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Authors: Deesri, Uthumporn, Lauprasert, Komsorn, Suteethorn, Varavudh, Wongko, Kamonlak, and Cavin, Lionel

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A new species of the ginglymodian fish *Isanichthys* from the Late Jurassic Phu Kradung Formation, northeastern Thailand

UTHUMPORN DEESRI, KOMSORN LAUPRASERT, VARAVUDH SUTEETHORN,
KAMONLAK WONGKO, and LIONEL CAVIN



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A new ginglymodian fish, *Isanichthys lertboosi*, is described from the Phu Kradung Formation, north-eastern Thailand, a freshwater deposit of probable Late Jurassic age. The species is represented by four specimens, from the Phu Noi locality, associated with a rich fauna of sharks, turtles, crocodiles, and theropod and sauropod dinosaurs. One specimen is an isolated braincase, which provides characters rarely observed in extinct ginglymodians. The species is referred to the genus *Isanichthys*, a taxon originally described on the basis of a single specimen from the Phu Nam Jun locality, a slightly younger site approximately 75 km from Phu Noi. *Isanichthys* is mainly distinguished by frontals slightly narrower anteriorly than posteriorly, two anterior infraorbitals not in contact with the orbit, reduced preorbital region, and a small orbit and a cheek region completely covered by bones. The new species is characterized, among other characters, by a dermal component of the sphenotic visible on the cheek, one pair of extrascapulars plus a small median one, the presence of few suborbitals (ca. 4 or 6) arranged in one row, and a median dorsal row of scales with spine. Comparisons with other ginglymodian taxa and a cladistic analysis indicates that *Isanichthys* (*Lepidotus*) *latifrons* from the Late Jurassic of England, as well as probably *Isanichthys* (*Lepidotus*) *luchowensis* from the Early or Middle Jurassic of Sichuan, China, form a clade with both Thai species of *Isanichthys*. The new species provides evidence of the high diversity of ginglymodian fishes in the Phu Kradung Formation and suggests a new hypothesis of phylogenetic relationships among extinct ginglymodians.

Key words: Actinopterygii, Holostei, osteology, braincase, phylogeny, Jurassic, south-east Asia.

Uthumporn Deesri [uthumporn_deesri@yahoo.com], Department of Biology, Faculty of Science, Mahasarakham University, Khamrieng, Kantharawichai District, Mahasarakham 44150, Thailand;

Komsorn Lauprasert [lauprasert@gmail.com], Department of Biology, Faculty of Science, Mahasarakham University, Khamrieng, Kantharawichai District, Mahasarakham 44150, Thailand and Palaeontological Research and Education Centre, Mahasarakham University, Khamrieng, Kantharawichai District, Mahasarakham 44150, Thailand;

Varavudh Suteethorn [suteethorn@hotmail.com], Palaeontological Research and Education Centre, Mahasarakham University, Khamrieng, Kantharawichai District, Mahasarakham 44150, Thailand;

Kamonlak Wongko [uree40@yahoo.com], Department of Mineral Resources, Rama VI Road, Bangkok 10400, Thailand; Lionel Cavin [lionel.cavin@ville-ge.ch], Department of Geology and Palaeontology, Muséum d'Histoire naturelle, CP 6434, 1211 Genève 6, Switzerland.

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Introduction

Ginglymodi is a clade of ray-finned fishes comprising the Lepisosteiformes (gars and extinct relatives), and the extinct “Semionotiformes” and Macrosemiiformes (Grande 2010). Lepisosteiformes and Macrosemiiformes are well characterized by osteological characters, but the “Semionotiformes”

are still poorly defined (Cavin 2010; Cavin et al. 2013). In these studies, the “Semionotiformes” are positioned as stem taxa to the Lepisosteiformes, but show poorly resolved intrarelationships. For more than a century, only a few species of well-preserved “Semionotiformes” have been described, mostly from Europe, and numerous taxa have been defined on the basis of incomplete and often fragmentary material. During the last few decades, however, re-examination of

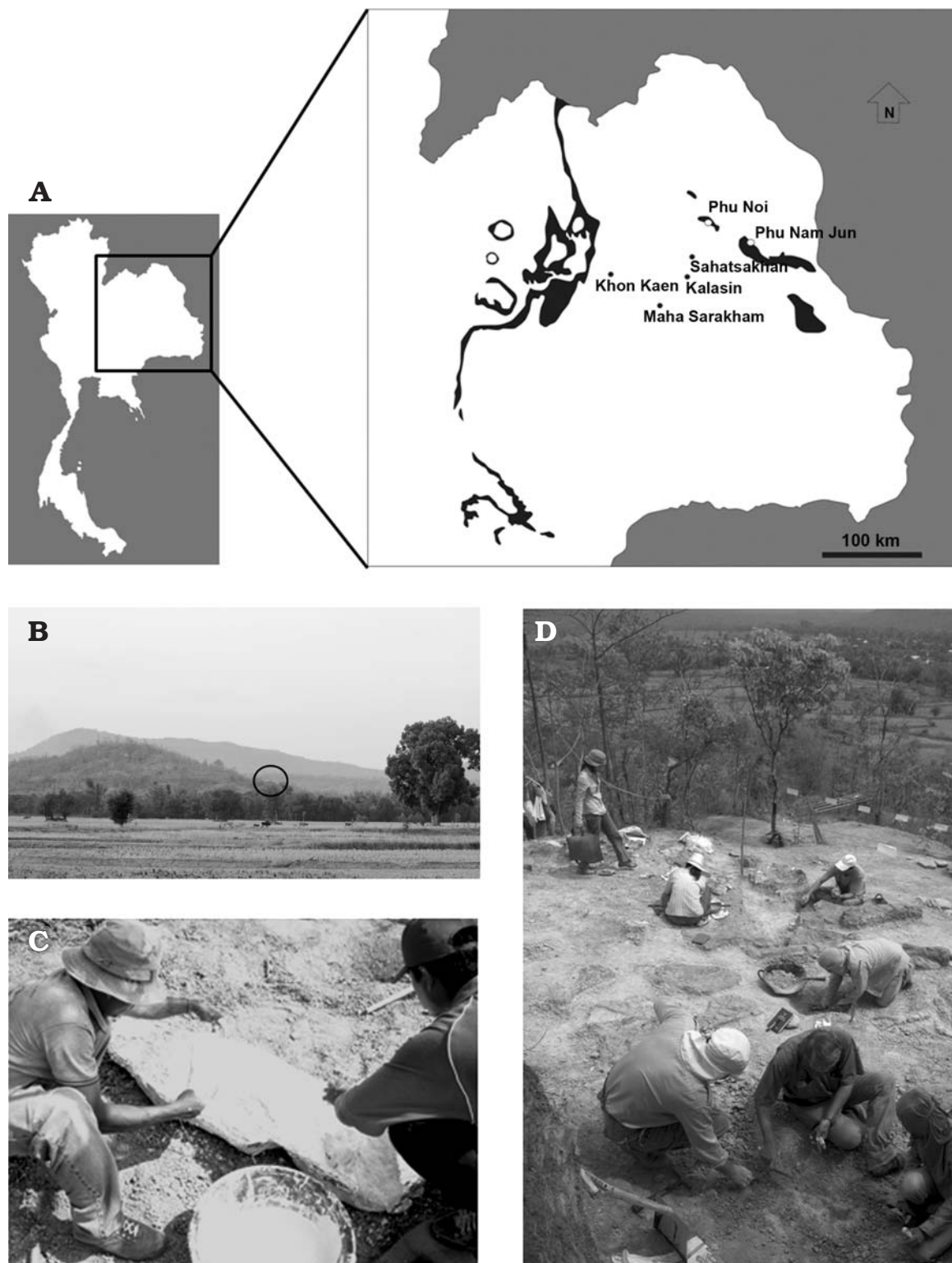


Fig. 1. **A.** Schematic map of Thailand with the Isan region (frame) showing the outcrops of the Phu Kradung Formation in black and the localisation of the site of Phu Noi. **B.** Landscape showing the localisation of the Phu Noi excavation site (circle) in the hilly landscape surrounded by rice pads. **C, D.** Views of the excavations in Phu Noi in February 2010. The fish specimens are extracted with the plaster jacket technique.

old specimens and new taxa found worldwide have greatly improved our knowledge of the group. Without evidence supporting the monophyly of “Semionotiformes” in the present analysis, we do not retain this term, and we use in-

stead *Ginglymodi*, which represents a broader monophyletic group. Recently, López-Arbarello (2012) provided important new results about ginglymodian relationships, showing that *Lepisosteiformes* includes *Lepisosteidae* and several

stem groups, i.e., the Obaichthyidae, *Pliodetes*, *Araripelepidotes*, *Lepidotes* (with a new definition, and including three Early Jurassic species), *Scheenstia* (with a new definition, and including seven species from the Late Jurassic and Early Cretaceous), as well as *Isanichthys palustris*. Importantly, a clade called Semionotiformes is resolved: it comprises the Semionotidae, the Callipurbeckiidae, and the Macrosemiidae. The set of characters used in López-Arbarello's analysis differs from the set of characters used in analyses of Cavin (2010), Cavin et al. (2013) and in the present study. We discuss and compare our results with those of López-Arbarello (2012).

