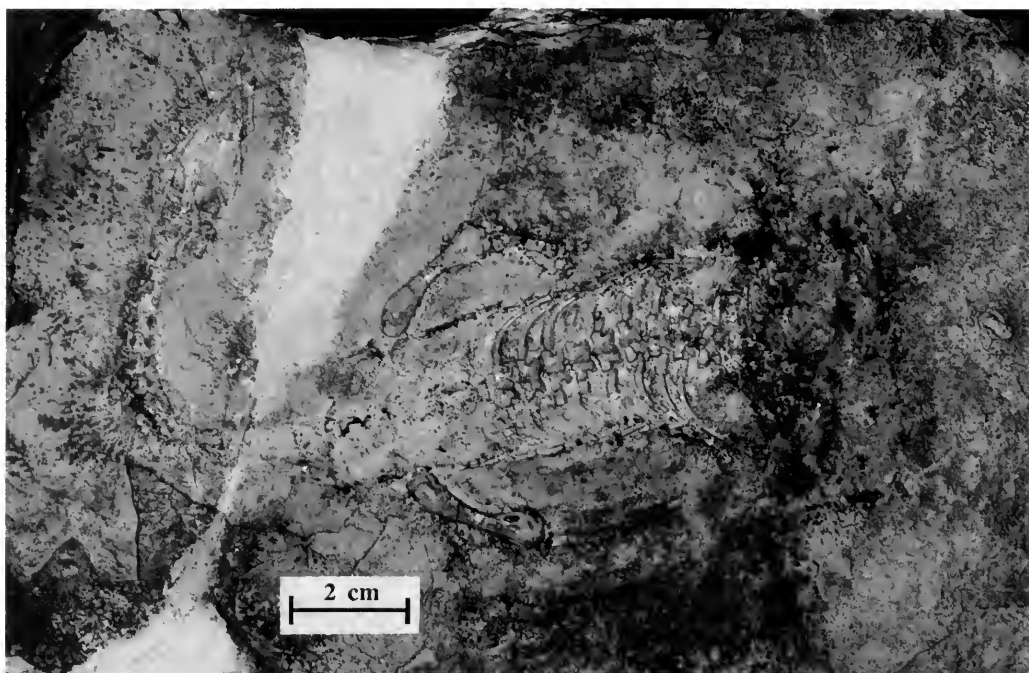


FIG. 13. *Dactylosaurus gracilis* Gürich from the lower Muschelkalk of Gogolin, Upper Silesia (Gorny Slask, Poland) (GPIT, uncatalogued).



FIG. 14. *Dactylosaurus gracilis* Gürich, humerus, from the lower Muschelkalk of Bobrek near Beuthen (BGR, drawer S 45/5 right). Scale bar = 10 mm.

type of *Dactylosaurus schroederi* Nopcsa, 1928. Cervical ribs can only be identified along the posterior part of the cervical vertebral column, and they are of typical structure with a free anterior process. The centra of four anterior dorsal vertebrae are preserved and exposed in ventral view on the actual specimen: they show no sign of constriction, but slightly convex lateral margins instead. The proximal part of the dorsal ribs (as far as preserved) shows no pachyostosis.

In the pectoral girdle, the distal end of the clavicle is seen to overlap with the anterior and medial aspect of the scapula in a typical pachypleurosaurid pattern. The interclavicle cannot be identified. The clavicle shows expanded lateral corners that are not as pronounced as in the holotype of *Dactylosaurus schroederi*, possibly a juvenile character. The coracoids are represented by impressions only. Their length is 7.4 (8) mm, their proximal width is 3.6 (3) mm, their minimal width is 3.4 (3.4) mm, and their distal width is 4.6 (5.3) mm (values in parentheses refer to the right element; all measurements were taken on the natural mold). The coracoids of both sides meet ventrally in a well-defined suture, but their proximal expansion is relatively weak, and the proximal margin shows no notch indicating the position of the

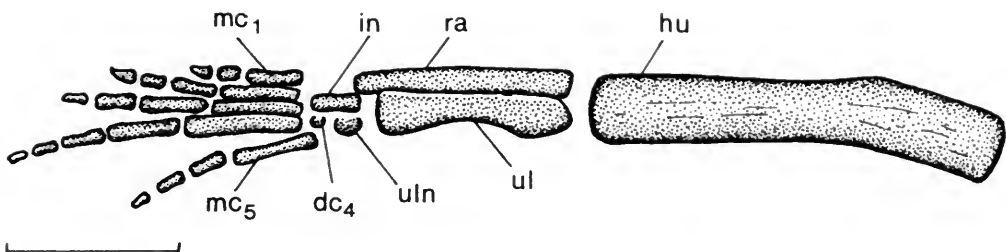


FIG. 15. *Dactylosaurus gracilis* Gürich, holotype (MGU Wr 3871s), right forelimb. Scale bar = 5 mm. Abbreviations: dc₄, distal carpal 4; hu, humerus; in, intermedium; mc₁, metacarpal 1; mc₅, metacarpal 5; ra, radius; ul, ulna; uln, ulnare.

coracoid foramen. This might indicate incomplete ossification of the coracoid in a juvenile specimen.

The right front limb is well preserved (Fig. 15). The right humerus is a slightly curved element that shows hardly any morphological differentiation, as is characteristic of juvenile pachypleurosaurs (Rieppel, 1989; Sander, 1989). The deltopectoral crest is hardly differentiated, and an entepicondylar foramen cannot be identified. In juvenile pachypleurosaurs, the entepicondylar foramen lies at the distal margin of the ossified part of the humerus or, in even earlier stages, beyond that (Rieppel, 1989; Sander, 1989). The total length of the humerus is 11.9 mm, its proximal width is 2.1 mm, its minimal width is 1.85 mm, and its distal width is 2 mm. The radius is incompletely exposed due to the overlapping ulna, but appears slightly longer than the ulna. Total length of the radius is 6.3 mm, that of the ulna is 5.8 mm. Some controversy surrounds the structure of the carpus (Gürich, 1886), but the new cast taken from the holotype corroborates Gürich's (1886) description of three ossified carpal elements. The intermedium is elongated and rectangular in shape; posterior to it lie the rounded ulnare and distal carpal 4. The phalanges are incompletely preserved, probably due to incomplete ossification. The cast shows a number of ossified elements that correspond to Gürich's (1886) illustration of 2-3-3-4-3. Unguals are unequivocally identified on digits 1 and 2 only; the count for the remaining digits may therefore be incomplete. Sander (1989) documented a proximo-distal sequence of ossification of the phalanges in *Neusticosaurus pusillus*.

The overall size of *Dactylosaurus gracilis*, and details of morphology throughout the skeleton, indicate that the holotype of that species is a juvenile specimen. The only character potentially contradicting this conclusion is the advanced degree of ossification in the carpus, but variation in the timing of ossification can be extensive in extant rep-

tiles (Rieppel, 1994a). The relatively low count of cervical vertebrae (17) is shared with *Dactylosaurus schroederi* Nopcsa, 1928, and is otherwise known only from lower Ladinian pachypleurosaurs (*Neusticosaurus peyeri*: Sander, 1989; *Neusticosaurus edwardsii*: Carroll & Gaskill, 1985). The latter taxa are characterized by a relatively smaller upper temporal fossa than is observed in *Dactylosaurus gracilis* and *D. schroederi*. On the basis of the limited data available, we conclude that *Dactylosaurus gracilis* Gürich, 1884 and *Dactylosaurus schroederi* Nopcsa, 1928, are subjective synonyms (see also Sues & Carroll, 1985); the first name has priority.

MORPHOLOGICAL DESCRIPTION—The morphological description of *Dactylosaurus gracilis* is based on new latex casts made from the original specimen (natural mold) described by Nopcsa (1928, holotype of *Dactylosaurus schroederi*), as well as on the rubber casts kept at the Senckenberg Museum, Frankfurt. The specimen is represented by natural molds of part and counterpart. The total length of the fossil must remain unknown because of the incompletely preserved tail, but it must have exceeded 213 mm; snout-vent length is 158 mm. Skull length (the length of the left lower jaw ramus in ventral view) is 27 mm; glenoid-acetabulum length (measured on the right side of the body) is 68 mm; standard length (length of the last four dorsal vertebral centra) is 15.5 mm (the length of the last dorsal vertebral centrum is 3.5 mm).

In the skull (Fig. 16), the snout complex is not well exposed. The nasal process of the premaxilla remains separated from the frontal by the broad nasals, which meet along a middorsal suture. The frontal forms a short anteromedial process entering between the nasals, as well as short anterolateral processes that meet the maxilla and thereby separate the prefrontal from the nasal. The prefrontal reaches high up along the anterodorsal margin of the orbit. The postfrontal forms a slen-

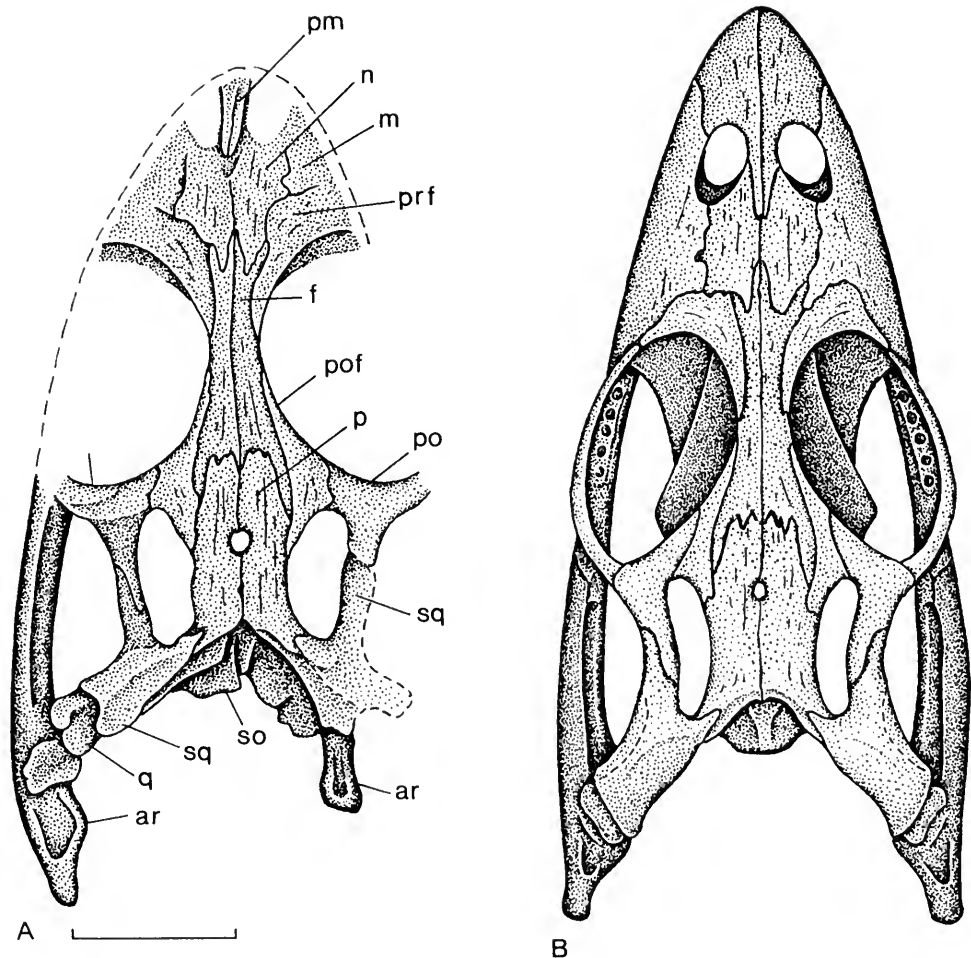


FIG. 16. Skull of *Dactylosaurus gracilis* Gürich (BGR, uncatalogued). A, Drawn after a new cast made from the original of Nopcsa (1928); B, reconstruction of the skull in dorsal view. Scale bar = 5 mm. Abbreviations: ar, articular; f, frontal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; q, quadrate; so, supraoccipital; sq, squamosal.

der anterior process running along the postero-dorsal margin of the orbit. The prefrontal and postfrontal fail to meet, however, allowing the frontal to enter into the dorsal margin of the orbit for a short distance. The interorbital bridge formed by the paired frontals is narrow (2 mm in the latex cast taken from the original specimen). The frontoparietal suture is in a rather forward position. The posterolateral processes of the frontals extend posteriorly between the parietal and postfrontal.

The skull table is well exposed. The upper temporal fossae are relatively large and of an elongated kidney shape. The length of the upper temporal fossa is 4.3 mm (right) and 4.5 mm (left), respectively; the width of the upper temporal fossa is 1.5

mm (right) and 1.3 mm (left), respectively. The postfrontal, the triradiate postorbital, the parietal, and the squamosal all participate in the formation of the margin of the upper temporal fossa. The paired parietals enclose the pineal foramen, which is positioned halfway along the length of the parietals.

The occiput is difficult to analyze. In particular, the occipital exposure of the parietal, and its relation to the squamosal, remain unclear.

The ventral view of the skull displays a dermal palate of typical pachypleurosauroid structure; little can be added to its description and illustration by Sues and Carroll (1985). The pterygoid shows a thickening (a rudimentary "transverse flange")

along the anterior margin of the subtemporal fossa. There is no positive evidence for the presence or absence of an ectopterygoid. A ceratobranchial element is preserved, overlying the posterior part of the left pterygoid.

Dactylosaurus gracilis shows a total of 36 presacral vertebrae, of which 17 are counted as cervical elements (Sues & Carroll, 1985), characterized by a keeled ventral surface of the centrum. The ventral surface of the dorsal centra is smooth, and the centra are not constricted. The neural arches are pachyostotic, and the neural spines are consistently low. Based on the Senckenberg casts, Sues and Carroll (1985) believed the neurocentral sutures to be closed in *Dactylosaurus gracilis*, but they are quite distinct in the cervical, posterior dorsal (where they pass below the transverse processes), sacral, and preserved caudal region (where they pass through the transverse processes). The material does not allow the presence of a neurocentral suture in the anterior dorsal region to be ascertained.

Sues and Carroll (1985) describe atlantal ribs, which are difficult to identify, however. The cervical ribs bear a distinct free anterior process. The dorsal ribs are not pachyostotic, and the last three dorsal ("lumbar") ribs are distinctly reduced in length.

Dactylosaurus gracilis shows three sacral vertebrae. The sacral ribs are broad, stout elements with a weak proximal expansion; they are not fused to the respective vertebrae. Caudal ribs (again not fused to caudal vertebrae) and chevron bones are not well exposed. Gastral ribs are likewise poorly preserved, but what little is present suggests that they are composed of five elements each, one medioventral and two lateral ones on either side.

