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The otic capsule of the Middle Triassic ichthyosaur *Mixosaurus* from Monte San Giorgio (Switzerland): New evidence on the braincase structure of basal ichthyosaurs

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Key words: Ichthyosauria, *Mixosaurus,* braincase, otic capsule, grundplan, Middle Triassic

ABSTRACT

For the first time, the otic capsule (proötic and opisthotic) of a Triassic ichthyosaur is described, based on a specimen of *Mixosaurus* cf. *cornalianus* from the Grenzbitumenzone of Monte San Giorgio, Switzerland. The otic capsule of *Mixosaurus* differs from that of more highly derived ichthyosaurs by several features, which are mainly related to the much higher degree of ossification found in *Mixosaurus*. The proötic is extensively ossified and shows an anteroventral facet for contact with the basisphenoid, a crista prootica lateralis, a foramen completely enclosed by bone for the exit of the nervus facialis, and a posterior sutural contact with the opisthotic, thus closing off the lateral wall of the internal ear capsule. The proötic also forms the anterior margin of a well ossified fenestra vestibuli and has a posterodorsal articulation facet for the supraoccipital. The opisthotic has an elongate, anteroposteriorly compressed, plate-like processus paroccipitalis and shows a well ossified crista interfenestralis, forming the posterior margin of the fenestra vestibuli and the anterior margin of the foramen metoticum. The anterodorsal contact with the supraoccipital is well defined.

For all these features, *Mixosaurus* is much closer to basal amniotes and basal diapsids, such as *Captorhinus*, *Procolophon* or *Youngina* than to more highly derived ichthyosaurs. The new data on the otic capsule of *Mixosaurus* are corroborated by the braincase of another Middle Triassic ichthyosaur, *Phantomosaurus*. It can be assumed that the reported features of the *Mixosaurus* braincase, which are unusual compared with other known ichthyosaurs, could be plesiomorphies retained from an unknown ichthyosaur ancestor, that is representative of the grundplan of ichthyosaurs. However, in the absence of further material the possibility that some features of the mixosaurid otic capsule are autapomorphic within ichthyosaurs can not be excluded.

ZUSAMMENFASSUNG

Anhand eines Exemplares von *Mixosaurus* cf. *cornalianus* (BASSANI, 1886) aus der Grenzbitumenzone des Monte San Giorgio (Schweiz) wird erstmals die Ohrkapsel (Prooticum und Opisthoticum) eines triassischen Ichthyosauriers beschrieben. Die Ohrkapsel von *Mixosaurus* unterscheidet sich von den Ohrkapseln höher abgeleiteter Ichthyosaurier in vielen Merkmalen, die im Wesentlichen auf den deutlich stärkeren Verknöcherungsgrad zurückzuführen sind. Das Prooticum ist umfangreich verknöchert und besitzt eine anteroventrale Facette für das Basisphenoid, eine Crista prootica lateralis, ein vollständig ossifiziertes Foramen zum Austritt des Nervus facialis und eine posteriore Sutur mit dem Opisthoticum, wodurch die Ohrkapsel lateral knöchern geschlossen wird. Das Prooticum bildet den anterioren Rand einer wohlverknöcherten Fenestra vestibuli und zeigt eine posterodorsale Facette für das Supraoccipitale. Das Opisthoticum hat einen langen, anteroposterior abgeflachten Processus paroccipitalis und eine gut ossifizierte Crista interfenestralis, die den posterioren Rand der Fenestra vestibuli und die anteriore Umgrenzung des Foramen metoticum bildet. Der anterodorsale Kontakt zum Supraoccipitale ist klar definiert.

