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The Pachypleurosauridae: an annotated bibliography. With comments on some lariosaurs

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ABSTRACT

The taxonomic literature on the pachypleurosaurid nothosaurs is reviewed and critical annotations are provided. Hypotheses of relationships put forward in recent publications are discussed.

ZUSAMMENFASSUNG

Die taxonomische Literatur über die Pachypleurosauridae wird kritisch bibliographiert. Verwandtschaftshypothesen, die in neueren Publikationen vorgeschlagen wurden, werden diskutiert.

Introduction

The Pachypleurosauridae are a diverse group of small to medium sized marine reptiles related to the Nothosauridae. The study of the taxonomic diversity of pachypleurosaurid genera and species has been thrown into focus by several recent research projects, including work in progress on the abundant pachypleurosaur material from the Middle Triassic of Monte San Giorgio, Switzerland. Comprehension of the group is rendered difficult, however, by a widely scattered literature, of which the older publications are difficult to obtain for workers outside Italy. Italian papers from around the middle of last century are not only the first treatments of pachypleurosaurid specimens, but they are also marred by sloppy treatment of nomenclatorial issues, and by statements distorted by polemics raging between early authors.

It is the purpose of the present contribution to provide a complete list of references dealing with the Pachypleurosauridae, and to trace the history of the investigation of this group of reptiles by critical annotations to the available literature. It is hoped that this contribution will provide a sound basis for the future treatment of the taxonomic diversity in that group.

Systematic Paleontology

Suborder *Pachypleurosauroidea* von HUENE, 1956

ARTHABER (1924) separated *Lariosaurus* (together with *Proneusticosaurus* and *Partenosaurus*) from pachypleurosaurids at the family level.

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NOPCSA (1928) recognized a basal dichotomy within nothosaurs, and grouped the genera within two families, the Nothosauridae and Pachypleurosauridae. His classification is not congruent with the currently accepted one: *Simosaurus* and *Proneusticosaurus* were referred to the Pachypleurosauridae (Neusticosaurinae), while *Phygosaurus* was referred to the Nothosauridae (Lariosaurinae) by NOPCSA (1928).

PEYER (1932, p. 16) suggested a close relationship of *Pachypleurosaurus* with *Dactylosaurus*, *Anarosaurus*, and *Neusticosaurus*.

PEYER (1934, p. 117–118) provided a diagnosis for the two families Pachypleurosauridae (*Anarosaurus*, *Dactylosaurus*, *Neusticosaurus*, *Pachypleurosaurus*, *Phygosaurus*, *Psilotrachelosaurus*) and Nothosauridae (*Ceresiosaurus*, *Cymatosaurus*, *Germanosaurus*, *Lariosaurus*, *Nothosaurus*, *Pistosaurus*, *Proneusticosaurus*, *Rhaeticonia*, *Simosaurus*).

ZANGERL (1935, p. 64) adopted the Pachypleurosauridae and Nothosauridae as defined by PEYER (1934).

VON HUENE (1948, p. 83–84) subdivided the Sauropterygia into three suborders. The Pachypleurosauridea (including the Pachypleurosauridae and Proneusticosauridae), the Nothosauridea (including the Lariosauridae and Nothosauridae) and the Plesiosauroida. The diagnosis of the Pachypleurosauridea neglects the characters enumerated by PEYER (1934, p. 117–118) to characterize the Pachypleurosauridae.

VON HUENE (1956, p. 382) again emphasized a basal dichotomy within the Sauropterygia, separating the Pachypleurosauroida as an “early offshoot” from the “true nothosaurs such as *Nothosaurus* ...”.

The Pachypleurosauroida was subdivided by VON HUENE (1956) into two families, the Pachypleurosauridae (*Dactylosaurus*, *Neusticosaurus*, *Pachypleurosaurus*, *Phygosaurus*, *Psilotrachelosaurus*, *Rhaeticonia*), and the Proneusticosauridae (*Proneusticosaurus*).

Current knowledge favours the inclusion of *Proneusticosaurus* and *Lariosaurus* within the same family. Characters such as the curved humerus, the enlarged upper temporal opening (see below) and the increase of sacral vertebrae (five or six) suggest that the two genera are to be grouped with more typical nothosaurs rather than with the pachypleurosauroids (SCHMIDT 1987). The Pachypleurosauroida are thus restricted to a single family, the Pachypleurosauridae.

***Pachypleurosauridae* NOPCSA 1928**

NOPCSA (1928) erected the family Pachypleurosauridae to include three subfamilies, the Pachypleurosaurinae (*Anarosaurus*, *Dactylosaurus*, *Pachypleurosaurus*), the Neusticosaurinae (*Neusticosaurus*), and the Simosaurinae (*Simosaurus*, *Proneusticosaurus*).

