



THE FIRST SPECIMEN OF THE MIDDLE TRIASSIC *PHALARODON ATAVUS* (ICHTHYOSAURIA: MIXOSAURIDAE) FROM SOUTH CHINA, SHOWING POSTCRANIAL ANATOMY AND PERI-TETHYAN DISTRIBUTION

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Abstract: *Phalarodon atavus* from the Germanic Muschelkalk Basin was previously represented only by cranial elements. Here we report a nearly complete and articulated specimen of *P. atavus* from the Middle Triassic Luoping Biota, Yunnan, South China. This is the first specimen of *P. atavus* from outside the Germanic Basin. This discovery demonstrates a peri-Tethyan distribution of *P. atavus*. The new specimen is also the first one preserving the postcranial

anatomy of this species, providing the opportunity to evaluate its sustained swimming ability. Inferences made on its functional morphology suggest that this species was probably adapted for active foraging. Tooth crown morphology suggests that *P. atavus* may have preferred externally soft prey.

Key words: ontogeny, functional morphology, feeding guild, sustained swimming, foraging mode.

ICHTHYOSAURS represent one of the most successful tetrapod groups that re-invaded the ocean, as part of the recovery of life following the devastating end-Permian mass extinction (Massare and Callaway 1990; Chen and Benton 2012). Their phylogenetic position within tetrapods was controversial (Massare and Callaway 1990), but they are now generally accepted as diapsid reptiles according to several independent studies (e.g. Motani *et al.* 1998; Müller 2004; Liu *et al.* 2011a). Ichthyopterygian fossils appear simultaneously in upper Olenekian (Early Triassic) strata of South China, Japan, Spitsbergen, and also probably British Columbia and Thailand where stratigraphic control is not very constrained (McGowan and Motani 2003). After their almost simultaneous appearance in the Early Triassic, ichthyosaurs remained some of the major predators in the Mesozoic oceans until their disappearance in the Cenomanian (Bardet 1992). Most euichthyosaurs (*sensu* Motani 1999a) had evolved a thunniform body shape since probably the Late Triassic,

which is suitable for long-distance pursuit and sustained swimming in the open ocean like their modern analogues such as tunas, whales, and lamnid sharks (Motani 2005). Thus, ichthyosaurs and these modern analogues represent an excellent example of convergent evolution (McGhee 2011).

Mixosaurids were a short-lived but extremely successful group of Middle Triassic ichthyosaurs (McGowan and Motani 2003). They are widely distributed in both Tethyan and Panthalassic deposits, with some specimens showing the earliest evidence of live birth among ichthyosaurs (Brinkmann 1996), indicating excellent adaptation to the aquatic environment as early as the Anisian (Middle Triassic). The mixosaurian body plan is recognized as an evolutionary intermediate between the basal stem plan represented by Early Triassic forms and the parvipelvic plan of largely post-Triassic ichthyosaurs (McGowan and Motani 2003). The monophyly of mixosaurids has rarely been questioned because they share many easily identified

synapomorphies (see Systematic Palaeontology section below; Motani 1999a; Maisch and Matzke 2000a; Sander 2000). The generic composition and taxonomic diversity of mixosaurids, however, have been controversial, largely because several taxa were named early in the history of palaeontology on the basis of very fragmentary type specimens. Currently two genera, including *Mixosaurus* and *Phalarodon*, are recognised within this family (Jiang *et al.* 2006). The genus *Mixosaurus* contains three valid species, namely *M. cornalianus* (Bassani, 1886), *M. kuhnschnyderi* (Brinkmann, 1998), and *M. panxianensis* Jiang *et al.*, 2006. They are all represented by nearly complete specimens. Recently a new species of *Mixosaurus*, *M. xindianensis* Chen and Cheng, 2010, was reported from Xindian, Pu'an County, Guizhou Province, China. The type locality is very close to Yangjuan Village, Panxian County, the source of *M. panxianensis*. The description by Chen and Cheng (2010), however, is insufficient to diagnose the new species, and currently the holotype is not available for examination. Hence this taxon is taken as species inquirendae here.

The second genus, *Phalarodon*, includes *P. atavus* (Quenstedt, 1852), *P. fraasi* Merriam, 1910, and *P. callawayi* (Schmitz *et al.*, 2004). The cranial and postcranial anatomy of *P. fraasi* and *P. callawayi* are relatively well known. Our current knowledge of the morphology of *P. atavus*, however, is limited to the cranial region (Maisch and Matzke 2001).

Phalarodon atavus is the first described and also the oldest known mixosaurid species (McGowan and Motani 2003; Jiang *et al.* 2006). It was believed to be an endemic species (Callaway 1997) because its distribution was restricted to the Germanic Muschelkalk Basin (Maisch and Matzke 2001). The material of this taxon is largely fragmentary and no postcranial material was ever confidently ascribed to this taxon due to the absence of articulated material (Maisch and Matzke 2001). This has prevented the use of postcranial characters in phylogenetic analysis, and consequently led to some controversy about the phylogeny of mixosaurids. Further, the lack of the postcranial skeleton left the question open of whether this earliest mixosaurid species had already acquired the typical body plan of later relatives. After more than 150 years of systematic collection of fossils from marine Lagerstätten of Central Europe and recent intense excavation of marine fossils from the Triassic of South China, there is still no indication of the existence of this species outside the Germanic Basin. This, combined with the existence of possible limitations to sustained swimming abilities and the presence of geographic barriers, could easily result in the conclusion that *Phalarodon atavus* was an endemic Germanic species (e.g. Callaway 1997).

In late 2007, a group of field geologists from the Chengdu Center of China Geological Survey (CCCGS) discov-

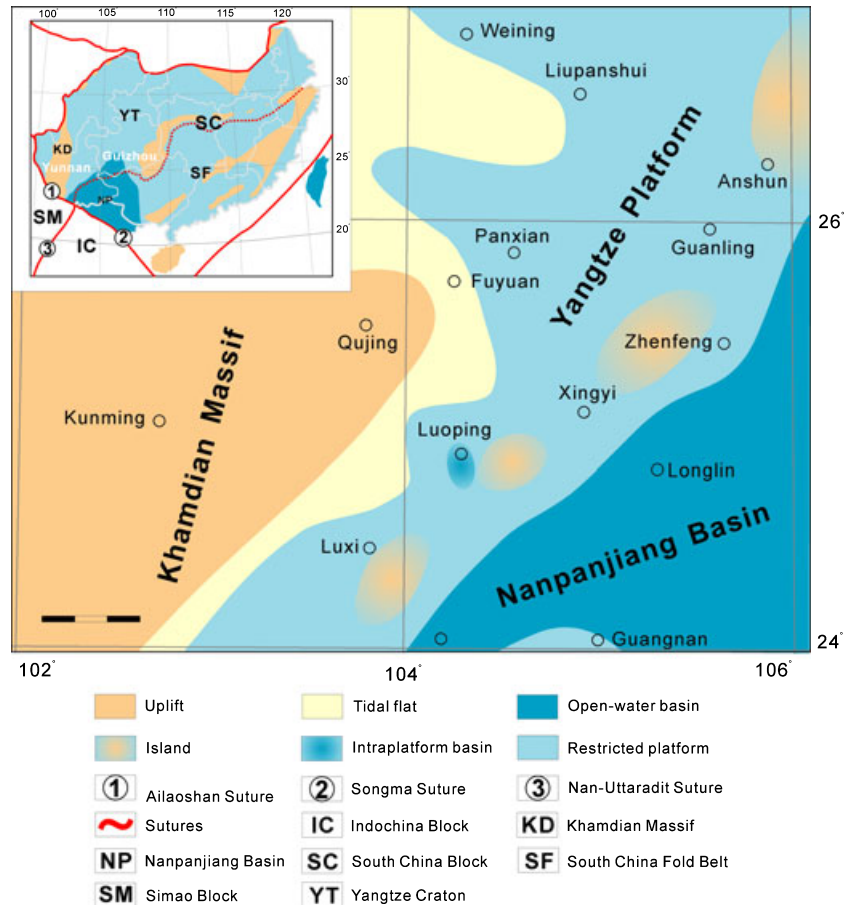
ered a new fossil Lagerstätte during regional geological mapping in Luoping County, Yunnan Province, South China. The following years witnessed the recovery of many articulated specimens of marine reptiles, accompanied by numerous fishes, invertebrates, and also rare terrestrial plants. This new Lagerstätte, the Luoping Biota, marks the full recovery of the oceanic ecosystem from the end-Permian mass extinction (Hu *et al.* 2011; Chen and Benton 2012). Preliminary survey of the marine reptiles from this Lagerstätte supports the full biotic recovery in terms of the biodiversity of top predators (Liu *et al.* 2010a).

To date, a new pachypleurosaur (Liu *et al.* 2011b) and a new marine reptile with uncertain systematic affinities (Li *et al.* 2011) from this biota have been formally described. An occurrence of *Mixosaurus kuhnschnyderi* has also been reported (Chen and Cheng 2009), the affinity of which, however, is doubtful (Liu *et al.* 2010b). This paper reports another mixosaurid ichthyosaur from the Luoping Biota, represented by an articulated and nearly complete specimen. This specimen is referred to *Phalarodon atavus* on the basis of exhibiting the diagnostic characters of this species. It is the only articulated specimen of *P. atavus* with a largely complete postcranial skeleton and also the first occurrence of this species outside the Germanic Basin. The Chinese specimen provides invaluable new information about *P. atavus* that is not available from the Germanic specimens. We present the postcranial anatomy of *Phalarodon atavus* for the first time and infer aspects of its ecology, with the aim of facilitating future reconstruction of the community structure of the Luoping Biota.

