

## A NEW MIXOSAURID ICHTHYOSAUR FROM THE MIDDLE TRIASSIC OF CHINA

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**ABSTRACT**—We describe the new ichthyosaur taxon *Mixosaurus panxianensis*, sp. nov., from the Middle Triassic of Guizhou Province, China. Diagnostic characters of the new species include a short posteroventral jugal process and the absence of external contact between jugal and quadratojugal. The morphologic description of the type specimens amends the knowledge of the postorbital region and the postcranium of the Mixosauridae. The holotype of *Mixosaurus maotaiensis*, which is very fragmentary and has no taxonomic value at the species level, is found to be undiagnostic, and hence the lately introduced, monospecific genus name for this species needs to be abandoned. Phylogenetic analysis strongly supports the monophyly of the family Mixosauridae. Furthermore, the analysis shows a bifurcation of the family into two sister groups, suggesting the presence of two genera, *Mixosaurus* and *Phalarodon*. *Mixosaurus*, characterized by a relatively short and wide humerus, includes *M. panxianensis* sp. nov., *M. cornalianus*, and *M. kuhnschnyderi*. Synapomorphies of *Phalarodon*, which contains *P. fraasi*, *P. callawayi*, and *P. atavus*, are a narial shelf and the absence of a maxillary dental groove.

### INTRODUCTION

The Mixosauridae Baur, 1887, are a geographically widespread family of Middle Triassic ichthyosaurs (Motani, 1999a, 1999b; Maisch and Matzke, 2000, 2001a, 2001b; Sander, 2000; Schmitz et al., 2004). These small to medium-sized ichthyosaurs are common faunal elements in the western Tethyan realm, Spitsbergen, and North America, but the fossil record of mixosaurids in Asia has been very sparse. In over four decades, only a single fragmentary specimen from Maotai County (China) was reported (Young, 1960, 1965). Young (1960) initially misinterpreted the specimen as a nothosaur, but later recognized its mixosaur affinities and established the name *Mixosaurus maotaiensis* Young, 1965. In subsequent studies, this taxon was rarely considered valid (but see Mazin (1983, 1986) and Callaway and Massare (1989)). Maisch et al. (2003) redescribed the holotype of *Mixosaurus maotaiensis* and found diagnostic characters in the humerus, coracoid, interclavicle, and clavicle. However, a definite generic assignment of this species was impossible, and Maisch et al. (2003) referred it to (?)*Mixosaurus*.

More recently, a team from Peking University discovered a new locality in the Middle Triassic of Guizhou Province, China. Two specimens were recovered from a Pelsonian bituminous limestone horizon (*Nicorella germanicus* conodont zone). Jiang et al. (2005) described the specimens, which preserve cranial and some postcranial remains, and found that the humerus and coracoid were sufficiently similar to those of *M. maotaiensis* to allow a formal referral. Furthermore, they erected a new genus based on *M. maotaiensis*. Lately, additional specimens have been recovered from the new locality, and the specimens described by Jiang et al. (2005) have been prepared in more detail. We now recognize features that are inconsistent with the taxonomy proposed by Jiang et al. (2005).

The morphologic description of the new specimens offers a wealth of new information which we use for a two-fold purpose: first, to remedy this taxonomic problem in the interest of stability, and second, to improve the phylogenetic hypothesis of mixosaurids by utilizing the data obtained from the new preparation and the new specimens. In the light of the improved phylogenetic tree, the generic composition of the Mixosauridae, which has been controversial in the past (e.g., Schmitz et al., 2004), is reassessed.

**Institutional Abbreviations**—CMC, Cincinnati Museum Center; GMPKU, Geological Museum of Peking University, Beijing; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing; NHM, British Museum of Natural History; NRM, Naturhistoriska Riksmuseet, Stockholm; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich; PMU, Paleontologiska Museet Uppsala; SMNS, Staatliches Museum für Naturkunde, Stuttgart; UCMP, University of California Museum of Paleontology, Berkeley.

### MATERIAL AND METHODS

The holotype of '*Mixosaurus maotaiensis*' is housed in the collections of IVPP under the number IVPP V2468. All specimens belonging to the new species are housed in GMPKU, bearing the numbers GMPKU-P-1008 (former GMPKU 2000008), GMPKU-P-1009 (former GMPKU 2000009), GMPKU-P-1033, GMPKU-P-1039. Dimensions were measured with callipers and are given in TABLES 1–2. Material for comparison was studied in CMC, NHM, NRM, PIMUZ, PMU, SMNS, and UCMP.

### THE STATUS OF *MIXOSAURUS MAOTAIENSIS*

*Mixosaurus maotaiensis* Young, 1965 was the first mixosaurid taxon documented in the eastern Tethyan realm. Maisch et al. (2003) carefully redescribed the holotype and attempted to establish diagnostic characters. However, the wealth of information gained from the new specimens and from new material from the Middle Triassic of Nevada (Schmitz et al., 2004) casts doubt on the proposed diagnosis. To achieve taxonomic stability, we analyzed proposed diagnostic characters of the holotype (IVPP V2468), and found that this very fragmentary specimen has no taxonomic value at the species level, as discussed below.

The humerus of the holotype has a maximum proximodistal length of 2.59 cm and a maximum anteroposterior width of 2.4 cm. In order to test the possible taxonomic significance of its short and wide humerus, dimensions of 27 humeri of *Mixosaurus* and nine other Triassic ichthyopterygian humeri (including *Phalarodon*) were compared. It is evident from the logarithmic plot of humeral width versus length that all species of *Mixosaurus* have a relatively wide humerus, showing a single allometric line (Fig. 1). Therefore, the humerus of the holotype is not particularly wider than long compared to the other humeri of the