PEYER (1934, p. 117–118) revised the content of the Pachypleurosauridae, and provided a diagnosis for the family, based on non-polarized characters: “Small temporal opening; humerus more or less straight, the middle portion showing a circular cross-sectional area; sacrum comprising 3 to 4 vertebrae; sacral ribs not in contact proximally; intermedium small, positioned distal to the ulna”.

The following genera are included within the Pachypleurosauridae: *Anarosaurus*, *Dactylosaurus*, *Neusticosaurus*, *Pachypleurosaurus*, *Phygosaurus* (without skull), *Psilotrachelosaurus* (without skull).

Pachypleurosaurus (CORNALIA 1854)

Pachypleurosaurus edwardsi (CORNALIA 1854) is the type species of the genus. The taxon cannot be discussed without reference to the older Italian literature dealing with the problem of demarcation of *Lariosaurus* and related forms from *Pachypleurosaurus* within the material of fossil saurians from three localities: Besano, Viggiù and Perledo. The stratigraphical correlation of these localities was recently reviewed by TINTORI et al. (1985).

The oldest fossiliferous layer at the Monte San Giorgio is the Grenzbitumen-horizon, corresponding to the Anisian-Ladinian boundary (RIEBER 1973): it yielded pachypleurosaur material informally referred to the genus *Phygosaurus* (RIEPPEL, work in progress). The deposits of Monte San Giorgio extend to progressively younger strata through the Ladinian (see KUHN-SCHNYDER 1974; CARROLL & GASKILL 1985, Fig. 10), up to the base of the "Upper Meridekalke"; the majority of the *Pachypleurosaurus edwardsi* specimens have come from the locality "Alla Cascina" of that horizon (CARROLL & GASKILL 1985). KUHN-SCHNYDER (1987) has recently described a *Lariosaurus* specimen from still younger deposits at Monte San Giorgio: it represents the geologically youngest tetrapod from this locality. The layers between the "Grenzbitumenzone" and the "Upper Meridekalke" have yielded the abundant material of "small pachypleurosaurids", provisionally referred to the genus *Neusticosaurus* by CARROLL & GASKILL (1985, p. 349) and currently under investigation by M. Sander.

Besano is a locality in Northern Italy southwest of Monte San Giorgio, at which the southern continuation of the deposits of the Monte San Giorgio basin crop out again. The same fauna is to be expected.

Viggiù is an Italian locality still further to the South, with outcrops corresponding to the geologically younger layers of Monte San Giorgio, viz. the "Alla Cascina-horizon". This follows from the angle at which the fossiliferous layers extend southwards.

Perledo, on the other hand, lying along the western slope of the Grigna Mountains, East of the Lake of Como, is geologically younger than the Monte San Giorgio deposits, or it overlaps with the youngest deposits at the latter locality: the lower part of the unit is Ladinian in age, the upper part may reach into the Carnian (TINTORI et al. 1985, p. 199). This corresponds with the occurrence of *Lariosaurus* in Perledo, as well as in the Monte San Giorgio deposits above the "Alla Cascina"-horizon. *Phygosaurus* was first described from Perledo. CURIONI (1863) claimed that all nothosaurs from Perledo have to be synonymized with *Lariosaurus balsami*, a conclusion which was contradicted by PEYER (1934) in accordance with CORNALIA (1854). The specimens in question are pachypleurosaurids, although the material described and figured by PEYER (1934) is very fragmentary and/or poorly preserved.

BALSAMO-CRIVELLI (1839) described and illustrated a fossil saurian from Perledo (PEYER 1934, p. 10), collected in the "monti che circondano il Lago di Como" (BALSAMO-CRIVELLI 1839, p. 423), which was later to become the type of *Lariosaurus balsami*. (CURIONI 1847). BALSAMO-CRIVELLI (1939, p. 425) informally referred the specimen to the "famiglia dei Paleosauri"; BOULENGER (1898, p. 1-2) and ARTHABER (1924, p. 499) referred to the specimen under the formal name of *Palaeosaurus*, which therefore becomes a junior synonym of *Lariosaurus* CURIONI.

CURIONI (1847) described and figured a second fossil saurian from Perledo named *Macromirosaurus Plinj* (CURIONI 1847, p. 161). CARNALIA (1854, p. 54) misspelt the generic name as *Macromerosaurus*, a spelling adopted by CURIONI (1863) and most later authors. PEYER (1934, p. 84, and Pl. 41, Fig. 1) prepared and re-described the original specimen of *Macromirosaurus*, noting the CURIONI's (1847) figure is a mirror-image and is also made up to some degree: the original lacks the facial region of the skull (see below: notes on some lariosaurs). PEYER (1934, p. 6) also emphasized, in accordance with BOULENGER (1898), that the name *Macromirosaurus* is misleading, as it indicates a relatively large humerus. This contrasts with CURIONI's (1847, p. 161) statement that the femur is "maggiore di quasi una teza parte" as compared to the humerus. This feature was cited as evidence for the distinctiveness of *Macromirosaurus* from yet another, similar fossil from Perledo (with a humerus of roughly equal length as the femur), and also from a specimen found at Viggù and belonging to the collection of the Count Vitaliano Borromeo (with a humerus distinctly longer than the femur).