In all diesen Merkmalen ähnelt *Mixosaurus* viel mehr basalen Diapsiden und basalen Amnioten wie *Captorhinus*, *Procolophon* und *Youngina* als abgeleiteten Ichthyosauriern. Die neuen Daten über die Gehörkapsel von *Mixosaurus* finden Bestätigung durch Beobachtungen am Hirnschädel von *Phantomosaurus*, einem weiteren mitteltriassischen Ichthyosaurier. Es kann angenommen werden, dass die meisten ungewöhnlichen Charakteristika der *Mixosaurus*-Gehörkapsel von unbekannten Vorfahren ererbte Plesiomorphien sind und den Grundplan der Ichthyosaurier widerspiegeln. Ohne weiteres Vergleichmaterial kann die Möglichkeit, dass einige Gehörkapsel-Merkmale von *Mixosaurus* innerhalb der Ichthyosauria autapomorph sind, jedoch noch nicht ausgeschlossen werden.

1. Introduction

Mixosaurus is the Triassic ichthyosaur genus which is represented by the most abundant and most well-preserved material. Most known specimens are from the famous Grenzbitumenzone of Monte San Giorgio in Southern Switzerland and Besano in Northern Italy. Despite the abundance of material, the anatomy of *Mixosaurus* remains poorly understood, and its osteology has only been partially described, particularly by Repossi (1902), Wiman (1912), Huene (1935, 1949) and more recently by Callaway (1997), Maisch & Matzke (1997, 1998a, b), Brinkmann (1998, 2004) and Motani (1999).

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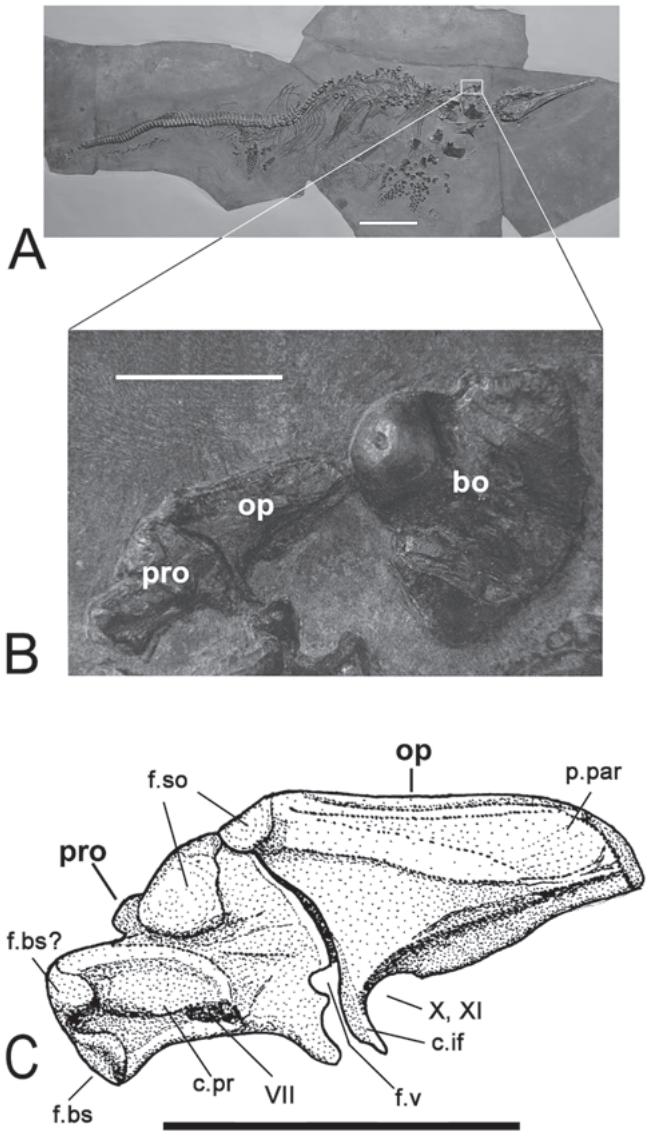

