



THE TAXONOMIC STATUS OF *MIXOSAURUS NORDENSKIOELDII* (ICHTHYOSAURIA)

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The Middle Triassic ichthyosaur *Mixosaurus nordenskiöldii* was originally described by Hulke (1873) based on material collected by Prof. A. E. Nordenskiöld in Spitzbergen (Saurie Hook, Ice Fjord) in 1864 and 1868. Most of the material was too poorly preserved for a taxonomic study, and thus Hulke (1873:3) only described the “less imperfect” specimens. Nevertheless he was able to diagnose two new ichthyosaur species: *Ichthyosaurus polaris* and *I. nordenskiöldii*. Dames (1895) referred the latter species to *Mixosaurus* Baur, 1887.

In recent years, the taxonomy of mixosaurid ichthyosaurs has been discussed controversially. One unsolved problem is whether both *Mixosaurus nordenskiöldii* (Hulke, 1873) and *Phalarodon fraasi* Merriam, 1910 are valid species. In most recent publications (Nicholls et al., 1999; Maisch and Matzke, 2000; Schmitz et al., 2004) *P. fraasi* was considered a junior synonym of *M. nordenskiöldii*. In contrast, McGowan and Motani (2003) tentatively recognized both species as valid and pointed out the need for comprehensive studies to clarify this taxonomic issue.

The aim of this note is to analyze the syntype series of *M. nordenskiöldii*. Hulke (1873) did not provide any figures, and it is still not clear which diagnostic characters are present in the syntypes. The reanalysis is even more important because the attempts by Nicholls et al. (1999) and Schmitz et al. (2004) to designate the holotype or the lectotype, respectively, did not comply with the ICZN, as explained below.

Institutional Abbreviations—**BMNH**, British Museum of Natural History; **NRM**, Naturhistoriska Riksmuseet, Stockholm; **PIMUZ**, Paläontologisches Institut und Museum der Universität Zürich; **PMU**, Paleontologiska Museet Uppsala; **TMP**, Royal Tyrrell Museum of Paleontology, Drumheller; **UCMP**, University of California Museum of Paleontology, Berkeley.

REDESCRIPTION OF THE SYNTYPE SERIES

The syntype series of *Mixosaurus nordenskiöldii* consists of five specimens, originally labeled 2a–e. Specimens 5 and 6 “may probably be referred” to *M. nordenskiöldii* (Hulke, 1873:7). Parts of this material were located in NRM, where it was originally deposited.

The material comprises poorly preserved remains of mainly the axial skeleton. Still bearing the historical label, four of the seven specimens were located in the collections of NRM: 2b, 2e, 5, and 6. Specimens 2a, 2c, and 2d could not be identified with certainty. There are two non-catalogued specimens that bear a historical number 2 and were collected at Saurie Hook in 1864 and 1868, respectively; however, the suffix is missing. They probably represent specimens 2c and 2d. To avoid a misinterpretation, I abstained from matching them and summarize Hulke’s descriptions instead.

According to Hulke (1873), the now missing specimen 2a contained two amphicoelous, subhexagonal vertebrae. The better preserved one was 3.98 cm high and wide, and only 0.84 cm long. Two rib articular facets were present. The diapophysis was apparently fused with the neural arch facet. The parapophysis was located about 5 mm more ventrally and is close to the anterior margin of the centrum. Hulke (1873) identified these specimens as thoracic vertebral centra. The specimen also contained a flat, four-sided limb ossicle.

Specimens 2b and 2c were described together by Hulke (1873). Specimen 2b was identified as NRM R 32 (Fig. 1A). The height of this damaged caudal vertebral centrum is 3.5 cm. The anteroposterior length is 0.9 cm, resulting in a ratio of centrum height to length of 3.9. The centrum is laterally compressed. The dimensions of NRM R 32 vary from those

given by Hulke (1873:6) for the better-preserved specimen (probably specimen 2c). The height of this centrum was 3.1 cm and the width was 1.45 cm.

According to Hulke (1873), specimen 2d showed a series of caudal vertebrae. The centra again had a vertical diameter greater than the horizontal one. Using his measurements, the ratio of centrum height to length can be given as less than 3.33. They had only one rib articular facet. Associated with the vertebrae are polygonal limb ossicles.

Specimen 2e was identified as NRM R 29 and has the best preservation of the syntype series. The specimen consists of three articulated caudal vertebral centra. They are higher than long (ratio 3.0 to 3.6) and strongly compressed laterally. The lateral outline is slightly sigmoidal, with thickened anterior and posterior margins (Fig. 1B). A single rib articular facet is present on the ventral margin of centra 2 and 3. The facets are preserved only on one side of the centra; this side is tentatively referred to as the right lateral side. Specimens 5 (NRM R 10) and 6 (NRM R 8), sensu stricto not part of the syntype series, are extremely poorly preserved, and consequently not described further herein.