In Thailand, ginglymodians constitute the most common fish remains in the continental Mesozoic deposits of the Khorat series in the northeastern part of the country, and well-preserved material has been uncovered since the 2000s (Cavin et al. 2009). The most productive locality, Phu Nam Jun, located in Tambon LaoYai, Kalasin province, exposes the Late Jurassic–Early Cretaceous Phu Kradung Formation (Cavin et al. 2004). It has yielded “*Lepidotes*” *buddhabutrensis* (Cavin et al. 2003), a ginglymodian that was recently referred to a new genus, *Thaiichthys* Cavin, Deesri, and Suteethorn, 2013. While *Thaiichthys buddhabutrensis* is represented in this locality by several hundreds of complete and subcomplete individuals (Deesri et al. 2009), a single specimen has been referred to another taxon by Cavin and Suteethorn (2006). In September 2008, a new excavation at the Phu Noi locality was opened in Kalasin District, approximately 75 km NW of Phu Nam Jun (Fig. 1). Although also exposing the Phu Kradung Formation, the new locality is at an older stratigraphical level than Phu Nam Jun (Cuny et al. 2013). Phu Noi has yielded an array of tetrapods, as well as isolated shark teeth and some ginglymodian remains. The latter material is described in this paper.

Institutional abbreviations.—CDUT, Palaeontological Museum of the Chengdu University of Technology, China; KS, Sirindhorn Museum, Sahat Sakhan, Kalasin Province, Thailand; NHMUK, Natural History Museum, London, UK.

Material and methods

The specimens have cracks filled with sediment caused by roots from the soil, and were coated with a few cm of calcareous sandstone. We extracted the fossils from the field with the plaster jacket technique in order to preserve their delicate and fragile fins. Preparation was performed using an air pen in the laboratory of the Sirindhorn Museum, where the specimens are housed. In the laboratory, the upper part of the jackets was sawed in order to free the upper side of the specimens, which were visible in the field. Details of the skulls were prepared under a binocular microscope. The available sample comprises four specimens in total. Nomenclature in the anatomical description follows Grande (2010).

Geological setting

The Phu Noi locality is located on the flank of a small hill at Ban Din Chi, Kam Muang District, Kalasin Province (Fig. 1B). Stratigraphically, it is in the lower part of the Phu Kradung Formation, which is characterized by sandstone beds alternating with silty to sandy claystone beds. This formation is low in the Khorat Group as currently defined, above the Upper Nam Phong Formation (Racey 2009). The Khorat Group comprises post-Triassic deposits on the Khorat Plateau and adjacent areas, and it has long been regarded as Late Jurassic, but palynological studies now suggest Early Cretaceous ages for most of the vertebrate-bearing horizons, i.e., the Phra Wihan, Sao Khua, Phu Phan and Khok Kruat formations (Racey et al. 1994, 1996). The dating of the Phu Kradung Formation is still problematic, but a recent synthesis suggests a Late Jurassic age for its lowermost part, in which the Phu Noi locality is located, and a basal Cretaceous (Berriasian) age for the upper part (Racey 2009; Cuny et al. 2013).

The sediments of the Phu Kradung Formation are fluvial and lacustrine in origin, and the main palaeocurrents are oriented towards the SW (Racey 2009). At Phu Noi, greenish grey sandy deposits are interbedded with maroon siltstone beds, which are mica rich and contain laminated plant debris. The fish remains have been found in two main layers. The upper layer consists of an accumulation of dinosaur skeletons, approximately 3 m thick and dips approximately 10° towards the SE. The fossil assemblage consists of fragments of skeletons of sauropod dinosaurs, isolated theropod bones, fragments of skeletons of crocodiles, turtle and shark remains, and includes two specimens of ginglymodian fishes. The lower layer is approximately 2 m below the dinosaur assemblage, and has yielded the other two ginglymodian specimens. However, there are no visible differences in terms of sediment deposition between these two layers.

Systematic palaeontology

Superdivision Holostei Müller, 1844 (sensu Grande 2010)

Division Ginglymodi Cope, 1872 (sensu Grande 2010)

Order Lepisosteiformes Hay, 1929 (sensu López-Arbarello 2012)

Genus *Isanichthys* Cavin and Suteethorn, 2006

Type species: *Isanichthys palustris* Cavin and Suteethorn, 2006; Phu Nam Jun, Upper part of the Phu Kradung Formation, probably Berriasian in age.

Emended diagnosis.—Ginglymodian fish with skull roof bones strongly ornamented, with no continuous ganoin cover; frontals slightly narrower anteriorly than posteriorly; ratio of frontal length to parietal length less than 2.5; ratio of skull length to orbit length more than 6; closed orbital ring; two anterior infraorbitals not in contact with the orbit, anteriormost

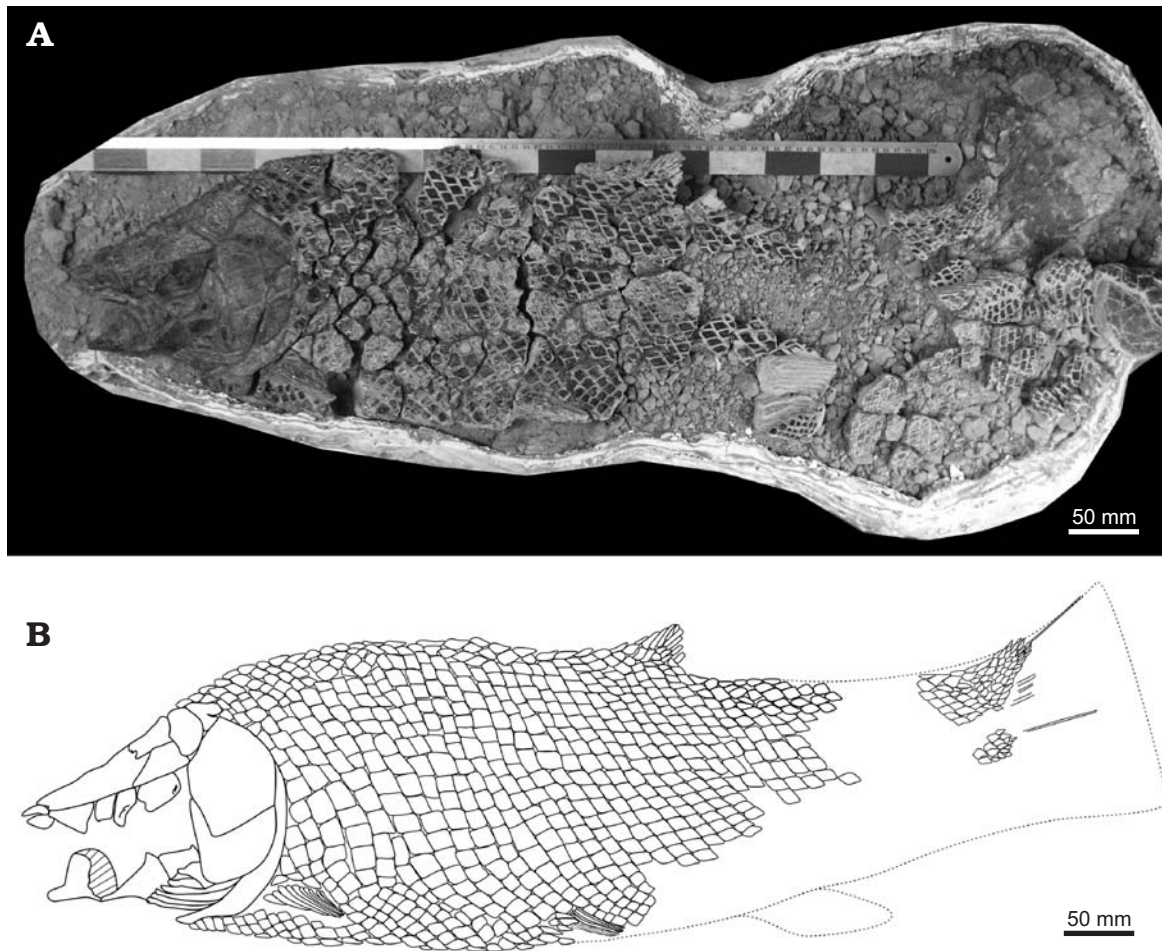


Fig. 2. Holotype of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS36-2 (holotype); Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand; in left lateral view. **A.** Photograph. **B.** Semi-interpretative line drawing.

infraorbital deeper than long; two supraorbitals, the anterior one generally elongated with anterior margin contacting the first and/or the second infraorbital; cheek region completely covered by bones; quadrate lies below the orbit; preopercle slightly curved; maxilla formed by a posterior rounded plate-like part and a thin anterior part, which precedes the articular process; one supramaxilla; epiotic with a short and simple posteriorly directed process; posttemporal fossa present; intercalar absent; basisphenoid present; presence of an oral sensory canal; 25 rays in caudal fin, 12 in upper lobe; 50 to 53 rows of ganoid scales along the flank and approximately 20 scales in the transverse row at the deepest level of the body.