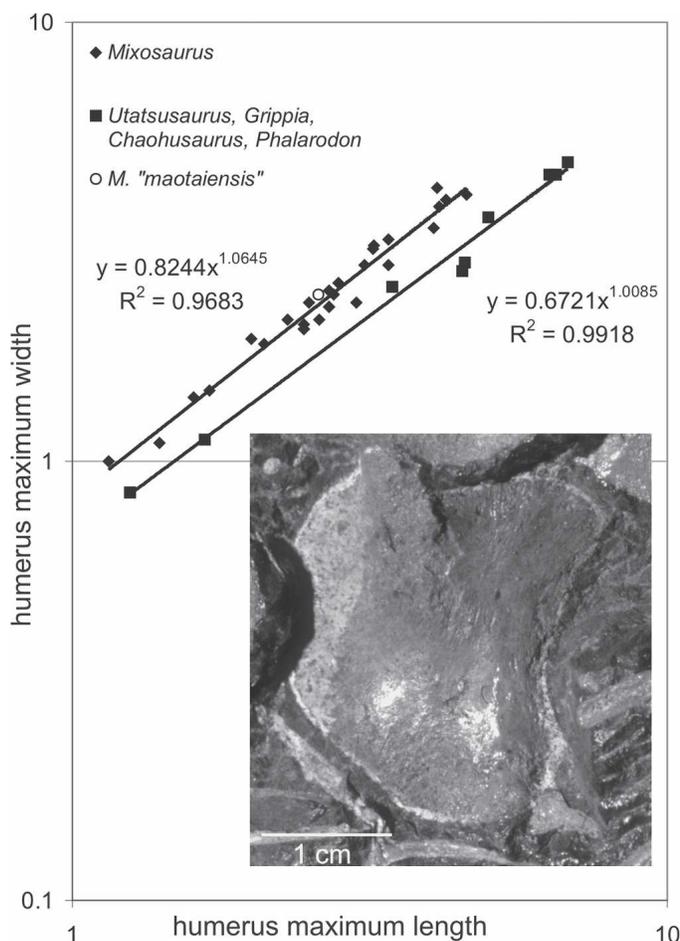


FIGURE 1. Logarithmic plot of maximum humerus width against maximum humerus length. *Mixosaurus* has a significantly greater relative humerus width than other Triassic ichthyopterygians. The humerus of *Mixosaurus maotaiensis*, nomen dubium (photograph), plots amidst the range of *Mixosaurus*. Data source: *Mixosaurus cornalianus*, Brinkmann, 1998b; *Mixosaurus panxianensis*, personal observation of Jiang and Schmitz; *Utatusaurus*, Motani, 1997; *Grippia*, personal observation of Schmitz; *Chaohusaurus*, Motani, 1998.

genus *Mixosaurus*. The lack of a postaxial facet on the humerus cannot be verified in the holotype, because this part of the humerus is damaged and additionally covered by a fragment of a gastral rib (Fig. 1). Thus, the humerus does not bear any diagnostic features.

A typical mixosaurid coracoid is distinguished from those of the other ichthyopterygians by an expanded anterior flange and a relatively short posterior extension (McGowan and Motani, 2003). The posterior extension of the coracoid can be defined as distance from the posterior end of the glenoid facet to the maximum posterior coracoid extension, measured parallel to the anteroposterior coracoid axis (Fig. 2A). When plotted against the complete anteroposterior coracoid length, the holotype of *M. maotaiensis* (Fig. 2A) falls in the range of other mixosaurids (Fig. 2B). The difference between left and right coracoids of the holotype indicates a considerable individual variability, questioning the taxonomic value of this feature at the species level. Based on this analysis, it is impossible to separate *M. maotaiensis* from the other mixosaurid species.

The interclavicle of the holotype is incompletely preserved and would not be distinguishable from those of other mixosaurids as illustrated by figures in Wiman (1910) and Brinkmann

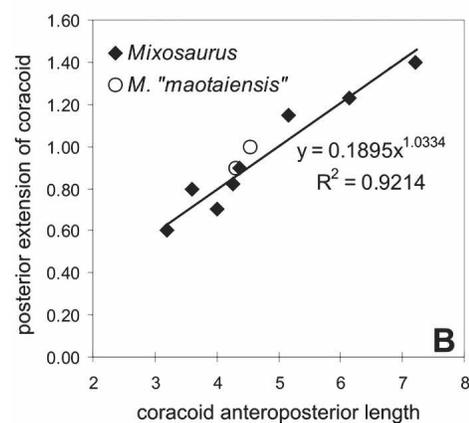
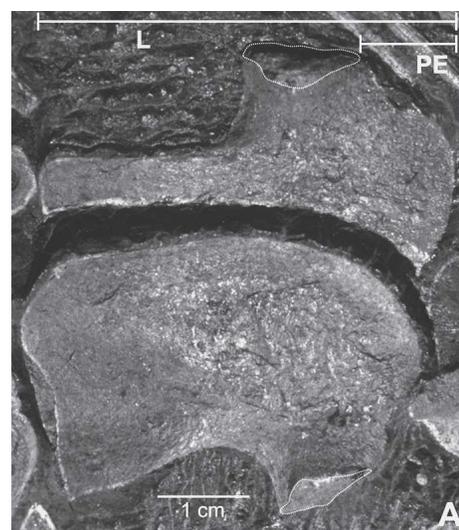


FIGURE 2. **A**, Coracoids of the holotype of *Mixosaurus maotaiensis*, nomen dubium (IVVP V 2468). **B**, plot of posterior coracoid extension against coracoid anteroposterior length. Ten mixosaurid coracoids were included in the analysis. *Mixosaurus maotaiensis* nomen dubium is within the range of the genus *Mixosaurus* (including *M. cornalianus* and *M. panxianensis*). Data source: *Mixosaurus cornalianus*, Brinkmann 1998; *Mixosaurus panxianensis*, personal observation of Jiang and Schmitz; *Mixosaurus maotaiensis* nomen dubium, Young, 1965, and personal observation of Jiang and Schmitz. **Abbreviations:** L, anteroposterior coracoid length; PE, posterior extension of the coracoid. The dotted line indicates the glenoid facet.

(1998b). The clavicles are also incompletely preserved, and do not have any taxonomic value at the species level.

Therefore, we conclude that the holotype is undiagnostic. In this case, the new generic name introduced by Jiang et al. (2005) should be abandoned because its type species is a nomen dubium (ICZN).

#### SYSTEMATIC PALAEOLOGY

ICHTHYOSAURIA de Blainville, 1835  
MIXOSAURIDAE Baur, 1887

**Revised Diagnosis**—Premaxilla posteriorly pointed, lacking supranarial process (character 1, state 1); dorsal margin of orbit formed by supraorbital crest (character 6, state 1); skull roof distinguished by long sagittal crest on nasal, frontal, and parietal (character 7, state 1); enlarged anterior terraces of upper temporal opening reaching nasal (character 8, state 1); mid-caudal

vertebral centra with significant height increase (character 23, state 1).

