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SHORT COMMUNICATION

FIRST RECORD OF PLACODONTOIDEA (REPTILIA, SAUROPTERYGIA, PLACODONTIA) FROM THE EASTERN TETHYS

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Placodontia is a monophyletic taxon that includes the unarmored Placodontoidea and the armored Cyamodontoidea. Until now, placodontoids were known only from the Middle Triassic of central and southern Europe, whereas cyamodontoids are known from a variety of localities throughout the western and eastern Tethyan faunal provinces, ranging from the Middle through the Upper Triassic (Sues, 1987; Rieppel, 1995, 2000a, b; Rieppel and Zanon, 1997; Li, 2000; Li and Rieppel, 2002). Whereas cyamodontoids are a very diverse group, unarmored placodonts are known from only two monotypic genera, viz. *Paraplacodus broilii* Peyer, 1931, and *Placodus gigas* Agassiz, 1833 (Rieppel, 1995, 2000a, b). Phylogenetic analysis shows these two taxa to be the successive sister-groups to the Cyamodontoidea, the tree topology being (*Paraplacodus* (*Placodus*, Cyamodontoidea)) (Rieppel, 2000a, b).

Here, we report the first unarmored placodont from outside Europe. The specimen was collected from Anisian deposits in Panxian County, Guizhou Province. The same horizon at the same locality has also yielded the mixosaurid ichthyosaur *Mixosaurus panxianensis* Jiang et al., 2006, as well as other vertebrates such as two nothosaurid sauropterygians (*Nothosaurus yangjuanensis* Jiang et al., 2006; *Lariosaurus hongguoensis* Jiang et al., 2006), one protorosaurian (*Dinocephalosaurus orientalis* Li, 2003), one marine archosaurian (*Qianosuchus mixtus* Li et al., 2006), and bony fishes associated with brachiopods, bivalves and conodonts (Jiang et al., 2003, 2004, 2005a, b, 2006a, b, c; Li, 2003; Li et al., 2004; Li et al., 2006). The sediments that yield the Panxian fauna are believed to have been deposited on a nearshore platform, possibly in a lagoonal basin (Li et al., 2006).

Institutional Abbreviations—GMPKU, Geological Museum of Peking University, Beijing;

Material—GMPKU-P-1054, holotype and only known specimen.

SYSTEMATIC PALAEONTOLOGY

Superorder SAUROPTERYGIA Owen, 1860
Order PLACODONTIA Cope, 1871
Suborder PLACODONTOIDEA Cope, 1871
Family PLACODONTIDAE Cope, 1871
Genus *PLACODUS* Agassiz, 1833

Type Species—*Placodus gigas* Agassiz, 1833

Diagnosis (as in Rieppel, 2000a)—A large sauropterygian with a spatulate rostrum; three enlarged and strongly procumbent, chisel-shaped premaxillary teeth; three transversally expanded palatine tooth plates; nasals, frontals and parietals fused in adult; jugal extends anteriorly beyond level of anterior margin of orbit; prefrontal and postfrontal in contact dorsal to orbit; pterygoid restricted to posterior position in dermal palate; basioccipital tubers in complex ventral relation to dermal palate; "alisphenoid bridge" underlying olfactory tracts; dentary forming most of large coronoid process, lateral exposure of coronoid bone restricted; mandibular symphysis elongate, formed by dentaries and splenials; coracoids reduced; thyroid fenestra in pelvic girdle reduced; humerus expanded and flattened distally; entepicondylar foramen absent.

PLACODUS INEXPECTATUS, sp. nov.

Holotype—GMPKU-P-1054, a nearly complete skeleton exposed in right lateral view. Ventral elements of the pectoral and pelvic girdles are missing or incomplete, as well as the left hind limb and the tip of the tail. As preserved, the specimen is 205 cm long (Figs. 1–3).

Type Locality—Yangjuan Village, Xinmin District, Panxian County, Guizhou Province, China.

Type Horizon—Upper Member, Guanling Formation; conodont biozone of *Nicoraella kockeli* Tatge, 1956; Pelsonian, Anisian, Middle Triassic (Yang et al., 1999; Sun, 2006).