GEOLOGICAL SETTING

The South China Block is composed of the Yangtze Craton and the South China Fold Belt (Fig. 1). Although it was proposed that the South China Fold Belt is a separate terrane that collided with the Yangtze Craton during the Late Triassic (Hsü *et al.* 1988, 1990), available palaeomagnetic and sedimentary evidence suggests that the South China Block had been a united plate since the Late Proterozoic or Early Palaeozoic (Lehrmann *et al.* 2005; Shen *et al.* 2006). From the Late Proterozoic to the end of the Middle Triassic, the Yangtze Craton of South China was a stable continent characterised by shallow-water carbonate deposition (Liu and Xu 1994; Ma *et al.* 2009). The Nanpanjiang Basin, with some smaller isolated platforms such as the Great Bank of Guizhou and Chongzuo-Pingguo Platform that developed during the Triassic (Lehrmann *et al.* 1998, 2007), was located at the southwestern margin of the Yangtze Craton and bordered by the Indochina and Simao blocks. The Khamdian

FIG. 1. Palaeogeographic map showing the location of the Luoping Biota (after Feng *et al.* 1994; Sun *et al.* 2009). Inset is a tectonic map illustrating blocks and sutures of South China and adjacent area (After Metcalfe 2006; Lehrmann *et al.* 2009; Ma *et al.* 2009). Scale bar represents 60 km.



Uplift, also located at the southwestern margin of the Yangtze Craton, had been a stable massif since the late Proterozoic (Liu and Xu 1994; Ma *et al.* 2009).

The Ailaoshan and Songma suture zones separate the South China Block from the Simao Block in the southwest and Indochina Block in the south. These zones represent former oceanic basins that were probably closed during the Triassic Indosinian orogeny (Lepvrier and Maluski 2008), which caused the formation of a series of intraplateau basins in the southwestern part of the Yangtze Platform between the Khamdian Uplift and the Nanpanjiang Basin (Fig. 1). These intraplateau basins provided a suitable environment for the preservation of fossil Lagerstätten including the Luoping (Hu *et al.* 2011), Panxian (Motani *et al.* 2008; Jiang *et al.* 2009), Xingyi and Guanling biotas (Wang *et al.* 2008).

The Luoping Biota may be attributed to the middle part of the upper Member of the Anisian Guanling Formation in Yunnan Province (Fig. 2). Biostratigraphical study of conodonts has suggested a Pelsonian age for this biota (Zhang *et al.* 2009; Huang *et al.* 2009), which is coeval with the Panxian fauna that was also discovered from the upper Member of the Guanling Formation (Sun *et al.* 2006; Motani *et al.* 2008; Jiang *et al.* 2009). The Anisian Guan-

ling Formation is widely distributed in northwestern and central Guizhou and southeastern Yunnan, representing the platform interior of the Yangtze Craton between the Nanpanjiang Basin and the Khamdian Uplift (Feng *et al.* 1994; Enos *et al.* 2006). It comprises mainly mudrock, argillaceous limestone, and dolostone in the lower part, and limestone and dolomitic limestone in the upper part. The Guanling Formation is thus conveniently divided into two members in regional geological mapping activities, although this lithological difference is not distinct in certain areas of central Guizhou (Feng *et al.* 1994; Enos *et al.* 2006). This unit is thought to have been deposited in a subtidal environment with restricted circulation and episodic elevated salinity (Enos *et al.* 2006). The base of the Guanling Formation is marked with bentonites ('green-bean rock' in Chinese literature). These alternating volcanic ash beds are widespread in southwestern China and roughly equivalent to the Olenekian–Anisian boundary (Lehrmann *et al.* 2006). The upper boundary of the Guanling Formation with the overlying Yangliujing Formation, as defined by the occurrence of coarsely crystalline dolostone and consequently, is diachronous in different sections.

The Luoping Lagerstätte is located in an intraplateau basin of the Yangtze Platform (Fig. 1), of which the

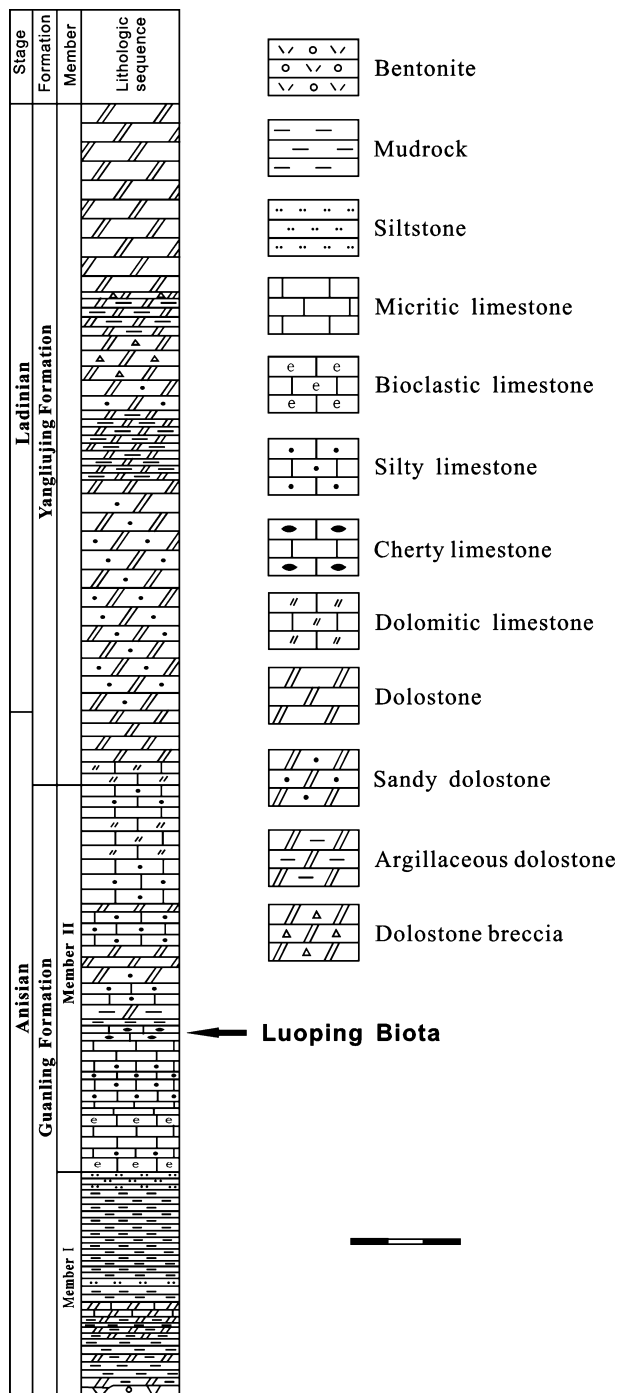


FIG. 2. Sedimentary log showing stratigraphic position of the Luoping Biota (after Zhang *et al.* 2009; Hu *et al.* 2011). Scale bar represents 150 m.

detailed extent is <200 km² (Hu *et al.* 2011). Abundant terrestrial fossils with excellent preservation (Hu *et al.* 2011) support the existence of nearby islands. Fossiliferous layers were most probably deposited in low-energy, dysoxic to anoxic conditions, with episodic oxygenation of bottom waters (Sun *et al.* 2009; Hu *et al.* 2011). The

proliferation of the Luoping Biota probably involved cyanobacterial blooms, which also help to enhance the preservation of organisms by the formation of microbial mats (Hu *et al.* 2011).

Anatomical abbreviations. c, clavicle; co, coracoids; en, external naris; f, frontal; fe, femur; fi, fibula; h, humerus; ic, interclavicle; in, intermedium; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pi, pisiform; pm, premaxilla; po, postorbital; pof, post-frontal; prf, prefrontal; q, quadrate; qj, quadratojugal; r, radius; ra, radiale; rb, rib; sc, scapula; sq, squamosal; st, supratemporal; svp, supratemporal ventral process; u, ulna; ul, ulnare; ut, upper temporal fenestra.

Institutional abbreviations. BMPI, Museum für Naturkunde der Alexander v. Humboldt- Universität, Berlin, Germany; CCCGS, Chengdu Center of China Geological Survey, Chengdu, China; CMC, Cincinnati Museum Center, Cincinnati, USA; GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Tübingen, Germany; MHI, Muschelkalkmuseum Hagdorn, Ingelfingen, Germany; PMU, Paleontological Museum of Uppsala University, Uppsala, Sweden; UCMP, University of California Museum of Paleontology, Berkeley, USA; WCCGS, Wuhan Center of China Geological Survey, Wuhan, China (formerly known as Yichang Institute of Geology and Mineral Resources).

SYSTEMATIC PALAEOLOGY

Order ICHTHYOSAURIA de Blainville, 1835

Family MIXOSAURIDAE Baur, 1887

Type genus. *Mixosaurus* Baur, 1887.

Included genera. *Mixosaurus* Baur, 1887 and *Phalarodon* Merriam, 1910.

Diagnosis. Mixosauridae is differentiated from other ichthyosaurs by possessing the following combination of autapomorphies (modified after Maisch and Matzke 2000a; Sander 2000; McGowan and Motani 2003; Schmitz *et al.* 2004; Jiang *et al.* 2006): premaxilla posteriorly pointed (convergent in *Qianichthyosaurus*); long sagittal crest reaching nasal; large anterior terrace of upper temporal fenestra reaching nasal; pubis much larger than ischium; distinctly high, narrow neural spines extending to the caudal peak; mid-caudal vertebral centra with increased size (absent in some specimens of *Mixosaurus cornalianus*); posterior teeth apparently more robust than anterior ones (convergent in *Chaohusaurus* and *Grippia*, and absent in *Mixosaurus cornalianus* and *Phalarodon atavus*); a pronounced notch present between the deltopectoral crest and the humeral head; distal carpal 1 slightly larger

than other distal carpals; three middle metacarpals flattened, relatively short but still retaining constricted shafts.