CURIONI (1847, p. 164) also noted morphological differences between *Macromirosaurus* and the fossil described by BALSAMO-CRIVELLI (1839), which he therefore named *Lariosaurus Balsami* (CURIONI 1847, p. 166), "alludendo al luogo in cui venne rinvenuto, cioè sui monti Lariani ...". The specimen from Perledo mentioned above, with a humerus of roughly equal length as the femur, was also referred to that genus and species (CURIONI 1847, p. 165).

CARNALIA (1854) described and figured a total of four specimens from Besano and Viggù under the name *Pachypleura Edwardsii*; no type specimen was designated by CARNALIA (1854).

The third specimen in the sample, coming from Viggù and belonging to the collection of Count Vitaliano Borromeo, later to the Museo Civico di Storia Naturale di Milano, was already mentioned by CURIONI (1847) and described as having a humerus which is distinctly longer than the femur. The specimen was figured by CARNALIA (1854, Pl. 2, Fig. 2) and referred to as "Esemplare minore". BOULENGER (1898, p. 7) concluded that it is this specimen which "must be taken as the type of *Pachypleurosaurus edwardsi*". The specimen from Besano, figured on Plate i, is possibly a *Neusticosaurus*. The "smaller specimen" from Besano thus became the lectotype for the species *Pachypleurosaurus edwardsi*, type species of its genus, a conclusion which was accepted by NOPCSA (1928, p. 22) and all later authors. The specimen had previously been used for comparison by DEECKE (1886) and BROILI (1927, p. 218–219): the latter author ascertained its generic distinctiveness from *Neusticosaurus* in contradistinction to LYDEKKER (1889), E. FRAAS (1896) and ZITTEL (1895).

LYDEKKER (1889, p. 285) noted that CARNALIA's (1854) generic name *Pachypleura* was preoccupied; he drew no consequences from this insight, however, as he considered *Pachypleura* to be synonymous with *Neusticosaurus* BROILI (1927, p. 220) ascertained the validity of both genera, and changed CARNALIA's (1854) generic name to *Pachypleurosaurus*; NOPCSA (1928) independently reached the same conclusion.

Pachypleurosaurus edwardsi was redescribed in a recent monograph by CARROLL & GASKILL (1985; see also CARROLL 1985) which includes the material from the Middle Triassic of Monte San Giorgio. As noted by these authors, it was the immature nature of the type specimen (lectotype) which introduced much confusion in the study of pachypleurosaurs, in particular with respect to the demarcation of *Pachypleurosaurus* from

Neusticosaurus and *Phygosaurus*. The origin of this confusion goes back to the initial descriptions of the Monte San Giorgio material by PEYER (1928, 1932) and ZANGERL (1935). The latter author recognized an extreme range of variability for the *Pachypleurosaurus* from Monte San Giorgio. Recent work has shown, however, that this extensive variability reported by ZANGERL (1935) is due to the fact that several taxa were included by him within the single genus and species *Pachypleurosaurus edwardsi* (CARROLL & GASKILL 1985; SANDER, work in progress). The descriptions of pachypleurosaurs by VIALLI (1941, three additional specimens from Besano), KUHN-SCHNYDER (1952; an incomplete specimen from the Ducantal, Kanton Graubünden, Switzerland), KUHN-SCHNYDER (1959; a specimen without skull from the Stulseralp, Kanton Graubünden, Switzerland, designated as type of a new species, *Pachypleurosaurws staubi*, but referred to the genus *Neusticosaurus* by CARROLL & GASKILL (1985, p. 348)] and MATEER (1976; two specimens from Vallone Caves near Lake Lugano, Northern Italy, referred to *Pachypleurosaurus* cf. *staubi* by MATEER but to *Neusticosaurus* by CARROLL & GASKILL [1985, p. 349]) deserve critical re-examination in the light of these recent findings.

Neusticosaurus SEELEY 1883

O. FRAAS (1881) described *Simosaurus pusillus* from the Lettenkohle (Lower Keuper) of Hoheneck, near Ludwigsburg, Southern Germany. The specimens were re-described by SEELEY (1882) who allocated them to a separate genus, *Neusticosaurus*. This genus was synonymized with *Lariosaurus* by DEZINGO (1883), BASSANI (1886) and MARIANI (1923), a view criticized by PEYER (1934, p. 12).

In 1896, E. FRAAS described numerous small *Neusticosaurus* specimens from the quarries of Egolsheim as a new species, *Neusticosaurus pygmaeus* (E. FRAAS 1896, p. 13). CARROLL & GASKILL (1985, p. 349) concluded that *Neusticosaurus pygmaeus* represents "almost certainly juvenile specimens of *N. pusillus*".