Fig. 1. *Mixosaurus* cf. *cornalianus*, PIMUZ T4848 (Middle Triassic, Grenzbitumenzone of Monte San Giorgio, Canton Ticino, Switzerland). A) Complete specimen in right lateral view, with framed left otic capsule and basioccipital bone. B) Left otic capsule in lateral view (left side of the photograph) and basioccipital bone in ventral view (right side of the photograph). C) Interpretative drawing of the left otic capsule as preserved, slightly compressed and seen in left lateral view. Abbreviations: bo, basioccipital; c.if, crista interfenestralis; c.pr, crista prootica lateralis; f.bs, f.bs?, facet and possible facet for basisphenoidal portion of parabasisphenoid; f.so, facet for supraoccipital; f.v, fenestra vestibuli or oval window; op, opisthotic, p.par, processus paroccipitalis; pro, proötic; VII, foramen nervi facialis; X, XI, foramen metoticum. Scale bars: A (10 cm); B, C (1 cm).

Few data have hitherto been published on the anatomy of the braincase of this taxon. Wiman (1912) provides some information on the basioccipital and the parabasisphenoid in ventral aspect. Maisch & Matzke (1997) described the dorsal surface of the parabasisphenoid, noting fundamental differences to more derived ichthyosaurs.

The purpose of this paper is to describe an important part of the braincase, the otic capsule, that is the proötic and opisthotic bones, which is hitherto completely unknown in mixosaurids and all more basal ichthyosaurs. The otic capsule of *Mixosaurus* differs in many ways from that of the better known, post-Triassic forms currently united as Neoichthyosauria (Maisch & Matzke 2000; Sander 2000). A comparison of *Mixosaurus* with the few other Triassic ichthyosaurs in which at least part of the otic capsule is known, as well as with highly derived post-Triassic forms on one hand, and non-ichthyosaurian basal amniotes and diapsids on the other hand, is also presented. It serves to suggest that the unusual features in the otic capsule of *Mixosaurus* could be mainly interpreted as plesiomorphic. This part of the braincase in basal ichthyosaurs appears considerably different from what is known in the more derived forms, which is useful to reconstruct the grundplan (sensu Hennig 1950) of ichthyosaurs and looking for their origin and ancestry.

2. Material

The bony otic capsule described below belongs to a well-preserved, almost complete, but somewhat disarticulated skeleton traditionally allocated to *Mixosaurus cornalianus*, PIMUZ T4848 (Paläontologisches Institut und Museum der Universität Zürich, Switzerland) (Fig. 1A). The fossil is the only representative of the genus *Mixosaurus* we have found in Zurich or any other collection showing this part of the cranial skeleton. The interarticulated proötic and opisthotic are found dislocated to a position six to seven centimetres posterior to the skull and dorsal to the moderately scattered cervical vertebrae. The otic capsule is situated immediately posterior to the likewise dislocated basioccipital, which is exposed in ventral view. The element here interpreted as the opisthotic is clearly reminiscent in shape of the opisthotic in the Middle Triassic cymbospondylid ichthyosaur *Phantomosaurus neubigi* (SANDER 1997) (Sander 1997; Maisch & Matzke in press) further corroborating its osteological identification.

3. Systematic palaeontology

Order Ichthyosauria DE BLAINVILLE 1835
Suborder Hueneosauria MAISCH & MATZKE 2000
Family Mixosauridae BAUR 1887
Genus *Mixosaurus* BAUR 1887
Type-species: *Ichthyosaurus cornalianus* BASSANI 1886

Mixosaurus cornalianus (BASSANI 1886) BAUR 1887

Comments: For revised diagnoses of genus and species, see Maisch & Matzke (2001). The taxon *Mixosaurus cornalianus* (BASSANI 1886) BAUR 1887 is under present revision by W. Brinkmann, and a re-allocation of PIMUZ T4848 to another

species of the same genus may be envisioned. In the following, *Mixosaurus* cf. *cornalianus* indicates the current, provisional, taxonomic status of PIMUZ T4848.

Mixosaurus* cf. *cornalianus

Age: Middle Triassic

4. Description

The dislocated otic capsule, consisting of the interarticulated left proötic and opisthotic bones exposed in generalized lateral view (Fig. 1B, C), has suffered some medio-lateral compression. The processus paroccipitalis of the opisthotic is now in the same plane as the rest of the bone (Fig. 1C: p.par).