### *MIXOSAURUS* Baur, 1887

**Revised Diagnosis**—Humerus relatively short and wide, being about as long as broad (character 20, state 1); maxilla with dental groove (character 14, state 0; plesiomorphic character absent in *Phalarodon*).

### *MIXOSAURUS PANXIANENSIS*, sp. nov. (Figs. 3–9)

**Holotype**—GMPKU-P-1033 (Figs. 3–5).

**Paratype**—GMPKU-P-1039 (Figs. 6–9).

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

**Type Horizon**—Upper Member, Guanling Formation, Middle Triassic. The Guanling Formation consists of alternating, thinly bedded bituminous limestones and marls. All specimens were excavated from a horizon about 50 cm in thickness. According to conodont data (Yang et al., 1999), this horizon is of Anisian age (Pelsonian; biostratigraphic zone of *Nicoraella germanicus* Kozur, 1990).

**Etymology**—Named after the type locality of the holotype, Panxian County.

**Referred Material**—GMPKU-P-1008 and GMPKU-P-1009.

**Diagnosis**—Jugal with short posteroventral process; external contact between jugal and quadratojugal absent (plesiomorphic character that is absent in other mixosaurid species).

### DESCRIPTION

The holotype (GMPKU-P-1033) consists of a well-preserved skull and mandible, visible in left lateral view, nearly complete forelimbs, clavicles, interclavicle, left coracoid, and left scapula (Figs. 3–5). The tip of the slender rostrum, which is largely formed by the premaxilla, is damaged. The paratype (GMPKU-P-1039) comprises a skull, mandible, and large parts of the postcranium (Figs. 6–9). The preserved length is 728.5 mm. GMPKU-

P-1008 and 1009, previously described by Jiang et al. (2005), are not as well preserved as the type specimens. Further preparation exposed the left side of the skull of GMPKU-P-1008 and also provided new information about dental and pectoral features.

### Skull

The specimens preserve important mixosaurid synapomorphies in the cranium, such as a long sagittal crest, extensive anterior terraces of the upper temporal opening, and a posteriorly pointed premaxilla. Skull dimensions are given in Table 1. This study focuses on two important aspects of the postorbital skull region: (1) dorsal extent of the postorbital; (2) ventral cheek embayment and surrounding bones.

Jiang et al. (2005) described the extreme dorsal extent of the postorbital, wedging in between postfrontal and supratemporal to reach the lateral border of the upper temporal opening. They observed this feature in GMPKU-P-1009, a specimen that exposes its right lateral aspect. The suture pattern is apparently well preserved; however, the skull is laterally compressed. In the holotype and paratype, the postorbital is overlapped by the squamosal posteroventrally and by the supratemporal posterodorsally to a certain degree, but dorsally it seems to extend to reach the lateral margin of the anterior terraces of the upper temporal opening and separates the supratemporal from the postfrontal (Figs. 4, 7). As known from Jurassic ichthyosaurs (Sollas, 1916; McGowan and Motani, 2003), cranial bones usually overlap other bones. This intricate suture pattern most likely presents for mixosaurids, as pointed to by observations of Motani (1999b) and Schmitz et al. (2004). Due to deformation, the bone elements could have been partially disarticulated, obscuring the suture pattern. Furthermore, the upper temporal opening is not visible in any of the specimens, as in other mixosaurids where the upper temporal opening is usually concealed by the supratemporal (e.g. Motani, 1999b), and thus we are unable to discern unequivocally if the postorbital truly reaches the upper temporal opening in the available specimens. More material is necessary to verify this important feature.



FIGURE 3. Holotype skeleton of *Mixosaurus panxianensis*, sp. nov. (GMPKU-P-1033) from the Upper Member of Guanling Formation (Pelsonian, Anisian, Middle Triassic) of Yangjuan village, Xinmin area, Panxian County, Guizhou Province, People's Republic of China. Scale bar equals 50 mm.

The deep, long ventral cheek embayment is surrounded by jugal, postorbital, squamosal, and quadratojugal (Fig. 4). Posterior to the very slender suborbital bar, the jugal forms a broad ascending ramus that is dorsally overlapped by the postorbital. The presence of a small posteroventral process, visible in the holotype and GMPKU-P-1008 (left side), is remarkable. This process has not been observed in any other mixosaurid species. The postorbital reaches the margin of the cheek embayment, and is intercalated between jugal and quadratojugal. This is a plesiomorphic character absent in the other mixosaurid species. In holotype and GMPKU-P-1009, the squamosal also reaches the embayment. However, as explained above, the suture pattern might be influenced by a partial disarticulation. Better-preserved specimens may reveal that this bone indeed reaches the cheek embayment, causing this character to be autapomorphic for the species.

### Dentition

The premaxilla carries at least nine (holotype) to 13 (paratype) teeth with 2–10 mm of space in between (Figs. 3–4, 7). The surface of these slender, pointed, and conical teeth bears distinct apicobasal striations. The tallest teeth are placed in the posterior part of the premaxilla and are 6.5 mm high and 2.5 mm long (Table 2). The mode of tooth implantation is subtheodont.

Both type specimens preserve seven maxillary teeth, which become more robust posteriorly and resemble those of *Mixosaurus kuhnschnyderi* (Brinkmann, 1998a) and *Phalarodon callawayi* (Schmitz et al., 2004). The anterior four to five maxillary teeth have bluntly pointed, conical crowns, and are distinguished by distinct apicobasal striations. In contrast, the posterior two to three teeth have blunt, wide, and low crowns. Strong posterior maxillary crushing teeth like those in *P. fraasi* and *P. callawayi* are absent. There may be retention of labyrinthodont infolding of the tooth roots, which seem to be elliptical to nearly round in cross section. Because the roots are not fully exposed and further preparation would most likely damage the teeth, their cross-sectional shape cannot be exactly determined. The roots lack an apicobasally oriented groove on their labial side, which Motani (2005) and Schmitz et al. (2004) identified in *Phalarodon*. The holotype has a dental groove throughout the upper jaw; tooth implantation is subtheodont.

The shape indices of maxillary teeth (as defined by Massare,

1987) decrease from more than 2 anteriorly to 1 posteriorly. The size indices of the maxillary teeth, here defined as the total tooth height divided by the anteroposterior length of the maxilla, vary from 0.074 to 0.152 (Table 2).