CARROLL & GASKILL (1985, p. 349–354) further concluded that the genus *Neusticosaurus* is represented in the abundant pachypleurosaurid material from the Middle Triassic of Monte San Giorgio, noting that the description of *N. pusillus* by SEELEY (1882) is erroneous with respect to two features: the presence of large suborbital vacuities, and the relative length of the metatarsals. The pattern of vertebral reduction through time in the genus *Neusticosaurus* from Monte San Giorgio was briefly discussed by CARROLL (1984).

Dactylosaurus GÜRICH 1884

GÜRICH (1884, p. 125, Pl. II, Figs. 1 and 2) described and figured *Dactylosaurus gracilis* from the lowermost Muschelkalk of "Oberschlesien" (Poland). The type and only known specimen preserved the posterior part of the skull, the cervical vertebral column, the pectoral girdle and the right fore-limb. The fate of the type specimen is unknown; a cast is preserved at the Museum für Naturkunde, Humboldt-Universität, East Berlin (SUES & CARROLL 1985, p. 1602). In 1886, GÜRICH rebutted the criticism of DEECKE (1886), confirming the presence of three carpal bones.

A second species of the genus, *Dactylosaurus schroederi*, was first described by NOPCSA (1928, p. 25–31) and recently re-studied by SUES & CARROLL (1985). NOPCSA's (1928, p. 27, 43) description is equivocal as to the number of sacral vertebrae; SUE &

CARROLL (1985, p. 1606) determined the presence of three pairs of sacral ribs. *Dactylosaurus schroederi* (but not *D. gracilis*) retains a “pisiform” in the carpus (NOPCSA 1928, p. 29), considered as a neomorph by SUES & CARROLL (1985, p. 1607); all other pachypleurosaurs have three or less ossified carpal elements. *Dactylosaurus* resembles *Anarosaurus* and *Keichousaurus* but differs from other pachypleurosaurs by the presence of relatively large upper temporal openings with a participation of the postorbital in their anteromedial margin (SUES & CARROLL 1985). In their re-description of *Dactylosaurus schroederi*, SUES & CARROLL (1985) emphasize the high degree of ossification reached by this species at relatively small overall size. The type specimen of *Dactylosaurus gracilis* is even smaller, what in SUES & CARROLL’s (1985, p. 1608) views raises doubts as to the two species being congeneric, although morphology does not preclude such an arrangement.

Anarosaurus DAMES 1890

DAMES (1890, p. 74) described an illustrated a specimen in the collection of the University of Göttingen as a new genus and species *Anarosaurus pumilio*. The specimen came from Remkersleben, west of Magdeburg; the lithology indicated its provenience from the uppermost Lower Muschelkalk. A second specimen, an isolated lower jaw from the Lower Anisian of the Lechtaler Alpen, Austria, was referred to the same genus but to a different species, *Anarosaurus multidentatus*, by v. HUENE (1958, p. 383).

The genus is characterized by elongated teeth in the front part of the upper jaws. The upper temporal openings were described by JAEKEL (1910, p. 325); his description was corroborated by NOPCSA (1928, p. 30). As in *Dactylosaurus*, the upper temporal openings of *Anarosaurus* are smaller than the orbits but larger than in other pachypleurosaurs, with the postorbital participating in the formation of the anteromedial margin (NOPCSA 1928, Pl. IV, Fig. 2; CARROLL 1981, p. 379, Fig. 32). The ribs are not pachyostotic. The number of sacral vertebrae does not appear to exceed three (DAMES 1890, p. 78; see also NOPCSA 1928, for a revision of vertebral counts of *Anarosaurus*).

According to PEYER (pers. comm., quoted by ZANGERL 1935, p. 68) *Anarosaurus* shares with *Phygosaurus* the combination of five (instead of three) elements in each gastralia, a character also recorded for *Proneusticosaurus* (VOLZ 1902, p. 134), *Lariosaurus* (BOULENGER 1898), and other nothosaurs such as *Ceresiosaurus* PEYER (1934, p. 78).

According to CARROLL & GASKILL (1985, p. 349; see also KUHN-SCHNYDER 1959, p. 652), “*Anarosaurus* is clearly distinguished from other pachypleurosaurids by the significantly greater length of the femur relative to the humerus. In the specimen described by NOPCSA (1928), the length of the femur exceeds that of the humerus by almost 30%”. This, as well as other characteristics such as the relatively large upper temporal fossae or the absence of rib pachyostosis, may be juvenile features, perhaps indicating paedomorphosis in the genus.

Psilotrachelosaurus NOPCSA 1928

NOPCSA (1928, p. 31–37) described *Psilotrachelosaurus Töplitschi* nov. gen. nov. sp. The specimen belongs to the Klagenfurt Museum; the exact locality at which it was found remains unknown – it may be the “Stadlbach-Graben” 2 km west of Töplitsch; the

limestone in which the fossil is embedded belongs to the “Muschelkalk”-series (Ladinian of the northern Austrian Alps: v. HUENE 1956, p. 384). The specimen lacks the head and the tip of the tail.

