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The status of the sauropterygian reptile *Partanosaurus zitteli* SKUPHOS from the Middle Triassic of the Austrian Alps, with comments on *Microleptosaurus schlosseri* SKUPHOS

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With 8 figures

Kurzfassung: *Partanosaurus zitteli* SKUPHOS 1893 aus den Partnachschichten (Ladin) von Vorarlberg (Österreich) wird als jüngeres Synonym von *Simosaurus gaillardoti* MEYER 1832 bestimmt. Die Gattung *Simosaurus* tritt im Germanischen Becken (Oberer Muschelkalk, *nodosus*-Zone) früher auf als in der Alpinen Trias (Partnachschichten). *Simosaurus* belegt einen Faunenaustausch zwischen der germanischen und der alpinen Trias zur Zeit des Mittleren bis Oberen Ladin. *Microleptosaurus schlosseri* SKUPHOS 1893 fußt auf sehr unvollständigem Material und wird als nomen dubium deklariert.

Abstract: *Partanosaurus zitteli* SKUPHOS 1893 from the Ladinian (Partnachschichten) of the northern Alps (Vorarlberg, Austria) is identified as a junior synonym of *Simosaurus gaillardoti* MEYER 1832. Its occurrence in the Germanic Basin (Upper Muschelkalk) predates its appearance in the Alpine Triassic, and suggests faunal interchange between these two faunal provinces during Middle and Upper Ladinian times. *Microleptosaurus schlosseri* SKUPHOS 1893 is represented by very incomplete material only and must be treated as a nomen dubium.

Introduction

SKUPHOS (1893a–c) described fragmentary fossil reptile remains collected at two different localities in the state of Vorarlberg (Austria), Northern Calcareous Alps, which came from the Partnachschichten of Ladinian age (the exact stratigraphic position of the fossil sites remains unknown). The fossils clearly represent two taxa of different size. The larger one, found in the vicinity of Braz, Klosterthal, was described by SKUPHOS (1893a, c) as *Partanosaurus zitteli*; the smaller taxon, found in the vicinity of Dalaas, was named by SKUPHOS (1893c) *Microleptosaurus schlosseri*. One of the diagnostic characters of the larger taxon, *Partanosaurus zitteli*, is the distal expansion of the dorsal ribs. Based on isolated bone fragments, a similar rib morphology was known to SKUPHOS (1893a, c) to occur in the Grenzbonebed of the Germanic Triassic which separates the Muschelkalk from the Keuper. Accordingly, SKUPHOS (1893a, c) referred those rib fragments to his new taxon, and used the occurrence of *Partanosaurus* in both deposits for a stratigraphic correlation of the Partnachschichten (misleadingly named "alpiner Muschelkalk") with the uppermost Germanic Muschelkalk. Comparison with other Sauropterygia, in particular with *Nothosaurus*, *Lariosaurus* and the pachypleurosaur *Neusticosaurus*, led SKUPHOS (1893c) to conclude that *Partanosaurus* is most closely related to *Nothosaurus*. FRAAS (1896: 11) disputed SKUPHOS' (1893c) conclusions, pointing to the occurrence of distally broadened ribs in the Upper Muschelkalk, and indicating that both taxa named by SKUPHOS were not based on diagnostic material.

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Since SKUPHOS' (1893c) detailed description, the status of *Partanosaurus zitteli* and *Microleptosaurus schlosseri* has never been critically reviewed. It is the purpose of this paper to redescribe the type material of these two taxa, and to critically evaluate their position within the Triassic stem-group Sauropterygia as well as their significance in the analysis of faunal interchange between the Germanic and Alpine Triassic.

Institutional abbreviations: BSP, Bayerische Staatssammlung für Paläontologie; GPIT, Geologisch-Paläontologisches Institut der Universität, Tübingen; SMNS, Staatliches Museum für Naturkunde, Stuttgart.

Systematic Paleontology

Sauropterygia OWEN 1860
Eosauropterygia RIEPPEL 1994a
Eusauropterygia TSCHANZ 1989
Simosaurus H. v. MEYER 1842

Type species: *Simosaurus gaillardoti* H. v. MEYER 1842.

Diagnosis: A large (3–4 meters total length) eusauropterygian with a brevirostrine skull, fully diagnosed in RIEPPEL (1994a). Among stem-group Sauropterygia, the vertebrae of *Simosaurus* are unique by combining high neural spines with high transverse processes that extend downwards to the base of the neural arch pedicels, and by centrally located pre- and postzygapophyses as well as infrapre- and infrapostzygapophyses. The dorsal ribs are characterized by a slender dorsal shoulder region and an expanded and flattened distal end.