The paratype contains an almost complete set of dentary teeth (Fig. 7). Eighteen teeth are counted, and the anterior 14 are conical and bluntly pointed, resembling those of the premaxilla and anterior maxilla. The posterior four teeth are larger than the corresponding upper teeth and seem to be mesiodistally elongated, but still retain bluntly pointed tips (Fig. 7). From anterior to posterior, the shape indices decrease from 2.25 to 0.71 (Table 2).

The preserved dentitions of GMPKU-P-1008 and 1009 are almost identical to the type specimens. From anterior to posterior, the shape indices of the maxillary teeth of GMPKU-P-1008 decrease from 1.67 to 1, and the size indices vary from 0.078 to 0.133. The shape indices of the two posterior dentary teeth of GMPKU-P-1009 are 0.80 and 0.75.

### Axial Skeleton

The paratype (GMPKU-P-1039; Fig. 6) preserves 70 fully articulated vertebrae, comprising cervicals, dorsals, and anterior caudals. The three posteriormost vertebrae are documented by neural spines only. Ribs are mostly preserved in articulation, and cover nearly the complete cervical to mid-dorsal centra row. As indicated by the position of the ilium, the presacral vertebrae count is 51. Because of the overlying ribs, the number of cervical vertebrae is not discernable.

All observable centra are distinctly higher than long. The ratio of centrum height to length is 1.57 in the posterior dorsals and increases to 1.87 in the anterior caudals; this is in the range for other mixosaurids (Schmitz et al., 2004). Rib articular facets are single in the mid-dorsal region (vertebrae 23 to 30) and in the anterior caudals (59–64), but double in the posterior dorsals to anteriormost caudals (39–58). Centrum 65 does not show a rib articular facet, which might be due to preservation.

Most neural arches carry tall neural spines, which are narrowest in the middle. In the mid-dorsal region they are about 2.8 times higher than the centrum, equivalent to proportions in the other mixosaurids (Schmitz et al., 2004). From anterior to posterior, the neural spines are first slightly inclined posteriorly, vertical in the mid-dorsal vertebrae, and slightly inclined anteriorly.

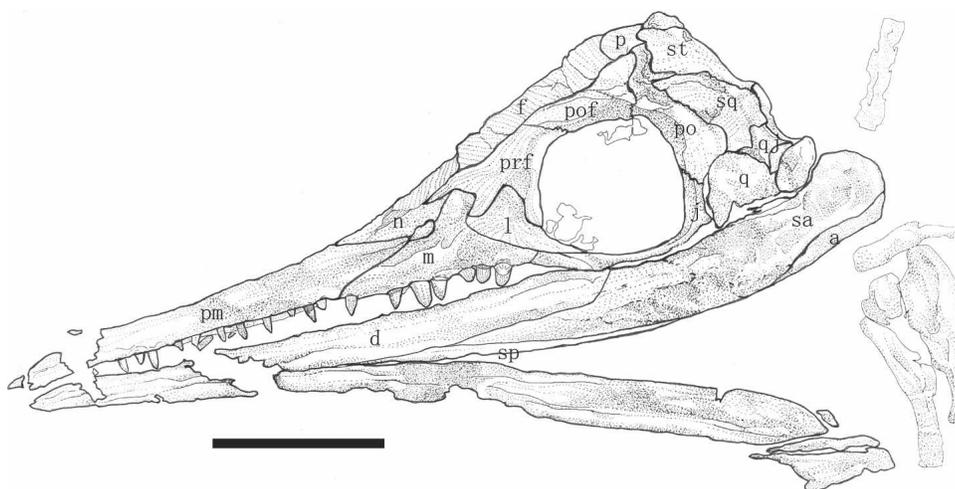


FIGURE 4. Line drawing of the skull of the holotype of *Mixosaurus panxianensis* (GMPKU-P-1033). **Abbreviations:** a, angular; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; po, postorbital; pof, postorbital; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal; st, supratemporal. Scale bar equals 50 mm.

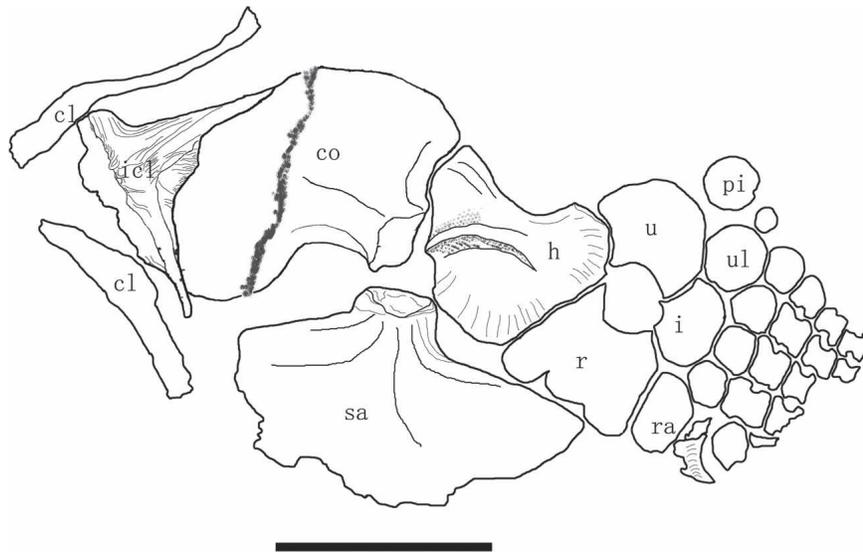


FIGURE 5. Drawing of the preserved pectoral girdle and the right forefin of the holotype of *Mixosaurus panxianensis* (GMPKU-P-1033). **Abbreviations:** cl, clavicle; co, coracoid; h, humerus; i, intermedium; icl, interclavicle; pi, pisiform; r, radius; ra, radiale; sa, scapula; u, ulna; ul, ulnare. Scale bar equals 50 mm.

only in the posterior dorsals (Fig. 6). The anterior caudal spines are distinguished by pronounced convex anterior margins, resulting from a strong posterior flexion. The onset of the caudal peak is marked by an anterior inclination of the neural spines.