Derivation of Name—From Latin, "inexpectatus" for unexpected, unforeseen.

Diagnosis—A species in the genus *Placodus* that differs from the type species *Placodus gigas* by the prefrontal entering the posterior margin of the external naris; narrow separation of orbit from external naris; orbit high and rounded rather that horizontally elongated; anterior postorbital spur projecting into the orbit absent; tooth-bearing part of dentary slender; posterior cervical vertebrae with laterally projecting diapophysis for cervical rib articulation; clavicle slender.

DESCRIPTION

The skeletal anatomy of the new specimen is closely similar to that of *Placodus gigas* (Drevermann, 1933; Sues; 1987; Rieppel, 1995, 2000a). In contrast, it differs in many of its features from *Paraplacodus broilii*, the only other placodontoid taxon known to date (Rieppel, 2000b)

Skull

The skull is exposed in right lateral view; it measures 18 cm from the tip of the rostrum to the posterior margin of the quadrate. The profile of the skull is typical for placodontoids, with a

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FIGURE 1. Holotype skeleton of *Placodus inexpectatus*, sp. nov. (GMPKU-P-1054) from the Upper Member of Guanling Formation (Pelsonian, Anisian, Middle Triassic) of Yangjuan village, Xinmin District, Panxian County, Guizhou Province, People' s Republic of China. Scale bar equals 10 mm.

flat rostrum formed by the premaxillaries set off from the deep orbital and postorbital region by a distinct preorbital step. The external naris is vertically oriented (21 mm long, 30 mm high), and surrounded by the premaxilla (anteroventrally and anteriorly), nasal (anterodorsally), prefrontal (posterodorsally) and the ascending (facial) process of the maxillary (posteriorly and posteroventrally). The premaxilla carries three chisel-shaped and strongly procumbent teeth that are 8 to 9 mm in length. The maxilla carries four flat to rounded maxillary teeth with an anteroposterior width of approximately 10 mm (Fig. 2). The premaxillary and maxillary dentition thus closely resembles that of *Placodus gigas* in tooth count and morphology.

The orbit is 33 mm long and 39 mm high, and hence of distinctly different shape than the elongated orbit of *Placodus gigas* (Rieppel, 1995, 2000a). The prefacial bridge between the orbit and the external naris is relatively narrower than in *Placodus gigas*. It is formed by the prefrontal and maxillary ascending process, without contribution of the nasal. Instead, the nasal remains separated from the maxillary ascending process by the prefrontal, which enters the posterodorsal margin of the external naris, an important difference from *Placodus gigas*. The nasal, frontal, and parietal are all fused, indicative of an adult age of the specimen. The relatively large pineal foramen is enclosed by the fused parietals and located behind the fronto-parietal suture at the level of the anterior margin of the upper temporal fenestra.

The prefrontal meets the postfrontal in the posterior part of the dorsal margin of the orbit. At the anterodorsal corner of the orbit, the prefrontal forms a thickened, anterolaterally projecting rim. The postfrontal defines the anteromedial margin of the upper temporal fenestra, as well as the posterodorsal margin of the orbit, and it forms a ventral process that meets the postorbital in the postorbital arch. The postorbital forms most of the posterior margin of the orbit, and extends posteriorly to form most of the lateral margin of the upper temporal fenestra. Unlike *Placodus gigas* (Rieppel, 1995, 2000a), an anteriorly projecting spur of the postorbital is not present, nor does the postorbital form a deep groove at the posterior margin of the orbit.

The postorbital part of the skull suffered extensive damage in the area behind the orbit and below the lateral margin of the upper temporal fenestra, which obscures most morphological detail. It is clear that the jugal enters the ventral margin of the orbit, and that the squamosal and parietal enclose the posterior part of the upper temporal fenestra. Beyond these observations, however, the exact contours of the jugal and squamosal, and their precise relations to neighbouring bones, cannot be established. In addition, in this damaged cheek region, a concavity appears in the ventral margin of the upper temporal arch between jugal and squamosal, looking like a ventrally opened cheek or temporal emargination which, probably caused by damage, differs from the condition observed in *Placodus gigas*, yet recalls the morphology of the skull of *Paraplacodus* (Rieppel, 1995, 2000a, b). Furthermore, the squamosal narrowly overlaps