Distribution: Upper part of Upper Muschelkalk (Ladinian, Middle Triassic) of eastern France, Baden-Württemberg and Bavaria, SW-Germany; Lettenkeuper (Lower Keuper) and Gipskeuper (lower Middle Keuper, Upper Ladinian) of Württemberg, Germany; Partnachschichten (Ladinian), Northern Alps (Vorarlberg, Austria).

Simosaurus cf. *gaillardoti* H. v. MEYER 1842

1893a *Parthanosaurus zitteli* – SKUPHOS: 67ff.
1893b *Partanosaurus zitteli* – SKUPHOS: 96.
1893c *Partanosaurus zitteli* – SKUPHOS: 1ff., pl. 1, figs. 1–14; pl. 2, figs. 1–5; pl. 3, figs. 1–4.
1924 *Partanosaurus zitteli* – ARTHABER: 74f.
1934 *Partanosaurus zitteli* – KUHN: 46.
1955 *Partanosaurus zitteli* – SAINT-SEINE: 428.
1956 *Partanosaurus zitteli* – HUENE: 389.
1956 *Partanosaurus zitteli* – ROMER: 662.
1964 *Partanosaurus zitteli* – KUHN: 11.

Description: The type material described by SKUPHOS (1893a, c) comprises a string of 15 completely or partially preserved, but articulated dorsal vertebrae, three additional but disarticulated dorsal vertebrae, the left scapula in articulation with a fragment of the clavicle, fragments of a coracoid, and a number of ribs or rib fragments including one probable sacral rib. All the material is kept at the Geologische Bundesanstalt in Vienna (uncatalogued). The material is, in general, rather poorly preserved, and distorted to a variable degree.

The string of 15 dorsal vertebrae figured by SKUPHOS (1893c: pl. 1, fig. 1) today is preserved in two parts. The high neural spines figured by SKUPHOS for the vertebrae 8 through 12 (SKUPHOS 1893c: pl. 1, fig. 1; his count) are idealized in the illustration, or have been broken since the original publication. The high transverse processes are conspicuous, but details of the intervertebral articulation are hardly visible. The centra show a distinct constriction in their middle portion, and vary in length from 26 mm through 30 mm (as preserved). The entire string of articulated dorsal vertebrae measures 435 mm in length, which results in an average length of 29 mm for each centrum. Subcentral foramina are absent.

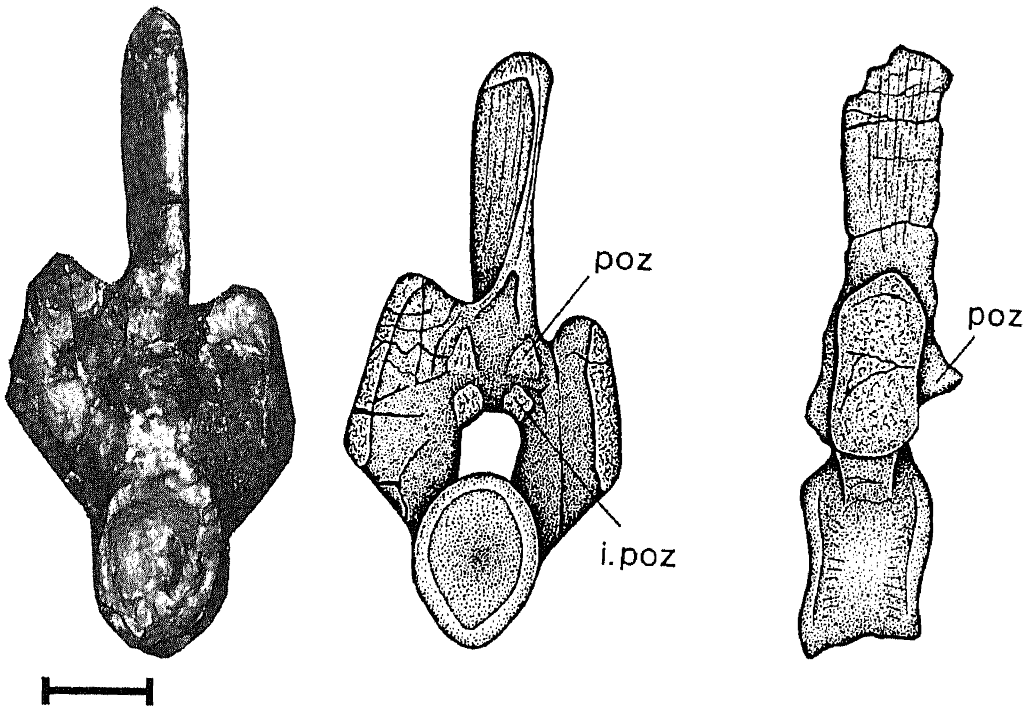

Fig. 1. Isolated dorsal vertebra of *"Partanosaurus zitteli"* (original of Skuphos 1893c: pl. 1, fig. 3). The scale bar equals 20 mm. Abbreviations: i.poz, infra-postzygapophysis; poz, postzygapophysis.