### Pectoral Girdle

The coracoid, corresponding well to the basal and mixosaurid plan (McGowan and Motani, 2003), has a fan-shaped distal expansion clearly offset from the stem-like glenoid process (Figs. 3 and 5). The ratio of the posterior extension of the coracoid (PE), measured from the posterior end of the glenoid facet to the posterior coracoid margin along the anteroposterior axis (Fig. 2 A), to total coracoid length (L) is around 0.2. Full preparation of the coracoid of GMPKU-P-1008 revealed that PE is significantly longer than previously thought and actually broken. Despite this damage, the ratio of PE to L is 0.18.

The fan-shaped scapula corresponds to the typical mixosaurid shape depicted by McGowan and Motani (2003). The proportion of anterior extension : glenoid : posterior extension of the scapula is 1.2 : 1 : 1.8.

The interclavicle is broadly T-shaped, with its posterior process being about as long as its transversal bar whose distal parts are slightly projected anteriorly (Fig. 5). Anteriorly, the transversal bar is expanded into a flattened flange that probably serves as an attachment area for the clavicles. This feature is



FIGURE 6. Paratype skeleton of *Mixosaurus panxianensis* (GMPKU-P-1039) from the Upper Member of Guanling Formation (Pelsonian, Anisian, Middle Triassic) of Yangjuan village, Xinmin area, Panxian County, Guizhou Province, People's Republic of China. Scale bar equals 100 mm.

known for Jurassic ichthyosaurs such as *Ichthyosaurus communis* (McGowan and Motani, 2003), and can to some extent also be observed in the neotype of *Mixosaurus cornalianus* (PIMUZ T2420; Brinkmann, 1998b:fig. 11). The clavicles are slender and slightly curved. Their proximal part is expanded into a flattened flange that corresponds to the shape of the anterior expansion of the interclavicle.

### Forelimb

The right and left forefin of the holotype are almost complete (Fig. 3) and expose their ventral sides. Most of the phalanges of the right forefin are split down the middle; however, their shape is easily observable. The paratype contains poorly preserved remains of the forelimbs only, which are not further described herein. The overall forelimb morphology corresponds to the detailed description provided by Jiang et al. (2005). Thus, only differences and new observations are given here.

The anterior margin of the radius of all studied specimens bears two deep notches, including GMPKU-P-1008. The double notch is very unusual and possibly indicates that the emargination is not homologous with the plesiomorphic shaft retention observed in long bones (Caldwell, 1997). Because the ontogenetic and individual variability of this feature is unknown, it is not included in the diagnosis.

The right and left forefin of the holotype contain two rounded pisiforms (Figs. 3 and 5), much like those of some specimens of *Mixosaurus cornalianus* (e.g., Motani, 1999c).

### Pelvic Girdle

The left half of the pelvic girdle of the paratype is fully articulated and exposes its slightly eroded ventral side (Figs. 6, 8). The triangular pubis is anteriorly expanded and is only slightly longer than wide, different from that of other mixosaurids. Usually, the anterior expansion of the pubis is larger, and the pubis is two times longer than wide. The acetabular facet is positioned on the acetabular neck at the posterolateral corner. The neck is set off from the straight lateral and posterior margin. Close to the posterior margin and near the acetabular region, a small, oval obturator foramen is present.



FIGURE 7. Skull of the paratype of *Mixosaurus panxianensis* (GMPKU-P-1039). Scale bar equals 50 mm.

The ischium reaches about 70 percent of the anteroposterior length of the pubis. Anterior and medial margins are straight, whereas the posterolateral margin, partly covered by the femur, is probably emarginated. The acetabular region formed by the pubis and ischium is surrounded by a thickened rim. The acetabulum is completed by the curved and relatively stout ilium.

#### Hind Limb

Except for the distal part of the fifth digit, the left hind limb of the paratype is almost completely preserved and is seen in ventral view (Fig. 9). The right hind fin, also in ventral view, lacks its distal-most parts and is slightly disarticulated (Fig. 6).

The femur has a weakly pronounced shaft and is distally widened. Most remarkable is a distinct ventral process that arises near the proximal end of the femur (Fig. 9). Although becoming less high, the process continues distally and contrasts the shaft margins. The straight articular facet for the tibia is about two times wider than the concave fibular facet, which corresponds to the neotype of *M. cornalianus*.

Tibia and fibula enclose a broad spateum interosseum and are distally separated by the astragalus (Fig. 9). The tibia has a well-defined shaft. Proximal and distal widths equal the length of the tibia. The bell-shaped fibula is distally much broader than proximally.

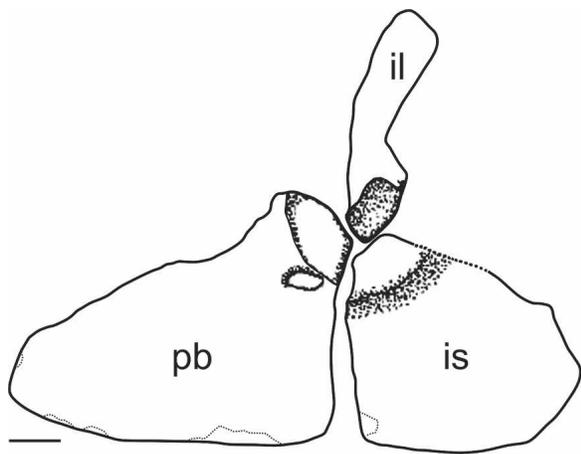


FIGURE 8. Drawing of the pelvic region of the paratype of *Mixosaurus panxianensis* (GMPKU-P-1039), partly reconstructed. The thick dotted lines indicate the area overlain by the femur; the thin dotted lines outline damaged parts. **Abbreviations:** pb, pubis; il, ilium; is, ischium. Scale bar equals 5 mm.