The proötic is anteroposteriorly elongate. Anteriorly it is narrower, expanding posteriorly in height towards the suture with the opisthotic. An anteroventral facet (Fig. 1C: f.bs) presumably was for contact with the dorsum sellae region of the basisphenoidal portion of the parabasisphenoid. A facet-like protrusion above it (Fig. 1C: f.bs?) possibly was part of the same joint structure indicating an original broad anterior contact of the proötic with the parabasisphenoid.

The ventral margin of the proötic is distinctly concave. Its dorsal margin is irregular and forms posteriorly a contact facet for the supraoccipital. The major part of the posterior margin of the proötic is slightly convex and fits closely into the anterior concave margin of the opisthotic. A sub-oval emargination at the lower end of the suture is interpreted as the fenestra vestibuli or oval window (Fig. 1C: f.v), which interpretation is supported by the presence of the stapedial basal plate in a similar emargination in the otic capsule of *Procolophon trigoniceps* shown in Fig. 2C. The space between proötic and opisthotic below the oval window presumably is an artefact in the form of a suture broken and opened during the post mortem medio-lateral flattening of the otic capsule. Long sutures above and below the oval window uniting relatively large proötic and opisthotic bones show that the lateral wall of the otic capsule was well ossified.

A ridge extending from the anterodorsal facet of the proötic towards its posteroventral corner is anteriorly produced into a pronounced lateral ledge. Ventral to the ledge and near the concave ventral margin of the bone is a relatively large foramen. Based on comparative morphology in amniotes with well ossified otic capsules the ridge is interpreted as crista prootica, and the foramen as the exit for nervus facialis or the seventh cranial nerve from the braincase.

The opisthotic consists of a short otic region and an elongate paroccipital process, the anterolateral surface of which is visible due to the compression of the specimen.

The otic region has anterodorsally a facet for contact with the supraoccipital bone. The facet is in close contact with the supraoccipital facet of the proötic and slightly overhangs that bone (Fig. 1C: f.so). Ventrally, posterior to the fenestra vestibuli, the opisthotic has a narrow crista interfenestralis, between the oval window and foramen metoticum. The metotic foramen (Fig. 1C: X, XI) transmitted the glossopharyngeal and vagus nerves along with the jugular vein (Rieppel 1993). The ridge continues in ventral direction on a narrow process of the bone curving around part of the metotic foramen. This, most likely, was closed posteriorly by the exoccipital, as is the case in *Phantomosaurus neubigi* (Maisch & Matzke in press).

The paroccipital process is preserved as a high and plate-like structure. Its dorsal and ventral margins are thin and sheet-like, whereas its central part is thicker, tapering to a ridge in posterior direction.

5. Comparison with Triassic ichthyosaurs

The otic capsule of Triassic ichthyosaurs is poorly known. The opisthotic was described and figured for the Late Triassic *Shonisaurus* by Camp (1980). It agrees with that of *Mixosaurus* cf. *cornalianus* in that it possesses a more elongate paroccipital process than characterizes Neoichthyosauria, such as *Ichthyosaurus communis* (Fig. 2E; e.g., McGowan 1973), in which the paroccipital process is usually reduced to a small knob of bone shorter than the otic region of the opisthotic.

Shonisaurus differs from *Mixosaurus*, by having a paroccipital process which is not plate-like (cf. Camp 1980: Figs. 9, 15, for comparison). The crista interfenestralis (and therefore the anterior margin of foramen metoticum) are apparently unossified in *Shonisaurus*, as they are in all neoichthyosaurs in which the opisthotic is known (Fig. 2E).

The braincase of the Middle Triassic cymbospondylid ichthyosaur *Phantomosaurus* (Fig. 2D), recently redescribed in detail by Maisch & Matzke (in press), shows strong similarities to *Mixosaurus*. Its paroccipital process is elongate, dorsoventrally wide and plate-like thin, particularly in its distal portion. The crista interfenestralis is ossified, and the foramen metoticum is completely enclosed by the bony exoccipital and opisthotic.