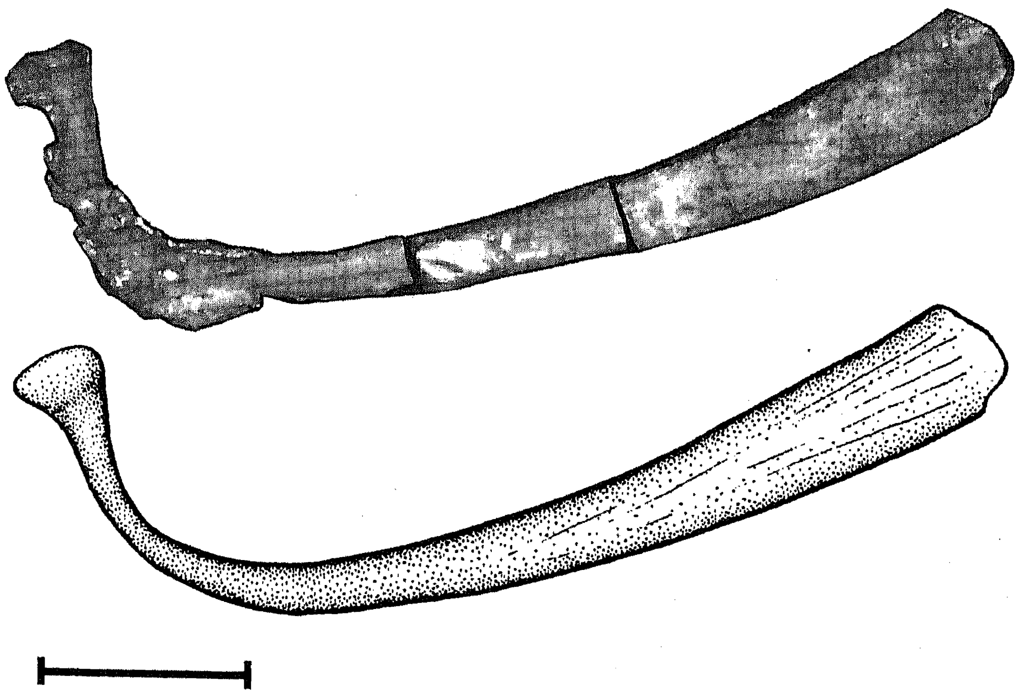

Fig. 2. Isolated dorsal rib of *"Partanosaurus zitteli"* (*Simosaurus*; original of Skuphos 1893c: pl. 2, fig. 4). The scale bar equals 50 mm.

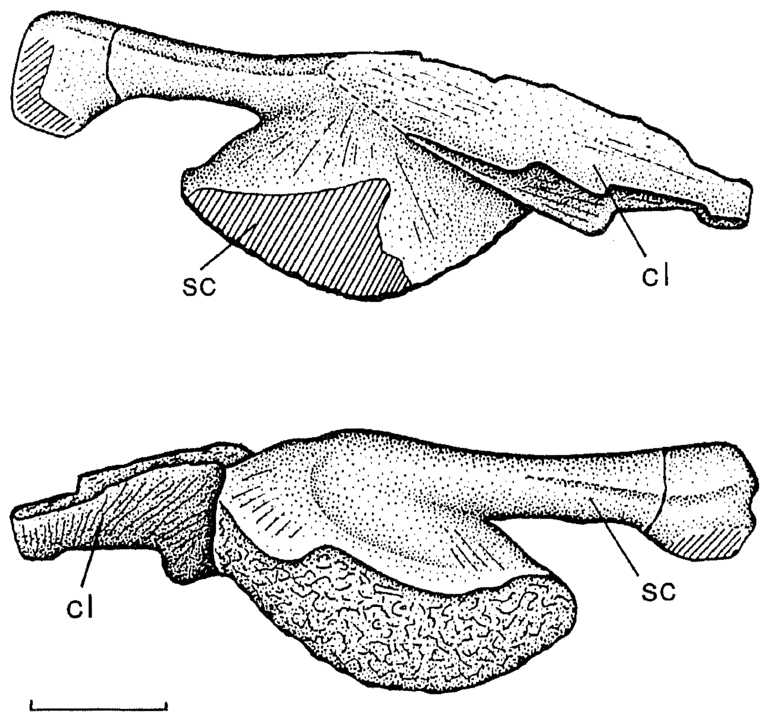

Fig. 5. Sacral rib (?) of *"Partanosaurus zitteli"* (*Simosaurus*; original of SKUPHOS 1893c: pl. 1, fig. 5). The scale bar equals 20 mm.