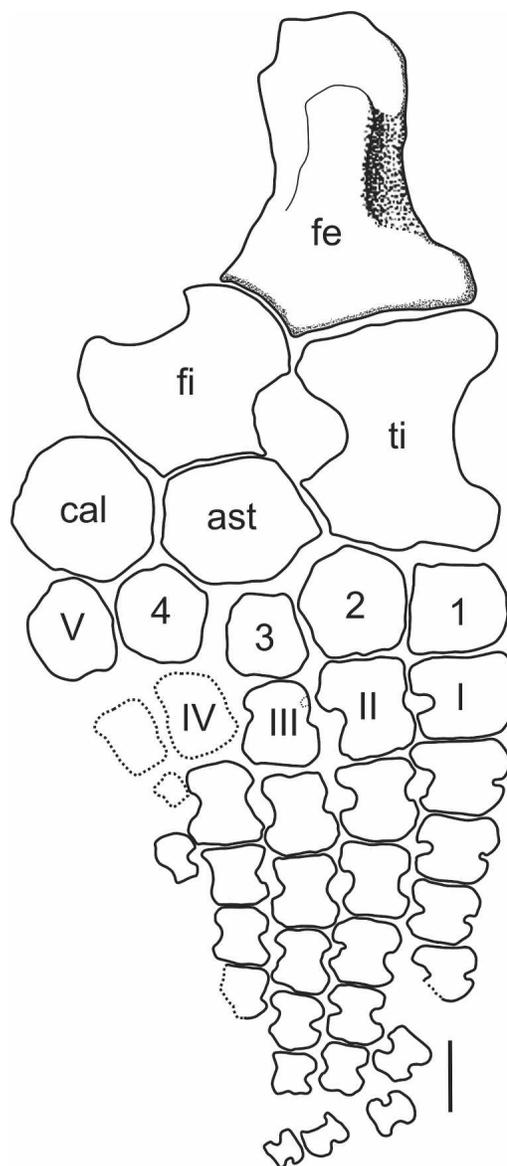


FIGURE 9. Drawing of the left hind limb of the paratype of *Mixosaurus panxianensis* (GMPKU-P-1039), ventral view. **Abbreviations:** ast, astragalus; ca, calcaneus; fe, femur; fi, fibula; ti, tibia; 1–4, distal tarsals; I–V, metatarsals. Scale bar equals 5 mm.

The fibula articulates with the hexagonal astragalus and the rounded calcaneum. Distally adjacent are four distal tarsals, with 1 and 2 being larger than 3 and 4. The shape of the distal tarsals is roughly squared (1 and 3) or pentagonal. Five metatarsals are present, and they also show two larger anterior elements. The leading edge of metatarsal I is convex, whereas metatarsals II and III are emarginated on both sides. Because metatarsals IV–V are poorly preserved, they are not further described herein. Up to five phalanges are present per digit, and all of them are emarginated. Along the anterior fin margin, the phalanges are very narrowly notched. The distal phalanges are disarticulated.

#### PHYLOGENY OF MIXOSAURIDAE

All major recent phylogenetic analyses of ichthyosaurs strongly supported the monophyly of Mixosauridae (Motani,

1999a; Maisch and Matzke, 2000; Sander 2000), but their ingroup relationships remained poorly understood. A first attempt to resolve the ingroup phylogeny by using a matrix-based analysis was pursued by Maisch and Matzke (2001a). Schmitz et al. (2004) questioned and briefly commented on problematic characters and concluded that it was most reasonable to keep the name *Mixosaurus* for all mixosaurid species, until new phylogenetic results were available. This view accords with that of Motani (1999a, b). Most recently, Jiang et al. (2005) incorporated new Chinese mixosaurid material in a phylogenetic analysis of mixosaurids. However, their data matrix was similar to that of Maisch and Matzke (2001a), including all characters criticized by Schmitz et al. (2004) because this latter paper was unavailable to the authors. Therefore, it is worthwhile to reanalyze the phylogeny of Mixosauridae with new data from the Chinese specimens.

### Matrix

The new matrix contains nine taxa and 23 characters (Appendices 1 and 2). Five new characters are introduced (4, 14, 18, 21, 22) and eight additional characters are modified from the previous analyses (7–10, 13, 15, 16, 23; see Appendix 1). All characters were polarized with respect to *Utatusaurus*, *Grippia*, and *Cymbospondylus*, which were used as outgroup taxa without a specified outgroup topology. Six valid mixosaurid species are recognized (*Mixosaurus cornalianus*, *M. kuhnschneideri*, *M. panxianensis*, sp. nov., *Phalarodon fraasi*, *P. callawayi*, and *P. atavus*). *M. nordenskiöldii* is considered a nomen dubium, following Schmitz (2005).

**Description of New Characters**—(4) Narial shelf: absent (0); present (1). Anterolateral to the external naris, *Phalarodon fraasi*, *P. callawayi*, and *P. atavus* have a flat, shelf-like area, which is medially bordered by the nasal-supraorbital ridge. This “narial shelf” cannot be recognized in *Mixosaurus*. However, this observation might be biased, because in contrast to *Mixosaurus*, all *Phalarodon* species are documented by almost three-dimensional skulls.

(14) Dentary labial shelf: absent (0); present (1). McGowan and Motani (2003) described a wide labial shelf in the dentary of *P. fraasi*. The dentary teeth are positioned far lingually; labially, the dentary is characterized by a broad, nearly even horizontal surface. This shelf can also be observed in *P. callawayi* and *Cymbospondylus*.

(18) Crown surface of at least one maxillary tooth with mesiodistal ridge: absent (0); present (1). Motani (2005) described a marked mesiodistal ridge on the crown surface of

crushing teeth of *Phalarodon fraasi*. Schmitz et al. (2004) mentioned chisel-like teeth in *P. callawayi*, referring to the same feature. Because the wrinkled crown surface is still intact, tooth wear can be excluded.

(21) Humerus shape: elongated, slightly flattened (0); distinctly flattened, nearly as wide as long (1). *Mixosaurus* has a relatively wider and shorter humerus than other Triassic ichthyopterygians (*Utatusaurus*, *Grippia*, *Chaohusaurus*, and *Phalarodon*). Figure 1 shows a logarithmic plot of humeral width against humeral length. All species of *Mixosaurus* have a relatively short and wide humerus and follow a uniform allometric line, as discussed earlier. The other Triassic taxa share another allometric line, because all considered genera have a relatively longer and narrower humerus. The humerus of *P. atavus* is unknown.

(22) Intermedium as wide as long or wider than long, and proximal margin wide, sometimes with deep proximal notch (0); intermedium longer than wide and proximally pointed, being wedged between distal ends of radius and ulna, which are almost in contact (1). Among mixosaurids, two different morphologies of the intermedium can be recognized. In all currently recognized species of *Mixosaurus*, the intermedium is at least as wide as long. The proximal margin of the intermedium is wide and usually straight, but some individuals have a deep proximal notch. The wide proximal margin broadly separates the distal ends of the radius and ulna. In *Phalarodon callawayi* and *P. fraasi*, however, the intermedium is longer than wide and proximally pointed, being tightly intercalated between the distal ends of the radius and ulna, which are almost in contact. The intermedium of *P. atavus* is unknown.