DISCUSSION

Does the Syntype Series Comprise Diagnostic Material?

It is obvious what Hulke (1873) considered diagnostic of ‘*Ichthyosaurus nordenskiöldii*. He noted that shape and proportion of the vertebral centra differed from all previously known ichthyopterygians (Hulke, 1873:6), referring to the lateral compression of caudal vertebral centra and their high ratio of dorsoventral height to anteroposterior length. This ratio ranges from 3.0–3.9 in the syntype specimens (Fig. 2). All mixosaurid species have an increase in mid-caudal vertebral centra height. This feature has been described as a synapomorphy of Mixosauridae (Motani, 1999). The degree of increase in height varies considerably among mixosaurids (Schmitz et al., 2004; Fig. 2). The ratio of height to length of vertebral centra ranges from about 2 in *Mixosaurus cornalianus* to up to 5 in *M. cf. M. callawayi*. The ratios observed in the syntype material plot well within the middle range of mixosaurids (Fig. 2). The vertebra could belong to different mixosaurid species, except perhaps *M. cornalianus*.

The lateral compression of posterior vertebral centra is observable in all mixosaurids and other Triassic ichthyopterygians, such as *Cymbospondylus* (e.g., Merriam, 1908), *Grippia* (PMU R 448, personal observation), or ‘*Pessosaurus*’ (e.g., Wiman, 1910). Mixosaurids are unique in the extent of the lateral compression which begins already in the pelvic area and reaches its maximum in the middle to posterior caudals. Schmitz et al. (2004) considered the lateral ‘flattening’ a synapomorphy of Mixosauridae. Thus, both of the characters Hulke (1873) considered diagnostic are actually synapomorphies of Mixosauridae. The two specimens of the syntype series still present in NRM are clearly undiagnostic. Three syntypes are missing. According to the descriptions of Hulke (1873) and personal observation of the two possible syntypes (compare above), they are undiagnostic.

Specimen 2a (now missing) was excluded from the analysis because its assignment to Mixosauridae is uncertain. Double rib articular facets are restricted to the cervical and pelvic region in mixosaurids (Brinkmann, 1997; Sander, 2000; Schmitz et al., 2004). For this reason, they could not have a thoracic position in the vertebral series, as Hulke (1873:5) had suggested. Because of their large horizontal diameter they are unlikely to be vertebrae of the pelvic region. Indicative of the cervical region is the fusion of the diapophysis with the neural arch facet. In this case, their

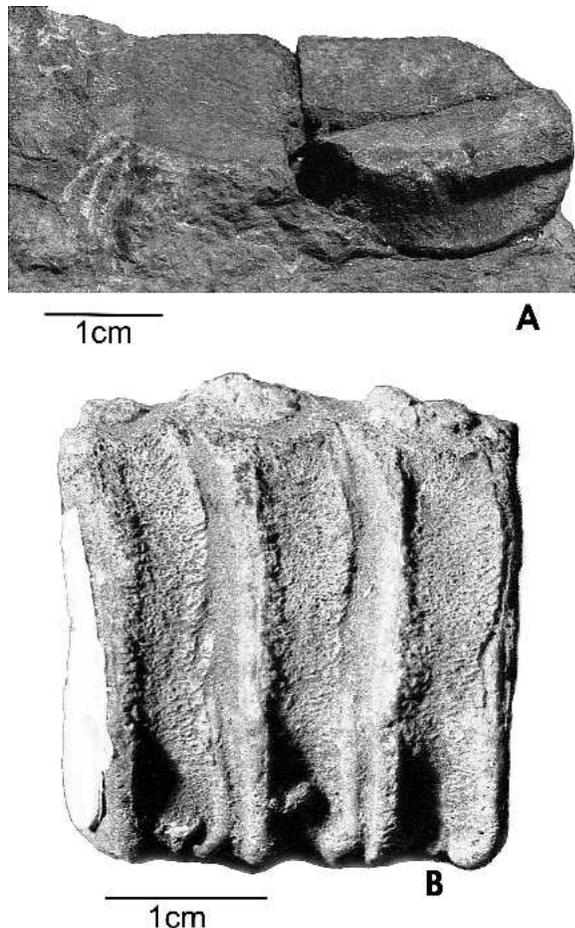


FIGURE 1. **A**, NRM R 32 (specimen 2b of Hulke (1873)), a damaged caudal vertebral centrum. The centrum is higher than long and laterally compressed. **B**, NRM R 29 (specimen 2e of Hulke (1873)), the best-preserved syntype specimen of *Mixosaurus nordenskiöldii* nomen dubium. Visible are three caudal vertebral centra in tentatively identified right lateral view. NRM R 32 and NRM R 29 are the only syntype specimens that could be identified. Three syntype specimens are missing.