Remarks. The generic composition of Mixosauridae has been highly controversial mainly because of the incomplete preservation of material. A traditional view is that *Phalarodon fraasi* is distinct from *Mixosaurus 'nordenskioldi'* in having more robust posterior teeth. Nicholls *et al.* (1999) demonstrated that this difference arises from the separation of upper and lower dentition of a single species and synonymized them. However, based on the new mixosaurid material from the Wapiti Lake area of eastern British Columbia, Canada, Nicholls *et al.* (1999) still insisted that there are two valid mixosaurid genera and listed several characters that differentiate *Phalarodon* from *Mixosaurus*. Motani's (1999b) work showed that one of the important characters, the long sagittal crest in Nicholls *et al.*'s (1999) *Phalarodon* can also be seen in *Mixosaurus*. Because all mixosaurid species can be differentiated from each other only by dental characters, Motani (1999b) suggested that it is more reasonable to consider that all species of Mixosauridae belong to a single genus with different feeding habits pending future cladistic analysis. This opinion was followed by McGowan and Motani (2003) and Schmitz *et al.* (2004). Maisch and Matzke (1998, 2001, 2005) argued there were more than three genera within Mixosauridae based on their own phylogenetic analysis. This opinion was then followed by Maisch (2010). The data matrix, however, has been updated by Jiang *et al.* (2006) based on the discovery of more complete material and new characters. Based on not only cranial characters but also postcranial data, the phylogenetic analysis of Jiang *et al.* (2006) recovered two clades within the family, which was also retrieved by Thorne *et al.* (2011). This view is thus followed here unless falsified by further phylogenetic analysis. Following Jiang *et al.* (2006), we assign all specimens listed by Schmitz *et al.* (2004) as *Mixosaurus 'nordenskioldii'* to *Phalarodon fraasi* (see Schmitz 2005 for discussion).

Genus PHALARODON Merriam, 1910

Type species. *Phalarodon fraasi* Merriam, 1910.

Included species. *Phalarodon atavus* (Quenstedt, 1852), *Phalarodon callawayi* (Schmitz *et al.*, 2004), and *Phalarodon fraasi* Merriam, 1910.

Diagnosis. Nasal region with pronounced narial shelf; dental groove absent in the maxillary region; premaxilla forming anterior half of the ventral border of external naris (unknown in *Phalarodon fraasi*); parietal forming

large part of the sagittal crest; humerus elongated (unknown in *Phalarodon atavus*); metacarpal V with anterior notch primitively (unknown in *Phalarodon callawayi*) (modified after Jiang *et al.* 2006, 2007).

Phalarodon atavus (Quenstedt, 1852)

Lectotype. GPIT/RE/411.

Referred material. LPV 30872 (Figs 3–9). Other specimens of *Phalarodon atavus* mentioned in this paper for comparison include BMPI R 2353 and MHI 1658, which were assigned to *Phalarodon atavus* by Maisch and Matzke (2001).

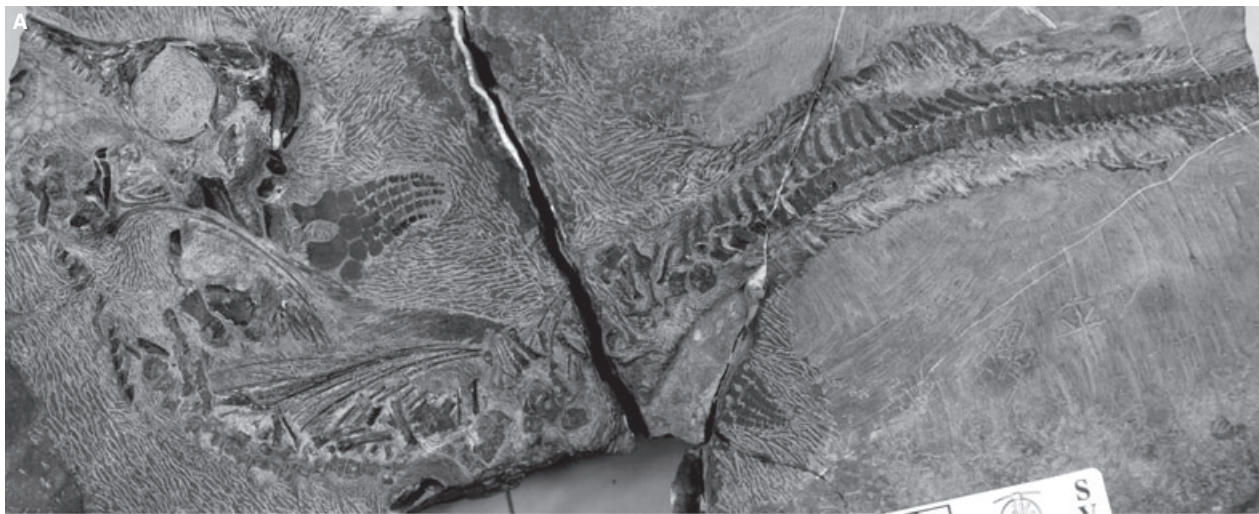
Diagnosis. Deep groove present on the root of most large and fully grown teeth; dental groove absent along the entire tooth-bearing jaw margin; homodont dentition with conical teeth (present also in *Mixosaurus cornalianus*); ventral margin of scapula straight (convergent in *Chaohusaurus*); metacarpal V larger than distal carpal 4 (modified after Maisch and Matzke 2001).

DESCRIPTION AND COMPARISON

The specimen described here was collected by the regional geological mapping team led by Q.Y.Z. in 2008. It is currently catalogued as LPV 30872 by CCCGS. This specimen is almost complete, with a three-dimensionally preserved skull, lacking only the anterior tip of the snout, posterior tip of the tail, and part of the hind limb (Fig. 3). The skull and tail are exposed in the left lateral view. The trunk region is slightly disarticulated and exposed in right lateral view. The specimen is contained in massive dark-grey micritic limestone, lacking the lamination commonly seen in most parts of the Lagerstätte. The following description is focused on the new specimen unless otherwise noted. Measurements of the skeleton and dentition are given in Tables 1 and 2, respectively.

Skull

The skull has been prepared from the left lateral, dorsal, and posterior views (Figs 4–6). The snout is incomplete, lacking the anteriormost tip. The orbit is almost circular and very large. The bones of the lower temporal region are disarticulated and the lower jaw is missing (Figs 3, 4). It is interesting that a similar pattern of preservation is also found in BMPI R 2353, the only specimen of *Phalarodon atavus* from the Germanic Muschelkalk Basin with a relatively complete skull (Maisch and Matzke 2001). This similar pattern may indicate a weak sutural articulation in this region of *P. atavus*. It is apparent that the cheek region is better viewed laterally than posteriorly in both specimens.



B



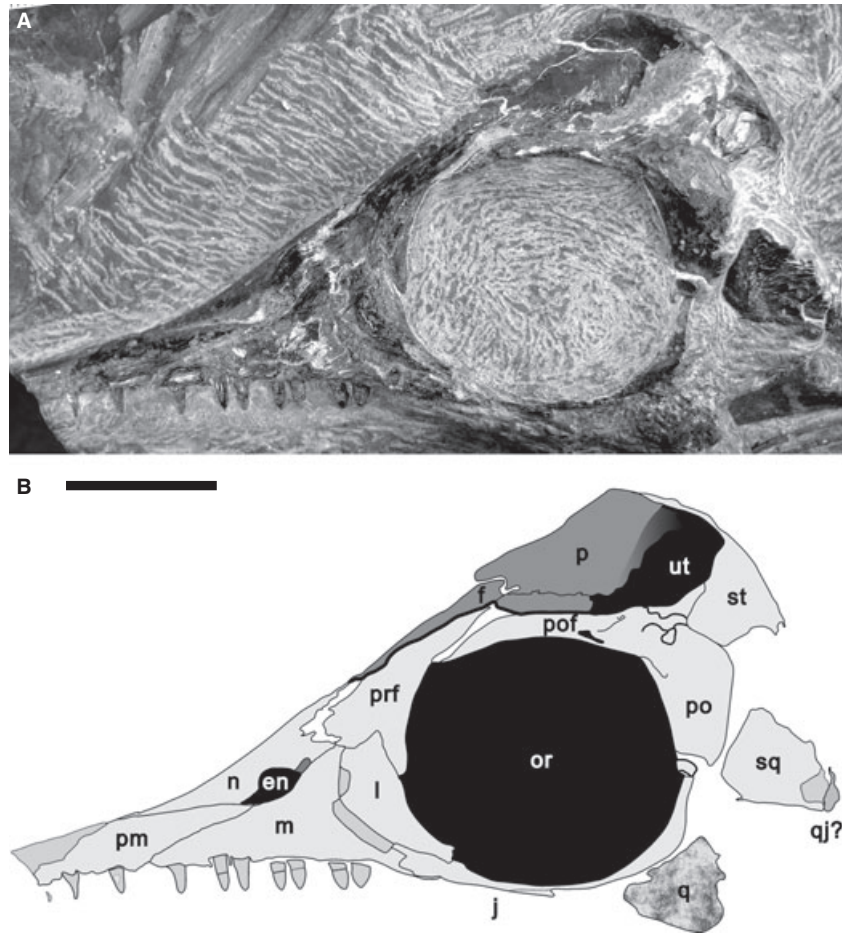
FIG. 3. Skeleton of the referred specimen of *Phalarodon atavus* (LPV 30872). A, photograph. B, interpretive drawing. Numbers denote the preservation sequence of centra. Scale bar represents 10 cm.