Isanichthys lertboosi sp. nov.

Figs. 2–17.

Etymology: The species is named after Lertboos Gongtong, former chief of Kam Muang District, honouring his important contribution to the systematic excavation at the type locality.

Holotype: KS36-2 (Figs. 2, 3). Subcomplete specimen with most of the dermal bones preserved, with partially preserved trunk and fins in right lateral view, standard length (SL) 800 mm.

Type locality: Phu Noi, Tambon Din Chi, Kam Muang district, Kalasin province, northeastern Thailand.

Type horizon: Lower part of the Phu Kradung Formation, probably Late Jurassic in age.

Referred material.—KS36-3, fragments of the squamation of a specimen with an almost complete skull except the snout region, which laid above the caudal region of KS36-2 (this part was destroyed during excavation) (Fig. 2A); KS34-281, portion of a skull showing in part the suspensorium; KS34-380, skull roof with part of the braincase.

Diagnosis.—*Isanichthys* with the body approximately 4.6 times longer than deep; total length approximately 3.8 times the head length; skull roof slightly sigmoidal in lateral view; preorbital region reduced; asymmetrical parietals; frontal almost quadrangular in shape; one pair of extrascapulars plus a small median one; infraorbital and suborbital bones weakly or not ornamented; few suborbitals (ca. 4 or 6) arranged in one row; dermal component of the sphenotic visible on the cheek; edentulous maxilla; dentary bears approximately 9 small cylindrical teeth; semi-tritorial dentition between the dermopalatines and the coronoid ossifications; median dorsal row of scales with spine; all fins with long basal and fringing fulcra.

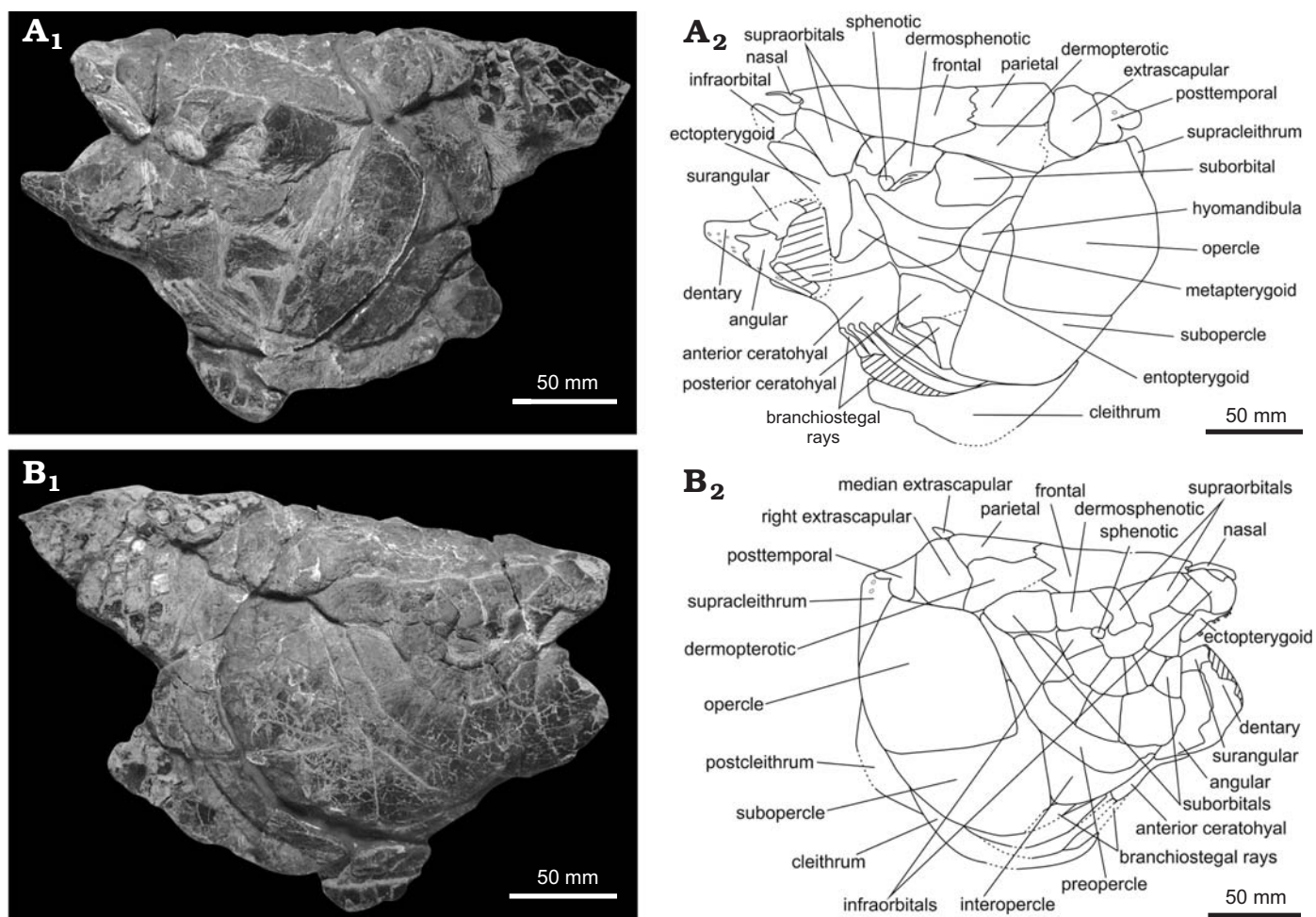


Fig. 3. Skull of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS36-2 (holotype); Phu Kradung Formation, Late Jurassic; Kalasin Province, North-eastern Thailand; in left (A) and right (B) lateral views. Photographs (A₁, B₁) and semi-interpretative line drawings (A₂, B₂).

Description

General features and proportions.—The body is proportionally shorter and deeper than in the type species, approximately 4.6 times longer than deep, and head length is proportionally shorter, being contained approximately 3.8 times in the total length. The head is 200 mm in average length (including the opercular series), and 175 mm in average depth. The ossifications of the head have no ganoin cover and most of the skull roof bones bear rugae and tubercles forming a reticulated pattern in the centers of ossifications and extending into radiating ridges to their margins (Fig. 5A).

Skull roof.—The frontal is the longest element of the dermal skull roof (Fig. 6). It is about twice as long as the parietal. The frontal is almost quadrangular, only slightly narrower anteriorly than posteriorly, with the maximum width at the level of the posterior margin of the orbit. The suture between both frontals is nearly straight. The suture between frontal and parietal on the left side is not aligned with the similar suture on the right side. The parietal is rectangular, approximately 1.5 times longer than wide. Both parietals are nearly equal in surface, but their shape is asymmetrical (Fig. 6). The parietal contacts the frontal anteriorly with an inter-digitating

suture in some specimens (Fig. 6A), or with an irregular but smooth suture in other specimens (Fig. 6B). It sutures with the dermopterotic laterally and the lateral extrascapulars posteriorly. The posterior margin of the parietal is arched, with a concavity situated at mid-length in KS34-380. The lateral and medial margins are straight, except in KS34-281, which presents a digitated pattern on the posterior half of the medial suture. The dermopterotic is massive, elongated and with an anterolateral expansion extending lateral to the frontal. The dermopterotic is longer than the parietal but is approximately equal to it in maximum width. Its lateral margin contacts the dorsalmost suborbital and the dorsal extremity of the preopercle. There is only one extrascapular on each side of the skull, plus a small median one that is triangular in shape (Fig. 6B). The external surface of the extrascapulars is coarse, with ornamentation mainly present in the centres of the bones. The extrascapular has an irregular posterior margin and its anterior border abuts against the sigmoid border of dermopterotics and parietals (Figs. 3, 4). The occurrence of a single pair plus a small median extrascapular differs from the general pattern of showing two extrascapulars in most Jurassic ginglymodians and generally multiple pairs in Cretaceous ginglymodi-