Little can be added to Sues and Carroll's (1985) description of the pectoral girdle. The right clavicle shows a rounded and somewhat expanded anterolateral edge (Fig. 17). This character is otherwise known from *Anarosaurus* only among other pachypleurosaurs (undescribed material from Winterswijk), but is distinctly developed in the eusauropterygian genera *Nothosaurus* and *Simosaurus* (pers. obs.). The overlap of the clavicles with the anterior and medial surface of the scapula is well exposed in dorsal view on the right side of the specimen. The shape of the interclavicle remains unknown. The scapula is of the typical sauropterygian structure with a reduced and posteriorly directed dorsal wing. The coracoid foramen is distinct and enclosed between the notched posteromedial margin of the scapula and the opposing

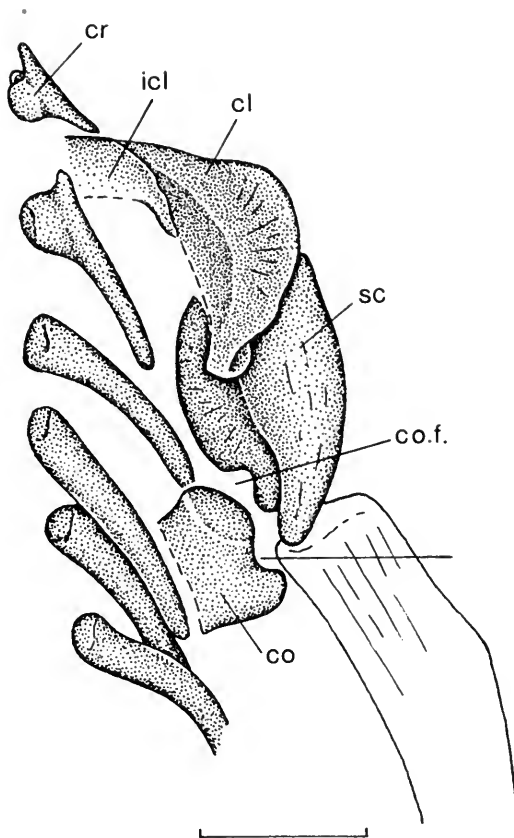


FIG. 17. Pectoral girdle of *Dactylosaurus gracilis* Gürich (BGR, uncatalogued), drawn after a new cast made from the original of Nopcsa (1928). Scale bar = 5 mm. Abbreviations: cl, clavicle; co, coracoid; co.f., coracoid foramen; cr, cervical rib; icl, interclavicle; sc, scapula.

posterolateral margin of the coracoid. The right coracoid measures 12.5 mm in length. In the pelvic girdle, the pubis shows a complete enclosure of the obturator foramen by bone (Fig. 18); the bone is completely fused between the obturator foramen and the posterior edge of the pubis. The pubis is a relatively broad element with a length of 11 mm, a proximal width of 6.8 mm, a minimal width of 5 mm, and a distal width of 7.8 mm. The right ischium is well exposed, and shows a markedly thickened proximal (acetabular) portion. The bone is 12 mm long, its proximal width is 4.5 mm, its minimal width is 3.5 mm, its distal width is 13 mm. Sues and Carroll (1985) describe a well-developed supra-acetabular buttress, but in ventral view the ilium does not display its acetabular portion; in dorsal view, the left ilium is concealed by sacral ribs.

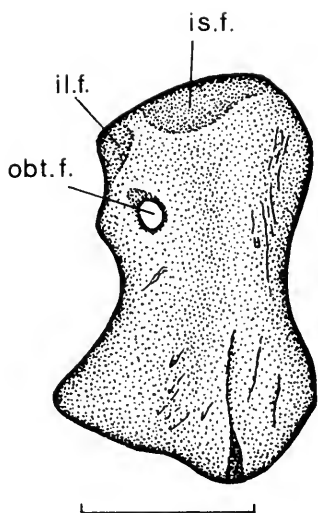


FIG. 18. Right pubis of *Dactylosaurus gracilis* Gürich (BGR, uncatalogued), drawn after SMNS R-4907a. Scale bar = 5 mm. Abbreviations: il.f., facet for ilium; is.f., facet for ischium; obt.f., obturator foramen.

The humerus of *Dactylosaurus gracilis* is very distinctive (Fig. 19), at least in sex γ (*sensu* Rieppel, 1989, and Sander, 1989; see also the discussion in Rieppel, 1993). The element bears a well-developed deltopectoral crest distinctly set off from the waisted diaphysis. The distal head is broadly expanded, with the entepicondyle forming a medial process distinctly set off from the articular head. The entepicondylar foramen lies at some distance from the distal articulation. The distal articular heads are level. A deep ectepicondylar ridge is present.

The radius of *Dactylosaurus gracilis* appears to be characterized by a distinct notch in the medial (preaxial) margin of the shaft (Fig. 20A). Sues and Carroll (1985, p. 1607) attribute this feature to a preservational artifact. Latex casts taken from the original specimen show the concavity on the preaxial margin of the radius in both limbs, more distinctly in their ventral exposure (and a similar concavity is also observed in the radius of undescribed *Anarosaurus* material from Winterswijk).

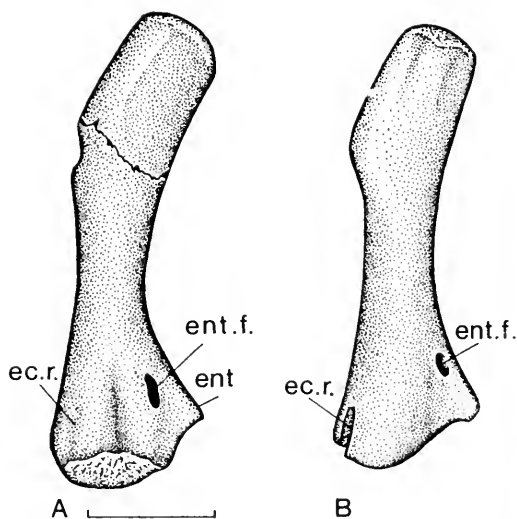


FIG. 19. Humerus of *Dactylosaurus gracilis* Gürich (BGR, uncatalogued). A, Right humerus in ventral view, drawn after SMNS R-4907a; B, left humerus in dorsal view, drawn after SMNS R-4907b. Scale bar = 5 mm. Abbreviations: ec.r., ectepicondylar ridge; ent, entepicondyle; ent.f., entepicondylar foramen.

The ulna is somewhat shorter than the radius and bears a weakly developed olecranon on its expanded proximal head.

The carpus (Fig. 20A) comprises three undisputed ossified elements, viz. the intermedium, the ulnare, and the fourth distal carpal. The intermedium is of subcircular shape and lies distal to the spatium interosseum between radius and ulna. A pisiform is distinct in Nopcsa's (1928) retouched photograph of the specimen, and its presence (or that of a neomorph in its position) was confirmed by Sues and Carroll (1985). Latex casts taken from the original specimen indicate the presence of a minute structure next to the ulnare in the left limb only. If that structure represents a carpal ossification, the pisiform (or a neomorph) would be extremely small and present in one limb only. In extant reptiles, the pisiform generally is the last of all carpal elements to ossify (Rieppel, 1992). Evidence that this bone (or a neomorph) is, indeed,

TABLE 4. Measurements of the humerus in articulated specimens of *Dactylosaurus gracilis* Gürich.

	Length		Proximal width		Minimal width		Distal width	
	Left	Right	Left	Right	Left	Right	Left	Right
Specimen Gürich (1884)		11.9		2.1		1.85		2
Specimen Nopcsa (1928)	20.5	21	4	4	3	2.8	7	6.5
Specimen in Tübingen	25.2	25.6	5.1	5	3	3	7	7.2

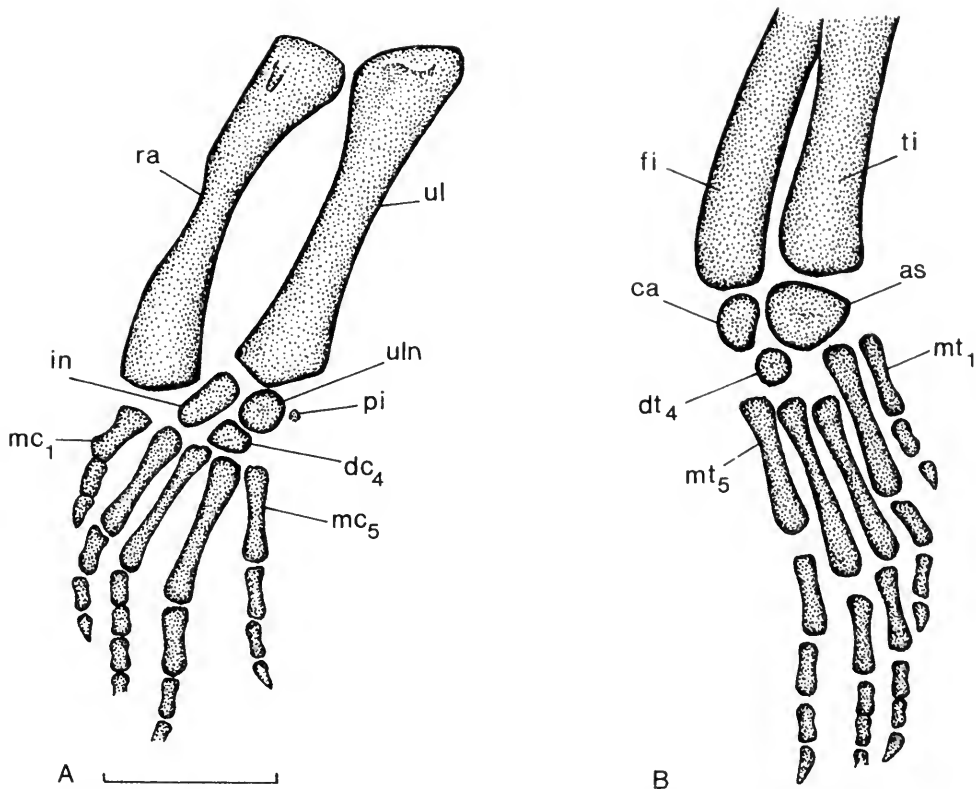


FIG. 20. Manus and pes of *Dactylosaurus gracilis* Gürich (BGR, uncatalogued). A, Left forelimb, dorsal view, drawn after SMNS R-4907b; B, right hindlimb, ventral view, drawn after SMNS R-4907a. Scale bar = 5 mm. Abbreviations: as, astragalus; ca, calcaneum; dc₄, distal carpal 4; dt₄, distal tarsal 4; fi, fibula; in, intermedium; mc₁, metacarpal 1; mc₅, metacarpal 5; mt₁, metatarsal 1; mt₅, metatarsal 5; pi, pisiform; ra, radius; ti, tibia; ul, ulna; uln, ulnare.

present in *Dactylosaurus gracilis* is here considered equivocal. The phalangeal count in the manus is 2-3-4-?-3. The presence of either four or five phalanges in the fourth digit cannot be ascertained unequivocally. Measurements of the humerus are given in Table 4.

Only the proximal head of the left femur and the distal head of the right femur are exposed. These indicate a slender bone with tibial and fibular articular heads level. The right fibula is only partially exposed. The right tibia is a little sturdier than the fibula but it is still a rather slender bone

TABLE 5. Measurements of the limb bones of *Dactylosaurus gracilis* (holotype of *Dactylosaurus schroederi* Nopcsa; BGR, uncatalogued).

	Length		Proximal width		Minimal width		Distal width	
	Left	Right	Left	Right	Left	Right	Left	Right
Humerus	20.5	21	4	4	3	2.8	7	6.5
Radius	11.1	11.1	2.5	2.2	1	1	1.8	1.6
Ulna	10.2	9.7	2.9	2.8	1.2	1.2	2.9	2.8
Metacarpal 3	4.5	4.7	—	—	—	—	—	—
Metacarpal 4	3.8	3.9	—	—	—	—	—	—
Femur	—	—	—	—	—	—	—	—
Tibia	—	9.8	—	3	—	2.0	—	2.3
Fibula	—	—	—	—	—	—	—	—
Metatarsal 3	—	6.5	—	—	—	—	—	—
Metatarsal 4	—	6.8	—	—	—	—	—	—

with a straight medial, and a slightly concave lateral, margin. Three ossified elements can be identified in the tarsus (Fig. 20B), viz. the astragalus, calcaneum, and the fourth distal tarsal. The phalangeal formula in the pes is 2-3-?-5-4, five phalanges in the fourth digit representing the plesiomorphic condition. Measurements of the limb bones of the specimen described by Nopcsa are given in Table 5.

DISCUSSION—The body proportions of *Dactylosaurus gracilis* fall squarely within the range of variability of the Monte San Giorgio pachypleurosaurs (Table 3). The upper temporal fenestrae are distinctly smaller than the orbit, yet distinctly larger than the upper temporal fenestrae in *Serpianosaurus* and *Neusticosaurus*. As in *Anarosaurus*, the postfrontal, postorbital, and parietal broadly enter the margin of the upper temporal fossa (unlike in *Serpianosaurus* and *Neusticosaurus*), but the upper temporal fenestrae in *Dactylosaurus gracilis* are rather narrow and elongated as opposed to the subcircular contours of the upper temporal fenestra in *Anarosaurus*. As in *Anarosaurus*, the upper temporal arch of *Dactylosaurus* is narrow and the cheek deeply excavated, unlike *Serpianosaurus* and *Neusticosaurus*, which show a broadened postorbital and squamosal. Like other pachypleurosaurs, *Dactylosaurus* shows a rather anterior position of the frontoparietal suture, with distinct posterolateral processes of the frontals extending backward between the parietal and postfrontal. *Dactylosaurus gracilis* differs from other pachypleurosaurs except *Keichousaurus* in the narrow interorbital bridge formed by the frontals; the close approximation of the prefrontal and postfrontal bones along the dorsal margin of the orbit is shared with undescribed *Anarosaurus* material from Winterswijk. The latter character is associated with the development of a long and slender anterior process of the postfrontal.

The cervical vertebral count in *Dactylosaurus gracilis* is low compared to other pachypleurosaurs, particularly those of the lower Muschelkalk (*Anarosaurus*: 19–20 [see above]; *Keichousaurus*: 26; *Serpianosaurus*: ?14–18 [Rieppel, 1989]; *Neusticosaurus*: 15–20 [Carroll & Gaskill, 1985; Sander, 1989], but the significance of this character is difficult to assess because of the lack of data on intraspecific variability. Vertebrae are difficult to count in the Tübingen specimen of *Dactylosaurus gracilis*, but there may be as many as 19 cervicals (and 17 preserved dorsals).

The morphology of the humerus of *Dactylosaurus* is quite distinctive. Nopcsa (1928; see also Sues

& Carroll, 1985, p. 1607) found it similar to isolated humeri from the lower Muschelkalk referred to “Macrotracheli” by H.v. Meyer (1847–1855). Huene (1942, Fig. 11) figured a humerus from much younger deposits (lowermost Lettenkohle of Schwäbisch Hall, southern Germany), which Sues and Carroll (1985, p. 1607) again found similar to that of *Dactylosaurus*, but the Lettenkohle specimen appears more curved rather than angulated as in the humerus of *Dactylosaurus*, and the entepicondyle is set off from the shaft by a crack rather than a notch. Indeed, the specimen figured by Huene (1942) closely resembles the humerus of *Neusticosaurus pusillus* (Sander, 1989, Fig. 15c), and does not indicate the extension of the stratigraphic occurrence of *Dactylosaurus* beyond the lower Muschelkalk.