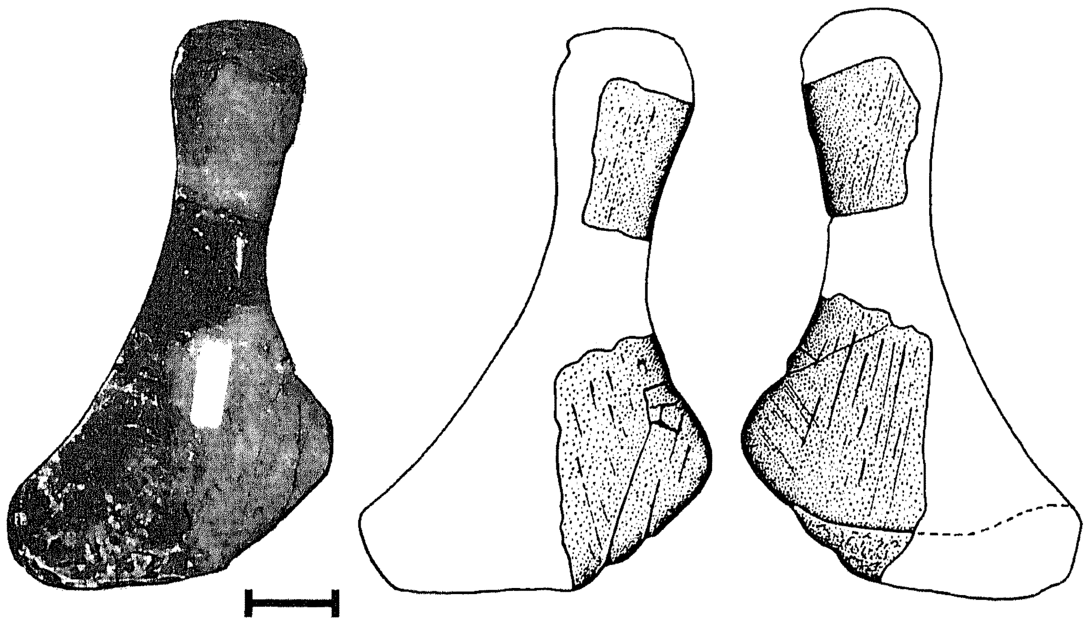

Fig. 4. Coracoid of *"Partanosaurus zitteli"* (*Simosaurus*; original of SKUPHOS 1893c: pl. 3, fig. 4). The scale bar equals 20 mm.

SKUPHOS (1893c: pl. 1, fig. 3) figured an isolated and incomplete dorsal vertebra which shows the relatively high and rectangular shape of the neural canal. The diameter of the centrum is 31 mm, the height of the neural canal is approximately 13 mm, its width is approximately 8.5 mm.

The vertebra shown by SKUPHOS (1893c) on pl. 1, fig. 2, is again incomplete and badly distorted. The best preserved isolated dorsal vertebra was figured by SKUPHOS (1893c) on pl. 1, fig. 4, but it, too, is badly broken and distorted (Fig. 1). The element confirms the presence of high neural spines, deep transverse processes, and an amphicoelous centrum. The total height of the element is 123 mm, the total width across the transverse processes is 54.5 mm (as preserved).

Distortion is particularly evident in the shape of the centrum, with a vertical diameter of 32.5 mm, and a horizontal diameter of 24 mm, while better preserved centra (SKUPHOS 1893c, pl. 1, fig. 3) show evenly rounded contours of the articular surface. The contours of the neural canal are hardly identifiable, but again approximate 31 mm in height and 8.5 mm in width. The transverse processes have been distorted in a dorsal direction; as preserved, the height of the articular surface is 37.5 to 38 mm. The height of the neural spine approximates 59 mm; the lateral surface of the neural spine shows distinct striations.

Details of the intervertebral articulation are identifiable on that specimen. On one side, two broken projections are located immediately above the neural canal, separated from the more dorsally located bases of the broken zygapophyses by a shallow depression. There is no evidence that the (broken) zygapophyses extended far laterally and merged into the dorsal surface of the transverse processes. Instead, the zygapophyseal projections must have been separated from the transverse processes by a deep notch. In spite of incomplete preservation, it is clear that the intervertebral articulation was centrally located on the neural arch, and consisted of zygapophyses and infra-zygapophyses diagnostic of the eusauropterygian genus *Simosaurus* (VON HUENE 1952; RIEPPEL 1994a).