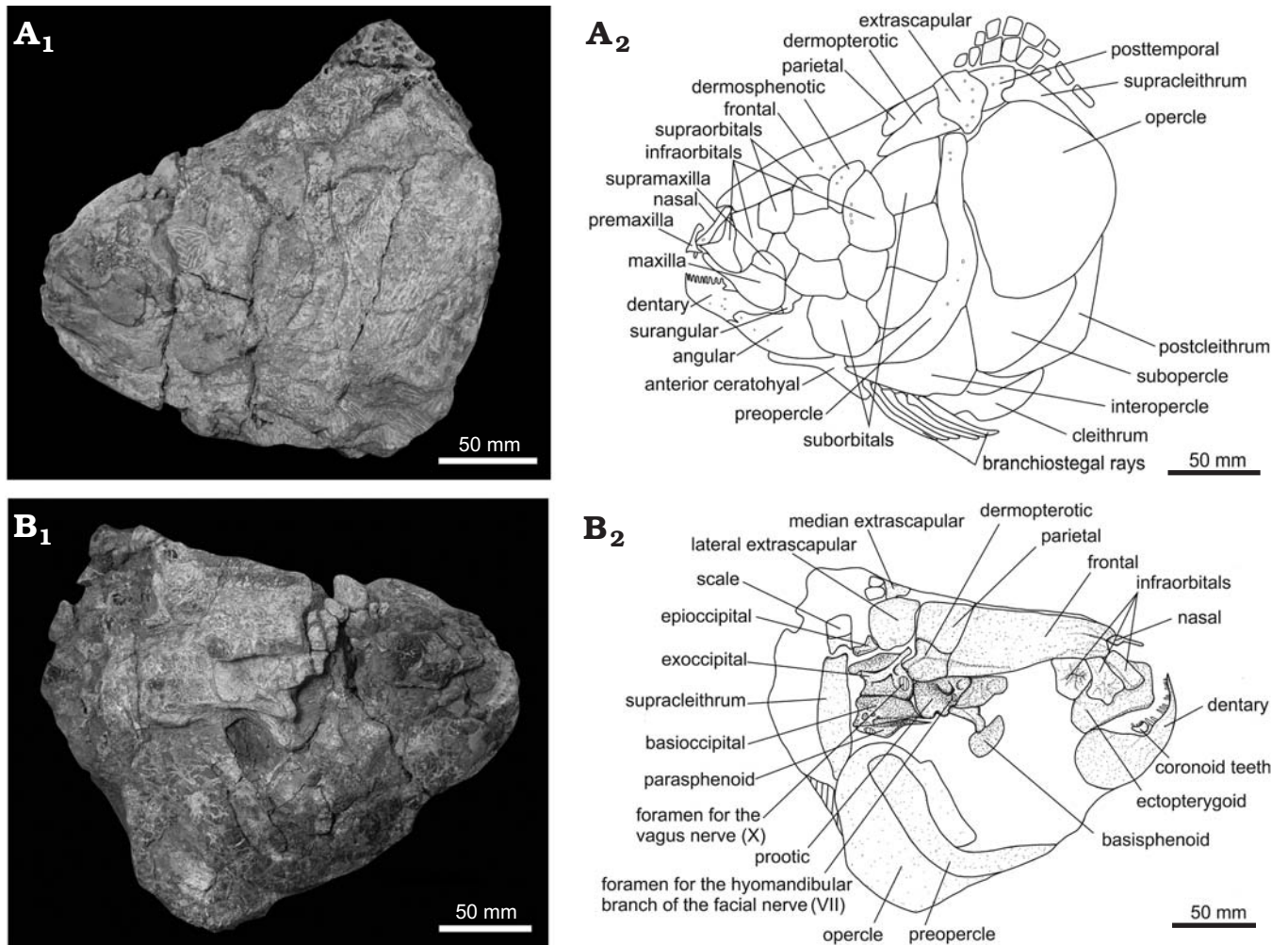


Fig. 5. Skull of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS34-281; Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand; in left (A) and right (B) lateral views. Photographs (A₁, B₁) and semi-interpretative line drawings (A₂, B₂).

soposterior edge of this ossification is a short process (Fig. 8C). The dorsal surface is irregular in shape and its anterior margin is marked by forked sutures with the posterior margin of the parietal (Fig. 6A). Both epioccipitals meet above the gap separating both exoccipitals. There is no supraoccipital. The prootic (Figs. 7, 8A, B) is well developed and contacts the exoccipital posteriorly. The bone has a crenulated posterior edge and bears a prominent straight ridge that runs vertically along the anterior margin. The dorsal and ventral ends of the ridge form sutural surfaces. The dorsal surface articulates with the sphenotic, while the ventral surface probably contacted the ascending ramus of the parasphenoid. There is a large foramen for the hyomandibular branch of the facial nerve (VII) in the centre of the bone. Three shallow grooves and two ridges radiating from the large foramen for the facial nerve mark the lateral face of the prootic. The ventral ridge is much more prominent than the dorsal one. Posterior to that large opening is a small foramen for the glossopharyngeal nerve (IX). The sphenotic (Figs. 7, 8A) is best preserved on the right side of KS34-380. It is sutured to the ventral side of the dermopterotic, and to the prootic posteriorly. This bone

has an expanding curved anteromedial margin and a straight posterior margin. It forms a well-developed anteriorly inclined rounded crest that extends laterally to the level of the circumorbital ossifications. The sphenotic is also visible on both sides of KS36-2 (holotype) and KS36-3, in which the ossification develops a lateral blunt process that is visible on the cheek along the ventral margin of the dermosphenotic (Figs. 3, 4). A small dermal component of the sphenotic process is also visible in specimens of other ginglymodians (see Cavin et al. 2013 for a review). In gars the sphenotic is visible laterally and separated from the dermosphenotic (Grande 2010). In *Isanichthys lertboosi* the tip of the lateral process of the sphenotic is separated from the orbit by a gap, but it is closely associated with the dermosphenotic. In obaichthyids, sphenotic and dermosphenotic are fused together (Grande 2010).

In KS34-380, the basisphenoid, pterosphenoid and orbitosphenoid surround the orbital cavity, with only a gap on the ventral margin that was occupied by the parasphenoid, as confirmed by the presence of attachment areas on the ventral surface of the basisphenoid and orbitosphenoid (Fig.

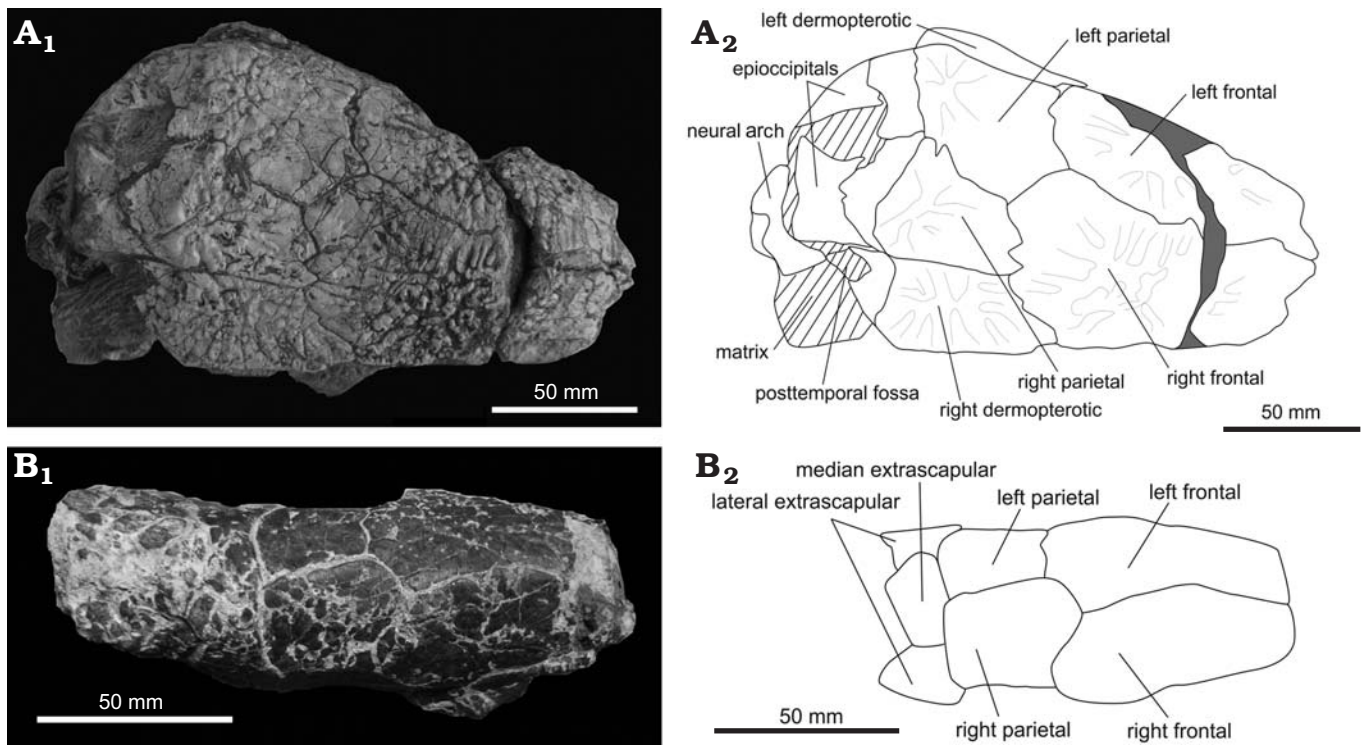


Fig. 6. Skull roof of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS36-2; Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand; in dorsal views. A. KS34-380. B. KS36-3. Photographs (A₁, B₁) and semi-interpretative line drawings (A₂, B₂).