absolute size and disc-shape is extremely unusual for mixosaurids. The biggest mixosaurid vertebral centra observed so far are 3.19 cm (BMNH R 5701, measurement courtesy of Ryosuke Motani) and 3.5 cm (UCMP 10624); they both belong to mid-dorsal vertebrae which are usually the tallest. It is most likely that this specimen does not belong to the Mixosauridae.

Previous Designation of the Lectotype

In the past few years, two attempts were made to validate *Mixosaurus nordenskiöldii* (Nicholls et al., 1999; Schmitz et al., 2004). Nicholls et al. (1999:6) designated specimen NRM R 33a, b as the “holotype”. However, this procedure is invalid. A holotype can only be designated in the original description (ICZN, article 73). The specimen probably was among material collected by Prof. Nordenskiöld, but it had not been described by Hulke (1873).

Schmitz et al. (2004) designated specimen NRM R 4 as the lectotype of *M. nordenskiöldii*. This specimen has mesiodistally elongated maxillary teeth, a feature commonly recognized as an autapomorphy of this species. Hulke (1873, specimen labeled 122 and 123; figure in Wiman, 1910:pl. V, fig. 8) obviously had considerable doubt to assign this fragmentary cranium to his new species “*Ichthyosaurus*” *nordenskiöldii*. The only connection between NRM R 4 and *M. nordenskiöldii* was given in the secondary header: “A small snout, reptilian?—incertae sedis—(of *I. Nordenskiöldii*?)” (Hulke, 1873:7). Even ichthyosaurian affinities were regarded provisionally by Hulke (1873:9). Ignoring this cau-

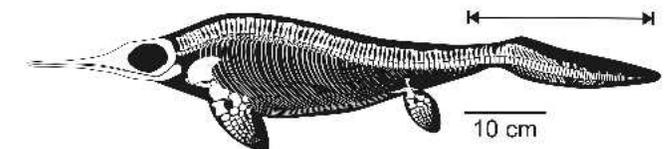
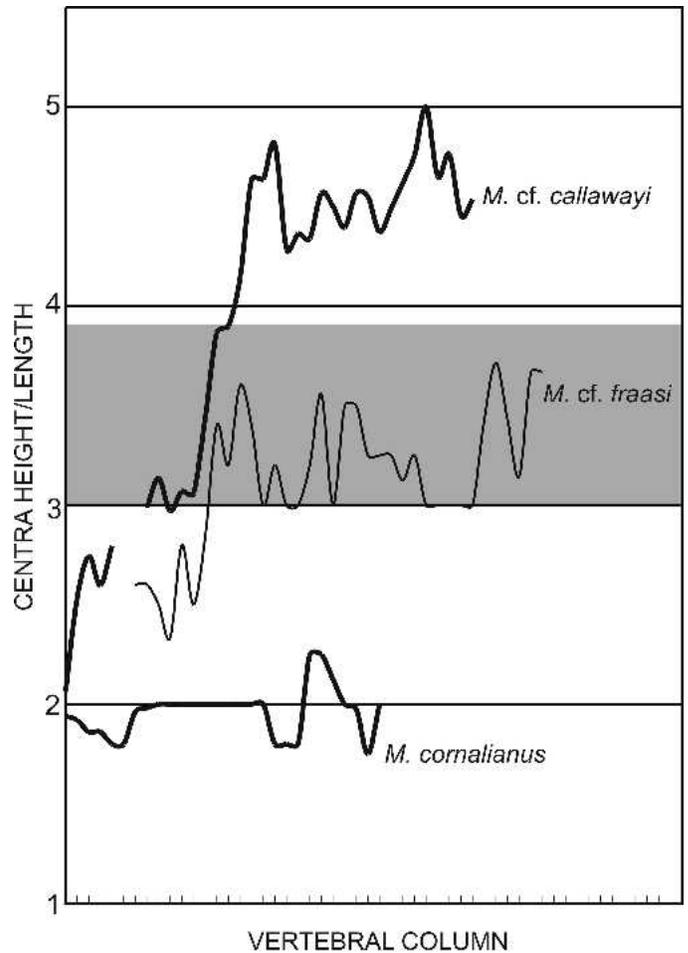