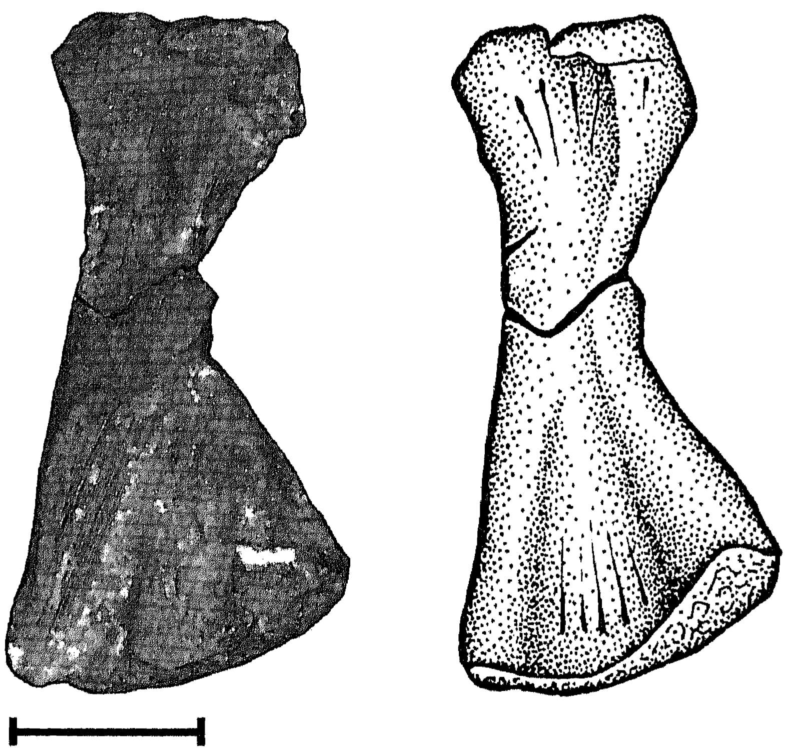

Fig. 3. Scapula of *"Partanosaurus zitteli"* (*Simosaurus*; original of SKUPHOS 1893c: pl. 1, fig. 14). The scale bar equals 20 mm. Abbreviations: cl, clavicle; sc, scapula.

Fig. 6. Sauropterygia indet.; two isolated dorsal ribs from the Upper Gipskeuper (Carnian) of southern Germany. The scale bar equals 50 mm.

SKUPHOS (1893a, c) repeatedly stressed the distinct rib morphology of *Partanosaurus*. The proximal articular head has a concave surface covered by unfinished bone. The dorsal shoulder of the rib is slender, but the distal end is distinctly broadened and flattened (Fig. 2). The total length of the complete dorsal rib figured by SKUPHOS (1893c: pl. 2, fig. 4) is 283 mm, its distal width is 28 mm.

The holotype of *Partanosaurus* also includes the slightly distorted left scapula (identified by SKUPHOS 1893c as right element), with a fragment of the clavicula attached to it (Fig. 3). The scapula is of typical eusauropterygian structure, with a broad ventral part and a slender posterodorsal process. The area of the coracoid foramen is eroded and has been reconstructed with plaster. SKUPHOS (1893c) considered the widened distal tip of the dorsal process of the scapula as a character diagnostic of a new genus. It appears, however, that the thickening of the distal end of the dorsal process of the scapula is the mere result of incomplete preparation. The clavicular fragment is attached to the anterior and medial aspect of the scapula.

The coracoid described by SKUPHOS (1893c: pl. 3, fig. 4) is of highly unusual shape, but inspection of the original material shows that SKUPHOS' reconstruction of the coracoid was based on two rather small bony fragments only (Fig. 4). The shape of the coracoid reconstructed by SKUPHOS (1893c) is not supported by natural bone margins.

A last piece of interest is the "unidentified element" of SKUPHOS (1893c: pl. 1, fig. 5). This strongly compressed bone has a characteristic hour-glass shape (Fig. 5). Its total length is 69 mm, its minimal width is approx. 27 mm, and the width of the distal ends is 37.2 mm and approx. 27 mm respectively. The element might represent a zeugopodial bone, but as such would be unusually short (about half as long as the zeugopodial elements of *Simosaurus*). Alternatively, this bone corresponds closely in size and shape to the principal sacral rib of *Simosaurus* (RIEPPEL 1994a).