The humerus of *Dactylosaurus gracilis* (sex *y sensu* Rieppel, 1989; Sander, 1989) is plesiomorphic with respect to all other pachypleurosaurs in the retention of a well-differentiated entepicondyle and a distinct ectepicondylar groove. The juvenile specimen described by Gürich (1884) indicates similar ontogenetic changes in the morphological differentiation as those known in other pachypleurosaurs (Rieppel, 1989; Sander, 1989), while a series of humeri from the lower Muschelkalk of Gogolin, Upper Silesia (GPIT 1744/1-10) indicates a similar sexual dimorphism in *Dactylosaurus gracilis* as is known for other pachypleurosaurs (Rieppel, 1989; Sander, 1989). As in other pachypleurosaurs, the index of minimal width/distal width is most informative with respect to ontogenetic changes and sexual dimorphism in the differentiation of the humerus. Plotting all available material (see referred material above) results in an index of 0.53–0.67 for sex *x* and/or juveniles, and 0.40–0.57 for adult specimens of sex *y*. Overlap of this ratio (in the range of 0.54–0.57) between sexes is restricted to three specimens (MB R. uncatalogued, GPIT 1744/1–2), and may reflect natural variability as well as wear of the ectepicondyle during postmortem transport.

Sauropterygia incertae sedis

Huene (1944) described an isolated humerus from the lowermost Muschelkalk (lower Gogolin beds) of Gogolin, Upper Silesia, which is housed in the Staatliches Museum für Naturkunde, Stuttgart (SMNS 16253). The humerus is noteworthy because of its well-developed deltopectoral crest,

the presence of a rudimentary supinator ridge, a distinct ectepicondylar groove, and the absence of an entepicondylar foramen (Fig. 21). The total length of the humerus is 104.1 mm, its proximal width is 28.5 mm, minimal width at mid-diaphysis is 12.4 mm, and the distal width is 29 mm.

The humerus is morphologically well differentiated and in one character (presence of the supinator ridge) more plesiomorphic than any other sauropterygian humerus known. It differs from the humerus of *Dactylosaurus* in the absence of an entepicondylar foramen and in the absence of an entepicondyle distinctly set off from the shaft of the bone. Humeri of *Nothosaurus* sp. from the lower Muschelkalk (Natural History Museum, Humboldt University, Berlin, MB R. 162.2; MB R. 162.4; MB R. 777; MB R. I. 007; Martin Luther Universität, Institut für Geowissenschaften, Halle, uncatalogued) differ from SMNS 16253 by the absence of the supinator ridge, by the presence of an entepicondylar foramen, and by a less distinctly developed ectepicondylar groove. Also, the humerus of *Nothosaurus* is relatively broader at mid-diaphysis than is SMNS 16253. Indeed, the slender appearance of the humerus SMNS 16253 renders it comparable to two humeri of *Cymatosaurus*, one from the lower Muschelkalk of Winterswijk, Netherlands (SMNS 58463), the other from the uppermost lower Muschelkalk (Schaumkalk) of Freyburg a.d. Unstrut (Institut für Geowissenschaften, Martin-Luther-Universität, Halle, uncatalogued) (Rieppel, 1994b). The ratio of humerus length to minimal width at mid-diaphysis is approximately 7.8 in *Anarosaurus*, and it ranges from 5.75 to 7.35 in *Dactylosaurus gracilis* sex *x*, 5.0 to 8.47 in *Dactylosaurus gracilis* sex *y*, 4.94 to 7.79 in *Nothosaurus* sp. from the lower Muschelkalk, and 8.3 to 8.85 in *Cymatosaurus*; the ratio is 8.39 in SMNS 16253. The humerus of *Cymatosaurus* approaches SMNS 16253 in overall size, but it differs from SMNS 16253 by the presence of an entepicondylar foramen (Halle specimen) or groove (SMNS 58463), an even deeper ectepicondylar groove, and in particular by separate articular condyles for radius and ulna, which are not level.

In conclusion, the humerus SMNS 16253 cannot be referred to any known sauropterygian taxon from the lower Muschelkalk. Huene (1944) believed the specimen to be of particular importance because of its "primitive" morphology, but the humerus of *Cymatosaurus* shows even more plesiomorphic characters, such as the presence of an entepicondylar foramen, well-differentiated ect- and entepicondyles, a deep ectepicondylar groove,



FIG. 21. Sauropterygia indet., an isolated humerus from the lower Muschelkalk of Gogolin, Upper Silesia (Gorný Slask, Poland) (original of Huene, 1944, SMNS 16253). Scale bar = 20 mm.

and separate articular condyles for the radius and ulna.

Phylogenetic Analysis

Reconstruction of the evolutionary and biogeographical history of the Pachypleurosauroidea must be based on a well-corroborated hypothesis of phylogenetic relationships. This study of pachypleurosaurs from the lower Muschelkalk provides a much expanded data matrix for the analysis of pachypleurosaur interrelationships, resulting in a modification of phylogenetic hypotheses presented in earlier studies (Rieppel, 1987, 1993). The terminal taxa of pachypleurosaurs entered in this analysis are *Anarosaurus*, *Keichousaurus* (Young, 1958, and pers. obs.), *Dactylosaurus*, the three species of *Neusticosaurus* (*N. edwardsii*: Carroll & Gaskill, 1985; *N. peyeri* and *N. pusillus*: Sander, 1989; *N. staubi* Kuhn-Schnyder, 1959, is a junior synonym of *N. pusillus*: Sander, 1989, p. 580), "*Psilotrachelosaurus*" *toeplitzchi* (Rieppel, 1993), and *Serpianosaurus* (Rieppel, 1989). The phylogenetic analysis was performed using the software package PAUP version 3.1.1. developed by David

L. Swofford (Swofford, 1990; Swofford & Begle, 1993). DELTRAN character optimization will be favored in the diagnosis of monophyletic taxa as it minimizes subsequent loss of diagnostic characters within the clade. In the listing of synapomorphies, 'D' will refer to DELTRAN, 'A' to ACCTRAN character optimization.

Monophyly of the Pachypleurosauroidea had generally been assumed, but evidence in its support remained scanty. Sanz, Alafont, and Moratalla (1993) recently published a phylogenetic analysis of Sauropterygia indicating paraphyly of the Pachypleurosauroidea: *Anarosaurus* was found to be more closely related to Eusauropterygia (*sensu* Tschanz, 1989) than to a clade comprising *Dactylosaurus* plus "*Pachypleurosaurus*." Reanalysis of their data matrix did not duplicate their results. Rooting the branch-and-bound search on an all-0 ancestor generates six equally parsimonious trees (tree length [TL]: 46 steps; consistency index [CI]: 0.826; rescaled consistency index [RC]: 0.723), which all indicate paraphyly of pachypleurosaurs, but in all six trees the *Dactylosaurus*-"*Pachypleurosaurus*" clade is closer to the Eusauropterygia than *Anarosaurus*. The character uniting the *Dactylosaurus*-"*Pachypleurosaurus*" clade with the Eusauropterygia is the relative length of the humerus exceeding that of the femur (in adults, and in sex γ [Rieppel, 1989; Sander, 1989] if applicable; reversed in "*Psilotrachelosaurus*" *toeplitzschii*). However, the relatively long femur is an autapomorphy of *Anarosaurus* among Sauropterygia.

Monophyly of the Pachypleurosauroidea remains an issue because *Anarosaurus* shares some characters with the Eusauropterygia that might indicate paraphyly, such as the sculpturing of dermal skull bones, the large and leaf-shaped nasals closely resembling those from the lower Muschelkalk *Nothosaurus* (undescribed material from Winterswijk; see also Schröder, 1914), the enlarged anterior teeth in the upper and lower jaws (*Anarosaurus heterodontus*), the anterolateral expansion of the clavicles (undescribed material from Winterswijk, also shared by *Dactylosaurus*), the high number of dorsal vertebrae, and the concave lower margin of the pubis (resulting in an anteroventral spine on the pubis). *Keichousaurus*, on the other hand, shares with *Lariosaurus* the broad ulna and hyperphalangy in the manus. However, *Keichousaurus* could potentially be the sister-taxon to all other Sauropterygia, since it lacks some of the sauropterygian synapomorphies such as anterolateral processes of the frontal, three or more sacral ver-

tebrae, lack of distal expansion of the sacral ribs, and a reduction of carpal ossifications to three or less in the adult (reversed in some specimens of *Lariosaurus*).

Previous studies (Rieppel, 1989) supported the monophyly of pachypleurosaurs on the basis of the two characters, that is, absence of an ectopterygoid, and presence of a trough on the dorsal surface of the retroarticular process to accommodate the mandibular condyle of the quadrate during jaw opening (Rieppel, 1989). Additional support for the monophyly of the Pachypleurosauroidea derives from additional character congruence, which hinges on the nesting of the clade within the Sauropterygia and relative to the position of *Placodus*.

Storrs (1991, 1993a) hypothesized placodonts as the sister-group of the Eusauropterygia, the two clades constituting his Nothosauriformes. The monophyletic pachypleurosaurs were shown to be the sister-group of the Nothosauriformes. Reanalysis of Storrs's (1993a) data matrix showed his characters 10, 40, 50, 54, 55, 56, and 72 to be uninformative (56 only becomes informative relative to an all-0 ancestor). The same strict consensus tree topology results for the unrooted network, rooting the tree on all-zero ancestor, or rooting the tree on *Captorhinus*, *Petrolacosaurus*, *Youngina*, and *Cladiosaurus*. The latter procedure results in 12 equally parsimonious trees with a tree length of 182 steps, CI = 0.665, and RC = 0.524. The strict consensus tree is the same as in Storrs (1993a), except for the unresolved position of *Silvestrosaurus*; the latter genus groups with the *Nothosaurus*-*Paranothosaurus* clade in the 50% majority rule consensus tree. The diagnosis of the monophyletic Pachypleurosauroidea is predicated on the position of *Placodus* as sister-taxon of the Eusauropterygia: neck length approximately equal to trunk length (D); suborbital fenestra absent (D, coded present in *Placodus*; for further discussion of this character, see Rieppel, 1994b); palatal dentition absent (coded present in *Placodus*); sacral ribs distally reduced (A, D; *Keichousaurus* was not included in the analysis. The character was coded unknown for *Placodus*); small iliac blade (A, D); radius longer than ulna (D).

Expansion of the database both in terms of taxa and characters (Rieppel, 1994b) resulted in a reversion of sauropterygian interrelationships. The Placodontia were shown to be the sister-taxon to all other Sauropterygia, the Eosauropterygia. Within the latter, *Corosaurus* turned out to be the sister-taxon to an unnamed clade comprising the monophyletic Pachypleurosauroidea and Eusauro-

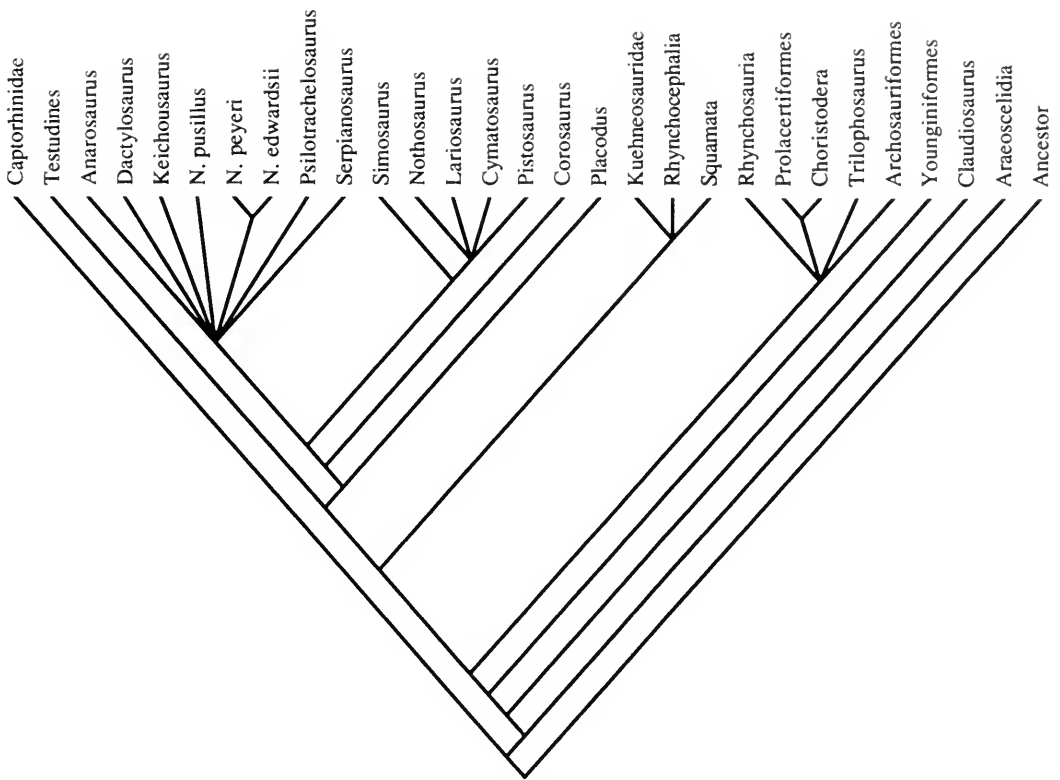


FIG. 22. Strict consensus tree of sauropterygian interrelationships, generated from 54 MPRs (28 taxa, 108 characters, TL = 415, CI = 0.629, RC = 0.475).

ropterygia. With *Corosaurus* and *Placodus* as successive outgroups, the characters diagnostic for the Pachypleurosauroidea changed dramatically, involving reversals (ACCTRAN) or convergences (DELTRAN), with important implications for the reconstruction of the evolutionary history of the group (Rieppel, 1994b).

The data matrix used in Rieppel (1994b) for the analysis of phylogenetic interrelationships of stem-group Sauropterygia (23 taxa, 94 characters) was expanded for the present study by the inclusion of all terminal taxa for pachypleurosaurs, and by the addition of new characters not already included in the previous analysis (Rieppel, 1994b; characters 8, 21, 23, 28, 29, 30, 31, 34, 40, 41, 43, 45, 46, 49, as defined below). These modifications result in a data matrix for a total of 28 taxa and 108 characters. A heuristic search rooted on an all-0 ancestor treated all characters as unordered except for character 22 (Rieppel, 1994b). It resulted in 54 equally parsimonious trees with a tree length of 415 steps, CI = 0.629, and RC = 0.475. All

trees show *Placodus* to be the sister-taxon to all other Sauropterygia (Eosauropterygia). All trees confirm monophyly of the Pachypleurosauroidea and their position as sister-group to the Eusauropterygia. Diagnostic characters of the Pachypleurosauroidea are: preorbital region of the skull longer than postorbital region (D, A); frontal with concave lateral edge (D), parietal skull table broad (A); mandibular articulation at the level of the occipital condyle (A); quadrate with concave posterior margin (A); ectopterygoid bone absent (D, A); trough on dorsal surface of retroarticular process present (D, A); anterior teeth not strongly precumbent (D, A); posterior process on interclavicle rudimentary or absent (D); radius longer than ulna, or both bones of equal length (D, A); iliac blade absent (D, A). The strict consensus tree (Fig. 22) remains highly unresolved within the pachypleurosaurs, which, however, may be an effect of the larger number of taxa and characters entered in the analysis. To resolve phylogenetic interrelationships within the Pachypleurosauroidea, a new

TABLE 6. Data matrix for 14 taxa and 50 characters.