In contrast to *Mixosaurus*, the exoccipital and opisthotic are fused in *Phantomosaurus* to form an otoccipital ossification, as found in many synapsids and diapsids (compare e.g. with the plesiosaur *Muraenosaurus*, Fig. 2B). This is interpreted by Maisch & Matzke (in press) as an autapomorphy of *Phantomosaurus* rather than as a plesiomorphic feature approaching the ancestral ichthyosaur condition, a hypothesis which is corroborated by the situation in the more basal *Mixosaurus*. Numerous specimens of *Mixosaurus* are known, in which the exoccipitals are preserved in isolation, but they never show any fusion to part of the otic capsule. Moreover, the sister-taxon of *Phantomosaurus*, *Cymbospondylus*, and all more highly derived, adequately known ichthyosaurs also show a lack of fusion between the exoccipital and opisthotic. It is therefore parsimonious to assume that the fusion in *Phantomosaurus* is autapomorphic.

The proötic has so far not been known in detail in any Triassic ichthyosaur. In *Phantomosaurus* it is incompletely pre-

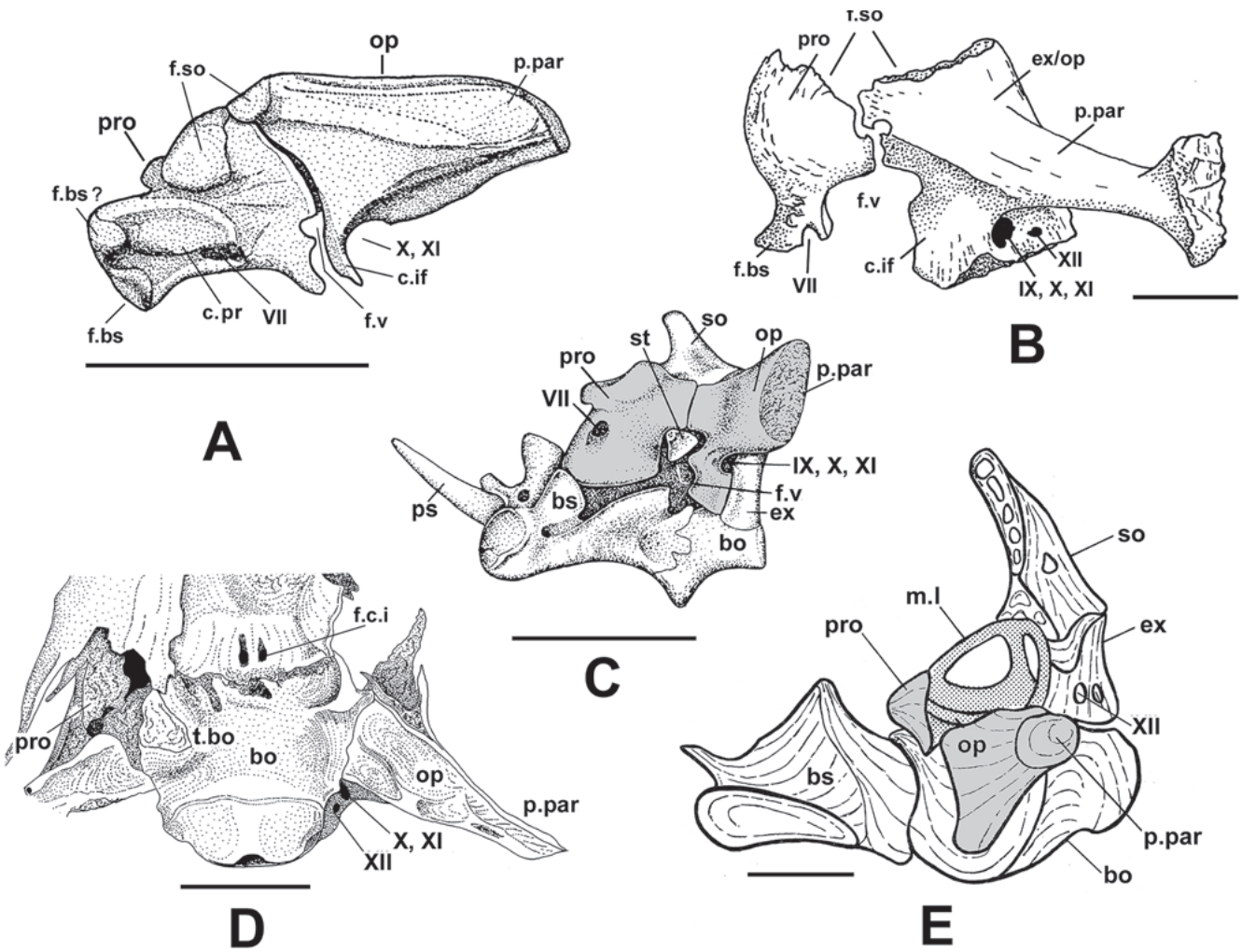

Fig. 2. Otic capsules and parts of braincases in ichthyosaurs and two other amniotes. A) *Mixosaurus* cf. *cornalianus* (PIMUZ T4848) left otic capsule in lateral view. B) The diapsid (sauropterygian) *Muraenosaurus leedsi* (SEELEY 1874) from the Middle Jurassic of England, left otic capsule in lateral view (redrawn from Maisch 1998). C) The parareptile *Procolophon trigoniceps* OWEN 1876 from the Lower Triassic of South Africa, reconstruction of the braincase in left lateral view, with otic elements shaded in grey (redrawn from Carroll & Lindsey 