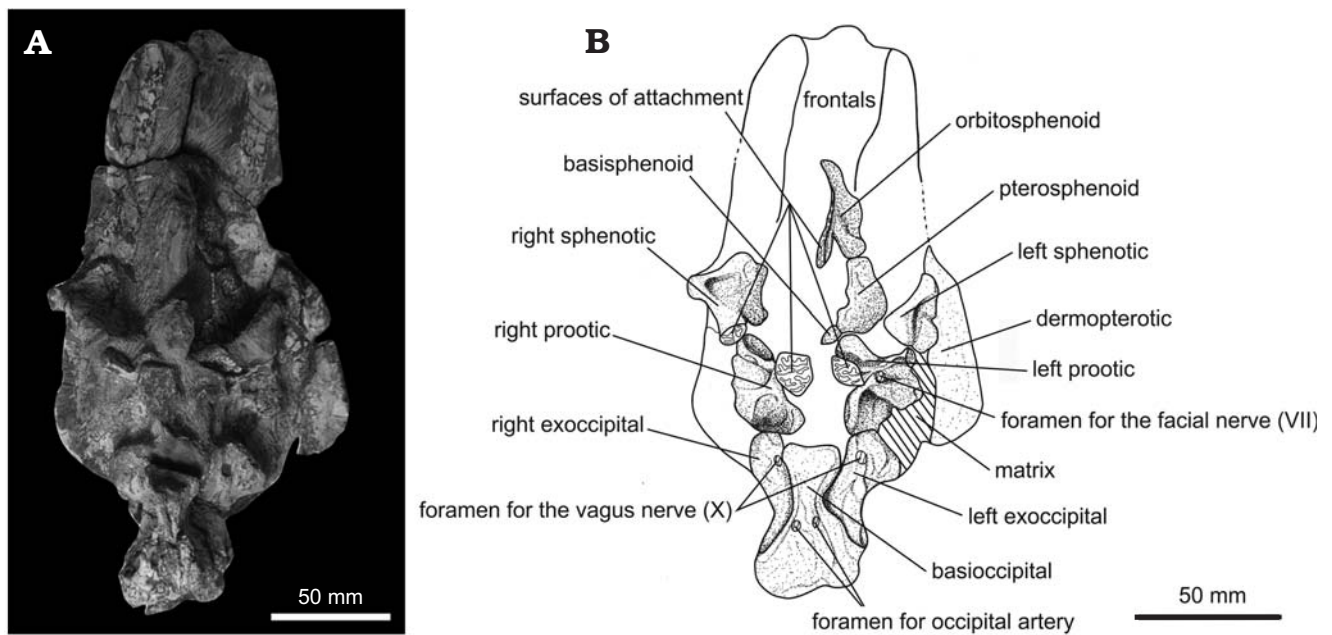


Fig. 7. Braincase of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS34-380; Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand; in ventral view. A. Photograph. B. Semi-interpretative line drawing.

8A). The basisphenoid is the smallest bone of the preserved series and is situated at the posteroventral edge of the orbit cavity. The posterior margin is covered with matrix, but we can estimate its shape. It is approximately triangular with a slightly curved anterodorsal margin, while the other margins are straight. Along the posterior margin runs a narrow groove that reaches the pterosphenoid. Although in KS34-380 the

pterosphenoid has slightly shifted, it is clear that the pterosphenoid was sutured to the basisphenoid ventrally and to the orbitosphenoid anteriorly. The pterosphenoid is wing-shaped with its dorsal margin forming a rounded rim and its ventral margin marking a broad angle, almost at its mid-length. The lateral surface of the bone presents alternating ridges and grooves. The orbitosphenoid has an irregular shape and is

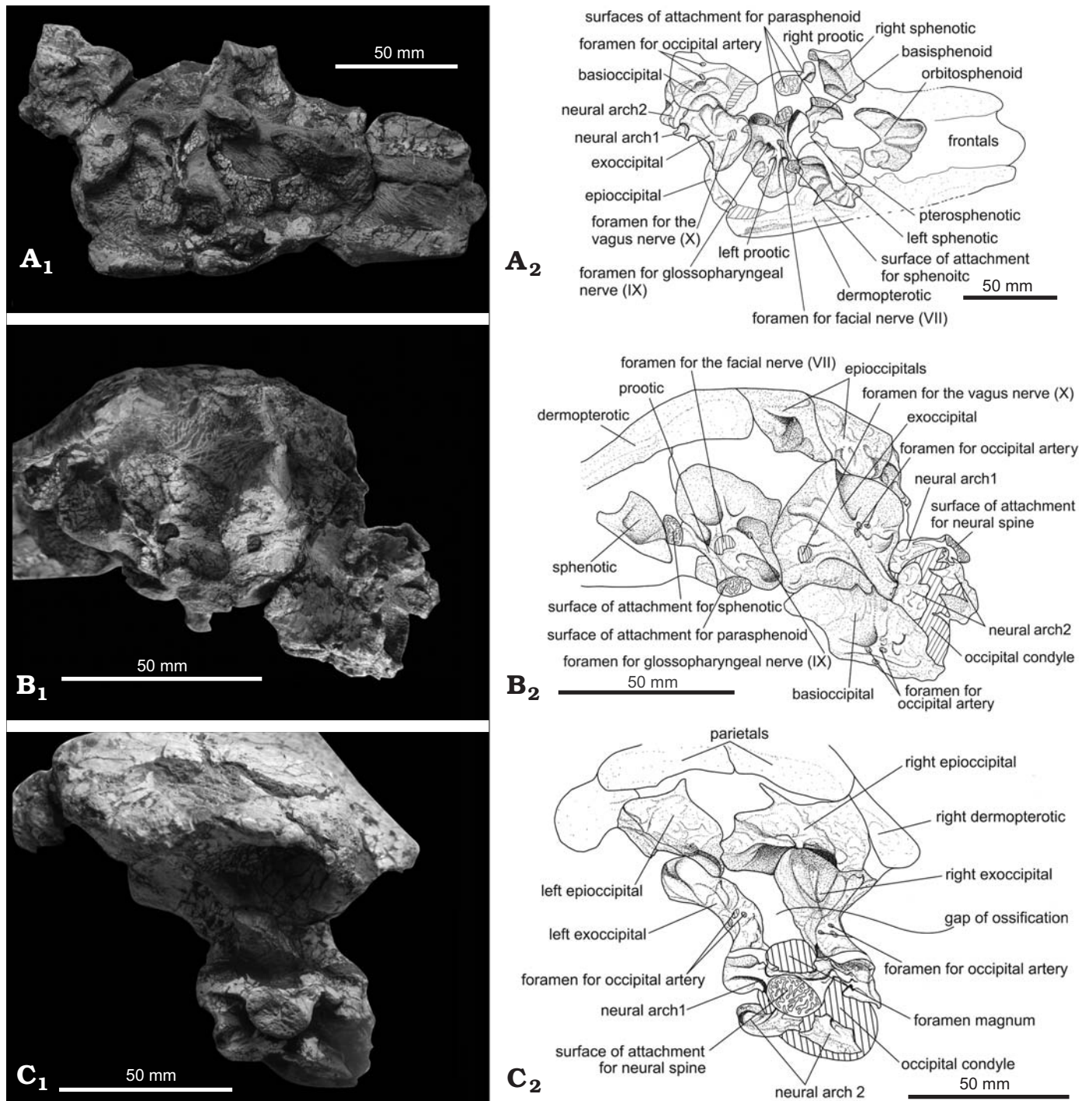


Fig. 8. Braincase of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS34-380; Phu Kradung Formation, Late Jurassic; Kalasin Province, North-eastern Thailand; in left ventrolateral view (the dorsal side faces down) (A), left posteroventral (B), and posterior (C) views. Photographs (A₁–C₁) and semi-interpretative line drawings (A₂–C₂). Shaded areas in B₂ and C₂ correspond to matrix.

located anteriorly to the orbit. Its posterior margin has a deep notch. It bears a blunt process on the posteroventral corner, which almost reaches the basisphenoid, while the postero-dorsal extremity sutures with the pterosphenoid. Laterally, two grooves run anteriorly from the centre of ossification. The anterior margin forms a slightly concave line and the dorsal margin is sutured with the ventral side of the frontal. The basisphenoid is absent in gars and in *Thaichthys bud-*

dhabutrensis, while it is present in most other ginglymodians in which this region is known (*Araripelepidotes*, *Scheenstia mantelli*, *Callipurbeckia minor*, *Lepidotes semiserratus*).