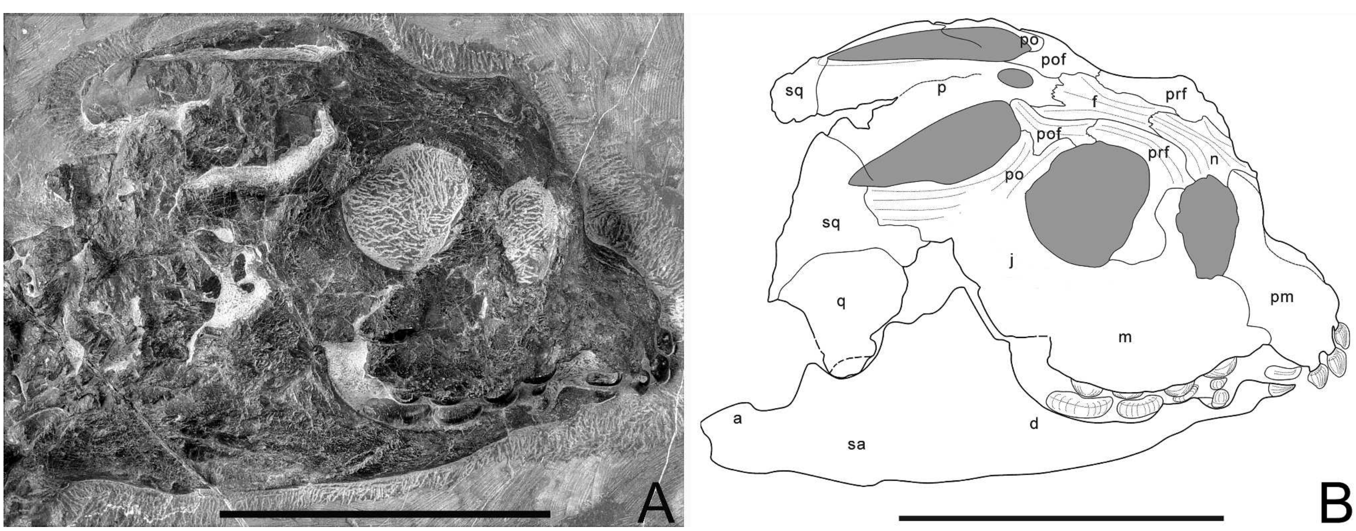

FIGURE 2. **A**, skull of the holotype of *Placodus inexpectatus* sp. nov. (GMPKU-P-1054). **B**, line drawing of the skull of the holotype of *Placodus inexpectatus* sp. nov. (GMPKU-P-1054). **Abbreviations**: **a**, angular; **d**, dentary; **f**, frontal; **j**, jugal; **m**, maxilla; **n**, nasal; **p**, parietal; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **prf**, prefrontal; **q**, quadrate**;** **sa**, surangular; **sq**, squamosal. Scale bars equal 10 mm.

the dorsal head of the quadrate posteroventrally, seemingly forming a short and pointed ventral projection that follows the posterior margin of the dorsal part of the quadrate. The resulting morphology (Fig. 2) seems similar to *Paraplacodus* but different from *Placodus gigas* (Rieppel, 1995, 2000a, b). But whether the 'open' cheek and short pointed projection of the squamosal in *Placodus inexpectatus* represent the natural conditions, or are consequences of postmortem damage to the skull, can no longer be ascertained, although the latter seems more probable.