1985). D) The basal ichthyosaur (cymbospondylid) *Phantomosaurus neubigi* (SANDER 1997) from the Middle Triassic of Germany, braincase in ventral view (redrawn from Maisch & Matzke in press). E) The derived ichthyosaur (ichthyosaurid) *Ichthyosaurus communis* CONYBEARE 1822 from the Lower Jurassic of England, reconstruction of part of the braincase in left lateral view with otic elements shaded in grey (redrawn from McGowan 1973). Abbreviations as in Fig. 1, and: bs, basisphenoid; ex, exoccipital; f.c.i, carotid foramen; m.l, membraneous labyrinth; ps, parasphenoid; so, supraoccipital; st, stapes; t.bo, tuber basioccipitale; IX, X, XI, metotic foramen; XII, hypoglossal foramen. Scale bars: A-C (10 mm); D, E (20 mm).

served (Fig. 2D). It can be observed, however, that the proötic and the opisthotic were in sutural contact, which together with the relatively large size of the bones suggest that the lateral wall of the otic capsule in *Phantomosaurus* was well ossified. This resembles conditions in *Mixosaurus* and distinguishes these Middle Triassic ichthyosaurs from the neoichthyosaurs, such as *Ichthyosaurus communis* (Fig 2E; e.g., Appleby 1956, 1961; McGowan 1973). The fenestra vestibuli, the borders of which are never well ossified in derived ichthyosaurs, is clearly demarcated in *Mixosaurus* and must have been enclosed between the proötic, opisthotic and the parabasisphenoid. A contribution of the basioccipital to the fenestra vestibuli appears unlikely, as there is no proötic-basioccipital contact in *Phantomosaurus*, but it cannot be completely ruled out without better articulated braincase material of *Mixosaurus* at hand.