### Results

The analysis of the data matrix with PAUP\* for Windows 4.0 beta 10 results in a fully resolved phylogenetic tree (Fig. 10). Using the branch-and-bound method with default settings, one single most-parsimonious tree was obtained. This tree has a length of 27 steps and a consistency index of 0.8519 (rescaled: 0.7545); the retention index is 0.8857.

The tree topology emphasizes the monophyly of Mixosauridae as supported by five synapomorphies, which are listed in the diagnosis. The bootstrap value (1000 replications) is 97.

The ingroup topology shows a split into two sister groups, representing *Mixosaurus* and *Phalarodon*. *Mixosaurus* is diagnosed by a relatively short and wide humerus (character 21, state1) as discussed above (Fig. 6). This node is weakly sup-

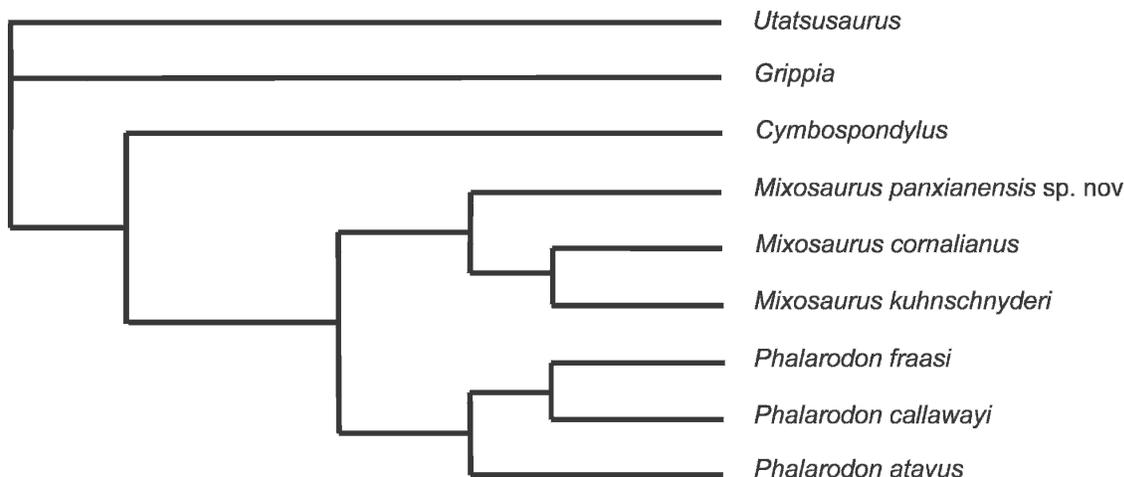


FIGURE 10. Phylogenetic position of *Mixosaurus panxianensis*, among mixosaurids. Tree length is 27 steps; CI = 0.8519, RI = 0.8857.

ported, having a bootstrap value of 63. Within *Mixosaurus*, *M. panxianensis*, sp. nov., is the sister taxon of *M. cornalianus* and *M. kuhnschnyderi*. The latter two species share the presence of a flat coronoid region (character 13, state 1), and the absence of dentine infolding (character 19, state 1). The node for *Phalarodon* is better supported, with a bootstrap value of 87. Synapomorphies of *Phalarodon* are a narial shelf (character 4, state 1) and the loss of a maxillary dental groove (character 15, state 1). *Phalarodon atavus* is the sister taxon of *P. fraasi* and *P. callawayi*; the latter two species share the presence of strong maxillary crushing teeth (character 16, state 1), which have a mesiodistal ridge on at least one of them (character 18, state 1).

The tree topology is generally similar to the tree obtained by Jiang et al. (2005), with the exception of the position of *Mixosaurus panxianensis* sp. nov. (equivalent for this purpose to '*Mixosaurus maotaiensis*,' because this taxon was coded for the referred specimens). Jiang et al. (2005) ascribed to this species a sister-taxon relationship to all other mixosaurids. The monophyletic relationships of *M. cornalianus*/*M. kuhnschnyderi* as well as *P. callawayi*/*P. fraasi* agree with those of Schmitz (2003). However, in the phylogenetic tree of Schmitz (2003), *P. atavus* forms the sister taxon of *M. cornalianus* and *M. kuhnschnyderi*, a relationship not supported here.

## CONCLUSIONS

The new locality discovered in the Guanling Formation (Anisian, Middle Triassic) in Panxian County (Guizhou Province, China) yields two mixosaurid species: *Phalarodon* cf. *P. fraasi* (Jiang et al., 2004) and *Mixosaurus panxianensis*. The fauna underlines the taxonomic diversity and wide geographical distribution of the Mixosauridae. From each major mixosaur locality (Monte San Giorgio, Spitsbergen, British Columbia, Nevada) at least two different species are known (Brinkmann, 1998b; Schmitz et al., 2004). The genus *Phalarodon* has a cosmopolitan distribution, being present in every fauna.

In addition to *Phalarodon atavus* (Quenstedt, 1852), *P. callawayi* (Schmitz et al., 2004), *P. fraasi* Merriam, 1910, *Mixosaurus cornalianus* (Bassani, 1886), and *M. kuhnschnyderi* (Brinkmann, 1998a), *M. panxianensis*, is the sixth valid mixosaurid species. This study shows that '*Mixosaurus maotaiensis*' Young, 1965, which had been erected upon fragmentary pectoral bones, is a nomen dubium. Therefore, the recently proposed new generic name for this species (Jiang et al., 2005) should be abandoned. The taxonomic treatment of *M. helveticus* Huene, 1916, *M. intermedius* Huene, 1916, *M. major* Fraas, 1891, and *M. timorensis* Broili, 1931, follows McGowan and Motani (2003), who considered these species as nomina dubia. Additionally, *Mixosaurus nordenskioeldii* (Hulke, 1873) is a nomen dubium (Schmitz, 2005). McGowan and Motani (2003) tentatively added *Tholodus schmidi* Meyer, 1851, to the Mixosauridae, but they already noted that this genus has ambiguous affinities. Because the syntype material only comprises dental material, it is difficult to establish taxonomic relationships. We consider *Tholodus schmidi* a species inquirenda.