Premaxilla. The premaxilla is incompletely preserved with the loss of the anteriormost tip. The preserved anterior half is damaged and exposes the underlying bone. The posterior half is largely preserved. The premaxilla is posteriorly pointed as in other mixosaurids. Its posterior process comprises the anterior half of the ventral margin of the external naris (Fig. 5), as in MHI 1658 (Maisch and Matzke 2001), which is also the situation in *Phalarodon callawayi* (Schmitz *et al.* 2004). The anteroposteriorly oriented surface striations of the premaxilla can be clearly seen on the preserved surface. Posterodorsally, the premaxilla contacts the nasal with a relatively straight suture that is almost anteroposteriorly oriented (Figs 4, 5). The premaxilla-maxilla suture extends posterodorsally from the ventral margin of the upper jaw to the ventral margin of the external naris.

Maxilla. The large maxilla is nearly triangular in lateral view (Fig. 4), with surface striations largely anteroposteriorly

oriented. The maxilla forms the posterior half of the ventral border of the external naris (Fig. 5). Posterior to the external naris the maxilla sends a postnarial process that prevents the lacrimal from extending to the external naris. Additionally, the postnarial process of the maxilla forms a shallow groove with the nasal dorsally and slightly overlaps the prefrontal. The posterior margin of the maxilla contacts the lacrimal in the same fashion as seen in MHI 1658 – the maxilla underlies the lacrimal in the dorsal half of the suture but overlaps the lacrimal in the ventral half of the suture (Maisch and Matzke 2001). Posteroventrally, the maxilla embraces the jugal laterally and ventrally. In lateral view, the maxilla extends posteriorly just at the level of the anterior margin of the orbit, but it may extend well behind the orbit ventrally if fully exposed. The level of posterior extension of maxilla in lateral view is in accordance with other mixosaurids except for *Phalarodon callawayi* where the maxilla extends well behind the anterior margin of the orbit (Schmitz *et al.* 2004).

FIG. 4. Skull of the referred specimen of *Phalarodon atavus* (LPV 30872) in left lateral view. A, photograph. B, interpretive drawing. Scale bar represents 2 cm.



External naris. The external naris is largely exposed in lateral aspect. Ventrally the maxilla forms an apparent narial shelf as in other specimens of *Phalarodon* where this area is preserved.

Nasal. The surface striations of the nasal are antero-posteriorly oriented. The nasal forms the dorsal margin of the external naris. Posterolaterally the nasal overlaps the prefrontal. To avoid

damage, the dorsal surface of the posterior part of the nasal was not completely prepared. It is clear, however, that the nasal forms a gentle border to the anterior terrace of the upper temporal fenestra (Fig. 5). Posteriorly the nasal is widely separated from the parietal and the postfrontal by the precluding prefrontal and frontal. The nasal also contributes to the sagittal crest, but this portion is relatively low compared to the contributions of the frontal and parietal.

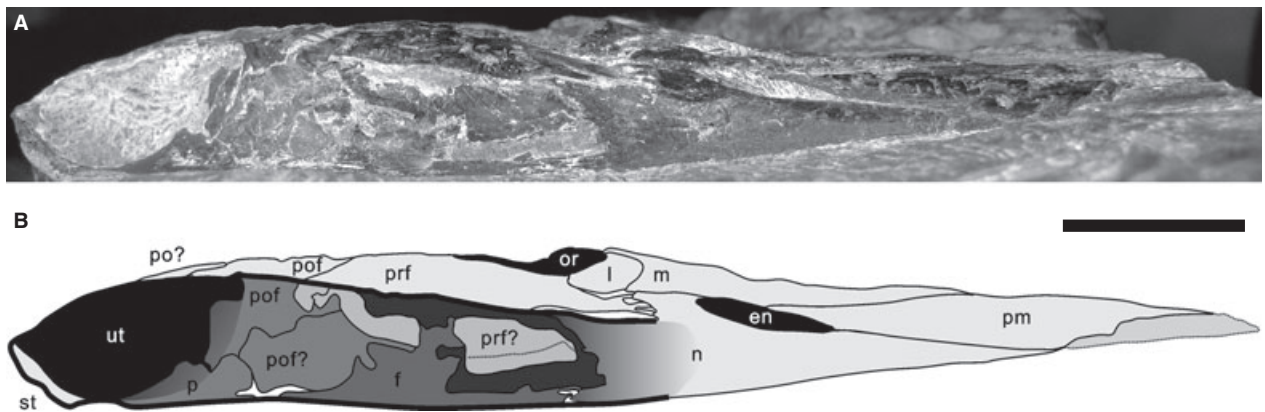


FIG. 5. Skull of the referred specimen of *Phalarodon atavus* (LPV 30872) in dorsal view. A, photograph. B, interpretive drawing. Scale bar represents 2 cm.

Lacrima. The lacrimal comprises the anteroventral corner of the orbit and forms a lateral crest anterior to the orbit (antorbital ridge of Schmitz *et al.* 2004). This antorbital ridge is almost continuous with the orbital ridge (defined by Schmitz *et al.* 2004) formed by the prefrontal and the postfrontal. The surface striations of the lacrimal are very complex. Dorsally the lacrimal overlaps the prefrontal. Posteroventrally it is covered by the jugal in lateral view.

Jugal. The jugal forms the entire ventral margin of the large orbit. Anteriorly, the jugal is embraced by the maxilla ventrolaterally and the lacrimal dorsomedially. The posterior margin of the jugal is smooth, with the posterodorsal tip covered by an isolated bone fragment (Fig. 4).

Prefrontal. The prefrontal forms the anterodorsal margin of the round orbit. The surface striations are very complex. In lateral view, the prefrontal forms a continuous ridge with the lacrimal and postfrontal along the anterodorsal margin of the orbit. Posteriorly the prefrontal contacts the postfrontal with a deep groove that extends posterodorsally. In dorsal view (Fig. 5), the prefrontal forms the majority of the lateral border of the anterior terrace of the upper temporal fenestra. Incomplete preparation and damage prevents the exact range of the prefrontal to be established in dorsal view. However, the prefrontal does extend medially to underlie the anterior terrace.

Postfrontal. In lateral view, the postfrontal forms the dorsal margin of the orbit. The relationship with the postorbital and the supratemporal is confounded due to severe postmortem damage in the upper temporal region. In dorsal view (Fig. 5), the postfrontal contributes to the lateral border of the upper temporal fenestra.

Frontal and parietal. The frontal and parietal comprise the majority of the sagittal crest. As in BMPI R 2353, the parietal forms a prominent part of the sagittal crest in lateral view. This is quite different from *Mixosaurus*, where the crest is mainly formed by the frontal (Maisch and Matzke 1998; Jiang *et al.* 2006). The surface of the sagittal crest is quite smooth. The height of the sagittal crest increases posteriorly, but is much lower than in some Germanic specimens of *Phalarodon atavus* (Maisch and Matzke 2001). Following Maisch and Matzke (2000b), this probably indicates a young ontogenetic stage for the new specimen (the ontogenetic stage of LPV 30872 will be discussed in detail below). In dorsal view the skull is roughened with many cracks, making the interpretation of sutures difficult. The frontal is probably excluded from the anterior margin of the upper temporal fenestra by the parietal and the postfrontal. It seems that the frontal underlies all other bones of the skull roof. The presence of a parietal ridge and the shape of the supratemporal cannot be determined because further preparation in this region will most probably destroy the bone.

Postorbital. The postorbital forms the posterior margin of the orbit. Surface striations are oriented posteroventrally. Dorsally,

the postorbital is overlapped by the large supratemporal. Damage to the surface of the upper temporal region prevents the dorsal extent of the postorbital to be determined. However, the postorbital likely contributed to the margin of the upper temporal fenestra (Fig. 5), as suggested for BMPI R 2353 (Maisch and Matzke 2001). The ventralmost tip of the postorbital was not prepared due to the presence of an isolated bone fragment preserved superficially (see Fig. 4).

Supratemporal. The large supratemporal forms the complete posterior margin of the upper temporal fenestra. The surface striations extend radially from the posteroventral point of the element. Both supratemporals are visible in posterior view (Fig. 6A, B) and a posterior slope and ventral process can be confirmed for the specimen. The ventral process has the same shape as in BMPI R 2353. The posterior ridge is present at the posterior end of the supratemporal. Dorsomedially, the supratemporal overlaps the parietal.

Quadrate, quadratojugal, and squamosal. As in BMPI R 2353 (Maisch and Matzke 2001), the squamosal, the quadratojugal, and the quadrate are all dislocated. The quadrate has shifted anteriorly and bears a roughened surface. As in MHI 1658 (Maisch and Matzke 2001), the quadrate is a large element with a thick articular condyle. The squamosal has been rotated by about 180 degrees, but cannot be completely prepared without damaging the postorbital. As in other specimens of *Phalarodon atavus*, the squamosal is fan-shaped with surface striations that extend radially. The bone located posteroventral and medial to the squamosal presumably represents the exposed part of the quadratojugal.

Dentition

Premaxillary dentition. The absence of the anteriormost tip of the premaxilla means the exact number of premaxillary teeth cannot be discerned. Three teeth are preserved on the premaxilla. The first tooth only preserves the impression of a partial crown with evident surface striations. The second tooth was cut in sagittal section prior to the collection. The surface of the third tooth is broken, exposing either a replacement tooth or a cast of the pulp cavity (Fig. 6C). The root is smooth and no surface ornamentation can be seen. As in Germanic specimens, a deep groove appears on the root, an important autapomorphy of *Phalarodon atavus* (Maisch and Matzke 2001). The associated socket for the third tooth is obvious and bony septa are also clearly visible. There is no indication of the presence of a premaxillary dental groove.