Discussion: Among all Triassic Eusauropterygia, only *Nothosaurus mirabilis* (MÜNSTER 1834; VON MEYER 1847–55) and *Simosaurus gaillardoti* (VON HUENE 1952; RIEPPEL 1994a) show dorsal neural arches with a high and slender neural spine as is characteristic for *Partanosaurus*. Of those two taxa, *Nothosaurus mirabilis* shows no distinct striations on the lateral surface of the neural spines, the transverse processes are slender and do not reach down to the base of the neural arch pedicels, and the pre- and postzygapophyses are not separated from the transverse

Fig. 7. Fragment (dorsal rib) of *Microleptosaurus schlosseri* (original of SKUPHOS 1893c: pl. 3, fig. 11). The scale bar equals 20 mm.

processes by a deep notch. In contrast, *Simosaurus* shows distinct striations on the lateral surface of the neural spine, it shares with *Partanosaurus* the high transverse processes which extend down to the base of the neural arch pedicels, and it shows pre- and postzygapophyses which are separated from the transverse process by a deep notch. *Simosaurus* is the only sauropterygian genus with infra-zygapophyses (VON HUENE 1952; RIEPPEL 1994a). As in *Partanosaurus*, but unlike *Nothosaurus*, the neural canal is relatively high and rectangular in *Simosaurus*. Also, the latter genus is the only Triassic stem-group sauropterygian which shares with *Partanosaurus* the distal expansion of the dorsal ribs. It is therefore concluded that *Partanosaurus* SKUPHOS 1893a–c is a junior synonym of *Simosaurus* VON MEYER 1832.

The only difference between *Simosaurus* and *Partanosaurus* is the amphicoelous structure of the centra in the latter genus, contrasting with the only very weakly amphicoelous or platycoelous vertebrae of *Simosaurus*. This (plesiomorphic) trait is here considered insufficient evidence to formally recognize a separate species within the genus *Simosaurus*, although the existence of a separate species in the Alpine Triassic cannot be ruled out. Until more complete material becomes available, *Partanosaurus zitteli* SKUPHOS 1893a–c is therefore referred to *Simosaurus* cf. *gaillardoti* VON MEYER 1832.

Within the Germanic Triassic, *Simosaurus* is most abundant in the upper part of the Upper Muschelkalk (Lower Ladinian), but is also known from the Lower Keuper (Lettenkeuper: Holotype of *Simosaurus "guilielmi"* VON MEYER 1847–55), and from the lower Middle Keuper of Upper Ladinian age (Grundgipsschichten; VON HUENE 1959). The occurrence of distally flattened ribs characteristic of *Simosaurus* in the Grenzbonebed (separating Muschelkalk from Keuper) is therefore no surprise, and reference of such rib remains to *Partanosaurus* by SKUPHOS (1893a, c) underlines the synonymy of the two genera (*Simosaurus* taking priority).

Taking the potential for distortion during fossilization into account, the degree of distal expansion of the dorsal ribs is closely similar in *Simosaurus* and in the holotype of *Partanosaurus*. As indicated above, a well preserved rib of the latter genus measures 283 mm in length, and its distal width is 28 mm. Dorsal ribs of *Simosaurus gaillardoti* (SMNS 14733; skeleton described by VON HUENE 1952) vary in length from 259 to 282 mm, and have a distal width ranging from 23 to 25 mm. There is a weak correlation between absolute length and distal width of the ribs. The specimen from the Gipskeuper of Obersontheim described by VON HUENE (1959; GPIT, uncatalogued; mounted on permanent exhibit) is somewhat smaller than SMNS 14733 from the Upper Muschelkalk of Tiefenbach near Crailsheim, and it shows ribs with a distal width of 20 mm (VON HUENE 1959).

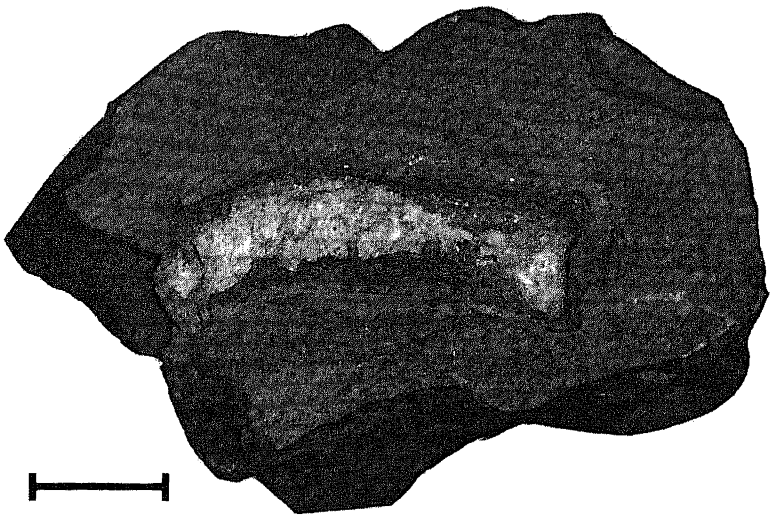

Fig. 8. A rib fragment of *Simosaurus* (*"Partanosaurus"*) from the Arlbergschichten (Middle Ladinian) of St. Anton, Tyrolia (BSP 1965.I.173). The scale bar equals 20 mm.