		1	2	3	4	5	6	7	8	9	10
1	Anarosaurus	0	0	0	0	1	1	0&1	0	0	0
2	Dactylosaurus	1	0	0	0	0	1	1	0	0	0
3	Keichousaurus	1	0	?	2	1	0	0	0	0	0
4	N. pusillus	1	0	1	1&2	1	1	0	0	1	0
5	N. peyeri	1	0	1	1&2	1	1	0	0	1	0
6	N. edwardsii	0&1	0	1	1&2	1	1	0	0&1	1	0
7	Psilotrachelosaurus	?	?	?	?	?	?	?	?	?	?
8	Serpianosaurus	1	0	1	1	1	1	0	0	1	0
9	Cymatosaurus	0	1	2	2	0	0&1	3	1	2	0&1
10	Lariosaurus	0	1	?	?	1	?	0	1	2	1
11	Nothosaurus	0	1	0	1&2	1	1	0	1	2	1&2
12	Pistosaurus	0	?	2	2	1	1	2	1	2	2
13	Simosaurus	0	0	1	2	1	1	0	1	2	1
14	Placodus	0	1	0	0	0&1	1	3	1	2	0
15	outgroup	0	0	0	0	0	0	0	0	0	0

data matrix was therefore constructed, including a total of 50 characters defined below and 14 taxa plus an all-0 ancestor for an outgroup (Table 6).

Definition of Characters

1. Bones in the dermatocranium distinctly sculptured (0) or rather smooth (1).

The plesiomorphic condition within the Rep-

tilia is sculpturing of the surface of dermatocranial bones. Sculpturing is present in the eusauroptrygian genera *Nothosaurus* and *Simosaurus*; sculpturing may be weak, but is present in some *Lariosaurus*, in *Cymatosaurus*, and in *Pistosaurus*. Among pachypleurosaurs, skull roof ornamentation appears present but is poorly visible in the cast of *Anarosaurus pumilio*; ornamentation of the dermatocranial bones in *Anarosaurus* is confirmed by undescribed material from Winterswijk. Among

TABLE 6. Continued.

		2	11	12	13	14	15	16	17	18	19	20
1	Anarosaurus	0	0	0	0	0	0	?	0	1	?	1
2	Dactylosaurus	0	0	0	0	0	0	?	0	1	0	1
3	Keichousaurus	0	1	1	0	0	0	0	0	1	?	1
4	N. pusillus	0	0	0	0	0	0	0	0	1	0	1
5	N. peyeri	1	0	0	0	0	0	0	0	1	0	1
6	N. edwardsii	1	0	0	0	0	0	0	0	1	0	1
7	Psilotrachelosaurus	?	?	?	?	?	?	?	?	?	?	?
8	Serpianosaurus	0	0	0	0	0	0	0	0	1	0	1
9	Cymatosaurus	0	1	0	0&1	1	1	1	1	0	1	0
10	Lariosaurus	0	1	2	0	1	?	?	1	1	?	0
11	Nothosaurus	0	1	2	0	1	1	1	1	1	1	0
12	Pistosaurus	0	1	1	1	0	1	1	1	0	?	0
13	Simosaurus	0	1	2	0	1	0	1	1	1	0	0
14	Placodus	1	0&1	0	0	0	0	1	1	0	1	0
15	outgroup	0	0	0	0	0	0	0	0	0	0	0

TABLE 6. *Continued.*

		3									
		2 1	2 2	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0
1	Anarosaurus	0	0	1	1	0	0	0	0	0	1
2	Dactylosaurus	0	0	1	0	0	0	0	1	1	0
3	Keichousaurus	1	0	1	0	0	0	0	0	2	0
4	N. pusillus	0	0	1	0	0	0	0	1	0&1	1
5	N. peyeri	0	0	1	0	0	0	0	1	0	0
6	N. edwardsii	0	0	1	0	0	0	0	1	1	0
7	Psilotrachelosaurus	?	?	?	?	?	?	0	1	?	0
8	Serpianosaurus	0	0	1	0	0	0	0	1	0	1
9	Cymatosaurus	1	1	0	1	1	0	?	?	?	?
1 0	Lariosaurus	1	1	0	1	1	1	1	1	1	1
1 1	Nothosaurus	1	1	0	1	1	1	1	0	1	1
1 2	Pistosaurus	1	?	0	1	0	0	1	?	?	?
1 3	Simosaurus	1	0	0	0	0	1	1	0	?	2
1 4	Placodus	1	1	0	0	1	0	0	0	0	0
1 5	outgroup	0	0	0	0	0	0	0	0	0	0

other pachypleurosaurs the skull roof bones are smooth except for very large specimens of *Neusticosaurus edwardsii*, where a weakly expressed ornamentation may appear (Carroll & Gaskill, 1985).

2. Snout unconstricted (0) or constricted (1).

The unconstricted rounded snout observed in *Dactylosaurus*, *Serpianosaurus*, and *Neusticosaurus* is the plesiomorphic condition. The snout is elongated and distinctly constricted in *Cymatosaurus*, *Lariosaurus*, and *Nothosaurus*. A very weak

embayment of the snout at the maxilla-premaxillary suture can be observed in *Anarosaurus* (undescribed material from Winterswijk), *Keichousaurus*, and *Simosaurus*, all of which are coded (0), however.

3. Nasals broad and leaflike (0), slender (1), or much reduced (2).

The nasals are broad elements defining most of the posterior margin of the external naris in *Anarosaurus* and *Dactylosaurus*. In *Serpianosaurus*

TABLE 6. *Continued.*

		4									
		3 1	3 2	3 3	3 4	3 5	3 6	3 7	3 8	3 9	4 0
1	Anarosaurus	0	1	1	0	1	2	1	1	0	0
2	Dactylosaurus	0	1	1	0	1	?	0	0	0	0
3	Keichousaurus	1	0	0	?	0	1	1	1	1	1
4	N. pusillus	1	1	1	1	0	1&2	0&1	0&1	0	1
5	N. peyeri	1	1	1	1	0	1&2	0&1	0&1	0	1
6	N. edwardsii	1	1	1	1	0	1&2	0&1	0&1	0	1
7	Psilotrachelosaurus	1	1	1	?	0	?	1	1	0	1
8	Serpianosaurus	0	1	1	0	0	1&2	1	1	0	1
9	Cymatosaurus	?	?	?	?	?	?	0	0	0&1	0
1 0	Lariosaurus	1	2	1	0	1	?	1	1	0	0
1 1	Nothosaurus	0	1	1	0	1	0&1	0&1	0&1	0	0
1 2	Pistosaurus	?	?	?	?	?	?	1	1	1	0
1 3	Simosaurus	0	1	0	0	1	0	1	1	1	0
1 4	Placodus	0	1	0	0	0	0	1	0	1	0
1 5	outgroup	0	0	0	0	0	0	0	0	0	0

TABLE 6. *Continued.*

		5	4 1	4 2	4 3	4 4	4 5	4 6	4 7	4 8	4 9	5 0
1	Anarosaurus	0	?	1	?	?	?	?	?	1	1	1
2	Dactylosaurus	0	1	1	0	1	0	0	0	1	0	0
3	Keichousaurus	1	1	0	0	0	1	0	0	1	0	0
4	N. pusillus	0	1	0	0&1	2	0	0	0	1	0	1
5	N. peyeri	0	1	0	0&1	2	0	1	1	1	0	0&1
6	N. edwardsii	0	1	0	0&1	1	0	1	1	1	0	1
7	Psilotrachelosaurus	0	1	0	1	1	0	?	?	1	0	1
8	Serpianosaurus	0	1&2	0	0	2	0	0	0	1	1	1
9	Cymatosaurus	0	?	?	?	?	?	?	?	?	?	?
10	Lariosaurus	1	2	0	0	0&1	1	0	0	1	0	?
11	Nothosaurus	0	2	0	0	1	0	0	0	0	1	0&1
12	Pistosaurus	0	2	?	?	?	?	?	?	0	?	?
13	Simosaurus	0	2	0	0	1	0	0	0	0	1	0
14	Placodus	0	?	0	0	1	0	0	0	0	0	0
15	outgroup	0	0	0	0	0	0	0	0	0	0	0

and *Neusticosaurus*, the nasals are slender and elongate elements, restricted to the posteromedial margin of the external naris. The exact contours of the nasals cannot be unequivocally identified in the *Keichousaurus* material available to us. The nasals are small in *Simosaurus* (1) but broad in *Nothosaurus*; the contours of the nasals remain poorly known in *Lariosaurus*. The strong reduction of the nasals (2) in *Cymatosaurus* and *Pistosaurus* results in their exclusion from the external naris.

4. Nasals in broad contact at midline of skull (0), nasals meet in a short suture only (1), or nasals are separated by the contact of the nasal processes of the premaxillae with the frontal (2).

This character is polymorphic in some taxa, where the nasals may come into narrow contact (1), or remain separate from each other (2) by a contact between premaxilla and frontal (*Neusticosaurus*: Sander, 1989; *Nothosaurus*, pers. obs.). However, a distinction can be made between taxa in which the nasals establish a broad contact (*Anarosaurus*, *Dactylosaurus*), a narrow contact (*Serpianosaurus*, Rieppel, 1989), or in which the nasals always remain separated by the premaxilla, which extends backward to meet the frontal (*Cymatosaurus*, *Simosaurus*, *Pistosaurus*). The condition in *Lariosaurus* remains unknown due to poor preservation of the available material. As far as is known, *Keichousaurus* always shows the premaxilla-frontal contact (Young, 1958; and per. obs.).

5. Frontals paired (0) or fused (1) in the adult.

6. Frontal(s) without (0) or with (1) distinct anterolateral process(es) entering between the prefrontal and the nasal.

7. Frontal broadly enters the dorsal margin of the orbit (0); participation of the frontal in the dorsal margin of the orbit is restricted due to an elongated anterior process of the postfrontal (1); participation of the frontal in the dorsal margin of the orbit is restricted due to an elongated posterior process of the prefrontal (2); the frontal remains excluded from the dorsal margin of the orbit due to a prefrontal-postfrontal contact (3).

Dactylosaurus and some specimens of *Anarosaurus* (undescribed material from Winterswijk) show a slender anterior process of the postfrontal extending along the dorsal margin of the orbit and narrowly approaching the prefrontal. A reduced participation of the frontal in the dorsal margin of the orbit is also observed in *Pistosaurus*, although in this taxon it is rather the prefrontal extending backward than the postfrontal extending forward. This condition, and the complete exclusion of the frontal from the dorsal margin of the orbit in *Cymatosaurus*, are autapomorphic for the respective taxa in this analysis.

8. Lateral edge of frontal concave (0) or straight (1).

In their analysis of sauropterygian interrelationships, Sanz, Alafont, and Moratalla (1993) listed a number of problematic characters such as the

relative size of the upper temporal fossa (their character 1), the relative size of the external nares (their character 3), and the relative size of the orbits (their character 4). All of these characters are subject to potential ontogenetic variation (allometric growth), and all may be interrelated, depending on how skull measurements are taken and how relative size is calculated.

Among the taxa included in this analysis, the ratio (longitudinal diameter of orbit/width of bony bridge between orbits) is distinctly larger in small pachypleurosaurs (>3.5) than in large eusauropterygians (<2.5), indicating relatively larger orbits or a relatively narrower frontal bridge in pachypleurosaurs (frontal constriction is extreme in *Keichousaurus* with an index of 7.2!). For most of the taxa entered in this analysis, very few specimens allow the size of the orbit (known to grow with negative allometry: Sander, 1989; Rieppel, 1994c) to be related to standard length defined as length of the last four presacral centra. This relation indicates a slightly smaller size of the orbits in *Nothosaurus* (holotype of *Nothosaurus* "raabi": Schroder, 1914) and *Lariosaurus* (neotype of *Lariosaurus balsami*: Kuhn-Schnyder, 1987), specimens of distinctly larger overall size than the small pachypleurosaurs. An overlap in the relative size of the orbit is observed in large specimens of *Neusticosaurus edwardsii* (Carroll & Gaskill, 1985). The character may therefore be directly related to overall body size.

Nevertheless, the relatively narrower frontal bridge between the orbits in *Anarosaurus*, *Dactylosaurus*, *Keichousaurus*, and small specimens of *Neusticosaurus* translates into a concave lateral margin of the frontal, whereas in large *Neusticosaurus* and eusauropterygians, the lateral edge of the frontal is rather straight.

9. Longitudinal diameter of upper temporal fossa about 50–60% of longitudinal diameter of orbit (0), 25–30% of orbital diameter (1), or 150–220% of orbital diameter (2).

As discussed above, the orbit shows negative allometric growth, which may affect this character as defined above to a certain degree. However, the Eusauropterygia show a marked elongation of the postorbital region of the skull (to a somewhat lesser degree in *Simosaurus* than in the other taxa), if compared to pachypleurosaurs or the plesiomorphic reptile condition (*Captorhinus*, *Araeoscelidia*, *Youngina*, *Claudiosaurus*). Within the pachypleurosaurs, a relatively large upper temporal fossa is observed in *Anarosaurus*, *Dactylosaurus*, and *Keichousaurus*, which compares to the lon-

gitudinal diameter of the orbit in a way closely similar to *Petrolacosaurus*, *Claudiosaurus*, and *Youngina*. In *Serpianosaurus* and *Neusticosaurus*, however, the upper temporal fenestra is strongly reduced, small, and keyhole shaped. The small size of the upper temporal fenestra correlates with a widening of the upper temporal arch and the transformation of the postorbital from a triradiate bone to a broad, triangular plate. *Serpianosaurus* is autapomorphic in the (variable) exclusion of the parietal from the medial margin of the upper temporal fossa. Exclusion of the postorbital from the reduced upper temporal fossa is polymorphic in *Neusticosaurus* and *Serpianosaurus*.

10. Posterior part of parietal skull table broad and flat (0), constricted (1), or forming a sagittal crest (2).

Pachypleurosaurs show a broad parietal skull table, whereas the parietal skull table is constricted between the posterior parts of the upper temporal fossa in eusauropterygians. *Cymatosaurus* is coded polymorphic for this character for reasons discussed in Rieppel (1994b). A sagittal crest may develop in some *Nothosaurus* (*Nothosaurus edingeriae*: Rieppel & Wild, 1994), as well as in *Pistosaurus*.

11. Width of upper temporal arch (i.e., temporal emargination) visible (0) or not visible (1) from above.

12. Parietal paired (0) or fused (1) in adult.

13. Pineal foramen located in center of skull table (0), or displaced anteriorly (1), or displaced posteriorly (2).

In pachypleurosaurs the pineal foramen is located in the center of the skull table except in *Keichousaurus*, where it is displaced anteriorly. The pineal foramen is in a central position in *Cymatosaurus*, displaced anteriorly in *Pistosaurus*, and displaced posteriorly in *Nothosaurus*; *Lariosaurus* shows the pineal foramen either in a central (Repetto, 1993, and pers. obs.) or in a posterior position.

14. Frontal excluded from upper temporal fossa (0) or narrowly enters the anteromedial edge of the upper temporal fossa (1).

The derived character state is observed in some specimens of *Cymatosaurus* as well as in *Pistosaurus* among the taxa considered in this analysis.

15. Jugal extends anteriorly along the ventral margin of the orbit (0) or remains restricted to a position behind the orbit (1).