Maxillary dentition. Seven teeth are preserved on the maxilla, but there may have been as many as 10 based on the spaces between teeth. This tooth count is also in accordance with Germanic specimens (Maisch and Matzke 2001). The dental groove is also absent in the maxillary region. The surface of the first tooth is largely broken but the root shows an apparent infolding. The second maxillary tooth is the only completely preserved tooth (Fig. 6D). The deep infolding is clearly visible on the root.

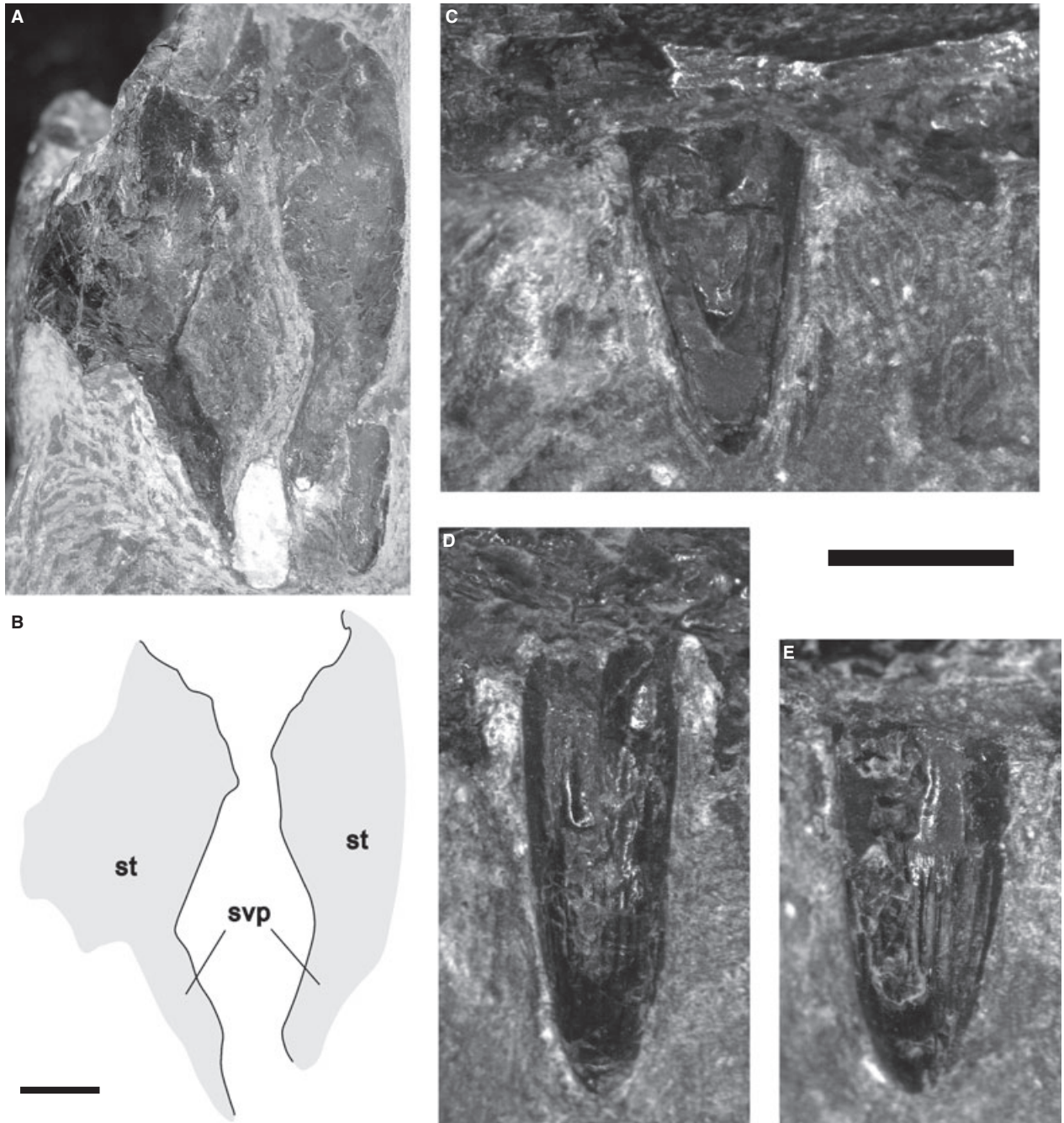


FIG. 6. Cranial skeleton of the referred specimen of *Phalarodon atavus* (LPV 30872). A, photograph of the skull in posterior view. B, interpretive drawing. C, the last premaxillary tooth showing the exposed replacement tooth or the cast of the pulp cavity. D, the second maxillary tooth showing the apparent root folding. E, the fourth maxillary tooth showing the weak constriction between the smooth root and the striated crown. Scale bar for A and B represents 5 mm. Scale bar for C, D and E represents 2 mm.

Surface striations are clear on the crown surface and disappear on the root. Bony dissepiments are also clearly visible around this tooth. The surface of the third tooth is completely damaged, preventing detailed observation. The fourth maxillary tooth is largely complete and bears a smooth root and striated crown. The division between the crown and the root is very clear, but

the root infolding seems to be absent (Fig. 6E). The fifth tooth is largely broken. Crown surface striations can be clearly seen in the last two teeth but both roots are broken. The crown shape index (sensu Massare 1987) decreases gradually toward the posterior dentition (Table 2), but the last maxillary tooth still has a pointed apex.

Axial skeleton

Centra. There are in total 73 centra exposed in LPV 30872. Thirty centra are preserved on the first block, which most probably belong to the trunk region based on their position, numbered according to preservation sequence (Fig. 3). Judging from the number and location of the preserved ribs anterior to the first centrum, the total number of presacral centra should approach the typical mixosaurian plan. The first centrum is almost completely exposed in posterior view, with an apparent ventral keel. The centrum has a largely elliptical shape excluding the ventral keel. Centra 2–19 are largely articulated and partly exposed in ventral view, with a ventral keel seen in some centra. Exposed centra 20–28 are disarticulated and also exposed in ventral view. The ventral keel can be seen in some centra. Centra 29 and 30 are disarticulated and exposed in anteroposterior view. Compared with centrum 1, centra 29 and 30 are more rounded (excluding their distinct ventral keels). Forty-three centra are preserved on the second block. Centra 31–33 are disarticulated and most likely belong to the tail region. Centra 31 and 32 are exposed in ventral view, while centrum 33 is exposed in posterior view. Centra 34–37 are slightly disarticulated and posterolaterally exposed. Compared with the centra in the first block, the ventral keel is a less distinct structure in these centra. Centra 38–73 are tightly connected and exposed in lateral view. The caudal peak is well represented in the tail region (Fig. 7). Centrum height increases posterior to the caudal peak (Fig. 7), representing another autapomorphy of Mixosauridae. When visible, all centra are distinctly discoidal and amphicoelous. Compared with *Phalarodon callawayi*, the height/length ratio of caudal centra in LPV 30872 is not distinctly high. In *Phalarodon callawayi*, the largest height/length ratio reaches five (Schmitz *et al.* 2004), while in LPV 30872 the largest value is approximately two.

Neural spines. The neural spines are generally high and straight. These high spines extend to the apical region of the tail and then the height decreases gradually (Fig. 7), another autapomorphy of Mixosauridae. The presacral neural spines are all disarticulated, whereas the spines of caudal vertebrae near the caudal peak remain articulated with their corresponding centra. It is apparent that spines incline anteriorly in the postflexural region.

Ribs and haemapophyses. All ribs are disarticulated from their respective centra. Grooves are observed on the lateral surfaces of the ribs. Distally, however, the ribs are flattened and broad. Gastralria are preserved along the entire trunk region. Haemapophyses are present beginning from centrum 33.

Pectoral girdle and forelimb

The right half of the pectoral girdle and forelimb are exposed in dorsal view (Fig 8A, B). The pectoral girdle elements are largely dislocated, but the right forelimb is still articulated except for the humerus, which is slightly rotated clockwise. The autopodial elements are completely exposed. They are all flattened and tightly packed, both interdigitally and interphalangeally. The

right humerus and right coracoid are still partly covered by other bones. The interclavicles and clavicles cannot be confidently identified. The following description is based on the right elements unless noted.

Pectoral girdle. The scapula retains the typical shape of basal and mixosaurian taxa, with a proximal stem and a distal fan-shaped expansion (McGowan and Motani 2003). The anteroventral margin of the scapula was slightly damaged during preparation. The shape of the scapula, however, looks more like *Chaohusaurus* (reconstructed by McGowan and Motani 2003) than other mixosaurids, with a straight ventral margin (Fig. 8A, B). The right coracoid is largely covered by other bone elements. The exposed part of the coracoid, however, presents no difference from other mixosaurids (McGowan and Motani 2003).

Humerus. The right humerus is partly exposed with its proximal end obscured by the coracoid (Fig. 8A, B). However, the exposed surface is relatively smooth and an anterior flange is well-developed. The anterior margin of the flange is almost smooth, but a weak anteroproximal notch can be observed, as in other mixosaurids (McGowan and Motani 2003). Distally, three facets are developed. The postaxial facet is not completely exposed. The radial facet is much wider than the ulnar facet. The left humerus is also partly exposed in ventral view (Fig. 8C). Its distal part is covered by the clavicle and the interclavicle that are not completely exposed (Fig. 8D). Compared with the dorsal surface, the ventral surface of the humerus is more roughened, a phenomenon generally observed in mixosaurid ichthyosaurs (*pers. obs.*). The proximal end of the left humerus is much narrower than the distal end of the right humerus. The deltopectoral crest on the left humerus is well developed, forming a pronounced notch with the humeral head, another autapomorphy of Mixosauridae. It seems that the deltopectoral ridge is less pronounced in LPV 30872 than in *Mixosaurus panxianensis* and *Mixosaurus natans* (UCMP 9873, *nomen dubium*, see Motani 1999c).