FIGURE 2. Ratio of caudal vertebral centrum dorsoventral height to anteroposterior length in different mixosaurid species. Each line is based on single individuals (*Mixosaurus* cf. *M. callawayi*: PMU R 188; *Mixosaurus* cf. *M. fraasi*: TMP 89.127.14; *Mixosaurus cornalianus*: PIMUZ T 4376). The gray shaded area indicates the range of the syntype series that coincides with different mixosaurid species. The body plan of *Mixosaurus* is taken from McGowan and Motani (2003:fig. 68c).

tious reasoning, Dames (1895) referred NRM R 4 to *M. nordenskiöldii*. Subsequently, all authors followed this view and eventually, Schmitz et al. (2004) designated this specimen as the lectotype. However, this procedure is also invalid. NRM R 4 is not in the syntype series of *M. nordenskiöldii*, because Hulke (1873) doubtfully attributed the specimen to this taxon (compare ICZN, articles 72.4 and 73.2). A lectotype can only be selected from among the syntypes (ICZN, article 74.1); otherwise it loses its status (ICZN, article 74.2).

CONCLUSIONS

The analysis of the syntype material of *Mixosaurus nordenskiöldii* (Hulke, 1873) reveals that this species is based on undiagnostic specimens. The commendable attempts of Nicholls et al. (1999) and Schmitz et al. (2004) to retain this historical species by designating the holotype and lectotype, respectively, are not in accordance with the ICZN. Therefore, *M. nordenskiöldii* is a nomen dubium. Two valid mixosaurid spe-

cies are recognized in the Middle Triassic of Nevada, British Columbia, and Spitzbergen: *Mixosaurus callawayi* Schmitz et al., 2004, and *Mixosaurus fraasi* (Merriam, 1910), hitherto considered a junior synonym of *M. nordenskiöldii* (e.g., Nicholls et al., 1999; Schmitz et al., 2004).

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LITERATURE CITED

- Baur, G. 1887. Über den Ursprung der Extremitäten der Ichthyopterygia. Jahresberichte und Mitteilungen des Oberrheinischen geologischen Vereines 20:17–20.
- Brinkmann, W. 1997. Die Ichthyosaurier (Reptilia) aus der Mitteltrias des Monte San Giorgio (Tessin, Schweiz) und von Besano (Lombardei, Italien)—der aktuelle Forschungsstand. Vierteljahresschrift der Naturforschenden Gesellschaft in Zürich 142:69–78.
- Dames, W. 1895. Über die Ichthyopterygier der Triasformation. Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin 46:1045–1050.
- Hulke, I. W. 1873. Memorandum on some fossil vertebrates collected by Swedish expeditions to Spitzbergen in 1864 and 1868. Bihang till Kungliga Svenska Vetenskaps Akademiens Handlingar, I, Afdelning IV 9:1–11.
- International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. Fourth edition, 306 pp.
- Maisch, M. W., and A. T. Matzke. 2000. The Ichthyosauria. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 298: 1–159.
- McGowan, C., and R. Motani. 2003. Ichthyopterygia; in Handbook of Paleoherpétology, Part 8. Verlag Dr. Friedrich Pfeil, München, 175 pp.
- Merriam, J. C. 1908. Triassic Ichthyosauria, with special reference to the American forms. Memoirs of the University of California 1:1–196.
- Merriam, J. C. 1910. The skull and dentition of a primitive ichthyosaurian from the Middle Triassic. University of California Publications, Bulletin of the Department of Geology 5(24):381–390.
- Motani, R. 1999. Phylogeny of the Ichthyopterygia. Journal of Vertebrate Paleontology 19:474–495.
- Nicholls, E. L., Brinkman, D. B., and J. M. Callaway. 1999. New material of *Phalarodon* (Reptilia: Ichthyosauria) from the Triassic of British Columbia and its bearings on the interrelationships of mixosaurs. Palaeontographica, Abteilung A 252:1–22.
- Sander, P. M. 2000. Ichthyosauria: their diversity, distribution, and phylogeny. Paläontologische Zeitschrift 74:1–35.
- Schmitz, L., Sander, P. M., Storrs, G. W., and O. Rieppel. 2004. New Mixosauridae (Ichthyosauria) from the Middle Triassic of the Augusta Mountains (Nevada, USA) and their implications for mixosaur taxonomy. Palaeontographica, Abteilung A 270:133–162.
- Wiman, C. 1910. Ichthyosaurier aus der Trias Spitzbergens. Bulletin of the Geological Institution of the University of Uppsala 10:124–148.

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