There is indication of the occurrence of an as yet only very incompletely known taxon (possibly related to *Simosaurus*) in the *Anatina*-bed of the *Estheria*-beds of the Upper Gipskeuper (of Carnian age) of Baden-Württemberg. The occurrence of this taxon is geologically significantly younger than that of *Simosaurus* (in the Germanic Triassic) or of the holotype of *Partanosaurus* (in the northern Alpine Triassic). The Carnian taxon is represented by two thoracic vertebral centra (SMNS 52981, and SMNS uncatalogued), and two isolated dorsal ribs (SMNS 18171, and SMNS uncatalogued, Fig. 6), which differ significantly from corresponding elements of *Simosaurus*, or from the holotype of *Partanosaurus*. Also, all of these elements are much too large to be attributed to the only (other) eusauropterygian known from corresponding layers, *Nothosaurus edingerae* (SCHULTZE 1970; RIEPPEL & WILD 1994).

The centrum SMNS 52981 (Gipskeuper, Ansbach) is 25 mm long and 40 mm high, with no signs of distortion. It is, therefore, distinctly shorter than it is high, a stark contrast to the dorsal centra of *Simosaurus* (SMNS 14733; VON HUENE 1952) with a length to height ratio of 0.81–0.9 (approx. 0.93 in the holotype of *Partanosaurus*). The shorter of the two isolated ribs (SMNS uncatalogued, Gipskeuper from Ansbach) is 225 mm long and has a distal width of 38.0 mm. The longer rib (SMNS 18171, Gipskeuper, Ochsenburg near Leonbrunn) measures 266 mm in length, and has a distal width of 43.7. As in *Simosaurus*, the degree of distal expansion is correlated with the absolute length of the rib, but again with no sign of distortion, these ribs from the Gipskeuper (Lower Carnian) show a significantly wider distal portion than those of *Simosaurus* (including the holotype of *Partanosaurus*).

Sauropterygia *incertae sedis*
Microleptosaurus schlosseri SKUPHOS 1893

1893c *Microleptosaurus schlosseri* – SKUPHOS: 2, 12ff, pl. 3, figs. 5–17.
1924 *Microleptosaurus schlosseri* – ARTHABER: 389.
1934 *Microleptosaurus schlosseri* – KUHN: 46.
1956 *Microleptosaurus schlosseri* – VON HUENE: 512f.
1956 *Microleptosaurus schlosseri* – ROMER: 662.
1964 *Microleptosaurus schlosseri* – KUHN: 11.

Distribution: Partnachschichten (Ladinian, Middle Triassic), Vorarlberg (Austria), Northern Calcareous Alps.

Description: The remains of this second taxon (SKUPHOS 1893c: pl. 3) are very fragmentary and hence not diagnostic at the genus or species level. The vertebral fragment (SKUPHOS 1893c: pl. 3, fig. 17) is very indistinct, and shows little more than the beginning constriction of the vertebral centrum. Cervical ribs identified by SKUPHOS (1893) lack the free anterior process characteristic of all other Sauropterygia, and are here re-interpreted as lumbar (SKUPHOS 1893c: pl. 3, figs. 10, 16) and caudal (SKUPHOS 1893c: pl. 3, figs. 12–13) ribs respectively. The one complete dorsal rib (SKUPHOS 1893c: pl. 3, fig. 11) is slender (no pachyostosis is apparent), and shows a rounded cross-section. Its total length is 81 mm (Fig. 7). The gastral ribs are indistinct except for one specimen (SKUPHOS 1893c: pl. 3, fig. 8) which is a cast taken from a natural mold, and which for this reason will remain difficult to interpret. The specimen does seem to show the fusion of two median gastral rib elements (not figured by SKUPHOS 1893c), otherwise known to occur in *Corosaurus* (STORRS 1991), *Nothosaurus* (KOKEN 1893), and *Simosaurus* (VON HUENE 1952). Of two further elements, considered by SKUPHOS (1893c: pl. 3, figs. 14–15) to represent posterior cervical ribs, one (SKUPHOS 1993c: pl. 3, fig. 14) is distinctly larger and much more massive than the other, and might, in fact, represent a stylopodial element. Based on its curvature, the element is best interpreted as an eusauropterygian humerus. No entepicondylar foramen can be identified.