The mandible of *Placodus inexpectatus* is again similar to that of *Placodus gigas*. Sutural details are difficult to ascertain on the laterally exposed right lower jaw ramus. The mandible is preserved in articulation with the quadrate. The coronoid process rises upwards immediately in front of the mandibular articulation, as in *Placodus gigas* (Rieppel, 1995, fig. 30A), but unlike in *Paraplacodus* (Rieppel, 2000b, fig. 3). In addition, the coronoid process is much higher in *Placodus inexpectatus* than in *Paraplacodus*, reaching a similar height as in *Placodus gigas* (Drevermann, 1933, plate 3, fig. 2d). Posterior to the mandibular articulation the lower jaw continues as a massive retroarticular process, another similarity shared with *Placodus gigas*. However, the mandible differs from that of *Placodus gigas* in that the tooth-bearing part of the dentary appears rather lightly built and slender as exposed in lateral view, a feature by which it differs from the dentary of both, *Placodus* and *Paraplacodus*. It is possible that the dentary of *Placodus inexpectatus* was subject to some limited damage, however, as is indicated by its irregular ventral margin. The dentary bears two anterior procumbent teeth, which are separated by a diastema from the four posterior crushing teeth measuring 5 mm, 8 mm, 15 mm and 21 mm in respective anteroposterior width. In *Placodus gigas* there are usually only three posterior dentary tooth plates, although a small, fourth, anterior tooth plate may variably occur (Rieppel, 1995).

Postcranial

Six cervical vertebrae, 19 dorsal, three sacral, and 36 caudal vertebrae can be counted. It is conceivable that the atlas—axis complex is buried in the deeply excavated occiput, which would bring the number of cervical vertebrae up to eight, the same as in *Placodus gigas*, while in *Paraplacodus* there is a minimum of six cervicals (Rieppel, 2000a). The cervical ribs show a free-ending anterior process that shifts laterally on the shaft of the rib in the posterior cervical region, as is also the case in *Placodus gigas* (Rieppel, 1995, 2000a, b). Unlike the latter taxon, the dorsal heads of the posterior cervical ribs articulate with the centra via a laterally projecting diapophysis. The transverse processes are distinctly elongated in the dorsal region, as is typical for placodonts in general (Rieppel, 2000a). The dorsal ribs lack an uncinate process as is present in *Paraplacodus* (Rieppel, 1995, 2000a, b). The three sacral vertebrae articulate with sacral ribs that are expanded both proximally and distally. The distal expansion is most prominently expressed in the second sacral rib in *Placodus inexpectatus*, but in the third sacral rib in *Placodus gigas* (Rieppel, 1995, 2000a, b). Free caudal ribs extend backwards to the 11th caudal vertebra.

The chevrons articulate on short pedicels located ventrally on the posterior margin of the caudal vertebral centrum. The chevrons show a distal expansion in the proximal tail region, a distal bifurcation in the middle section of the tail, while the shanks of the distally bifurcated chevrons become aligned with the longitudinal axis of the tail in the posterior tail section. This peculiar morphology of the chevrons is shared by *Paraplacodus*, but is not known for *Placodus gigas* (Rieppel, 1995, 2000a, b).

The gastral ribs are composed of five elements of which the lateral ones are strongly angulated, as is the case in *Placodus gigas* and *Paraplacodus* (Rieppel, 1995, 2000a, b). A single row of osteoderms extends along the dorsal midline of the body, as is also the case in *Placodus gigas*, but not in *Paraplacodus*, where osteoderms are absent (Rieppel, 1995, 2000a, b). The osteoderms of *Placodus inexpectatus* are almost round and small in the posterior cervical region capping the neural spines, and become larger in the dorsal, sacral, and proximal caudal region, but smaller again in the more distal tail region, further decreasing in size posteriorly and terminating in the gap between the 17th and 18th caudal vertebrae.

The partially exposed right clavicle is a boomerang-shaped element, with its posterolateral shank applied to the medial surface of the scapular blade (Fig. 3). The scapula is a tall, blade-like structure with the glenoid facet located at its posteroventral corner. The curved humerus shows a relatively straight preaxial margin and deeply concave postaxial margin. It is distinctly expanded and flattened distally (Fig. 3). The length of the right humerus is 142 mm, its proximal width is 27 mm wide, its minimal width is 23 mm, and its distal width is 43 mm. The entepicondylar foramen is absent, as is an ectepicondylar foramen or notch. The flattened radius of 79 mm in length is slightly shorter than the ulna, which is 81 mm long. The more robustly built ulna has a biconcave shaft with broadly expanded proximal and distal ends. The more lightly built radius is angulated, and lacks a distinct proximal or distal expansion. The ulna is also more robust than the radius in *Paraplacodus*, but the element is unknown in *Placodus gigas* (Rieppel, 1995, 2000a, b). Two rather small and rounded carpal ossifications, the intermedium with a diameter of 10 mm, and the ulnare of 7 mm width, are present. This differs from *Placodus gigas*, for which a single carpal ossification has been described (Drevermann, 1933), as well as from *Paraplacodus broilii*, which has three or four ossified carpals (Rieppel, 2000b). Of the five metacarpals, the first is only 10 mm long and thus the shortest in the series, while the third and fourth metacarpals are the longest with a length of 31 mm. The phalangeal formula is incompletely preserved but closely approaches the primitive condition 2-3-4-5-3.