Circumorbital and suborbital series.—The circumorbital ring is complete. It is composed of a large dermosphenotic forming the posterodorsal edge of the orbit, two supraorbitals above the orbit and six to eight infraorbitals located

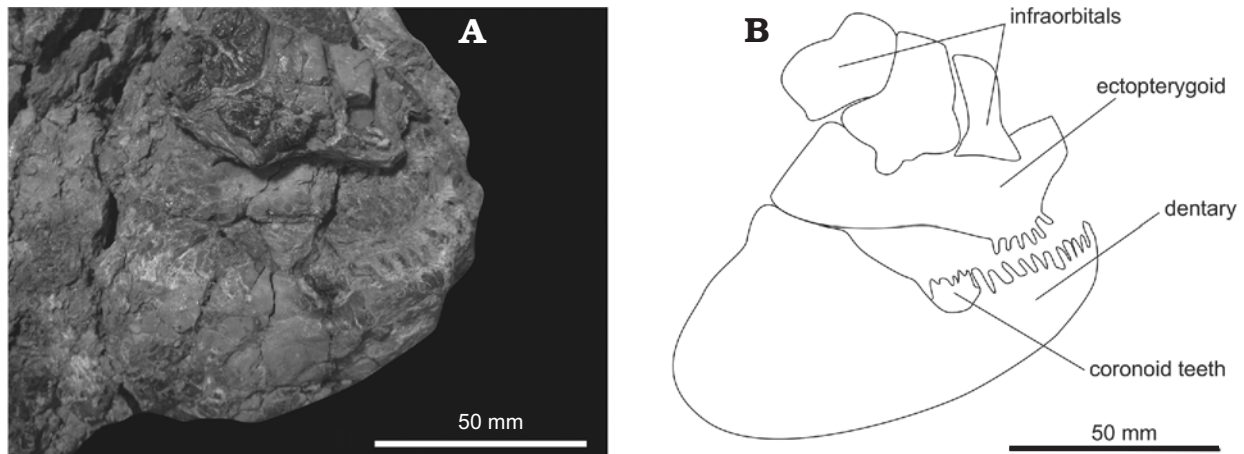


Fig. 9. Part of suspensorium and mandible of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS34-281; Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand; in right lateral view. **A.** Photograph. **B.** Semi-interpretative line drawing.

posteriorly, ventrally and anteriorly to the orbit. The number of infraorbitals is generally eight but KS34-281 contains six large infraorbitals only (Fig. 5A). Two infraorbitals anteriorly are not in contact with the orbit. The first, anterior-most, infraorbital is deep and irregular in shape with a dorsal margin shorter than the ventral margin, which is gently convex (Fig. 3B). The second infraorbital is approximately rectangular or ovoid in shape, slightly deeper than long. The third infraorbital, which forms the anteroventral corner of the orbit, and the remaining ones, situated below and behind the orbit, are deeper than long. On the left side of KS36-3, the infraorbitals are ornamented with strong knobs and grooves in the centres of all ossifications, except the large posteroventral one, which lacks ornamentation (Fig. 4A). The shape of the dermosphenotic varies: it is elongated and trapezoidal in KS36-2, large and rectangular in KS36-3 and narrow and rectangular in KS34-281. The supraorbitals consist of two large bones. The anteriormost is elongate and rectangular in shape, tapers anteriorly, and the posterior one is smaller and deeper than long. In the holotype (KS36-2), there are six suborbitals arranged in one row located between the dermosphenotic, the infraorbitals and the preopercle. In some specimens (KS36-3, KS34-281) four suborbitals only are present (Figs. 4, 5). The largest one, situated anteroventrally, is irregular in shape with its dorsal margin straight, and its ventral margin slightly undulating. It articulates posteriorly to the adjacent suborbital and dorsally to the infraorbitals, and contacts posteroventrally the blunt extremity of the preopercle. The dorsalmost suborbital is large and rectangular, longer than deep and articulates with the dermosphenotic dorsally, the dermosphenotic anteriorly, the dorsal portion of the preopercle posteriorly and the adjacent suborbital ventrally. The remaining suborbitals are deeper than long (Fig. 4). On its right side, KS36-2 presents a small triangular suborbital located at the anterior end of the series (Fig. 3B).

Jaws.—There are some variations in the arrangement of jaw bones and in tooth morphology. The maxilla is best preserved

on the left side of KS34-281. It is an elongate bone with a thin, slender anterior part and a plate-like, rounded posterior part. Its narrow anterior portion is edentulous (Figs. 5A, 10). The anterior articular process, prolonging the anterior thin part and corresponding to one third of the length of the bone, is inwardly curved. A supramaxilla rests on the dorsal margin of the posterior plate. Its depth is nearly half the depth of the maxilla, and it has a curved dorsal margin and a straight ventral margin that borders the maxilla. The nasal process of the premaxilla extends posterodorsally under the nasal and the frontal, and the alveolar portion extends laterally as blunt processes. Only one tooth is preserved on the premaxilla of KS34-281 but the exact number of teeth on the anterior transversal margin of the bone is unknown. The tooth is similar in shape and size to the teeth borne by the dentary and ectopterygoid. It is well developed, about 4 mm in height with an acrodine tip, which is about 0.5 mm high (Figs. 10, 11).

The lower jaw is massive. The visible ossifications are a dentary, one or two coronoids, a large angular, and a surangular located on the posterodorsal edge of the mandible and visible just anterior to the coronoid process in lateral view (Fig. 5A). The angular forms most of the posterior part of the mandible. It contacts the dentary along a suture, whose pattern varies within the set of available specimens. An elongated posterior process of the dentary is present on the holotype. The dentary is robust and slightly tapering at its anterior extremity, which bears a row of approximately 13 conical teeth with bulbous and pointed acrodine caps. Each tooth is composed of a high cylindrical base, approximately 4 mm in height and 1 mm in width, topped by a bulbous cap that is shallow (0.5 mm) compared to its base. All teeth are held on a single row along the anterior portion of the dorsal rim of the dentary. A second row of teeth, similar in both shape and size to the dentary teeth, lies behind the anterior marginal teeth. These teeth are regarded as coronoid teeth. A second coronoid (or the posterior part of the anterior one) is visible as a thin blade of tooth-bearing bone wedged in a notch of

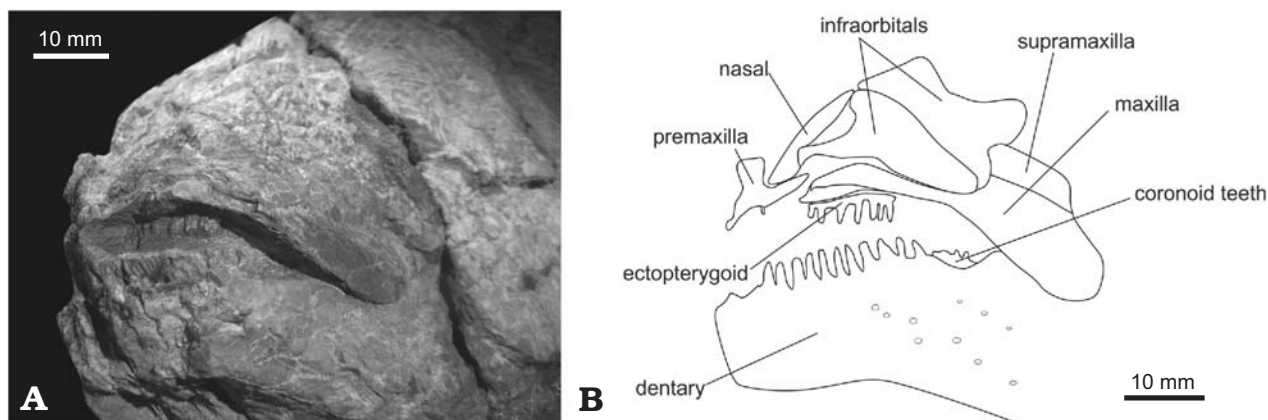


Fig. 10. Snout region and mandible of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS34-281; Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand; in left lateral view. **A**. Photograph. **B**. Semi-interpretative line drawing.

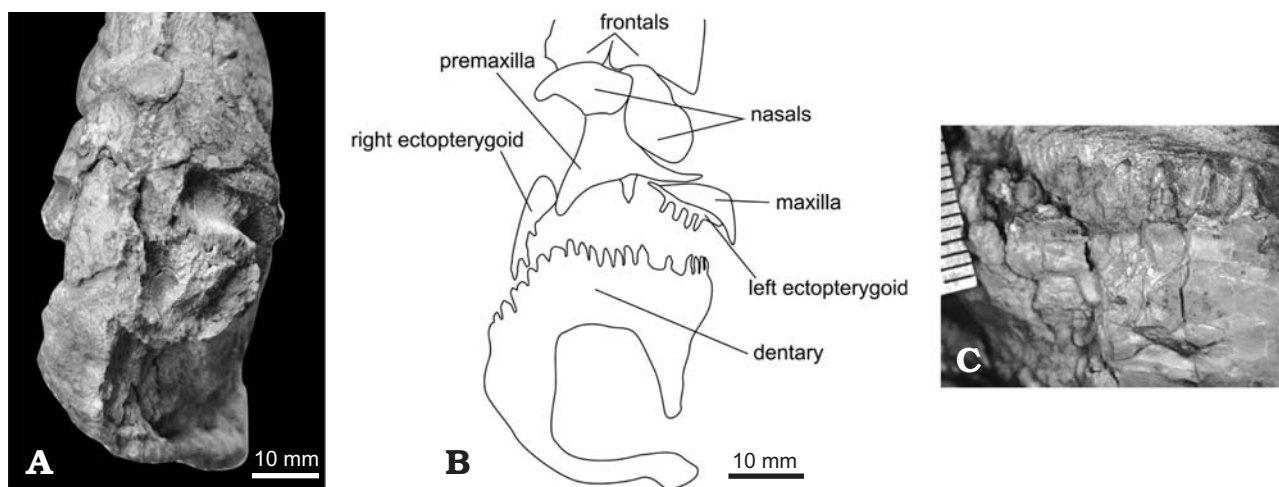


Fig. 11. Snout of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS34-281; Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand; in anterior view. **A**. Photograph. **B**. Semi-interpretative line drawing. **C**. Photograph of the teeth on dentary (scale in mm).

the dentary, anteriorly to the coronoid process and visible on both sides of KS34-281 (Figs. 9, 10).