Radius. The radius is slightly thickened compared to the ulna and autopodium. It bears an almost straight humeral articular facet. Both the leading and the trailing edges of the shaft are smoothly concave, which is also observed in *Mixosaurus cornalianus* (Maisch and Matzke 1998; Motani 1999c) and *Phalarodon fraasi* (PMU R 186, see Motani 1999c; CMC VP 7276, see Schmitz *et al.* 2004). The radii of *Mixosaurus panxianensis* (Jiang *et al.* 2006; Liu *et al.* 2010a, b) and *Phalarodon callawayi* (PMU R 191, see Motani 1999c) are different in their morphology, in that two notches are present on the leading edge of the shaft. Distally, the radius bears a slightly concave facet for articulation with the radiale. At the posterodistal margin of the radius, a short straight facet for the intermedium is seen. The surface striations extend along the long axis of the shaft and parallel with the anterior and posterior margins.

Ulna. The ulna is much more flattened than the radius. It is lunate in outline with proximal and distal ends of subequal width. The posterior margin is smoothly convex, as in *Mixosaurus cornalianus* (Maisch and Matzke 1998; Motani 1999c), *M. panxianensis* (Jiang *et al.* 2006), and *Phalarodon fraasi* (PMU R 186, see Motani 1999c). The ulnar shape of *P. callawayi* is dif-

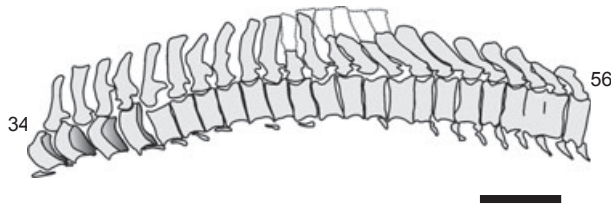


FIG. 7. Drawing of the caudal region of the vertebral column showing the caudal peak and the high centrum height/length ratio. Numbers denote the preservation sequence of centra. Scale bar represents 2 cm.

ferent from other mixosaurid species in the presence of a notch on the posterior margin (PMU R 191, see Motani 1999c; Schmitz *et al.* 2004), which was also reported to occur in *M. 'xindianensis'* (Chen and Cheng 2010). The distal end of the ulna bears three articular facets. The anterior and the middle facet are straight and subequal in length, and correspond to the intermedium and the ulnare, respectively. The more posterior pisiform facet is slightly convex. The anterior margin of the ulna is smoothly concave, forming a well-developed spatium interosseum with the radius (Fig. 8A, B). The surface striations extend radially from the middle point of the anterior margin.

Proximal carpals. Four proximal carpals, including the radiale, intermedium, ulnare, and pisiform, are preserved. The intermedium is slightly larger than the other three elements which are subequal in size. All of them develop weak striations that extend radially from the middle point of the bones. The proximal margin of the radiale is slightly convex, corresponding to the concave margin of the radius. The anterior and posterior margins of the radiale are relatively straight and parallel to each other. Distally, two straight facets are developed for articulation with distal

carpals 1 and 2. The intermedium retains a roughly hexagonal shape. It is as wide as long and separates the radius widely from the ulna, a morphology previously thought to be limited to *Mixosaurus* (Jiang *et al.* 2006). A notch is present proximally; this feature is polymorphic in *Phalarodon fraasi* (compare PMU R 186 with CMC VP 7276, see Motani 1999c and Schmitz *et al.* 2004) and *Mixosaurus cornalianus* (Motani 1999c), but consistently present in *M. panxianensis* (Jiang *et al.* 2005, 2006) and *P. callawayi* (PMU R 191, see Motani 1999c). The other sides are more or less straight and contact radius, radiale, distal carpals 2–4, ulnare, and ulna. The ulnare is subcircular in outline. The articular facets for the ulna, intermedium, distal carpal 4 and metacarpal V are relatively straight while the one contacting the pisiform is convex. The pisiform has a subcircular shape. No other postaxial element is present except for the pisiform, which is subcircular in outline. However, a neomorph distal to the pisiform is present in the holotype of *M. panxianensis*, some specimens of *M. cornalianus*, and *P. fraasi* (Motani 1999c). This character is unknown in *M. kuhnschnyderi* (Brinkmann 2004) and *P. callawayi* (Schmitz *et al.* 2004).

Distal carpals. Four distal carpals are present. Distal carpal 1 is slightly larger than the other three distal carpals, representing an autapomorphy of Mixosauridae that was already noted by Maisch and Matzke (2000a). Distal carpals 1 and 3 have a quadrangular shape and are wider than long. Distal carpals 2 and 4 have a pentagonal shape.

Metacarpals. Metacarpals I–IV are located adjacent to one another in a line. Metacarpal I has a convex anterior margin and a notched posterior margin. This is generally seen in other mixosaurids, except for *Phalarodon fraasi* (PMU R 186, see Motani 1999c) where this notch seems to be absent. Metacarpals II–IV all have a similar shape and size. They are all flattened,

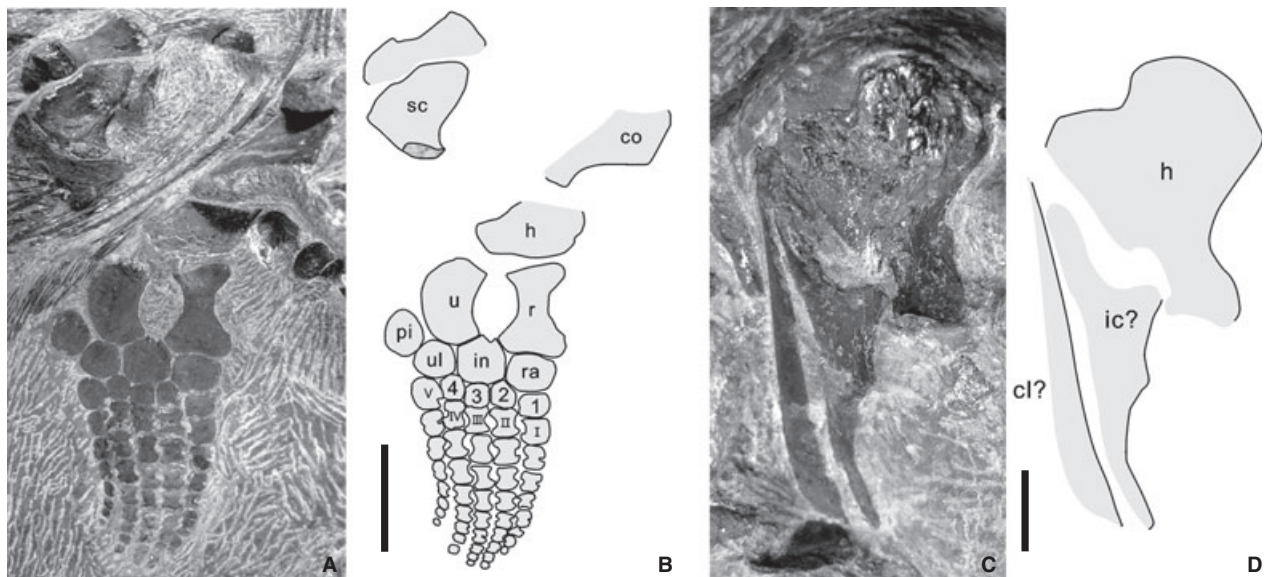


FIG. 8. Pectoral girdles and forelimbs of the referred specimen of *Phalarodon atavus* (LPV 30872). A, photograph of the right half of the pectoral girdle and forelimb in right lateral view. B, interpretive drawing. C, photograph of the left humerus in medial view. D, interpretive drawing. Scale bar for A and B represents 2 cm. Scale bar for C and D represents 5 mm.

relatively short, and retain constricted shafts. This is another autapomorphy of Mixosauridae (Maisch and Matzke 2000a). The anterior and posterior notches of each metacarpal are well developed. Metacarpal V is located more proximally than metacarpals I–IV, larger than the other metacarpals, and is subcircular with a notched anterior margin. This anterior notch is also well-developed in *Phalarodon fraasi* (PMU R 186 and CMC VP 7276, see Motani 1999c and Schmitz *et al.* 2004), but is consistently absent in *Mixosaurus cornalianus* (Motani 1999c) and *M. panxianensis* (Jiang *et al.* 2005, 2006). Metacarpal V is also larger than distal carpal 4, a character primitively present in Lower Triassic ichthyosaurs but absent in other mixosaurids (McGowan and Motani 2003).

Phalanges. The phalangeal formula of LPV 30872 is 7-8-8-7-7. However, this should be taken as the minimum estimate for *Phalarodon atavus* because the distal phalanges in ichthyosaurs are very small elements (McGowan and Motani 2003), and can easily be lost during preparation. The proximal four phalanges of digit 1 bear both anterior and posterior notches. The fifth phalanx is not completely exposed, and the sixth develops a posterior notch but lacks an anterior notch. The distalmost element is round. The first six phalanges of digit 2 exhibit both anterior and posterior notches, whereas the seventh phalanx bears only a posterior notch. The distalmost phalanx is a round element, as in the first digit. The proximal six phalanges of digit 3 develop both anterior and posterior notches. The seventh phalanx develops only an anterior notch, whereas the distalmost phalanx is rounded. The first five phalanges of digit 4 bear anterior and posterior notches, the sixth develops a very weak anterior notch, and the distal phalanx is rounded. The first four phalanges of digit 5 develop both anterior and posterior notches, although the posterior notches are generally weaker than their anterior equivalents. The fifth phalanx is a round element with a very weak anterior notch. The two distalmost phalanges are round in outline without any indication of notching.