The plesiomorphic condition is known or assumed to exist in all pachypleurosaurs, as well as in *Simosaurus*. The jugal is restricted to a position

behind the orbit in *Lariosaurus* and *Nothosaurus*. For reasons discussed elsewhere, *Cymatosaurus* is coded (1), *Pistosaurus* (0) for this character (Rieppel, 1994b).

16. Quadratojugal present (0) or absent (1).

Presence of a quadratojugal is documented for *Serpianosaurus*, *Keichousaurus*, and *Neusticosaurus* among pachypleurosaurs, as well as for *Simosaurus* among eusauropterygians. Its absence is documented for *Cymatosaurus*, *Nothosaurus*, and *Pistosaurus*.

17. Quadrate with straight posterior margin (0) or with concave posterior margin (1).

18. Pterygoid flanges well developed (0) or strongly reduced (1).

Among the taxa here considered, pterygoid flanges are strongly reduced in all except *Cymatosaurus* and *Pistosaurus*.

19. Premaxillae enter internal nares (0) or remain excluded therefrom (1).

Because of poor preservation, this character is known for few taxa only. The premaxilla enters the internal naris in *Serpianosaurus* and *Neusticosaurus*, probably also in *Dactylosaurus* (Sues & Carroll, 1985—as in all other pachypleurosaurs), as well as in *Simosaurus*, but it remains excluded from the internal naris in *Nothosaurus* and *Cymatosaurus* (coded unknown for *Lariosaurus* and *Pistosaurus*).

20. Ectopterygoid present (0) or absent (1).

There continues to be no unequivocal evidence for the presence of an ectopterygoid bone in pachypleurosaurs (*Dactylosaurus*, *Keichousaurus*, *Serpianosaurus*, *Neusticosaurus*).

21. Scleral ossicles present (0) or absent (1).

Scleral ossicles are present in all pachypleurosaurs except, apparently, *Keichousaurus*. Scleral ossicles have never been reported for stem-group eusauropterygians, but are present in some plesiosaurs.

22. Mandibular symphysis short (0) or elongated (1).

The mandibular symphysis is short in all pachypleurosaurs (including *Anarosaurus*: undescribed material from Winterswijk), but is elongated in all eusauropterygians except *Simosaurus* (unknown in *Pistosaurus*).

23. Trough on dorsal surface or retroarticular process absent (0) or present (1).

24. Premaxillary and anterior dentary teeth small (0) or enlarged (1).

The plesiomorphic character state is observed in all pachypleurosaurs except for *Anarosaurus* (undescribed material from Winterswijk; see also

Oosterink, 1986, Foto 40). The derived character state is observed in all eusauropterygian taxa except *Simosaurus*.

25. One or two maxillary fangs present (0) or absent (1).

Maxillary fangs are absent in all pachypleurosaurs but present in all eusauropterygians here considered with the exception of *Simosaurus* and *Pistosaurus* (although that genus shows larger anterior than posterior maxillary teeth).

26. Tooth row restricted to a level in front of the posterior margin of orbit (0) or extending backward to a position below the anterior part of upper temporal fossa.

This character is discussed in detail in Rieppel (1994b).

27. Vertebrae amphicoelous (0) or platycoelous (1).

The vertebrae of pachypleurosaurs are amphicoelous; those of *Lariosaurus*, *Nothosaurus*, *Pistosaurus* (Sues, 1987), and *Simosaurus* are platycoelous. The vertebrae of *Cymatosaurus*, are unknown except for *Cymatosaurus multidentatus*, which shows amphicoelous vertebrae, possibly a juvenile feature (Rieppel, 1995).

28. Dorsal centra constricted (0) or unconstricted (1) in ventral view.

Nopcsa (1928) drew attention to the fact that the dorsal centra of *Anarosaurus* appear constricted in ventral view, whereas those of *Dactylosaurus* do not. This character is not related to pachyostosis, which is absent in the dorsal ribs of *Dactylosaurus* and *Serpianosaurus*, but present in the dorsal ribs of *Neusticosaurus* and “*Psilotrachelosaurus*,” all of which have unconstricted centra. The dorsal centra of *Keichousaurus* are slightly constricted.

29. Neck less than 80% of trunk length (0), 80–100% of trunk length (1), or distinctly more than 100% of trunk length (2).

These relations are calculated on the number of vertebrae in the cervical and dorsal region, although it must be admitted that the two regions are sometimes difficult to delineate from one another. In *Dactylosaurus* and *Neusticosaurus edwardsii*, the dorsal region comprises two more vertebrae than the neck (perhaps three in one poorly preserved specimen of the latter species). In *Anarosaurus*, *Neusticosaurus pusillus*, *Neusticosaurus peyeri*, and *Serpinaosaurus*, the difference between trunk and neck is generally larger, involving a minimum of three and a maximum of nine more dorsal vertebrae; a slight overlap between two or three vertebrae may exist between *Neusticosaurus ed-*

wardsii and *Neusticosaurus pusillus*. Of all specimens of *Serpianosaurus*, one has been reported with 18 cervicals and 20 dorsals (T 1071; Rieppel, 1989), compared to the average difference within the whole sample of four to nine more dorsals than cervicals, the count for T 1071 seems erroneous and could have been caused by a slight backward shift of the pectoral girdle during fossilization. A neck that is longer than the trunk is autapomorphic for *Keichousaurus*.

30. Number of dorsal vertebrae: 20 or below (0), 20 or more (1), 30 or more (3).

The number of dorsal vertebrae is variable within taxa, and the ranges of variation overlap to some slight extent (*Serpianosaurus*, *Anarosaurus*). Nineteen to 20 dorsal vertebrae is considered the plesiomorphic condition (0), present in *Dactylosaurus*, *Keichousaurus*, *Neusticosaurus edwardsii*, *Neusticosaurus peyeri*, and "*Psilotrachelosaurus*." Twenty to 24 (26) dorsal vertebrae is the derived condition observed in *Anarosaurus* (25 or 26 dorsals!), *Neusticosaurus pusillus*, *Serpianosaurus*, *Lariosaurus*, and *Nothosaurus* (holotype of *Nothosaurus raabi*: Schroder, 1914). *Simosaurus* is autapomorphic with a minimum of 32 dorsal vertebrae (Huene, 1959). The number of dorsal vertebrae is unknown for *Cymatosaurus* and *Pistosaurus*.

31. Dorsal ribs without (0) or with (1) pachyostosis.

Pachyostosis is subject to ontogenetic variation, but it is present in adult *Neusticosaurus* and "*Psilotrachelosaurus*." It is absent, or only very weakly developed, in adult *Anarosaurus*, *Dactylosaurus*, and *Serpianosaurus*. Rib pachyostosis appears variable in *Keichousaurus*, which is coded as polymorphic for that character. Among Eusauropterygia, only *Lariosaurus* shows pachyostotic ribs.

32. Number of sacral ribs: two (0), three (1), four (2).

Two sacral ribs have been described for *Keichousaurus* (Lin Kegang, quoted in Sues, 1987), and this is the character state accepted here. It should be noted, however, that only one sacral rib shows a distinct distal expansion abutting the medial side of the ilium; a second sacral rib with no distal expansion extends toward the posterolateral aspect of the ilium. In some specimens, an anterior (i.e., last dorsal) rib converges toward the anterolateral aspect of the ilium. Three sacral ribs is the typical condition observed in all other pachypleurosaurs, as well as in *Simosaurus* and *Nothosaurus* (Rieppel, 1994b). Four sacral ribs is autapomorphic for *Lariosaurus* among the taxa included

in this analysis. The sacrum of *Cymatosaurus* and *Pistosaurus* remains unknown.

33. Sacral ribs with (0) or without (1) distinct distal expansion.

The one principal sacral rib in *Keichousaurus* shows a distal expansion, whereas the distal expansion of the sacral ribs is not pronounced in other pachypleurosaurs, or in *Lariosaurus* or *Nothosaurus*. The sacral ribs are distally expanded in *Simosaurus*.

34. Gastral ribs composed of five (0) or three (1) segments.

In an earlier analysis of pachypleurosaurian interrelationships (Rieppel, 1987), the number of segments included in each gastral rib was used as a character, with three segments being the derived condition. With *Pachypleurosaurus* a junior synonym of *Neusticosaurus* (Sander, 1989), this character is autapomorphic for the latter genus (not known for "*Psilotrachelosaurus*").

35. Clavicles without (0) or with (1) expanded corners.

In *Anarosaurus* (undescribed material from Winterswijk) and *Dactylosaurus*, the clavicles are expanded into distinct anterolateral corners, as is also the case in *Lariosaurus*, *Nothosaurus*, and *Simosaurus*. These clavicular "corners" (Storrs, 1991, 1993a) are absent in all other pachypleurosaurs.

36. Posterior stem on interclavicle distinct (0), rudimentary (1), or absent (2).

The interclavicle of *Simosaurus* retains a distinct (yet short) posterior stem (Huene, 1952). In articulated specimens of *Nothosaurus*, the interclavicle carries no posterior process, but isolated interclavicularae most probably referable to *Nothosaurus* may retain a very rudimentary process (Rieppel, 1994b). A rudimentary process is also observed in *Keichousaurus*, and in some specimens of *Neusticosaurus* and *Serpianosaurus*. No trace of a posterior process is observed in *Anarosaurus* (undescribed material from Winterswijk). The interclavicle of *Dactylosaurus*, "*Psilotrachelosaurus*" and *Lariosaurus* is poorly known; that of *Cymatosaurus* and *Pistosaurus* remains unknown.

37. Ectepicondylar groove on humerus notched anteriorly (0) or without notch (1).

Humerus morphology has traditionally played an important role in sauropterygian systematics (see Storrs, 1991, 1993a, and Rieppel, 1994b, for a discussion). In the most recent analysis, Sanz, Alafont, and Moratalla (1993) defined yet different character states for humerus morphology, all of which are difficult to recognize. The major prob-

lem is that humeral morphology is subject to ontogenetic variation and sexual dimorphism. The shape of the humerus can also be quite variable, as in the genera *Keichousaurus* and *Lariosaurus*. In an earlier analysis, a “curved” humerus was accepted as a sauropterygian synapomorphy (Rieppel, 1994b); the rather straight humerus of *Cymatosaurus* is autapomorphic among the genera included in this analysis.

The ectepicondylar groove is generally present on sauropterygian humeri, and it is “notched” anteriorly in *Dactylosaurus* (sex *y*), large individuals of *Neusticosaurus edwardsii* (sex *y*; Carroll & Gaskill, 1985; Sander, 1989), in large *Nothosaurus*, and in *Cymatosaurus*.

38. Humerus with (0) or without (1) distinct entepicondyle.

Sues and Carroll (1985) commented on the distinct morphology of the humerus in *Dactylosaurus*, with an entepicondyle distinctly set off from the humeral shaft by a notch (in sex *y*; see also Rieppel, 1993, Fig. 8). Similar humeri have been recorded for *Neusticosaurus pusillus* and other species of *Neusticosaurus* (Carroll & Gaskill, 1985; Sander, 1989). The entepicondyle is less distinct in *Anarosaurus*, *Keichousaurus*, “*Psilotrachelosaurus*,” and *Serpianosaurus*.

39. Entepicondylar foramen present (0) or absent (1).

Among the genera considered in this analysis, an entepicondylar foramen is absent in *Keichousaurus*, some specimens of *Cymatosaurus*, *Simosaurus*, and *Pistosaurus*.

40. Humerus without (0) or with (1) vermiculate surface.

Serpianosaurus, “*Psilotrachelosaurus*,” and *Neusticosaurus* share a peculiar “orange-peel” ornamentation of endochondral bone surface, most conspicuously developed on the humerus (Sander, 1989; Rieppel, 1993). A similar ornamentation of the bone surface occurs in *Keichousaurus*.

41. Ulna with slender shaft (0) or distinctly broadened (1).

Among the genera included in this analysis, the ulna is distinctly broadened in *Keichousaurus* and *Lariosaurus*.

42. Radius shorter than ulna (0), radius slightly longer than ulna (1), or bones of approximately equal length (2).

The radius is slightly longer than the ulna in *Dactylosaurus*, *Keichousaurus*, *Neusticosaurus*, and “*Psilotrachelosaurus*”; in *Serpianosaurus*, the radius may be slightly longer than the ulna, or the two bones may be of equal length (the elements

are unknown in the holotype of *Anarosaurus pumilio*). In Eusauropterygia, the radius and ulna are of equal length (the character is not known for *Cymatosaurus*).

43. Radius without (0) or with (1) distinct concavity in the medial (preaxial) margin of the shaft.

44. The intermedium is rounded (0) or a rectangular elongate element located at the preaxial margin of the distal tip of the ulna (1).

The derived condition is observed in some specimens of *Neusticosaurus* and in “*Psilotrachelosaurus*” (Rieppel, 1993) among the genera included in this analysis.

45. Number of ossified carpal bones in adult: five (0), three (1), or two (2).

The carpus of *Anarosaurus* is unknown. *Dactylosaurus* shows three undisputed carpal ossifications, with the possible occurrence of a pisiform (perhaps a neomorph: Sues & Carroll, 1985). In *Serpianosaurus*, *Neusticosaurus pusillus*, and *Neusticosaurus peyeri*, only two carpals ossify (Sander, 1989); large *Neusticosaurus edwardsii* show three carpal ossifications (Carroll & Gaskill, 1985). Adult *Keichousaurus* show five carpal ossifications. *Simosaurus* and *Nothosaurus* (*Nothosaurus “raabi”*: Schroder, 1914) show three ossified carpals. In *Lariosaurus*, adults (of perhaps two different species) may show three (neotype of *Lariosaurus balsami*: Kunn-Schnyder, 1987) or up to five ossified carpals. The carpus of *Cymatosaurus* and *Pistosaurus* is unknown.

46. Phalangeal formula of manus 2-3-4-5-3 (0) or characterized by hyperphalangy (1).

Hyperphalangy is observed in *Keichousaurus* and *Lariosaurus* among the genera included in this analysis.

47. Phalangeal formula in pes 2-3-4-5-3 (0) or less than 2-3-4-4-3 (1). The formula 2-3-4-4-3 itself is coded (0) because of incomplete or problematic preservation (*Keichousaurus*: Young, 1958; *Dactylosaurus*: Sues & Carroll, 1985) or ontogenetic variation (*Neusticosaurus*: Sander, 1989). The reduction of the phalangeal count in the pes (beyond 2-3-4-4-3) is autapomorphic for *Neusticosaurus edwardsii* (Sander, 1989).

48. Dorsal part of ilium forming an iliac blade (0) or a simple dorsal process (1).

An iliac blade is absent in all pachypleurosaurs, as well as in *Lariosaurus*, among the genera included in this analysis.