The sacrum comprises three vertebrae, testifying to the pachypleurosaurid nature of the genus. Otherwise, its validity is questionable, however. The coracoid is unusually long and narrow (CARROLL & GASKILL 1985, p. 349), what might be an effect of preservation and/or preparation, however (SUES & CARROLL 1985, p. 1608). The last four cervical vertebrae appear to be distinctive, but their shape might result from their fraction in a horizontal plane at the base of the neural arch (NOPCSA 1928, p. 32). The last character apparently distinctive for *Psilotrachelosaurus* is the approximately equal length of all metacarpals and metatarsals (CARROLL & GASKILL 1985, p. 349).

SUES & CARROLL (1985, p. 1608) concluded: “Too little is known about ... *Psilotrachelosaurus* at present to allow a definitive phylogenetic assessment”.

Phygosaurus ARTHABER 1924

DEECKE (1886) described the Strassburg-specimen, collected in the Grigna mountains (Perledo) under the name of *Lariosaurus balsami*; a cast of the original specimen described by BALSAMO-CRIVELLI (1839) served as basis for comparison (PEYER 1934, p. 14–15). The description of the gastral ribs in the Strassburg-specimen by DEECKE (1886, p. 175), and Pl. 3, Fig. 3) as being composed of three elements is erroneous.

DAMES (1890) expressed doubts about DEECKE’s (1886) assignment of the Strassburg-specimen to *Lariosaurus balsami*. He pointed out that in the first specimen the humerus is not as distinctly curved as would be typical for *Lariosaurus*. The bone is constricted in the middle portion and distally expanded in a manner similar to *Neusticosaurus*. On the other hand, DAMES noted the absence of rib pachyostosis in the Strassburg-specimen in contradistinction to *Neusticosaurus*.

DÖDERLEIN (in STEINMANN & DÖDERLEIN 1890, p. 627, Fig. 770) reconstructed the pectoral girdle and gastral ribs of the Strassburg-specimen in ventral view, assigning the latter to *Lariosaurus balsami* following DEECKE (1886). DÖDERLEIN correctly reproduced the composition of the gastral ribs as being composed of five elements each.

BOULENGER (1898, p. 7) could “see no ground for regarding Deecke’s specimen as generically distinct from *Neusticosaurus pusillus*”.

MARIANI (1923, p. 224) referred the Strassburg-specimen to *Lariosaurus*.

ARTHABER (1924, p. 493) assigned the Strassburg-specimen from Perledo to a new genus and species, *Phygosaurus perledicus*, noting the absence of rib-pachyostosis, the presence of three sacral vertebrae only (in contrast to *Lariosaurus*), and the composition of gastral ribs of five elements each as described by DÖDERLEIN – a similarity shared with the *Lariosaurus* specimen from Frankfurt described by BOULENGER (1898).

PEYER (1934) prepared and re-described the Strassburg-specimen. He corroborated the validity of the genus and also DÖDERLEIN’s description of the gastral ribs. PEYER (1934, p. 120) provided an amended diagnosis for the genus which will have to be critically revised following the analysis of the Monte San Giorgio material (RIEPPEL, work in progress).

ZANGERL (1935) questioned the generic distinctiveness of *Phygosaurus*, as most of the diagnostic features (such as rib cross-sectional area and extended coracoid symphysis) are

also observed in the *Pachypleurosaurus* material from the “Alla Cascina” – horizon of Monte San Giorgio. Gastral ribs being composed of five elements each are also observed in *Anarosaurus* (PEYER, pers. comm., quoted in ZANGERL 1935, p. 68).

Keichousaurus YOUNG 1958

The genus was first described by YOUNG (1958, p. 73), the material coming from the Middle Triassic of S. W. Keichow Province, China. Two species are currently recognized: *Keichousaurus hui* (YOUNG 1958), and *Keichousaurus yuananensis* (YOUNG 1965; see also SHUOPNAN, BAIMING & LUCAS 1985).

The allocation of the genus to the Pachypleurosauridae was questioned by KUHN-SCHNYDER (1959, p. 656; v. HUENE 1959, referred the genus to the “Simosauridae”), who emphasized the relatively large upper temporal openings of *Keichousaurus*. His criticism was rebuked by YOUNG (1965); as can be seen from YOUNG’s illustration (1958, Pl. 1, Fig. 1), the upper temporal openings are indeed relatively large, but they remain distinctly smaller than the orbit. Their relative size does not exceed that observed in *Dactylosaurus* and *Anarosaurus*, and as in the latter genera, the postorbital appears to participate in the formation of their anteromedial margin.

CARROLL & GASKILL (1985, S. 349) write of *Keichousaurus*: “In most features it appears typical of pachypleurosaurids, but the ulna is a massive element, quite unlike that of any European genera”.