6. Discussion and conclusion

The otic capsule of *Mixosaurus* shows several differences to that of neoichthyosaurs, as exemplified by *Ichthyosaurus* described in detail by McGowan (1973) (Fig. 2E); all other neoichthyosaurs in which the braincase is reasonably well

known, including *Temnodontosaurus*, *Eurhinosaurus*, *Suevoleviathan*, *Stenopterygius*, *Ophthalmosaurus* and *Platypterygius*, basically correspond to this pattern (Appleby 1956; Maisch & Matzke 2000; McGowan 1973; Kear 2005). They can be summarized as follows. The proötic is well ossified. It has a clear anteroventral articulation facet for the parabasisphenoid. It bears a crista prootica lateralis and has a foramen completely enclosed by bone for the exit of the nervus facialis from the braincase. It has a posterior sutural contact with the opisthotic, the two bones together closing off the lateral wall of the internal ear capsule. It forms a well ossified anterior margin of the fenestra vestibuli. There is a clear posterodorsal facet for the articulation with the supraoccipital. The opisthotic has an elongate, high and plate-like processus paroccipitalis. There is a well ossified crista interfenestralis forming the posterior margin of the fenestra vestibuli and the anterior margin of the foramen metoticum. The anterodorsal contact with the supraoccipital is well defined. All these features demonstrate that the otic capsule of *Mixosaurus* has a much higher degree of ossification than that of the neoichthyosaurs.

If the braincase of *Mixosaurus* is compared to that of other amniotes, particularly basal forms, including parareptiles like the Early Triassic *Procolophon* (Carroll & Lindsey 1985; Fig. 2C), captorhinids such as the Early Permian *Captorhinus* (Price 1935; Modesto 1998), early diapsids like the Late Permian *Youngina* (Evans 1987) and the Early Triassic *Prolacerta* (Evans 1986), and the Late Jurassic basal sauropterygian *Muraenosaurus* (see Maisch 1998 for a detailed account why *Muraenosaurus* has to be regarded as a basal sauropterygian; Fig. 2B) – at least regarding the osteology of its well known braincase –, the apparently unusual features of *Mixosaurus* are proposed as plesiomorphies. They are all found in all the outgroup taxa, except for the extreme anteroposterior flattening of the paroccipital process, which is, however, matched in another rather basal Triassic ichthyosaur, *Phantomosaurus*, and might be an autapomorphic character of a larger group of comparatively basal ichthyosaurs. Despite this potentially autapomorphic feature, the braincase of *Mixosaurus*, seems consistent with that of a wide array of relatively basal Permo-Triassic amniotes, as can be expected from an early ichthyosaur.

Specific similarities to a certain amniote group – basal diapsids, captorhinids, and parareptiles – are not evident from the structure of the otic capsule of *Mixosaurus*. It is instead of a much generalized, basal amniote pattern. The structure of the otic capsule of *Mixosaurus* thus suggests that ichthyosaurs must have arisen from terrestrial or aquatic ancestors in which there was considerable ossification of the braincase, particularly the otic capsule. In neoichthyosaurs, the ossification of the braincase in general and of the otic capsule in particular are strongly reduced (see above), this highly derived condition can not further be used for comparing ichthyosaur braincases to that of other amniotes, as done in previous studies (e.g., Appleby 1961). Despite some general trends and tendencies become more and more apparent, the precise evolution of the ichthyosaur braincase is still poorly known because of the paucity of adequate material, notably for the Triassic taxa, and the lack of detailed descriptions of the available specimens. In order to make braincase osteology an important factor in the continuing debate on the origin and ancestry of ichthyosaurs, it is necessary to find well-preserved specimens of even more basal ichthyosaurs. The very basal *Mixosaurus*, although being the most plesiomorphic known ichthyosaur with useful data on braincase osteology, is a relatively late Triassic ichthyosaur (Anisian-Ladinian). The tendency to reduce braincase ossification has maybe already affected the mixosaurids to such a degree as to blur aspects of the ancestral ichthyosaurian braincase morphology, what would be crucial for a meaningful comparison to other amniote groups. New findings of mixosaurids may also indicate additional braincase autapomorphies. So that *Mixosaurus* may not be regarded as a typical basal ichthyosaur in this context. Nevertheless, it is important to emphasize that the reported *Mixosaurus* specimen hitherto represents the earliest known ichthyosaur with well ossified otic capsules.

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