49. Pubis without (0) or with (1) anteroventral process.

In *Anarosaurus*, the pubis forms a distinct anteroventral process that is also observed in *Ser-*

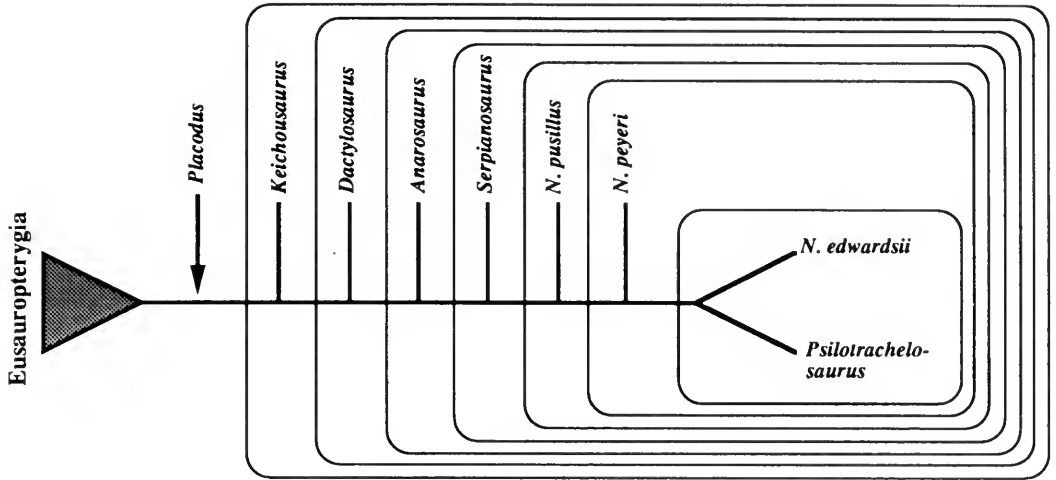


FIG. 23. Unrooted network for *Placodus*, Pachypleurosauroidea, and selected representatives of the Eusauropterygia. For further discussion see text.

pianosaurus, among other pachypleurosaurs. This anteroventral process of the pubis results from a concavity of the medial (ventral) margin of the pubic plate, which is also observed in *Simosaurus* and *Nothosaurus*, but not in *Lariosaurus* among the Eusauropterygia. The pubis of *Cymatosaurus* and *Pistosaurus* is unknown.

50. Obturator foramen closed (0) or open (1) in adults.

The obturator foramen is open or slitlike in *Anarosaurus*, *Serpianosaurus*, and “*Psilotrachelosaurus*”; both conditions may occur in *Neusticosaurus*. The foramen is closed in *Dactylosaurus* and *Keichousaurus*. The obturator foramen is closed in *Simosaurus*, but may be closed or open in *Nothosaurus*. The character is unknown in *Cymatosaurus*, *Lariosaurus*, and *Pistosaurus*.

In a first analysis, an unrooted network was reconstructed for all taxa except *Placodus* and the all-0 ancestor. The branch-and-bound algorithm found one single most parsimonious reconstruction (MPR) with TL = 123, CI = 0.756, and RC = 0.555. The addition of *Placodus* to the analysis increased the lack of resolution within the Eusauropterygia, resulting in five MPRs with TL = 134, CI = 0.709, and RC = 0.506. The addition of *Placodus* did not alter the relative adjacency of pachypleurosaurs in the unrooted network, however. The unrooted network suggests the possibility of grouping pachypleurosaurs into a nested hierarchy of monophyletic taxa (Fig. 23), which is exactly the pattern observed if pachypleurosaurs

(assumed to be monophyletic) are rooted on the monophyletic Eusauropterygia, their sister-group (Rieppel, 1994b). When *Placodus* and the all-0 ancestor were excluded, the branch-and-bound algorithm found one single most parsimonious tree (Fig. 24) with TL = 123 steps, CI = 0.756, and RC = 0.555. The *Serpianosaurus*–*Neusticosaurus* clade shows the same substructure as in Sander (1989), but “*Psilotrachelosaurus*” no longer appears as the sister-taxon to that clade (Rieppel, 1993) but rather is nested within that clade as the sister-taxon to *Neusticosaurus edwardsii*. *Anarosaurus* is the sister-taxon to the *Serpianosaurus*–*Neusticosaurus* clade, *Dactylosaurus* is the next successive sister-taxon, and *Keichousaurus* is the sister-taxon to all other pachypleurosaurs. The relative position of *Anarosaurus* is weakly supported and breaks in a tree one step longer (TL = 124), in which *Anarosaurus* and *Dactylosaurus* fall into an unresolved trichotomy with the *Serpianosaurus*–*Neusticosaurus* clade. The position of *Anarosaurus* as sister-taxon to the *Serpianosaurus*–*Neusticosaurus* clade is accepted here, because it also appears in the strict consensus tree (Fig. 25) generated from four MPRs (heuristic search, tree bisection-reconnection [TBR] branch swapping, random stepwise addition, 10 replications; TL = 137, CI = 0.701; RC = 0.483), which result from rooting the 13 taxa included in the analysis (Table 6; *Placodus* excluded) on an all-0 ancestor as out-group. The position of *Anarosaurus* as the sister-group to the *Serpianosaurus*–*Neusticosaurus* clade is further supported by the stratigraphic position

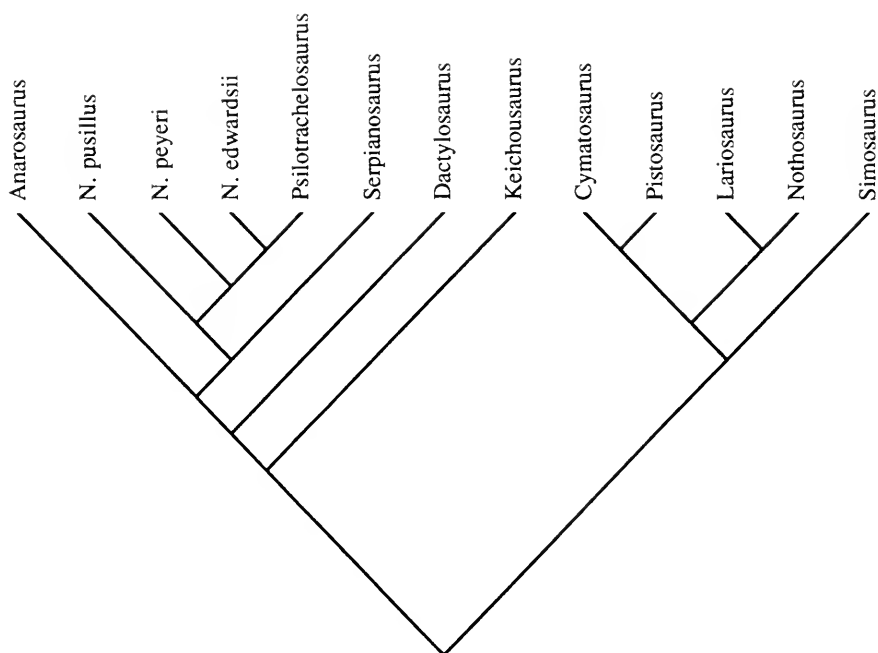


FIG. 24. The single most parsimonious tree for pachypleurosaur interrelationships, with the monophyletic Pachypleurosauridae rooted on the monophyletic Eusauropterygia (TL = 123 steps, CI = 0.756, RC = 0.555).

of *Anarosaurus*, which is somewhat younger than *Dactylosaurus*.

As pachypleurosaur and eusauropterygians are rooted on an all-0 ancestor (Fig. 25), *Dactylosaurus* and *Keichosaurus* fall into an unresolved position with respect to other pachypleurosaur. The relative position of *Dactylosaurus* and *Keichosaurus* at the base of the pachypleurosaur cladogram is of major historical biogeographical importance, because *Dactylosaurus* is the first genus to appear in Europe, whereas *Keichosaurus* is restricted to China. It is tempting to resolve the basal polytomy in the pachypleurosaur cladogram with reference to stratigraphy, but the stratigraphic control on the occurrence of *Keichosaurus* is rather poor. If *Placodus* is included in the analysis and all 14 taxa are rooted on an all-0 ancestor, resolution within the Eusauropterygia drops again, and the result is 10 MPRs (heuristic search, TBR branch swapping, random stepwise addition, 10 replications; TL = 147, CI = 0.667; RC = 0.455) with no improved resolution for *Dactylosaurus* and *Keichosaurus* in the strict consensus tree (Fig. 26). Previous work has shown *Placodus* to be the sister-taxon to all other Sauropterygia (Rieppel, 1994b). Using this information to root pachypleurosaur and the eusauropterygians considered in this analysis on *Placodus* results in five MPRs (heuristic

search, TBR branch swapping, random stepwise addition, 10 replications; TL = 134, CI = 709, RC = 506), which all confirm the position of *Keichosaurus* as sister-taxon to all other pachypleurosaur. This is the position of *Keichosaurus* provisionally accepted in this analysis (Fig. 27).

The cladogram of the Pachypleurosauridae thus reads: (*Keichosaurus* (*Dactylosaurus* (*Anarosaurus* (*Serpianosaurus* (*N. pusillus* (*N. peyeri* (*N. edwardsii*, "*Psilotrachelosaurus*")))))))). The monophyly of the Pachypleurosauridae was discussed above. With the restricted data set (Table 6), monophyly is supported by the following unequivocal synapomorphies (CI = 1, ACCTRAN and DELTRAN optimization, rooting pachypleurosaur on Eusauropterygia [Fig. 24], or together with eusauropterygians on *Placodus* [Fig. 27]): 8—lateral edge of frontal concave; 9—longitudinal diameter of orbit 50–60% of diameter of orbit; 17—quadrate with concave posterior margin; 20—ectopterygoid absent; 23—trough on dorsal surface of retroarticular process present; 42—radius slightly longer than ulna.

Continuing to root pachypleurosaur on the Eusauropterygia (Fig. 24), or together with eusauropterygians on *Placodus* (Fig. 27), then *Dactylosaurus*, *Anarosaurus*, and the *Serpianosaurus*–*Neusticosaurus* clade group to the exclusion of *Kei-*

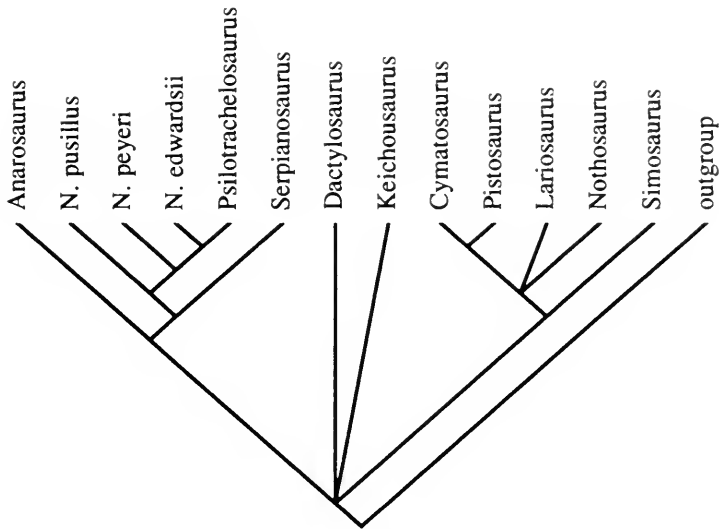


FIG. 25. Strict consensus tree for pachypleurosaurs and selected eusauropterygians, rooted on an all-0 ancestor (four MPRs, TL = 137, CI = 0.701, RC = 0.483).

chousaurus on the basis of the following characters: 4—nasals in broad contact (CI = 1; D, A); 12—parietals paired in adult (CI = 1; D, A); 21—scleral ossicles present (D, A); 28—dorsal centra unconstricted (CI = 0.5; A); 33—sacral ribs with-

out distal expansion (CI = 0.5; D, A); 36—posterior stem on interclavicle absent (CI = 1; A); 39—entepicondylar foramen present (CI = 0.667; D, A); and 43—radius with distinct concavity on preaxial margin (CI = 0.5; A). *Anarosaurus* and

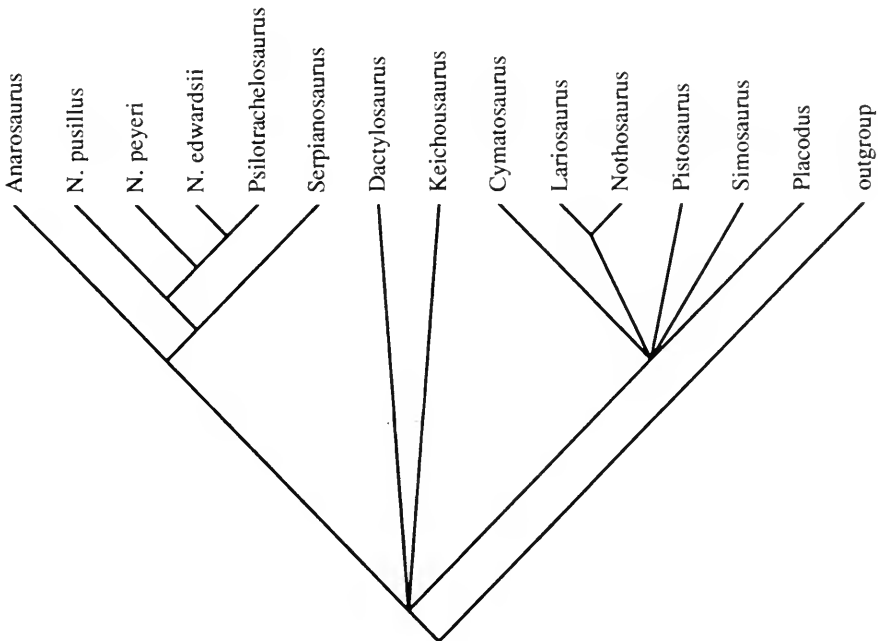


FIG. 26. Strict consensus tree for *Placodus*, pachypleurosaurs, and selected eusauropterygians, rooted on an all-0 ancestor (10 MPRs, TL = 147, CI = 0.667, RC = 0.455).