The ilium is similar to that in *Placodus gigas* (Rieppel, 1995,

FIGURE 3. **A**, the preserved pectoral girdle and the right forelimb of the holotype of *Placodus inexpectatus* sp. nov. (GMPKU-P-1054). **B**, the preserved pelvic girdle and the right hindlimb of the holotype of *Placodus inexpectatus* sp. nov. (GMPKU-P-1054). **Abbreviations**: **cl**, clavicle; **f**, femur; **fi**, fibula; **h**, humerus; **il**, ilium; **r**, radius; **sc**, scapula; **ti**, tibia; **u**, ulna. Scale bars equal 10 mm.

2000a), in that a ventral acetabular part is separated by a distinctly constricted neck region from the low dorsal iliac blade. The latter possesses a preacetabular process, and differs distinctly from the tall and narrow iliac blade, characteristic of *Paraplacodus* (Rieppel, 2000b, fig. 9B). The right femur with a length of 135 mm, is much more lightly built than the humerus, being shorter, more slender, and rather straight. The distal end of the femur is somewhat expanded. Unless it is buried in the matrix, the internal trochanter is rather poorly differentiated, quite unlike the condition observed in *Paraplacodus* and *Placodus gigas*. The slender tibia and fibula are almost of the same length of 96 mm and both longer than the zeugopodial elements in the forelimb. With straight outside margins and concave inside margins, the tibia and fibula enclose a spatium interosseum. Two rounded tarsal ossifications, the astragalus with a diameter of 23 mm and the calcaneum of 21 mm width, are present, both remarkably larger than the carpal ossifications. There are five metatarsals, of which the first one with a length of 13 mm is the shortest. The longest metacarpals are the third and the fourth, with a length of 40 mm and 42 mm respectively. Compared to the forelimb, the distal hindlimb is longer than the corresponding part of the forelimb. The phalanges preserved in the right pes are 2-3-4-4-1 (Fig. 3). Given that a crack runs through the slab right distal to the right pes, it is very well possible that the phalangeal formula originally corresponded to the primitive condition (2-3-4-5-4).

DISCUSSION

Diagnostic features of the new species of unarmored placodont here described include the prefrontal entering the posterior margin of the external naris; narrow separation of orbit from external naris; orbit high and rounded rather that horizontally elongated; anterior postorbital spur projecting into the orbit absent; tooth-bearing part of dentary slender; posterior cervical vertebrae with laterally projecting diapophysis for cervical rib articulation; clavicle slender. *Placodus inexpectatus* n. sp. shares a number of characters with *Placodus gigas*, characters by which it also differs from *Paraplacodus broilii*. These include the general morphology of the dentition, the absence of a curved (boomerang-shaped) jugal, the high coronoid process with an anteroposteriorly expanded base, the absence of an uncinate process on the dorsal ribs, the tall, blade-like and unconstriced scapula, the low but antero-posteriorly expanded iliac blade forming a preacetabular process, and the presence of a row of osteoderms located above and between the neural vertebral spines in the posterior cervical, dorsal, and tail region. At the same time, the new specimen also shares some characters with *Paraplacodus*, most notably the morphology of the chevrons that changes from front to back within the tail. This very closely resembles the chevron morphology in *Paraplacodus*, but whether similar chevrons were, in fact, present or absent in *Placodus* remains unknown. Only very few chevrons are known from the incompletely preserved tail that is part of the specimen described by Drevermann (1933, pl. 5, figs. 30b, 31b, 32b; pl. 16, fig. 97), and those that are known have been noted to be of a "very delicate structure" (Drevermann, 1933: 343) and may well be distally incomplete. The radius is characteristically angulated in the new placodont, as is also the case in *Paraplacodus*, yet only the incomplete proximal end of the radius is known from *Placodus gigas* (Drevermann, 1933). The new specimen shows a ventrally open cheek like in *Paraplacodus*, but this is very likely the result of postmortem damage. It is for these reasons that the new specimen here described is referred to the genus *Placodus.*