The generic composition of the family Mixosauridae has been controversial in the past, and the goal of this study was to improve this situation. While Motani (1999) and Schmitz et al. (2004) hold a conservative view and suggested that all mixosaurid species should be referred to the single genus *Mixosaurus*, other authors recognized two to four genera (e.g. Maisch and Matzke, 2000, Sander, 2000, Jiang et al., 2005).

The phylogenetic analysis presented in this paper resulted in a fully resolved tree. Important nodes of the tree are defined by one or two characters only, making the taxonomic interpretation of this result difficult. However, the presence of two genera, *Mixosaurus* and *Phalarodon*, seems to be sufficiently supported

at this point. A detailed study of ontogenetic and intraspecific variability is crucial for a better understanding of mixosaurid phylogeny.

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## APPENDIX 1

Descriptions of characters used in phylogenetic analysis. Characters were polarized with respect to *Utatusaurus*, *Grippia*, and *Cymbospondylus* as outgroup taxa.

- (1) Supranarial posterior process of premaxilla: present (0); absent (1). (Maisch and Matzke, 2001a:character 12). This character describes a widely accepted synapomorphy of the Mixosauridae and has also been used in the analysis of, e.g., Motani (1999a). For the purpose of this study, we follow the formulation of Maisch and Matzke (2001a).
- (2) Maxilla: excluded from prefrontal (0); meeting prefrontal (1). (Maisch and Matzke, 2001a:character 12).
- (3) External naris orientation: dorsolateral (0); lateral, scarcely visible in dorsal view (1). (Motani, 1991a:character 4).
- (4) Narial shelf: absent (0); present (1).
- (5) Anterior orbital margin: irregular (0); of regular rounded shape (1). (Maisch and Matzke, 2000:character 23).
- (6) Supraorbital crest on prefrontal and postfrontal: absent (0); present (1). (Maisch and Matzke, 2000:character 22).
- (7) Sagittal crest on nasal, frontal, and parietal: absent (0); present (1). (Modified from Motani, 1999a:character 16).
- (8) Anterior terrace of temporal opening: small or absent (0); enlarged, reaching nasal (1). (Modified from Motani, 1999a:character 14).
- (9) Postfrontal and supratemporal: separated by postorbital (0); in contact (1). (Modified from Sander, 2000:character 28).
- (10) Pre- and postfrontal external contact: absent, dorsal margin of orbit being formed by frontal (0); present, eliminating frontal from dorsal margin of orbit (1). (Modified from Motani, 1999a:character 8).
- (11) Jugal/quadratojugal dorsal contact: absent (0); present (1). (Motani, 1999a:character 23).
- (12) Deep jugal-quadratojugal notch, forming pronounced ventral embayment of cheek: present (0); absent (1). (Jiang et al., 2005:character 24).
- (13) Coronoid region: slightly elevated or high (0); flat (1). (Modified from Sander, 2000:character 41).
- (14) Dentary labial shelf: absent (0); present (1).
- (15) Maxillary dental groove: present (0); absent (1). (Modified from Motani, 1999a:character 41). In difference to previous analyses, *Cymbospondylus* is coded with a question mark. The tooth-bearing part of the maxilla of the holotype of *C. petrinus* (UCMP 9950) is not fully prepared.
- (16) Maxilla teeth: conical, sometimes blunt (0); strong crushing (1). (Modified from Motani, 1999a:character 38; Maisch and Matzke, 2001a:character 1; Jiang et al. 2005:character 2).
- (17) Tooth size relative to skull width: smaller than 0.05 (0); higher than 0.1 (1). (Motani, 1999a:character 39).
- (18) Crown surface of at least one maxillary tooth with mesiodistal ridge: absent (0); present (1).
- (19) Dentine infolding of tooth root: present (0); absent (1). (Jiang et al., 2005:character 5).
- (20) Manual pisiform 2 (neomorph): absent (0); present (1). (Modified from Nicholls et al., 1999:character 12).
- (21) Humerus shape: elongated, slightly flattened (0); distinctly flattened, nearly as wide as long (1). Compare Figure 1.
- (22) Intermedium as wide as long or wider than long, proximal margin wide and straight, sometimes with deep proximal notch (0); intermedium longer than wide and proximally pointed, being wedged between distal ends of radius and ulna, which are almost in contact (1).
- (23) Caudal vertebral centra with significant height increase: absent (0); present (1). (Modified from Motani, 1999a:character 98).

## APPENDIX 2

Character-taxon matrix used for phylogenetic analysis.

	1	2	3	4	5	6	7	8	9	10	11	12
<i>Utatusaurus</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Grippia</i>	0	0	0	0	0	0	0	0	0	1	0	0
<i>Cymbospondylus</i>	0	1	0	0	1	0	0	0	1	1	1	0
<i>Mixosaurus panxianensis</i>	1	1	1	0	1	1	1	1	?	1	0	0
<i>Phalarodon fraasi</i>	1	1	1	1	1	1	1	1	1	1	?	0
<i>Phalarodon callawayi</i>	1	1	0	1	1	1	1	1	1	1	1	0
<i>Phalarodon atavus</i>	1	1	1	1	1	1	1	1	1	1	1	0
<i>Mixosaurus cornalianus</i>	1	1	1	0	1	1	1	1	1	1	1	1
<i>Mixosaurus kuhnschnyderi</i>	1	1	?	0	1	1	1	1	1	1	1	?

	13	<u>14</u>	15	16	17	18	19	20	21	22	23
<i>Utatusaurus</i>	0	<u>0</u>	0	0	0	0	0	0	0	0	0
<i>Grippia</i>	0	<u>0</u>	0	0	0	0	0	0	0	0	0
<i>Cymbospondylus</i>	0	<u>1</u>	<u>2</u>	0	0	0	0	?	0	?	0
<i>Mixosaurus panxianensis</i>	0	<u>0</u>	0	0	1	0	0	1	1	0	1
<i>Phalarodon fraasi</i>	<u>2</u>	<u>1</u>	1	1	1	1	0	1	0	1	1
<i>Phalarodon callawayi</i>	0	<u>1</u>	1	1	1	1	0	1	0	1	1
<i>Phalarodon atavus</i>	?	<u>2</u>	1	0	1	0	0	?	?	?	?
<i>Mixosaurus cornalianus</i>	1	<u>0</u>	0	0	0	0	1	1	1	0	1
<i>Mixosaurus kuhnschnyderi</i>	1	<u>0</u>	0	0	1	0	1	?	1	?	1