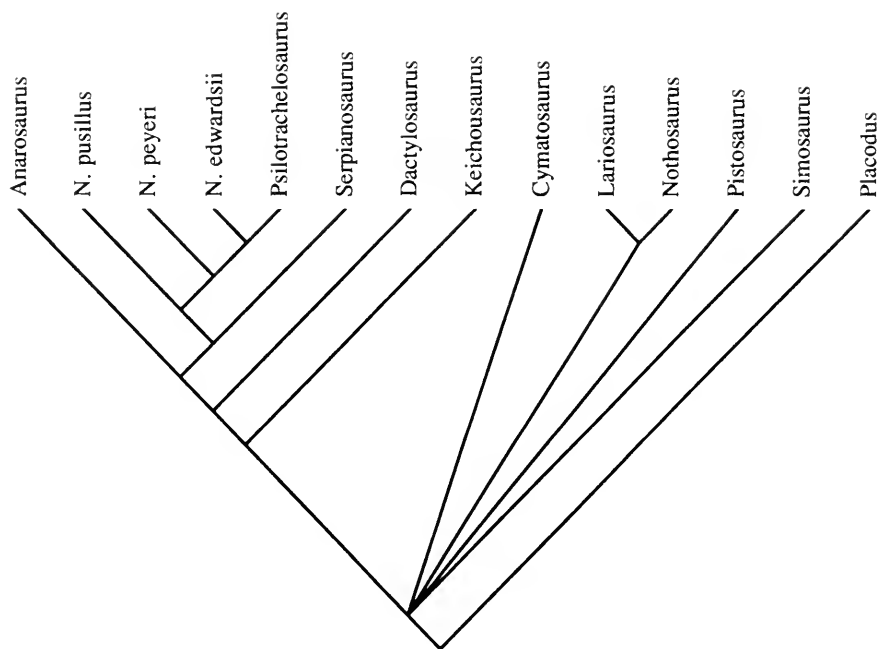


FIG. 27. Strict consensus tree for pachypleurosaur interrelationships, with the pachypleurosaurs plus selected eusauropterygian taxa rooted on *Placodus* (five MPRs, TL = 134, CI = 709, RC = 506).

the *Serpianosaurus*–*Neusticosaurus* clade group to the exclusion of *Dactylosaurus* on the basis of: 29—neck less than 80% of trunk length (CI = 0.75; D, A if rooted on Eusauropterygia; CI = 0.6; A, if rooted on *Placodus*); 30—20 or more dorsal vertebrae (CI = 0.5; D, A); 36—posterior stem on interclavicle absent (CI = 1; D); 45—carpal ossifications reduced to two (CI = 0.75; A); 49—pubis with anteroventral process (CI = 0.25; A); and 50—obturator foramen open in adults (CI = 1; D, A). The *Serpianosaurus*–*Neusticosaurus* clade is united by the following synapomorphies: 3—nasals slender (CI = 0.5–1; D, A); 4—nasals meet in short suture (CI = 0.857–1; D, A); 9—longitudinal diameter of upper temporal fossa 25–30% of orbital diameter (CI = 1; D, A); 28—dorsal centra unconstricted (CI = 0.333; D); 35—clavicles without expanded corners (CI = 0.33–0.5; D, A); 40—humerus with vermiculate surface (CI = 0.5; D, A); 43—radius without distinct concavity on preaxial margin (CI = 0.5; A); and 45—carpal ossifications reduced to two (CI = 10.75; D). The genus *Neusticosaurus* is diagnosed by: 31—dorsal ribs pachyostotic (CI = 0.333; D, A); 34—gastral ribs composed of three segments (CI = 1; D, A); 44—rectangular and elongated intermedium (CI =

1; A); and 49—pubis without anteroventral process (CI = 0.25; A). *Neusticosaurus peyeri*, *N. edwardsii*, and “*Psilotrachelosaurus*” are united by: 11—upper temporal arch broad (i.e., temporal emargination not visible from above) (CI = 0.5–1; D, A—not known for “*Psilotrachelosaurus*”); 30—19–20 dorsal vertebrae (CI = 0.5; D, A); and 47—phalangeal reduction in manus (CI = 1; D, A—not known for “*Psilotrachelosaurus*”). *Neusticosaurus edwardsii* and “*Psilotrachelosaurus*” are united by: 29—neck 80–100% of trunk length (CI = 0.6–0.75; A); and 45—three carpal ossifications (CI = 0.75; D, A—this character was miscoded for *Neusticosaurus edwardsii* in Rieppel, 1993).

Genera and Species of Pachypleurosauroidea in the Middle and Upper Triassic

The morphological and phylogenetic analyses presented above show *Anarosaurus*, *Dactylosaurus*, and *Keichousaurus* to represent well-diagnosed genera from the lower Middle Triassic. The diagnoses of *Anarosaurus* and *Dactylosaurus* are

given above. Characters diagnostic of *Keichousaurus* Young, 1958, are the relative length of the neck (130–140% of trunk length as expressed by the number of vertebral elements), the narrow frontal with no anterolateral processes, the fused parietal with an anteriorly located pineal foramen, the gently curved humerus with no entepicondylar foramen but with a vermiculate surface, the broad ulna, and hyperphalangy in the manus.

Upper Middle Triassic pachypleurosaurs form the *Serpianosaurus*–*Neusticosaurus* clade. “*Psilotrachelosaurus*” is shown by the above analysis to be nested within species referred to the genus *Neusticosaurus* and hence must be included in that genus as a fourth species, *N. toepfilschi*. The association with *Neusticosaurus edwardsii* is weak, however, based only on the presence of three carpal bones (other synapomorphies are unknown for *toepfilschi*; see discussion above). In a tree one step longer (122 steps), *N. peyeri*, *N. edwardsii*, and *N. toepfilschi* fall into an unresolved trichotomy, with *N. pusillus* being the sister-taxon to those three. The systematics of Middle Triassic Pachypleurosauroidea may be formalized as follows.

Genus *Neusticosaurus* Seeley, 1882

TYPE SPECIES—*Neusticosaurus pusillus* Seeley, 1882.

DIAGNOSIS—Small to medium-sized pachypleurosaurs with pachyostotic dorsal ribs; gastral ribs composed of three segments; pubis without anteroventral process; intermedium may be rectangular and elongate, located at the postaxial margin of the distal tip of the radius.

DISTRIBUTION—Middle Triassic (Ladinian), western Europe (western Tethyan Province).

REFERRED SPECIES

Neusticosaurus peyeri Sander, 1989

DIAGNOSIS—A small pachypleurosaurs (450–550 mm overall length, 90–130 mm trunk length) with a distinctly wedge-shaped skull (shared with *N. edwardsii*); relatively large orbits; keyhole-shaped upper temporal fossae; 19–20 dorsal vertebrae (shared with *N. edwardsii* and *N. toepfilschi*); no accessory intervertebral articulations; relatively small pectoral fenestra; two carpal ossifications in adult; phalangeal reduction in manus (shared with *N. edwardsii*).

LOCUS TYPICUS—Cava Superiore horizon, low-

er Meride Limestone (middle Ladinian), Monte San Giorgio, Switzerland.

Neusticosaurus pusillus Seeley, 1882

DIAGNOSIS—A small pachypleurosaurs (400–520 mm overall length, 85–105 mm trunk length); skull table with parallel margins; orbits relatively small; oval upper temporal fossae; 22–24 dorsal vertebrae; no atlas rib; two carpal ossifications in adult (Sander, 1989).

LOCUS TYPICUS—Lettenkeuper (lower Keuper, middle to lower upper Ladinian) of Hoheneck near Ludwigsburg, southwestern Germany.

DISTRIBUTION—Middle Triassic of southern Germany (Germanic Triassic), Switzerland, and northern Italy (northern and southern Alpine Triassic).

Neusticosaurus edwardsii (Cornalia, 1854)

DIAGNOSIS—A large pachypleurosaurs (up to 1,200 mm overall length) with a wedge-shaped skull; upper temporal fossae oval; neck 80–100% of trunk length; 19–20 dorsal vertebrae; relatively short femur; three carpal ossifications in adult; phalangeal reduction in manus and pes.

LOCUS TYPICUS—Uppermost part of upper Meridekalke (upper Ladinian; lower Carnian according to Tintori et al., 1985), Ca’ del Frate near Besano, Italy.

DISTRIBUTION—Middle and upper Ladinian (lower Carnian?) of southern Switzerland and northern Italy (southern Alpine Triassic).

Neusticosaurus toepfilschi (Nopcsa, 1928)

DIAGNOSIS—A small pachypleurosaurs (56 mm trunk length) with 19–20 dorsal vertebrae (shared with *N. edwardsii*); relatively short humerus; relatively broad ventral elements in the pelvic girdle; three carpal ossifications (shared with *N. edwardsii*); fourth distal tarsal ossified.

LOCUS TYPICUS—Upper unit of the Partnach-Plattenkalk (middle Ladinian), Stadelbachgraben, Gailtaler Alps, Austria.

Genus *Serpianosaurus* Rieppel, 1989

TYPE SPECIES: *Serpianosaurus mirigiolensis* Rieppel, 1989.

DIAGNOSIS: A medium-sized pachypleurosaur (up to 750 mm overall length; up to 187 mm trunk length); skull relatively long; lower jaw straight; upper temporal fenestra small and oval with possible exclusion of parietal from its medial margin; 20–23 dorsal vertebrae; distinct striations on neural spines; two carpal ossifications.

LOCUS TYPICUS—Grenzbitumenzone (Anisian–Ladinian boundary), Monte San Giorgio, Switzerland.

REFERRED SPECIES—*Serpianosaurus mirigiolensis* is the only known species of its genus.

Historical Biogeography of the Pachypleurosauroidea

Stem-group Sauropterygia are known from the Lower and Middle Triassic of China, from the Middle to Upper Triassic of Europe, and from the upper Lower and Middle Triassic of the western United States. As presently known, the stratigraphic and geographic distribution of the Pachypleurosauroidea is restricted to the Middle Triassic (perhaps extending into the lower Upper Triassic) deposits of coastal stretches and epicontinental seas of the Tethyan Province. The only possible record of pachypleurosaurs from the western hemisphere is represented by as yet undescribed material from the Wupatki Member of the Moenkopi Formation (Lower Triassic: Colbert & Gregory, 1957), in northeastern Arizona, but their resemblance to pachypleurosaurs is only superficial and their relationship with the group has not been established on the basis of shared derived characters (Storrs, 1991).

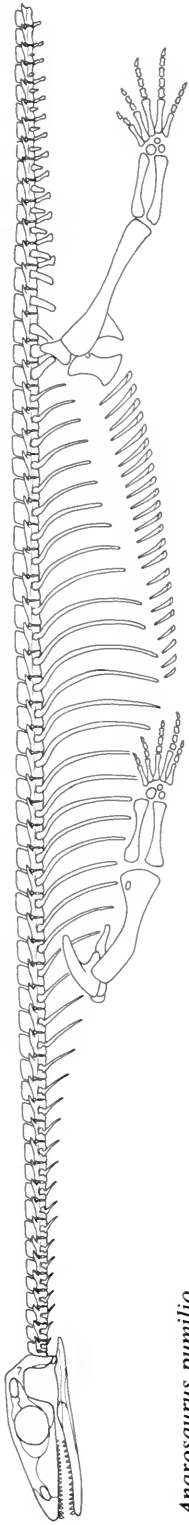
With stem-group Sauropterygia in the Lower Triassic of China (Young, 1965), Europe, and the western United States (Storrs, 1991), a reasonable assumption would be to locate the origin of the clade in the eastern Tethyan Province, from where the group spread eastward (into the eastern Pacific Province, western United States) and westward (western Tethyan Province, Europe). Whereas the phylogenetic positions of Placodontia and *Corosaurus* as currently understood continue to challenge this broad scenario, an eastern Tethyan origin of the Pachypleurosauroidea is indicated by the phylogenetic position of *Keichousaurus*. It is relatively the most plesiomorphic genus within the clade, sister-taxon to all other Pachypleurosauroidea, and its distribution is restricted to the Middle Triassic epicontinental sea of China. The hypothesis of immigration of Sauropterygia into the

Middle Triassic epicontinental sea of Europe (Muschelkalk Basin) from the East is supported by independent evidence derived from geology and invertebrate fossils.

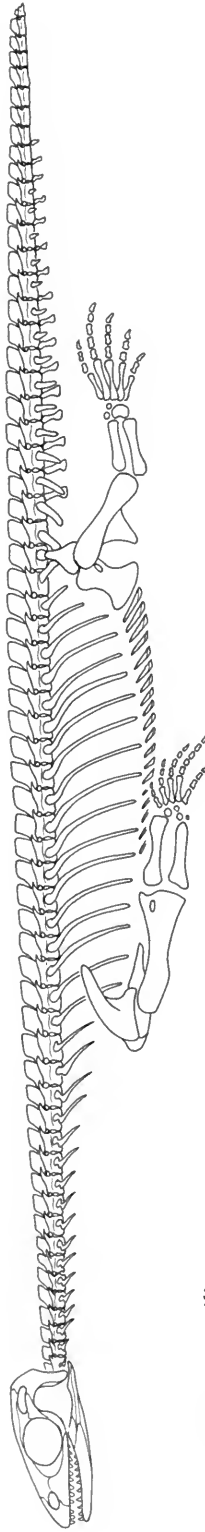
The history of the Muschelkalk Basin has recently been reviewed by Hagdorn (1985, 1991; see also Ziegler, 1982). A relative rise in sea level in early Anisian time induced the Muschelkalk transgression. The base of the lower Muschelkalk is in the lower Anisian (Kozur, 1974; Hagdorn, 1985). The analysis of invertebrate faunas indicates immigration into the Muschelkalk Basin from the east, through the East Carpathian Gate (Kozur, 1974; Ziegler, 1982, 1988; Hagdorn, 1985, 1991; Urlichs & Mundlos, 1985), but westward dispersal was stopped by a salinity barrier. With a second sea level rise during the lower Anisian, the invertebrate fauna expanded throughout the basin. During Pelsonian times, the main faunal exchange occurred through the Silesian–Moravian Gate, although the East Carpathian Gate persisted. Study of longshore transport directions in the area of the Silesian–Moravian Gate indicates a fan-shaped current diagram changing from a SE–NW direction in western Upper Silesia to a SW–NE direction in eastern Upper Silesia (Szulc, 1991). Marine faunas populating the Muschelkalk Basin may have dispersed into the intraplatform basins of the Alpine Triassic (Mostler, 1993). In late Anisian times (lower Illyrian, middle Muschelkalk), a southern connection from the Muschelkalk Basin to the Tethys, the Burgandy Gate, opened.

The earliest pachypleurosaur to appear in the Germanic Triassic is *Dactylosaurus* (Fig. 28), from the lower Muschelkalk (lower Gogolin beds, *Dadocrinus* biozone: Hagdorn, 1991; corresponding to Kozur's [1974] "assemblage zone" with *Beneckeia buchi*, *Myophoria vulgaris*, and *Dadocrinus gracilis* at the transition from the Röt to the lower Muschelkalk; see also Wysogorski, 1903–1908) of Upper Silesia. Its early appearance in the Muschelkalk Basin indicates immigration from the east, perhaps through the East Carpathian Gate, although crinoid data also support immigration through the Silesian–Moravian Gate at that time (Hagdorn, 1985). Pachypleurosaurs, however, have not (yet) been reported from Transylvanian deposits east of the Silesian–Moravian Gate (Jurcsak, 1973, 1976, 1977, 1982). *Dactylosaurus* is the sister-taxon to *Anarosaurus* and the *Serpianosaurus*–*Neusticosaurus* clade.

Early westward dispersal of pachypleurosaurs through the Muschelkalk Basin is documented by the genus *Anarosaurus* (Fig. 28). The undescribed



Anarosaurus pumilio



Dactylosaurus gracilis

FIG. 28. Reconstruction of the skeletal anatomy of *Anarosaurus pumilio* (top, approximately $\frac{1}{2}$ times natural size) and *Dactylosaurus gracilis* (bottom, approximately $\frac{4}{5}$ times natural size).

Anarosaurus material from the lower Muschelkalk of Winterswijk (Oosterink, 1986; here referred to *Anarosaurus heterodontus* n. sp.) is geologically younger than the vertebrates from the Gogolin beds, since the deposition of marine sediments started earlier in the eastern part of the Muschelkalk Basin than in the western part (Hagdorn, 1991). The temporal occurrence of *Anarosaurus* may be closer to the *Anarosaurus heterodontus* material from the upper lower Muschelkalk in the eastern part of the Muschelkalk Basin (Schaumkalk, Freiburg/Unstrut). The holotype of *Anarosaurus pumilio* comes from the *orbicularis* beds of Remkerleben near Magdeburg, now referred to the basal part of the middle Muschelkalk (Hagdorn & Simon, 1993), which renders *Anarosaurus pumilio* (upper Pelsonian or lower Illyrian) distinctly younger than *Dactylosaurus* (Bithynium), and also younger than *Anarosaurus heterodontus*. The genus *Anarosaurus* is the sister-group to the *Serpianosaurus-Neusticosaurus* clade of the Alpine Triassic.