Notching along the anterior margin of the most proximal phalanx of digit 1 is present in *Mixosaurus panxianensis* (pers. obs., GMPKU-P-1033). Notching can also be confirmed in *Phalarodon callawayi* (PMU R 191, see Motani 1999c), but intraspecific and ontogenetic variation is unknown because of the lack of additional specimens. Notching is absent in *M. cornalianus* (Motani 1999c) and unknown in *P. fraasi* and *M. kuhnschnyderi*. Notching along the posterior margin of the most proximal phalanx of digit 5 is absent in *M. panxianensis* (pers. obs., GMPKU-P-1008, GMPKU-P-1033, GMPKU-P-1039) and *M. cornalianus* (Motani 1999c). It is unknown in other mixosaurids.

Pelvic girdle and hind limb

No pelvic girdle element can be unequivocally identified due to incomplete preservation or exposure. Of the hind limb, only the right femur, right fibula, and distal part of the left digits can be recognised (Fig. 9), all of which are exposed in dorsal view.

Femur. The left femur is completely exposed. It is distinctly widened and more similar to *Phalarodon fraasi* (Schmitz *et al.* 2004) than other mixosaurids. The proximal end of the femur

is convex, has a roughened surface and is triangular in outline with a notch on its ventral (medial) face. The distal end is widened and bears two articular facets. The anterior facet is significantly longer and quite straight, corresponding to the proximal end of the tibia. The posterior facet is much shorter and slightly concave, corresponding to the convex proximal end of the fibula.

Fibula. The anteroproximal part of the fibula is still covered by the femur. The shaft is well defined. Distally, the fibula bears two facets to articulate with the astragalus and calcaneum.

Phalanges. The phalangeal formula of the hind limb is 6-8-7-6-5. As in the forelimb, this should be taken as a minimum estimate. Metatarsals II–IV are partially preserved, Metatarsals I and V, together with the other tarsal elements, have been lost. The phalanges of digit 1 bear both anterior and posterior notches, except for the distalmost two that are round in shape. The proximal five phalanges of digit 2 bear both anterior and posterior notches. Phalanx six and seven only develop the posterior notch, while the distalmost phalanx is rounded. The first six phalanges of digit 3 show both anterior and posterior notches, whereas phalanx seven is round in outline. The proximal four phalanges of digit 4 retain their shafts and the distalmost two phalanges are rounded. Phalanx one through four of digit 5 are notched along their anterior and posterior margins, but the latter are only weakly developed compared to the former. Phalanx five is a round element.

DISCUSSION

Systematics

LPV 30872 retains nine synapomorphies among 10 listed in the diagnosis of Mixosauridae above. Its assignment to Mixosauridae is thus undoubted. Generic assignment seems also indisputable, as evidenced by the presence of five out of the six diagnostic characters of *Phalarodon* listed above. Even so, we acknowledge the possibility that *Phalarodon* is a paraphyletic group, as already stated by Jiang *et al.* (2006). A further cladistic analysis of mixosaurid ichthyosaurs is required to resolve this issue, but we do not propose a new phylogenetic hypothesis here because of the absence of a detailed description of *Mixosaurus* spp. from the Monte San Giorgio region (Brinkmann 2004) and the existence of new taxa of mixosaurids from the Panxian and Luoping biotas (Liu *et al.* 2010b, 2011a).

LPV 30872 shares a uniquely derived character with other specimens of *Phalarodon atavus* from the Germanic Basin (Maisch and Matzke 2001), i.e. a deep groove on the tooth root. This tooth morphology has never been observed in any other mixosaurid ichthyosaur. Like other specimens of *Phalarodon atavus* (Maisch and Matzke 2001), LPV 30872 also retains another unique trait among mixosaurids, the thecodont implantation along the entire

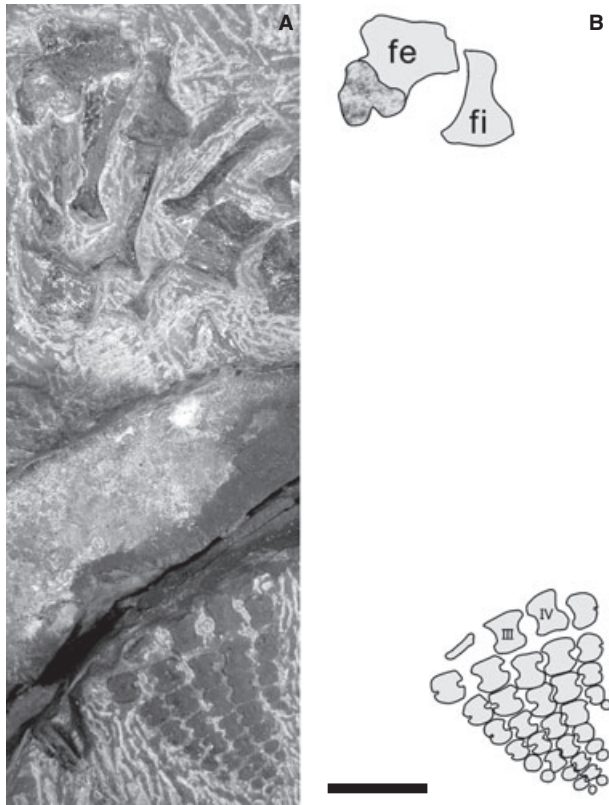


FIG. 9. Hind limb of the referred specimen of *Phalarodon atavus* (LPV 30872) in lateral view. A, photograph. B, interpretive drawing. Scale bar represents 1 cm.

jaw margin. The only difference presented between this new specimen and the classical Germanic specimens is the height of the sagittal crest. As has been already noted by Maisch and Matzke (2000b), however, the sagittal crest of *P. atavus* grows higher during ontogeny. The lower height of the sagittal crest in the new specimen thus corresponds well to its ontogenetic stage, as discussed below. In addition, the size of the sagittal crest in *Mixosaurus panxianensis* is quite variable. The highest sagittal crest is found in the paratype, of which the skull is smaller than the holotype of the same species but larger than the other two referred specimens (Jiang *et al.* 2005, 2006). Therefore, the size of the sagittal crest is not a stable character to differentiate species among mixosaurids. We cannot exclude the possibility that the Germanic specimens represent a different species, but this would require the

discovery of new articulated specimens with postcranial skeletons that differ consistently from the specimen reported here. Without such positive evidence, however, we will conservatively propose this specimen is conspecific with those from the Germanic Basin.

Ontogenetic stage

Johnson (1977) proposed several size-independent criteria for estimation of the relative age of *Stenopterygius*, a Jurassic ichthyosaur. Based on the examination of 26 specimens of *Stenopterygius*, she divided the ontogenetic stages of *Stenopterygius* into early immature, late immature, sexually mature, and osteologically mature stages. Preliminary examination of different sized specimens of mixosaurids catalogued in the GMPKU and CCCGS shows that the three largest humeri (CCCGS LPV-30281, GMPKU-P-1033, and GMPKU uncatalogued) all reach a similar size and have a smooth humeral head, indicating an osteologically mature stage. LPV 30872, however, shows both rugose humeral and femoral heads, suggesting an osteologically immature stage. The new specimen here retains a convex humeral head and a smooth texture on the dorsal surface of its shaft, indicating a subadult stage. This is in accordance with the lower height of the sagittal crest of LPV 30872, as compared to some larger specimens from the Germanic Basin (Maisch and Matzke 2000b, 2001). If dividing the maximum diameter of the orbit by the minimum external naris-orbit distance (Table 1), the value in the new specimen is much larger than in BMPI R 2353, also indicating a younger ontogenetic stage in the new specimen.

Ecological implications

Hu *et al.* (2011) presented a preliminary food web of the Luoping Biota. This reconstruction, however, largely relied on comparative information from other time-equivalent Lagerstätten and modern communities. In order to facilitate the reconstruction of the community structure of the Luoping Biota, we analysed the ecological guild of the new specimen here. In the original definition proposed by Root (1967), a guild was defined as 'a group of species that exploit the same class of environmental

TABLE 1. Measurements of the skeleton of *Phalarodon atavus* (LPV 30872).

Minimum distance between external naris and orbit	Maximum diameter of orbit	Skull length (snout excluded)	Skull width (left half)	Distance between atlas and apex of tailbend	Body depth (sensu Massare 1988)
14 mm	34 mm	50 mm	13.5 mm	c. 300 mm	c. 91 mm

TABLE 2. Measurements of the dentition of *Phalarodon atavus* (LPV 30872).

	Exposed height (mm)	Proximal width (mm)	Crown height (mm)	Crown width (mm)	Crown shape index	Crown ratio (sensu Motani 1996)
Premaxillary teeth						
1	2.72	1.54	–	–	–	–
2	3.45	1.82	2.63	1.51	1.74	0.76
Maxillary teeth						
1	3.94	2.19	–	–	–	–
2	3.83	1.66	2.62	1.52	1.72	0.68
3	3.8	1.64	–	–	–	–
4	3.88	1.68	2.75	1.66	1.66	0.71
5	4.21	1.85	–	–	–	–
6	3.85	2.31	2.74	1.88	1.46	0.71
7	3.42	2.27	2.47	2.08	1.19	0.72

resources in a similar way'. Following this definition, Massare (1997) divided the Mesozoic marine reptiles into 12 somewhat overlapping guilds based on tooth morphology and rare gut contents (Massare 1987), and relative swimming ability (Massare 1988, 1994).