Incomplete pachypleurosaur material

v. HUENE (1942) described isolated postcranial material from the lowermost Lettenkohle (Lower Keuper), 1.8 meters above the Muschelkalk, from the surroundings of Gaidorf, southern Germany. The elements fall into the range of variability of the pachypleurosaurids from Monte San Giorgio as described by PEYER (1932) and ZANGERL (1935).

SANZ (1983) described isolated pachypleurosaur vertebrae from the Spanish Muschelkalk, Aiguafreda, near Barcelona.

SCHULTZE & MÖLLER (1986) described isolated postcranial elements referred to the Pachypleurosauridae from the Middle Muschelkalk near Göttingen, Germany.

Comments on some lariosaurs

CURIONI (1847) described a fossil from Perledo under the name of *Macromirosaurus Plinj*, and referred the specimen previously described by BALSAMO-CRIVELLI (1839) to a separate genus and species, *Lariosaurus balsami*.

In 1854, CORNALIA appended to his description of *Pachypleurosaurus edwardsi* some comments on incomplete specimens from Perledo in the possession of the Museo Civico di Storia Naturale di Milano, which he also referred to his new genus.

CURIONI (1863) interpreted these comments of CORNALIA (1854) as to generally imply the synonymy of the fossil saurians from Perledo with those from Besano and Viggiù, a supposition against which he strongly objected in his paper of 1863. This polemic is worth mentioning because in 1863, CURIONI distorted his views as published in 1847 (BOULENGER 1898; PEYER 1934).

In contradiction to his 1847 paper, CURIONI claimed in 1863 (p. 266) that in his earlier publication he had described and figured a specimen from Perledo under the name of *Lariosaurus balsami*; a second specimen, found both in Perledo and Viggiù, was given the name *Macromirosaurus* (*Macromerosaurus*), characterized by the relative length of the humerus.

Both BOULENGER (1898) and PEYER (1934) agree, however, that with his claim, CURIONI (1863) misconstrued what he had said in 1847. The description and figure given by CURIONI in 1847 are those of *Macromirosaurus*, although the name of the genus is misleading, as pointed out above.

In his reply to CORNALIA's (1854) appendix, CURIONI (1863, p. 266) continued to point out that new and better preserved material from Perledo, collected after 1847, demonstrated that all the fossil saurians from this locality can in fact be referred to one single genus and species, viz. *Lariosaurus balsami*, which is different from the taxa found at Besano and Viggiù. PEYER (1934: 10) noted that CURIONI (1863) was wrong with this claim, and described pachypleurosaur from Perledo which are too incomplete, however, to permit specific identification.

What continued to be a problem, however, was the validity of the genus *Macromirosaurus* (*Macromerosaurus*). With his claim that all fossil saurians from Perledo have to be referred to *Lariosaurus* CURIONI (1863) implicitly synonymized *Macromirosaurus* with the latter genus. DAMES (1890, p. 84), BOULENGER (1898) and PEYER (1934, p. 82) considered it possible that CURIONI (1863) treated *Macromirosaurus* as a juvenile specimen of *Lariosaurus*. The synonymy of *Macromirosaurus* with *Lariosaurus* was accepted by DE ZINGO (1883), BASSANI (1886), DAMES (1890), and BOULENGER (1898). PEYER (1934) redescribed the original specimen of *Macromirosaurus* (CURIONI 1847) finding no differences from *Lariosaurus balsami*: he referred to it as *Lariosaurus balsami* varietas *plinii* CURIONI (PEYER 1934: 128).

The synonymy of *Macromirosaurus* with *Lariosaurus* was not accepted unanimously, however. BAUR (1886, p. 247) erected the family Macromirosauridae to include the genera *Macromirosaurus* and *Neusticosaurus*. In a postscript (BAUR 1886, p. 323) he noted that this family is identical with the "Lariosauridae" sensu GERVAIS (1859, p. 485; the family Lariosauridae was erected by LYDEKKER 1889, p. 284). DEECKE (1886, p. 190–191) on the other hand stressed the similarities which *Macromirosaurus* supposedly shares with protorosaurs and lacertids (see also LYDEKKER 1889, p. 286).

ARTHABER (1924, p. 489–490) emphasized the distinctiveness of *Macromirosaurus* (*Macromerosaurus*) as opposed to *Lariosaurus*, stressing amongst other features the different morphology of the interclavicle. However, PEYER (1934: 83) pointed out that ARTHABER's (1924) reconstruction of the pectoral girdle of *Macromirosaurus* is based on the erroneous interpretation of CURIONI's (1847) original figure.