The earliest pachypleurosaur from the Alpine Triassic is an isolated neural arch (not diagnostic) found in lower Anisian (*Dadocrinus* biozone) deposits of the Vicentinian Alps, northeastern Italy (coll. H. Hagdorn, MH1 1292). It is contemporaneous with, or only slightly younger than, the occurrence of *Dactylosaurus* in Upper Silesia. The specimen might indicate a very early southward migration from the Germanic into the Alpine Triassic, or alternatively an independent migration of pachypleurosaurs with Asiatic affinities into the European epicontinental sea (Muschelkalk Basin) and into the intraplatform basin facies along the northwestern shores of the Tethys. This latter scenario would be supported by a position of *Anarosaurus* as sister-taxon to *Dactylosaurus*, that clade in turn forming the sister-group to the *Serpianosaurus-Neusticosaurus* clade [(*Anarosaurus*, *Dactylosaurus*) (*Serpianosaurus*, *Neusticosaurus*)]. It has been pointed out that the phylogenetic position of *Anarosaurus* is weakly supported, since the genus falls into an unresolved trichotomy with *Dactylosaurus* and the *Serpianosaurus-Neusticosaurus* clade in a tree one step longer than the most parsimonious reconstruction. Also, *Anarosaurus* (undescribed material from Winterswijk) and *Dactylosaurus* share two potential synapomorphies, viz. the close approximation of postfrontal and prefrontal along the dorsal margin of the orbit (due to an anterior process of the postfrontal) and the notch on the preaxial side of the radius. However, on the basis of the currently available evidence (Table 6), no tree could be generated that shows

Anarosaurus to be closer to *Dactylosaurus* than either is to the *Serpianosaurus-Neusticosaurus* clade.

The earliest diagnosable pachypleurosaur from the Alpine Triassic is *Serpianosaurus* from the Grenzbitumenzone (Anisian-Ladinian boundary) of Monte San Giorgio, Switzerland (Rieppel, 1989). Stratigraphically, this occurrence corresponds to the transition from mo₁ to mo₂ in the lower part of the upper Muschelkalk (i.e., to the boundary between Illyrian and Fassanian) (Kozur, 1974). It also corresponds to a time period when the Burgandy Gate had established a southern connection of the Muschelkalk Basin to the western Tethys, although a migration of marine faunal elements from the Muschelkalk Basin southward into the southern Alpine carbonate platform facies was possible earlier (Mostler, 1993). The sister-group relationship of the geologically older *Anarosaurus* from the Germanic Triassic and the geologically younger *Serpianosaurus-Neusticosaurus* clade from the Alpine Triassic may indicate a southward dispersal of pachypleurosaurs from the Muschelkalk into the southern Alpine intraplatform basins.

Diagnostic remains of *Serpianosaurus* are restricted to the Grenzbitumenzone (Anisian-Ladinian boundary) of Monte San Giorgio, Switzerland (Rieppel, 1989). An incomplete pachypleurosaur from the Calcare di Perledo, recognized as the Perledo Member of the Perledo-Varenna Formation (northern Italy) of upper Ladinian age (Gaetani et al., 1992), was referred to as *Phygosaurus* by Arthaber (1924). The name is a nomen dubium (Rieppel, 1989), and the specimen is now lost, but early and informal comparison of pachypleurosaurs from the Grenzbitumenzone of Monte San Giorgio with Arthaber's (1924) genus *Phygosaurus* (Peyer, 1933-1934) indicates the possibility of the occurrence of *Serpianosaurus* outside the Monte San Giorgio Basin, and at a younger geological age. Isolated pachypleurosaur remains from the basal part of the middle Muschelkalk (lower Illyrian) of Eberstadt near Heilbronn (Baden-Württemberg) have been referred to *Anarosaurus pumilio* of closely similar geological age (Hagdorn & Simon, 1993), although they are typically larger than the corresponding elements in the skeleton of *Anarosaurus*. The (disarticulated) material includes a slender femur, a pubis with a concave ventral (medial) margin, an open obturator foramen, and a left clavicle. The clavicle lacks an expanded anterolateral corner, present in undescribed material of *Anarosaurus* from Winterswijk, unknown in the holotype of *Anarosaurus*

pumilio, but absent in *Serpianosaurus*. The pubis morphology of the Eberstadt material is similar to that of *Serpianosaurus*, and isolated posterior dorsal and anterior caudal vertebrae from Eberstadt show distinctly striated neural spines, a character known to occur within the *Serpianosaurus*–*Neusticosaurus* clade (particularly in *Serpianosaurus*: Rieppel, 1989), but unknown (for lack of adequately preserved and/or prepared material) in *Anarosaurus*. The fragmentary remains from Eberstadt might indicate the early occurrence of *Serpianosaurus* in the Germanic Triassic (Hagdorn & Simon, 1993), from where it might have spread southward into the intraplatform basin facies of the southern Alpine region.

Serpianosaurus is the sister-taxon of the genus *Neusticosaurus*. The genus *Neusticosaurus* occurs in the Monte San Giorgio deposits with three species, each relatively short-lived and following one another in stratigraphic succession within the lower Meridekalke (Sander, 1989) of lower to middle Ladinian age: the earliest species, *Neusticosaurus pusillus*, comes from the Cava Inferiore beds, followed by *Neusticosaurus peyeri* from the Cava Superiore beds, which in turn is followed by *Neusticosaurus edwardsii* from the Alla Cascina beds. The intrageneric cladistic structure fits the stratigraphic succession of *Neusticosaurus* species at Monte San Giorgio, but the pattern becomes complicated if the distribution of the species is considered over a wider range.

The most widespread species of *Neusticosaurus* is *N. pusillus*, the first species of *Neusticosaurus* to occur in the Monte San Giorgio deposits and the sister-taxon to all other species of *Neusticosaurus*. Restricted to the Cava Inferiore beds (lower or middle Ladinian) at Monte San Giorgio, the species is abundant in the Lettenkeuper deposits of the Germanic Triassic (Hagdorn & Simon, 1993), considered to be of lower to middle Ladinian age by Brinkmann (1986). However, Kozur (1974, p. 62) identified the first Cordevolian faunal elements in the Grenz dolomit, which he places at the very base of the middle Keuper. This indicates that the lower Keuper (Lettenkeuper) corresponds to the upper Longobardian, that is, to the middle to upper Ladinian. *Neusticosaurus pusillus* has also been reported from the middle Ladinian Prosanto formation of the eastern Alps (Bürgin et al., 1991), and it occurs in the Perledo Member of the Perledo–Varenna formation (northern Italy) of upper Ladinian age (Rieppel, in prep.). This pattern of geographic and temporal distribution suggests a faster faunal turnover rate at Monte San Giorgio

compared to other localities. Diagnostic remains of *Neusticosaurus peyeri* are known only from the Monte San Giorgio deposits, which might indicate that the genus *Neusticosaurus* originated in the intraplatform basin facies of the southern Alps. Such a conclusion is difficult to support, however, because the identification of *Neusticosaurus* species is contingent on the availability of fairly complete skeletons. These are not available from the upper Muschelkalk, in which disarticulated pachypleurosaur remains are abundant.

The holotype of *Neusticosaurus edwardsii* is from Ca' del Frate, a locality in northern Italy that has been correlated with the Kalkschieferzone (uppermost Meridekalke) and has been assigned a middle Carnian age by Tintori et al. (1985). In southern Switzerland, the Meridekalke do not extend into the Carnian (Scheuring, 1978), and the Kalkschieferzone of Monte San Giorgio has yielded *Lariosaurus* (Kuhn-Schnyder, 1987), as have northern Italian outcrops (Tintori & Renesto, 1990; Renesto, 1993). A middle Carnian age may be too young for the Ca' del Frate locality (which may be upper Ladinian), but the occurrence of *Neusticosaurus edwardsii* at Ca' del Frate indicates a longer persistence of this species in the latter locality than in Monte San Giorgio and hence again a faster faunal turnover rate in the Monte San Giorgio Basin than in other similar intraplatform basins of the southern Alps.

Diagnostic remains of *Neusticosaurus toepflichi* are restricted to middle Ladinian deposits of the Gailtaler Alps. Other, less complete pachypleurosaur specimens from the same deposits (Zapfe & König, 1980) cannot be identified to species level.

For taphonomic reasons, articulated vertebrate skeletons are generally preserved in intraplatform basins of the southern Alps and allow species diagnoses based on meristic data. The identification of disarticulated pachypleurosaur remains from the upper Muschelkalk to the species level is difficult if not impossible. Furthermore, the delineation of genera and species within a fully resolved tree ("Hennigian comb": Panchen, 1992) of monophyletic taxa is a purely conventional one. Nevertheless, current knowledge of the Pachypleurosauroidea indicates an increase in taxic diversity among crown-group pachypleurosaurs (*Serpianosaurus*–*Neusticosaurus* clade) from the Ladinian, as compared to the stem-group pachypleurosaurs from the Anisian. Based on the hypothesis that pachypleurosaurs invaded the western Tethyan Province from the east, it might be

argued that the increased taxic diversity of crown-group pachypleurosaurs is correlated with a greater habitat fragmentation and habitat diversity in the intraplatform basin facies of the southern Alps, as compared to the more contiguous habitat in the Muschelkalk Basin. Pachypleurosaurs also document the fact, however, that faunal interchange did take place between the two environments throughout the Middle Triassic (Wild, 1972).

The Paleocology of Pachypleurosaurs

Using generalized reptiles such as *Captorhinus*, *Petrolacosaurus*, *Claudiosaurus*, and *Youngina* as outgroups, and comparing pachypleurosaurs to Eusauropterygia (Storrs, 1991, 1993a), indicates a relatively plesiomorphic morphology for the Pachypleurosauroidea (Rieppel, 1989): retention of the posteriorly excavated quadrate, no distinct posterior displacement of the mandibular articulation, no constriction of the skull table and no posterior elongation of the tooth row beyond the posterior margin of the orbit. All of these characters indicate that pachypleurosaurs retained an impedance-matching middle ear and a simple jaw adductor system.

The Eusauropterygia have reduced or lost the tympanum and the large, air-filled middle ear cavity to avoid problems generated by hydrostatic pressure during diving (Taylor, 1992). Advanced stem-group Sauropterygia, as well as crown-group taxa, are also characterized by an elongation of the upper and lower jaws and dorsoventral depression of the skull, changes that reduce hydrostatic drag during lateral snapping bites. In association with these modifications there developed a specialized dual system of jaw adduction (Rieppel, 1989; Taylor, 1992; Storrs, 1993b) in correlation with a relative elongation of the postorbital region of the skull. The reorientation of the jaw adductor muscle groups is correlated with a posterior extension of the tooth row beyond the posterior margin of the orbit, and with changes in the morphology of the mandibular joint preventing disarticulation of the lower jaw. All of these morphological correlates suggest that Eusauropterygia became progressively more adapted to an open marine environment than is typical for pachypleurosaurs, which inhabit intraplatform basin and shallow epicontinental marine habitats (Sues, 1987).

Currently available evidence supports the position of Placodontia as sister-taxon to all other

Sauropterygia (Eosauropterygia) and *Corosaurus* as sister-taxon to a clade comprising pachypleurosaurs plus Eusauropterygia (Rieppel, 1994b). Such changes in the relative relationships of sauropterygian taxa require the impedance-matching middle ear and the simple jaw adduction system to have re-evolved in pachypleurosaurs (on the basis of ACCTTRAN optimization; DELTRAN optimization treats the loss of the impedance-matching middle ear and the evolution of the dual jaw adduction system in *Corosaurus* and Eusauropterygians as convergent) as an adaptation to a coastal environment.

The correct interpretation of character evolution within the Sauropterygia will depend on further tests of sauropterygian interrelationships. Several faunas have not yet been brought to bear on that problem, such as sauropterygians from the Triassic deposits in Transylvania (Jurcsak, 1982) and Israel (Brotzen, 1955; Peyer, 1955; Haas, 1963), the Eusauropterygia from the Lower and Middle Triassic of China, and new material from the Middle Triassic of northwestern Nevada. Nevertheless, the morphology of pachypleurosaurs, whether relatively plesiomorphic or apomorphic, as well as the geographic and geologic occurrence of the group, indicates that pachypleurosaurs were inhabitants of shallow epicontinental seas or intraplatform basins along coastal stretches (Sues, 1987; Rieppel, 1989; Storrs, 1993b). In the upper Muschelkalk, the occurrence of pachypleurosaurs tends to be correlated with the beginning of a transgressive phase, or the waning of marine conditions during a regressive phase, and the frequency of their occurrence is increased in deposits close to the paleocoast (Hagdorn & Simon, 1993). Intraplatform basins along the northwestern coast of the Tethys temporarily communicated with the open sea, but pachypleurosaurs have so far not been recorded outside coastal environments.

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Appendix: Material Included and Institutional Abbreviations

Institutional Abbreviations

Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin: BGR; The Natural History Museum, London: BMNH; Institut und Museum für Geologie und Paläontologie, Georg-August-Universität, Göttingen: Gö; Institut und Museum für Geologie und Paläontologie, University of Tübingen: GPIT; Natural History Museum, Humboldt University, Berlin: MB; Institute of Geological Sciences, University of Wrocław: MGU; Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a.M.: SMF; Staatliches Museum für Naturkunde, Stuttgart: SMNS.

Anarosaurus heterodontus n. sp.

Institut für Geowissenschaften, Martin-Luther-Universität, Halle; right dentary and left premaxilla (M4/12); Schaumkalk (upper lower Muschelkalk), Freyburg/Unstrut. Museum Freriks, Winterswijk (uncatalogued): skull; lower Muschelkalk, Winterswijk, Netherlands.

Anarosaurus pumilio

Institut und Museum für Geologie und Paläontologie, Georg-August-Universität, Göttingen, Gö 409-1; Museum für Naturkunde, Berlin (MB R. 57.1–3, dorsal view; MB R. 58, ventral view); Institut für Geowissenschaften, Martin-Luther-

Universität, Halle (uncatalogued, skull only, dorsal view); The Natural History Museum, London (BMNH R-5691, dorsal view; MBNH R-5866, ventral view); Staatliches Museum für Naturkunde, Stuttgart (SMNS 59073).

Charitosaurus tschudii

Humboldt Museum, Berlin (MB R. 61–62); Staatliches Museum für Naturkunde, Stuttgart (SMNS 80082–83); lower middle Muschelkalk, Remkersleben.

Dactylosaurus gracilis

Museum für Naturkunde, Berlin (MB R. 63, cast of original specimen of Gürich, 1884); Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin

(BRG, uncatalogued, original specimen of Nopcsa, 1928; MB R. 772.1., MB R. 769, and uncatalogued; humeri from lower Muschelkalk of Gogolin); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a.M. (SMF R-4097 a, b; original specimen of Nopcsa, 1928, cast); Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin (BGR, drawer S 45/5 right; humerus from lower Muschelkalk of Bobrek near Beuthen); Institut und Museum für Geologie und Paläontologie, University of Tübingen (GPIIT 1744/1-10; humeri from lower Muschelkalk of Gogolin, Poland; and an uncatalogued articulated skeleton from the same deposits).

Sauropterygia incertae sedis

Staatliches Museum für Naturkunde, Stuttgart (SMNS 16253, humerus, lower Muschelkalk, Gogolin, Upper Silesia [Poland]).

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