The holotype, KS36-2 (Figs. 12, 13), shows a different arrangement of its jaws. The premaxillae have no preserved teeth. Posteriorly, the narrow and elongate nasal process of the premaxilla extends under the frontal, and anteriorly the bone extends transversely to form the alveolar processes (Fig. 13A). On this specimen, the lower jaw is broken but we observe a piece of mandible shifted close to the skull. This piece of bone bears two rows of crushing teeth. The teeth, approximately 5 mm high, have a cylindrical base with a bulbous acrodine cap, which is 2.5 mm high, 2 mm wide (this morphology corresponds to the “moderately tritorial dentition” as defined by Cavin 2010). The teeth are not attached to the dentary, and we regard them as coronoid teeth (Fig. 13B). Based on the location of the articulation between the lower and upper jaws, it seems that this fish had a wide gape.

Hyopalatine series.—The suspensorium is visible on both sides of the holotype (KS36-2), but it is poorly preserved and identification of the ossifications remains uncertain. The hyomandibula is partially exposed; the anteroventral part only

is visible, while the rest is hidden by the opercle and subopercle. Based on the surface of the exposed region, it seems that the bone is a massive and relative large ossification. The metapterygoid (Fig. 3A) is irregular in shape, with its posterior part expanding and with a tapering anterior extremity. It contacts the hyomandibula posteriorly and the entopterygoid anteriorly, but we cannot see if there was a contact with the quadrate. The entopterygoid is a triangular bone wedged between the metapterygoid dorsally and the ectopterygoid anteriorly. The ectopterygoid is preserved as a crescent-shaped ossification suturing posteriorly with the entopterygoid. The anterior portion of the ectopterygoid bears at least 7 small cylindrical-based teeth along its ventral border. Each of these teeth is tipped with a bulbous cap. In KS36-2, the dermopalatine is covered with teeth (Fig. 12). The teeth are variable in size and irregularly arranged, but two main rows of crushing teeth appear to be present. In KS34-281, the right ectopterygoid is also visible as a thin bone lying under the infraorbitals (Figs. 9, 10). It bears 6–7 conical teeth restricted to its anterior margin. The arrangement of the palatine dentition is unknown in other specimens.

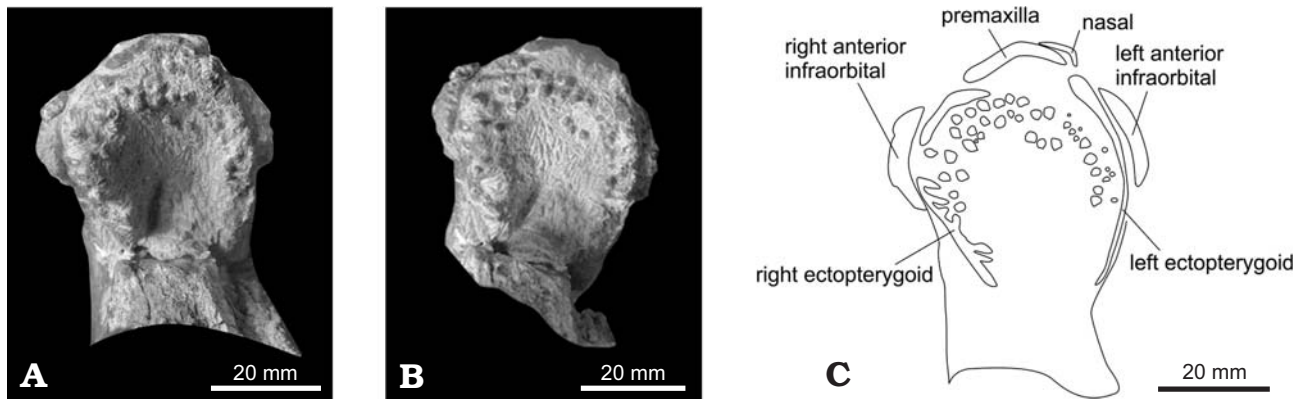


Fig. 12. Ventral views of the snout of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS36-2; Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand; showing vomerine and ectopterygoid teeth. Photographs in different angles (A, B) and semi-interpretative line drawing (C).

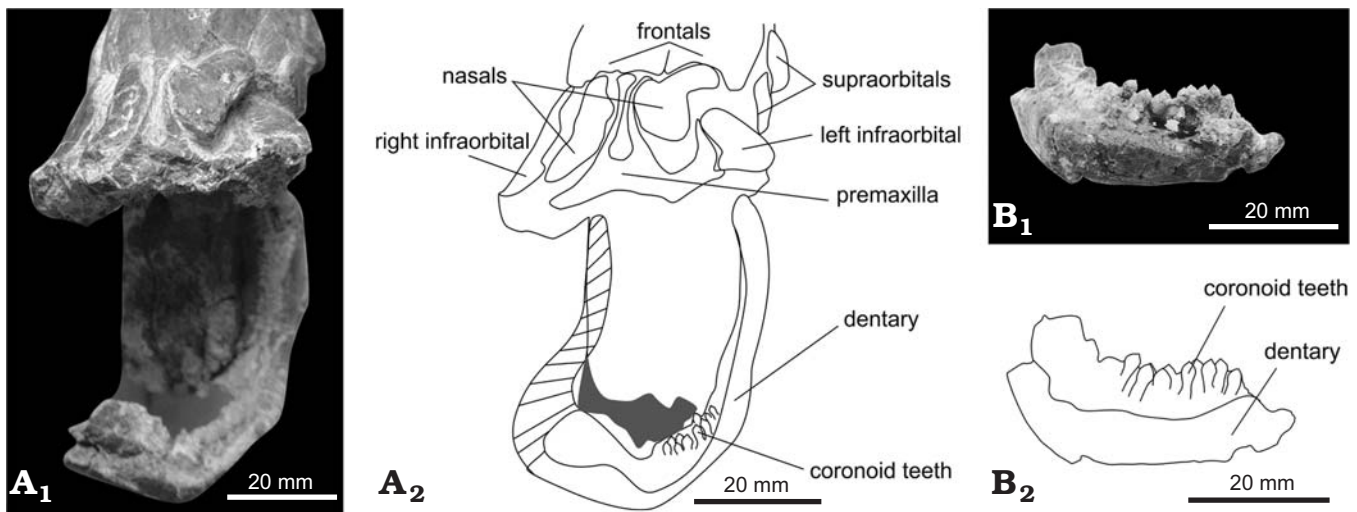


Fig. 13. Snout region and coronoid dentition of the ginglymodian fish *Isanichthys lertboosi* sp. nov., KS36-2; Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. A. Snout region in ventral view. The grey area corresponds to matrix; the shade area corresponds to the reconstructed limit. B. Coronoid dentition in left lateral view. Photographs (A₁, B₁) and semi-interpretative line drawings (A₂, B₂).

Opercular series.—The opercular series is complete, formed by the preopercle, opercle, subopercle, and interopercle.

In the holotype, KS36-2, the preopercle (Figs. 3–5) is preserved only on the right side. It is narrow with a poorly developed ventral limb, and is slightly bent forward. The ossification is crescent-shaped, with no marked angle between both limbs. In KS34-281, the preopercle of the right side shows two limbs forming a more closed angle than in the holotype, and the horizontal limb is shorter than the vertical (Fig. 5B), but it is unclear if this arrangement is genuine or caused by preservation. The vertical branch has parallel margins that do not converge dorsally, and the ossification ends anteriorly as a blunt spine. The extremity of the horizontal branch slightly widens in its anterior part before the blunt spine. The preopercular sensory canal extends enclosed within the thickened anterior margin of the ossification. The opercle (Fig. 3) is roughly quadrangular and slightly deeper than long, but in one specimen (KS34-281) the ossification is more rounded (Fig. 5A). The anterior border is straight, while the posterior border is strongly convex and widely overlaps

the supracleithrum. The dorsal border reaches the dermal skull roof. The surface is smooth in KS36-2 (holotype) but in some specimens, such as KS36-3, the external surface is ornamented with fine grooves, and in KS34-281 rough tubercles are present. The subopercle is well developed with a vertical limb reaching half the depth of the opercle. The anterior margin of the bone is vertical and straight, and contacts the posterior border of the interopercle. The ventral margin of the bone is convex. The interopercle is visible as a triangular bone wedged between the subopercle and the posteroventral edge of the preopercle (Fig. 3B). The anterior tip tapers and it runs toward the ventral extremity of the preopercle. In KS36-3, however, the interopercle is visible as a narrow bone along the ventral margin of preopercle (Fig. 4A).