BROILI (1927, p. 216) again stressed the validity of the genus *Macromirosaurus*, noting that it differs from *Lariosaurus* by the snout which is distinctly set off from the more posterior portion of the facial region of the skull. This is also the character which, according to his opinion (BROILI 1927, p. 223) proves the close relationship of *Macromirosaurus* with his own new genus and species, "Rhaeticonia Rothpletzi" from the Upper Ladinian of Austria ("Arlbergerschichten" near Bludenz). The sacrum of *Rhaeticonia* is unfortunately not known (BROILI 1927, p. 209), but the impressions of the upper temporal

openings appear large (BROILI 1927, p. 207), what justifies the tentative inclusion of *Rhaeticonia* within the Nothosauridae by PEYER (1934).

The problem is, however, that the facial region of the skull of the type specimen of *Macromirosaurus* is not preserved (PEYER 1934, p. 84, and Pl. 41, Fig. 1). On the other hand, PEYER's (1934) sample of *Lariosaurus* from Perledo was not homogeneous with respect to this character: the snout is distinctly set off in the Münich-specimen (PEYER 1934, Pl. 32, Fig. 1 and Pl. 33, Fig. 3), first described by ZITTEL (1887–1890, p. 484–486), and in the Frankfurt-specimen (PEYER 1934, Pl. 41, Fig. 3) first described by BOULENGER (1898). The fine specimen of *Lariosaurus* described by MAZIN (1985) does not share this feature, however. From this it appears that the lariosaur genera and species might deserve critical re-evaluation.

Character analysis

A diapsid derivation of nothosaurs was first suggested by JAEKEL (1910), a proposition which was supported by KUHN-SCHNYDER (1967) and CARROLL (1981). A basal dichotomy is currently recognized within the diapsid (neodiapsid sensu BENTON 1985) reptiles, the Archosauromorpha constituting the sistergroup of the Lepidosauromorpha (GAUTHIER 1984; EVANS 1984; BENTON 1985). Whereas GAUTHIER (1984), EVANS (1984, 1987) and BENTON (1985) classify *Youngina* within the Lepidosauromorpha, GAFFNEY (1980) considered the genus to represent the sistergroup of both archosaurs and lepidosaurs. CARROLL (1981) described *Claudiosaurus* from the Upper Permian of Madagascar as a primitive diapsid reptile "structurally intermediate" between such forms as *Youngina* on the one hand and sauropterygians on the other. BENTON (1985) and EVANS (1987) classify *Claudiosaurus* as sistergroup of archosauromorphs plus lepidosauromorphs which in turn constitute the Neodiapsida of BENTON (1985). The plesiomorph sistergroup of *Claudiosaurus* plus the Neodiapsida is the Araeoscelidia, including the genera *Petrolacosaurus* (REISZ 1981) and *Araeoscelis* (REISZ, BERMAN & SCOTT 1984). In view of the uncertainty as to the sistergroup relations of nothosaurs, it is suggested to use *Araeoscelis*, *Petrolacosaurus*, *Youngina* and *Claudiosaurus* as potential outgroups for character analysis, giving the latter genus precedence over the others.

A number of characters was lifted from the available literature as reproduced in Table 1.

The sacrum of *Youngina* comprises two sacral vertebrae (GOW 1975), and so does that of *Claudiosaurus*, although it begins to incorporate a third (sacral) rib for the support of the pelvic girdle (CARROLL 1981). The sacrum of pachypleurosaurids never incorporates more than three (variably an occasional but equivocal fourth) sacral vertebrae, and it is therefore relatively plesiomorph as compared to other nothosaurs with five or six sacral vertebrae.

The small upper temporal openings have been cited as a pachypleurosaurid synapomorphy by SUES & CARROLL (1985, p. 1608), while the same character was interpreted as primitive by CARROLL & GASKILL (1985, p. 361). They compared the small upper temporal fossa to that of *Youngina*, concluding that this condition might be plesiomorph for nothosaurs in general. Indeed, the upper temporal opening is smaller than the orbit in *Youngina*, *Claudiosaurus* (CARROLL 1981) and in pachypleurosaurids. This does seem to represent the primitive condition for nothosaurs in general. Nothosaurs other than pachypleurosaurids are therefore characterized by the apomorphic enlargement of the upper temporal fossa, which becomes larger than the orbit.

Table 1: Data matrix for the currently recognized taxa of the Pachypleurosauridae. Characters are the following:

- a) sacral vertebrae: 4 or less (0); 5 or more (1).
- b) upper temporal fossa: smaller than orbit (0); larger than orbit (1).
- c) postorbital: enters upper temporal fossa (0); excluded from upper temporal fossa (1).
- d) humerus: straight (0), curved (1).
- e) "pisiforme" (4th carpal ossification): retained (0); lost (1).
- f) number of carpal ossifications: more than three (0); three (1); two (2).
- g) gastralia composed of: five elements (0); three elements (1).
- h) ribs: not pachyostotic (0); pachyostotic (1).

(Characters b, c, and e/f cannot be checked on the type and only known specimen of *Phygosaurus*).