In order to test the generic affinity of the new placodont, we conducted a phylogenetic analysis based on the data matrix in Rieppel (2000b), to which two characters were added. Character **68**: External naris not distinctly higher than long (0); distinctly higher than long (1); character **69**: chevron morphology simple, y-shaped (0); complex as described by Rieppel (2000b) for *Paraplacodus* (1). To strengthen the test of the generic affinities of *Placodus inexpectatus*, latter character was coded (1) for *Placodus inexpectatus* and *Paraplacodus*, but (0) for all other taxa, including *Placodus gigas*. The vector for *Placodus inexpectatus* (in groups of five) is: 10001 0?010 00?00 1???? 0???? ????0 111?? ????? ????? ??0?? 0??20 ?0??1 1111? ??11. Pachypleurosaurs, *Simosaurus* and *Nothosaurus* constituted the outgroup, *Placodus gigas*, *Placodus inexpectatus*, *Cyamodus*, *Henodus*, *Macroplacus*, *Protenodontosaurus*, *Placochelys*, and *Psephoderma* were included in the in-group. A branch-and-bound search yielded one single parsimonious tree (TL = 119; CI = 0.689, RI = 0.706), which is the same as the one discussed in Rieppel (2000b, fig. 10), but with *Placodus inexpectatus* coming out as sister-taxon of *Placodus gigas*. The generic affinity of the new placodont with *Placodus* is thus confirmed.

With the referral of the new species to the genus *Placodus*, the latter's geographical range is significantly expanded. Previously known exclusively from the lower Anisian to lower Ladinian of central and southern Europe (Rieppel, 1995, Rieppel and Dalla Vecchia, 2001), it is now also known to occur in the Anisian of Panxian, Guizhou Province, southwestern China, indicating that the genus *Placodus* had a wide geographical distribution within the Tethyan realm during the Middle Triassic. It further enforces the close affinities between the Middle Triassic marine reptile faunas of China and Europe, i.e., of the eastern and western Tethyan faunal provinces.

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LITERATURE CITED

Agassiz, L. 1833–45. Recherches sur les Poissons Fossiles. Imprimerie de Petitpierre, Neuchâtel.

Cope, E. D. 1871. The systematic arrangement of the Reptilia. Proceedings of the American Association for the Advancement of Science 19:226–247.

Drevermann, F. 1933. Die Placodontier. 3. Das Skelett von *Placodus gigas* AGASSIZ im Senckenberg Museum. Abhandlungen der senckenbergischen naturforschenden Gesellschaft 38:319–364.

Li, C. 2000. Placodont (Reptilia: Placodontia) from Upper Triassic of Guizhou, China. Vertebrata PalAsiatica 38(4):314–317.

Li, C. 2003. First record of protorosaurid reptile (Order: Protorosauria) from the Middle Triassic of China. Acta Geologica Sinica 77(4): 419–423.

Li, C., and O. Rieppel. 2002. A new cyamodontoid placodont from Triassic of Guizhou, China. Chinese Science Bulletin 47(5):403–407.

Li, C., O. Rieppel, and M. C. LaBarbera. 2004. A Triassic aquatic protorosaur with an extremely long neck. Science 305:1931.

Li, C., X. C. Wu, Y. N. Cheng, T. Sato, and L.-T. Wang. 2006. An unusual archosaurian from the marine Triassic of China. Naturwissenschaften 93:200–206.