The class of prey the marine reptiles could consume depends on their tooth morphology and skull width (Massare 1987). The longest tooth preserved in LPV 30872 has a crown height of 2.75 mm (Table 2). The left half of the skull of LPV 30872 has a width of about 13.5 mm (Table 1). Thus, the width of the skull is inferred to be 27 mm in LPV 30872. It should be noted, however, that this is a minimum estimation for the skull width of LPV 30872 considering the postmortem alteration. The tooth size index is defined as the crown height of the longest tooth divided by the skull width (Massare, 1987). Thus, LPV 30872 has a relative tooth size of about 0.1. In addition, LPV 30872 develops a bluntly pointed tooth apex, and its dentition lacks cutting edges. These characteristics of tooth crown morphology indicate the smash or crunch feeding guild of Massare (1987). All tooth apices in LPV 30872, however, lack rough surfaces, but they have longitudinal ridges, suggesting a likely preference for externally soft prey (Massare 1987) such as belemnoids and fishes with few scales, both of which are present in the Luoping Biota (Tintori *et al.* 2007, 2010; Hu *et al.* 2011; Wu *et al.* 2011; Wen *et al.* 2012).

The foraging mode of the predator is another factor of the guild definition, which also plays an important role in the community structure (e.g. Schmitz 2008). Numerous studies suggest that predators typically employ one of two basic methods for foraging (McLaughlin 1989). Ambush predators wait for their prey to enter into their visual field and then capture it with a lunge or short chase, while widely foraging predators actively search for their prey (McLaughlin 1989). Although the foraging mode adopted by predators is controlled by many biological factors, model simulations predict that the advantage of active for-

aging increases rapidly with an increase in sustained velocity (Scharf *et al.* 2006). This is largely consistent with empirical studies that relatively fast predators with streamlined body shape will more likely adopt an active foraging mode, especially in aquatic vertebrates (Webb 1984).

The optimal morphology for sustained swimming of aquatic vertebrates is represented by thunniform swimmers, which are characterized by a large lunate tail with a high aspect ratio and a relatively rigid streamlined body with a fineness ratio around 4.5 (Weihs and Webb 1983; Massare 1988). A large lunate tail of high aspect ratio maximizes the thrust while a rigid and streamlined body with an optimum fineness ratio minimizes the drag in the water. A large lunate tail morphology had not yet developed among Middle Triassic marine reptiles, including mixosaurid ichthyosaurs (McGowan and Motani 2003). However, the body shape of mixosaurids, including the specimen reported here, approached an optimal morphology that minimizes drag. There are two lines of evidence for this argument. Firstly, the maximum values of centrum height/length ratio in mixosaurid ichthyosaurs range from about two to five (Schmitz *et al.* 2004; this study). It is possible to infer that a high ratio of centrum height/length minimizes the intervertebral flexibility (Motani *et al.* 1996). The centrum height/length ratios of mixosaurid ichthyosaurs are similar to those of lamnid sharks, which have a stiff body, indicating also a relatively rigid body in mixosaurids (Motani *et al.* 1996). Secondly, the fineness ratios of mixosaurids (see below) fall within the optimal range to minimize drag (Massare 1988). This relatively rigid and optimal body shape of mixosaurids has never been observed in any other marine reptile group of the Middle Triassic (Massare 1997; Motani *et al.* 2008; Liu *et al.* 2010a). Thus, if there is a group of widely foraging predators of marine reptiles in the Middle Triassic oceans, mixosaurids appear to be the best suited candidates. This is likely the case as differentiation of foraging modes reduce competition among similar predators.

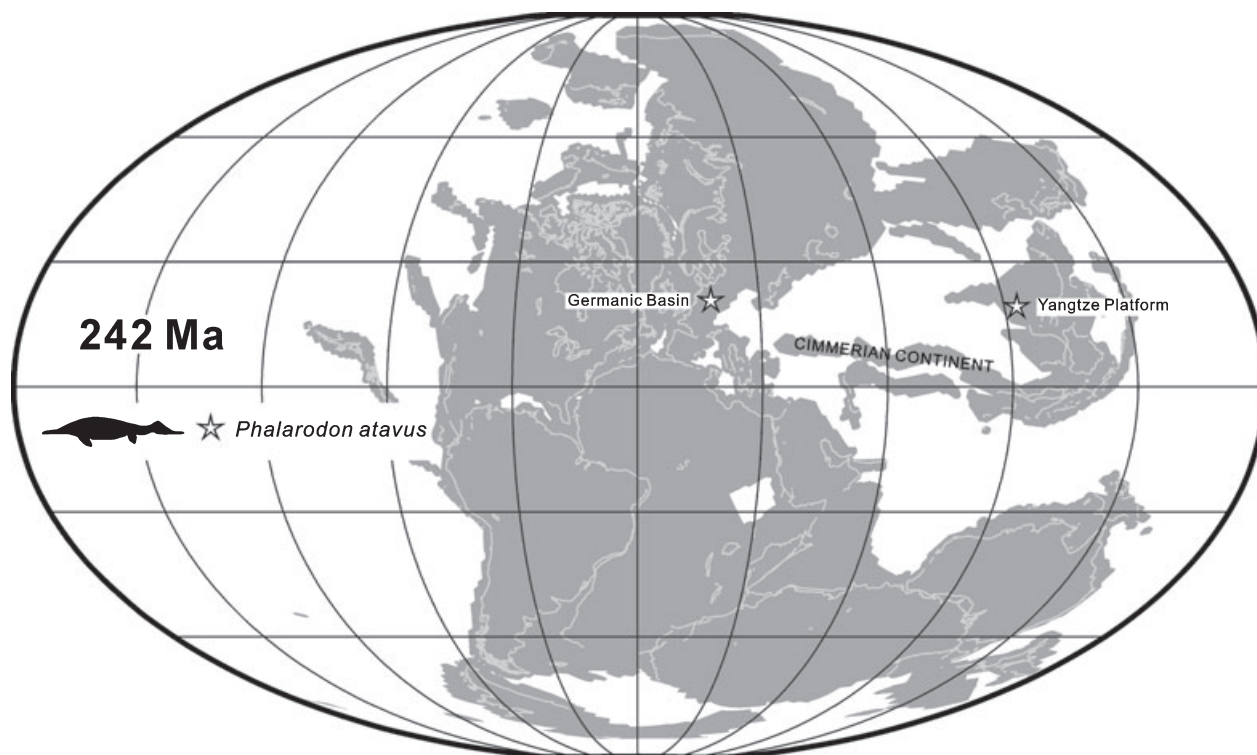


FIG. 10. Global palaeogeographic reconstruction showing the peri-Tethyan distribution of *Phalarodon atavus* (Generated using the plotting software designed by John Alroy, available free at <http://pbd.org>).

Mixosaurus from Monte San Giorgio in Switzerland has already been hypothesized as an active predator by Massare (1997), based on the principles proposed by Massare (1988, 1994). Although the formula for calculating absolute speed has been modified by Motani (2002), the evaluation of relative sustained swimming ability among Mesozoic marine reptiles proposed by Massare (1988) is still valid (Motani 2002). The posterior tip of the tail of LPV 30872 is missing, so it is not possible to measure the total length of this new specimen. If we assume the same ratio of postflexural/postcranial length between *Mixosaurus cornalianus* (reconstruction by McGowan and Motani 2003) and LPV 30872, we can calculate the fineness ratio of LPV 30872 as 5.3 (see Table 1 for measurements of LPV 30872). The new specimen thus has a more optimal fineness ratio compared with the reconstruction of *Mixosaurus cornalianus* by McGowan and Motani (2003, fineness ratio *c.* 5.4), implying an improved sustained swimming ability by the new specimen. Assuming the hypothesis that *Mixosaurus* from Monte San Giorgio of Switzerland is an active predator is valid, LPV 30872 also appears well-suited to an active foraging mode.

Phalarodon atavus had only been discovered previously in the Germanic Muschelkalk Basin, and LPV 30872 is the first example reported from elsewhere. During the Middle Triassic, there was an almost continuous coastal region (Cimmerian Continent, see Fig. 10) between the eastern

and western Tethyan provinces, which connected to the biotas of these respective regions. The Luoping Lagerstätte is located in a semi-enclosed intraplateau basin of the Yangtze Platform, connected to the Nanpanjiang Basin during high stands of sea level, which was again connected to the open Tethyan ocean represented by the Songma, Ailaoshan, and Nan-Uttaradit suture zones during the Triassic (Fig. 1). The Germanic Basin was also connected to the Tethyan ocean by the Carpathian Gate during the Middle Triassic (Ziegler 1990; Diedrich, 2009). As discussed above, *Phalarodon atavus* exhibits an optimum fineness ratio for sustained swimming that would have allowed it to access the open ocean. Thus, there appears to be no morphological or physical barriers to prevent the migration of *Phalarodon atavus* between the western and the eastern Tethyan provinces.

CONCLUSIONS

LPV 30872 is a subadult of *Phalarodon atavus*. Discovery of this new specimen shows that the distribution of *P. atavus* extends at least to the eastern extent of the Tethyan ocean, rather than being restricted to the Muschelkalk Germanic Basin as previously suggested. As the earliest mixosaurid species, *P. atavus* already had a typical mixosaurian body plan that allowed it to adapt to the coastal region of the

peri-Tethyan ocean. Tooth crown morphology and postcranial anatomy shows that this taxon was likely an active predator that may have preferred externally soft prey.

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