	<i>Araeoscelis</i>	<i>Petrolacosaurus</i>	<i>Youngina</i>	<i>Claudiosaurus</i>	<i>Lariosaurus</i>	<i>Anarosaurus</i>	<i>Dactylosaurus</i>	<i>Keichousaurus</i>	<i>Neusticosaurus</i>	<i>Pachypleurosaurus</i>	<i>Phygosaurus</i>	<i>Psilotrachelosaurus</i>
a	0	0	0	0	1	0	0	0	0	0	0	0
b	0	0	0	0	1	0	0	0	0	0	?	0
c	0	0	0	0	0	0	0	0	0/1	0/1	?	?
d	0	0	0	0	1	0	0	0	0	0	0	0
e	?	0	?	0	?	?	0/1	1	1	1	?	1
f	?	0	0	0	0/1	?	0/1	1/2	2	1/2	?	1
g	?	?	?	0	0	0	0	?	1	1	0	?
h	0	0	0	0	0/1	0	0/1	1	1	1	0	1

The humerus is straight in captorhinid stem reptiles (HOLMES 1977) and in early diapsids. The humerus is straight or slightly curved in pachypleurosaurids, dependent on sex. In other nothosaurs, the humerus is distinctly curved, the apomorphic character state.

SCHMIDT (1987, 365) characterized the Pachypleurosauridae by the small upper temporal fossa from the margin of which the postorbital is excluded. The postorbital enters the upper temporal fossa in *Youngina*, *Araeoscelis* (REISZ, BERMANN & SCOTT 1984), *Petrolacosaurus* (REISZ 1981) and *Claudiosaurus* (CARROLL 1981). The postorbital enters the upper temporal opening in *Anarosaurus*, *Dactylosaurus*, *Keichousaurus* and variably in *Neusticosaurus* and *Pachypleurosaurus* (CAROLL & GASKILL, 1985). A reduction of the size of the upper temporal fossa, on the other hand, appears to be synapomorph at a less inclusive level (RIEPPEL, work in progress).

Another synapomorphy evoked by SCHMIDT (1987) to diagnose the Pachypleurosauridae is a reduction of the phalangeal formula in manus and pes. A pachypleurosaurid from the Grenzbitumen-horizon of Monte San Giorgio displays the primitive phalangeal formula both in hand and foot, however.

SUES & CARROLL (1985, p. 1608) mention two further shared derived characters diagnosing the Pachypleurosauridae, viz. the reduction of the posteromedial process of the interclavicle, and the reduction of ossified elements in the carpus, maximally four being present (in *Dactylosaurus schroederi*). The reduction of the posterior stem of the

interclavicle is synapomorphic at a more inclusive level, however, while the pattern of reduction of the carpal bones does not yield any useful hypothesis of grouping. Most taxa included in the analysis either preserve the primitive set of carpal bones, or include variably two or three ossifications in their carpus.

The conclusion is that current literature provides no evidence in support of the monophyly of the Pachypleurosauridae. A potential synapomorphy diagnosing the group is the presence of a tympanum, suspended on a posteriorly excavated quadrate bone, as described by CARROLL & GASKILL (1985), but the assessment of the significance of this character must await a more detailed analysis of the relationships of sauropterygians to diapsid reptiles. On the other hand, all other nothosaurs, the Nothosauridae sensu PEYER (1934), are well characterized by a suite of shared derived characters (see also SCHMIDT 1987), including the enlarged upper temporal openings, the posterior displacement of the mandibular joint, the increased number of sacral vertebrae, and the distinctly curved humerus.

Within the taxa conventionally referred to pachypleurosaurids, some are diagnosed by autapomorphies: *Anarosaurus* (if adult) is distinguished by the relation of humerus to femur length; *Keichosaurus* has a broad and massive ulna; and in *Psilotrachelosaurus* the metatarsal and metacarpal bones are claimed to be all of equal length with the exception of the first (NOPCSA 1928).

Resolution within the pachypleurosaurids is poor on the basis of available data. It might appear possible to group all pachypleurosaurid taxa to the exclusion of *Dactylosaurus schroederi* on the basis of the shared derived loss of the pisiform, if this is the correct homology of the element in question. If, however, *Dactylosaurus gracilis* has to be referred to that genus too, its placement implies either a convergent loss of the pisiform, or the interpretation of the latter as a neomorph. On the other hand, SUES & CARROLL (1985) have already expressed doubts as to the congenericity of the two taxa, based on size differences. Beyond that, the genera *Keichousaurus*, *Psilotrachelosaurus*, *Neusticosaurus* and *Pachypleurosaurus* group together on the basis of pachyostotic ribs, admittedly a feature of questionable significance [*Dactylosaurus* and *Lariosaurus* (PEYER 1934) are polymorphic with respect to this character, which may furthermore be age-related in some taxa]. *Neusticosaurus* and *Pachypleurosaurus* pair off on the basis of the structure of their gastral ribs. These are composed of three elements only (the character is unknown at present for *Keichousaurus* and *Psilotrachelosaurus*).

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