Jiang, D.-Y., W.-C. Hao, Y.-L. Sun, M. W. Maisch, and A. T. Matzke. 2003. The mixosaurid ichthyosaur *Phalarodon* from the Middle Triassic of China. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte (11):656–666.

Jiang, D.-Y., L. Schmitz, and W.-C. Hao. 2004. Two species of Mixosauridae (Ichthyosauria) from the Middle Triassic of southwestern China. Journal of Vertebrate Paleontology 24 (3, supplement):76A.

Jiang, D.-Y., W.-C. Hao, M. W. Maisch, A. T. Matzke, and Y.-L. Sun. 2005a. A basal mixosaurid ichthyosaur from the Middle Triassic of China. Palaeontology 48:869–882.

Jiang, D.-Y., M. W. Maisch, W.-C. Hao, H.-U. Pfretzschner, Y.-L. Sun, and Z.-Y. Sun. 2005b. *Nothosaurus* sp. (Reptilia, Sauropterygia, Nothosauridae) from the Anisian (Middle Triassic) of Guizhou, southwestern China. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte (9):565–576.

Jiang, D.-Y., L. Schmitz, W.-C. Hao, and Y.-L. Sun. 2006a. A new mixosaurid ichthyosaur from the Middle Triassic of China. Journal of Vertebrate Paleontology 26(1):60–69.

Jiang, D.-Y., M. W. Maisch. W.-C. Hao, Y.-L. Sun, and Z.-Y. Sun. 2006b. *Nothosaurus yangjuanensis* n. sp. (Reptilia, Sauropterygia, Nothosauridae) from the middle Anisian (Middle Triassic) of Guizhou, southwestern China. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2006:257–276.

Jiang, D.-Y., M. W. Maisch, Z.-Y. Sun, Y.-L. Sun, and W.-C. Hao. 2006c. A new species of *Lariosaurus* (Reptilia, Sauropterygia) from the Middle Anisian (Middle Triassic) of Guizhou, southwestern China. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 242:19–42.

Owen, R. 1860. Palaeontology; or, a systematic summary of extinct animals and their geologic remains. Adam and Charles Black, Edinburgh, xv+420 pp.

Peyer, B. 1931. *Paraplacodus broilii* nov. gen. nov. sp., ein neuer Placodontier aus der Tessiner Trias. Vorläufige Mitteilung. Centralblatt für Mineralogie, Geologie und Paläontologie, B 1931:570–57.

Rieppel, O. 1995. The genus *Placodus*: Systematics, Morphology, Paleobiogeography, and Paleobiology. Fieldiana (Geology) n.s. 31:1–44.

Rieppel, O. 2000a. Sauropterygia I; pp 1–134 in: P. Wellnhofer (ed.), Encyclopedia of Paleoherpetology part 12A. Verlag Dr. Friedrich Pfeil, München.

Rieppel, O. 2000b. *Paraplacodus* and the phylogeny of the Placodontia (Reptilia: Sauropterygia). Zoological Journal of the Linnean Society 130:635–659.

Rieppel, O., and F. M. Dalla Vecchia. 2001. Marine reptiles from the Triassic of the Tre Venezie Area, Northeastern Italy. Fieldiana (Geology) n.s. 44:1–25.

Rieppel, O., and R. T. Zanon. 1997. The interrelationships of Placodontia. Historical Biology 12:211–227.

Sues, H.-D. 1987. On the skull of *Placodus gigas* and the relationships of the Placodontia. Journal of Vertebrate Paleontology 7:138–144.

Sun, Z.-Y. 2006. Studies on the Middle and Upper Triassic biostratigraphy in western Guizhou and eastern Yunnan, China. Ph.D. dissertation, Peking University, Beijing, 110pp.

Tatge, U. 1956. Conodonten aus dem germanischen Muschelkalk, Teil II. Paläontologische Zeitschrift 30(3–4):129–147.

Yang, S.-R., W.-C. Hao, and X.-P. Wang. 1999. Triassic conodont sequences from different facies in China; pp. 97–112 in A. Yao, Y. Ezake, W.-C. Hao, and X.-P. Wang (eds.), Biotic and Geological Development of the Paleo-Tethys in China. Peking University Press, Bejing.

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