Discussion: *Microleptosaurus* differs from *Simosaurus* not only in size, but also in dorsal rib morphology (no expansion of the distal end of the rib). Whereas *Microleptosaurus* might approach a small species of *Nothosaurus* in size, the latter genus shows weak pachyostosis in the dorsal shoulder region of the rib (e.g., the holotype of *Nothosaurus raabi* SCHRÖDER 1914) absent in *Microleptosaurus*. A small (juvenile?) *Cymatosaurus* has been recorded from the Lower Anisian of the Austrian Alps (*"Anarosaurus" multidentatus* VON HUENE 1958; see redescription in RIEPPEL 1995), but the lack of articulated postcranial material renders the meaningful comparison of *Cymatosaurus* with *Microleptosaurus* impossible. The genus *Lariosaurus* (CURIONI 1847; see PEYER 1933–34, for a review) is widespread in Middle to Upper Ladinian deposits of the southern Alps (see summary in RIEPPEL 1994b), and it would seem to resemble *Microleptosaurus* in the morphology of the evenly curved humerus with no distinct deltopectoral crest (providing that this element is correctly identified in the latter genus). However, *Lariosaurus* generally shows some degree of rib pachyostosis which is absent in *Microleptosaurus*. The same is true of Ladinian pachypleurosaurs which would match *Microleptosaurus* in size (and hence be of adult age: SANDER 1989).

In conclusion, the remains of *Microleptosaurus schlosseri* SKUPHOS 1893c, are too incomplete to be considered diagnostic; the name is therefore considered a nomen dubium.

Conclusions

SKUPHOS (1893c) gave no precise indication of the stratigraphic position of *"Partanosaurus"* within the Partnachschichten, which as a whole correspond to the Ladinian, with an extension into the Lower Carnian in Tyrolia. His (SKUPHOS 1893c: 1f) detailed description of the circumstances under which he collected *"Partanosaurus"* indicates, however, that the latter was found in the upper part of the Partnachschichten, not far below the Raibler Schichten of Carnian age. SKUPHOS' (1893c) stratigraphic indications are problematic because Arlbergschichten of about 400 m depth separate the Partnachschichten from the Raibler Schichten in the "Vorarlberger facies" (TOLLMANN 1976). Since SKUPHOS (1893c) indicates outcrops of the Raibler Schichten not too far above the locality which yielded the holotype of *"Partanosaurus"*, it may be concluded that the latter was collected in the Upper Ladinian, perhaps in the lowermost Carnian. A second occurrence of *Simosaurus ("Partanosaurus")* in the Austrian Alps, other than the specimen described by SKUPHOS (1893a, c), is documented by a rib fragment from the Arlbergschichten (Middle Ladinian) of St. Anton, Tyrolia (Lorfe-Grat, 2270 meters above Steissbachfall; BSP 1965.I.173; Fig. 8).

Other diagnostic eusauropterygians that have been reported from the Austrian Alps include *Cymatosaurus* from the Lower Anisian (VON HUENE 1958; RIEPPEL 1995), and *Lariosaurus* from the Middle Ladinian (ZAPFE & KÖNIG 1980; RIEPPEL 1994b; *Proneusticosaurus carinthiacus* ARTHABER 1924 is considered a junior synonym of *Lariosaurus*). Poorly preserved and fragmentary material also documents the occurrence of a pachypleurosaur (*Neusticosaurus sp.*, cf. *N. pusillus*) in Middle Ladinian deposits of the Austrian Alps (ZAPFE & KÖNIG 1980). *Rhaeticonia* BROILI 1927 may be a separate taxon from the Arlbergschichten of Vorarlberg (Austria), but the holotype and only known specimen can no longer be located today (destroyed during World War II).

The occurrence of *Cymatosaurus* and *Simosaurus* in the Germanic Triassic predates their occurrence in the northern Alpine Triassic. *Cymatosaurus* was part of an early (Lower Anisian) dispersal of sauropterygians from the Germanic into the Alpine Triassic (RIEPPEL & HAGDORN 1996), whereas *Simosaurus* documents a faunal interchange between the two biotas at Middle to Upper Ladinian times.

Faunal interchange between the Germanic and Alpine Triassic during Middle to Upper Ladinian times is also indicated by the occurrence of the pachypleurosaur *Neusticosaurus pusillus*, and representatives of the eusauropterygian *Ceresiosaurus-Lariosaurus*-clade, in both realms. Diagnostic remains of *Neusticosaurus pusillus* are widespread in the Alpine Triassic, but considering the widespread occurrence of isolated (and hence not diagnostic) small pachypleurosaur remains in the Upper Muschelkalk (VON HUENE 1942), details of the paleobiogeography of *Neusticosaurus pusillus* are difficult to reconstruct. The first occurrence *Ceresiosaurus-Lariosaurus*-clade is in the Alpine realm, where the clade seems to have diversified, and from where it may have expanded into the Germanic Basin during the Lower Keuper (see RIEPPEL & HAGDORN 1996 for a full discussion). In contrast, the genus *Simosaurus* evidently expanded from the Germanic into the Alpine Triassic, since its occurrence in the Upper Muschelkalk (Lower Ladinian) predates its appearance in the Alpine Triassic (Middle and Upper Ladinian). The available evidence therefore indicates that faunal exchange between the Germanic and Alpine Triassic was possible in both directions during Middle and Upper Ladinian times.

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