Hyoid arch and branchiostegal rays.—Six thin and elongated branchiostegal rays are preserved on the left side of holotype, KS36-2 (Fig. 3A); the posteriormost one is the shortest but the widest. The four anterior rays articulate with the anterior ceratohyal and the two posterior ones with the posterior ceratohyal. The anterior ceratohyal is hourglass-shaped, with a

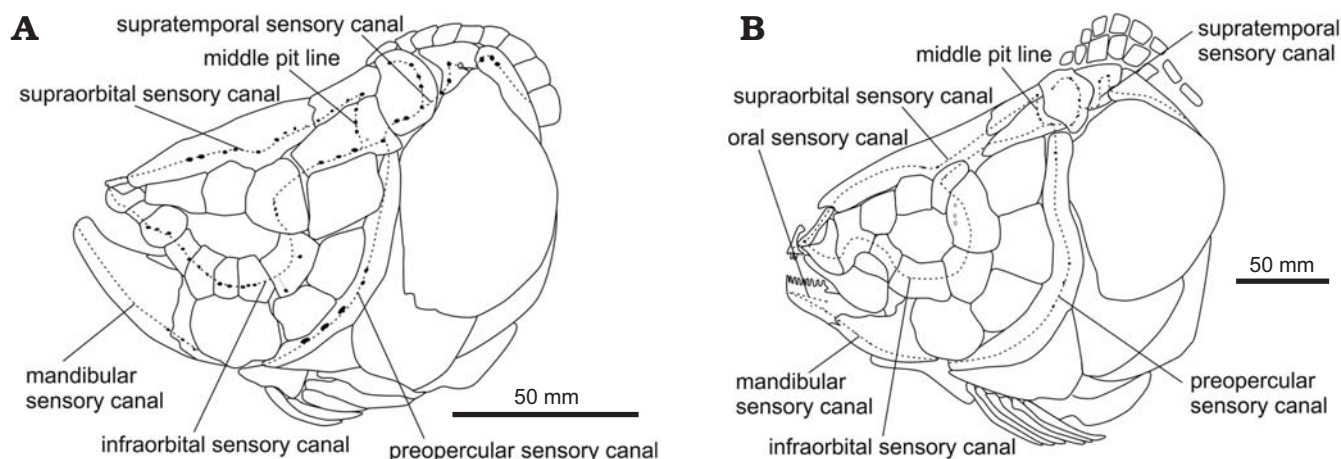


Fig. 14. Ginglymodian fish *Isanichthys lertboosi* sp. nov.; Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. Reconstructions of the skull with the path of sensory canals. **A.** KS36-3. **B.** KS34-281. The head is 200 mm in average length.

slightly convex posterior border. There is a weak groove running on the median region of the lateral surface of the bone. The posterior ceratohyal is roughly triangular in shape, with a regularly curved margin contacting the anterior ceratohyal.

Pectoral girdle.—The posttemporal is visible as a crescent-shaped ossification with a notch along its posterolateral margin for the exit of the sensory canal (Fig. 4). The supra-cleithrum is an ovoid ossification and its dorsal border articulates with the posterior margin of the posttemporal. The path of the sensory canal is indicated by three pores that open adjacent to the exit of the sensory canal. The cleithrum is a long and curved ossification, proportionally narrow on its exposed part, which is overlapped by the opercular series. The lateral face of the cleithrum bears traces of enamel. The posterior margin of the bone is curved. In KS34-281, the ventral margin of the cleithrum shows a concavity for the insertion of the pectoral fin (Fig. 5A). The horizontal limb of the cleithrum is rather short and deep, with its lateral face marked by a smooth ridge. One gently curved postcleithrum is visible.

Cephalic sensory canal.—The anterior part of the lateral line is indicated by a series of pores located on the dorsal margin of the supra-cleithrum, then by a pore located in the concavity of the middle part of the posttemporal and by one on the anteroventral edge of this ossification. The occipital sensory canal (forming the supratemporal commissure) is indicated by a series of pores that open along the posterior edges of extrascapular ossifications. The supraorbital canal marks an angle at the level of the posterodorsal corner of the orbit, and several pores along the lateral margin of the frontal and along the lateral margin of the parietal. The canal passes through the nasal along the longitudinal axis of the bone. There is one pore visible on the anterior tip of the nasal in specimens KS36-2 and KS34-281. The middle pit line is indicated by a groove and pores opening between parietal and dermopterotic close to the posterior edge of these bones. The supratemporal sensory canal extends along the dermopterotic through the dermosphenotic, which marks the connection with the in-

fraorbital sensory canal. The infraorbital sensory canal runs in the centre of the infraorbital ossifications, and gives off openings located near the ventral and posterior margin of the infraorbitals located respectively ventrally and posteroventrally to the orbit. There is no evidence of a sensory canal running within the supraorbital bones. The preopercular sensory canal presents several pores along the horizontal and vertical branches of the ossification: three elongate pores open in the curvature of the bone near its ventral margin and two smaller pores open more dorsally (KS36-3), and two pores are visible close to the dorsal margin of the preopercle in KS34-281. The mandibular sensory canal gives off two or three pores in the angular, and approximately six pores in the dentary arranged in two lines in KS34-281, the dorsal one corresponding to the oral canal.

Pectoral fins.—The pectoral fin of KS36-2 is composed of three basal fulcra—the anterior one, unpaired, is followed by two elongate and paired ones—and two fringing fulcra (only two basal fulcra are visible in Fig. 15A because of the angle). The unsegmented basal portions of ten rays are visible in KS36-2.

Pelvic fins.—The pelvic fin consists of two basal fulcra, the anterior of which is unpaired and the second paired (both halves of the paired fulcrum are visible in Fig. 15B), five thin fringing fulcra and five rays. The rays are very long, representing 47% of the head length (KS36-2; fin length 90 mm, head length 190 mm)

Unpaired fins.—The dorsal fin is visible on KS36-2 and more completely on KS36-3 (Fig. 16) while the anal fin is lacking in all specimens. The dorsal fin is composed generally of four basal fulcra (the anterior one is unpaired and the other are paired on KS36-2), approximately eight fringing fulcra and 12 rays (KS36-3, Fig. 16C). The fringing fulcra are slightly curved and very elongated, the first one being equal to half the length of the first ray. The first third of the length of the rays is not segmented. A first longitudinal division of the ray occurs at mid-length, and a second division occurs approxi-

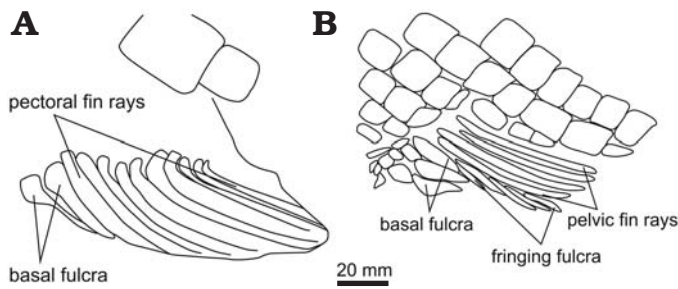


Fig. 15. Ginglymodian fish *Isanichthys lertboosi* sp. nov., KS36-2 (holotype); Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. **A.** Pectoral fin. **B.** Pelvic fin.

mately at the third quarter of the length of the rays. Although the very tips of the rays are usually not preserved, the outline of the fin observed in KS36-3 seems to indicate that the distal margin of the fin was straight.

As for the other fins, the caudal fin is poorly preserved (Fig. 17). The dorsal lobe is preceded by an indeterminate number of fulcra, whose arrangement cannot be exactly described. The ventral lobe is preceded by at least two basal fulcra and 12 small and thin fringing fulcra. There are probably 25 rays, 12 in the ventral lobe separated by a deep fork in the squamation from the 13 in the dorsal lobe. Each ray divides three times. The ventral lobe of the caudal fin equals approximately 60% of the head length and we can infer that the dorsal lobe, poorly preserved on the available material, was similar in size (the tail is usually externally homocercal in ginglymodians).

Squamation.—Based on the general outline, we can estimate the number of scales along the lateral line as approximately 53, 12 scales along a row from the anterior extremity of the dorsal fin to the lateral line and 25 scales in the mid-line between the head and the dorsal fin. The shape of the scales varies depending on position on the body. The anterior margin of individual scales bears a peg articulation as in most ginglymodians (see Cavin et al. [2009] and López-Arbarello [2012] for a discussion of this character). The lateral line scales are marked with a small pore on their surface. The posterior extremity of the scales forms a blunt spine, sometimes more acute, especially in the posterior part of the trunk. In KS36-2, the median dorsal scales are longer than broad, rhomboidal in shape and have a slightly concave surface. There are very elongate spines in KS36-3.

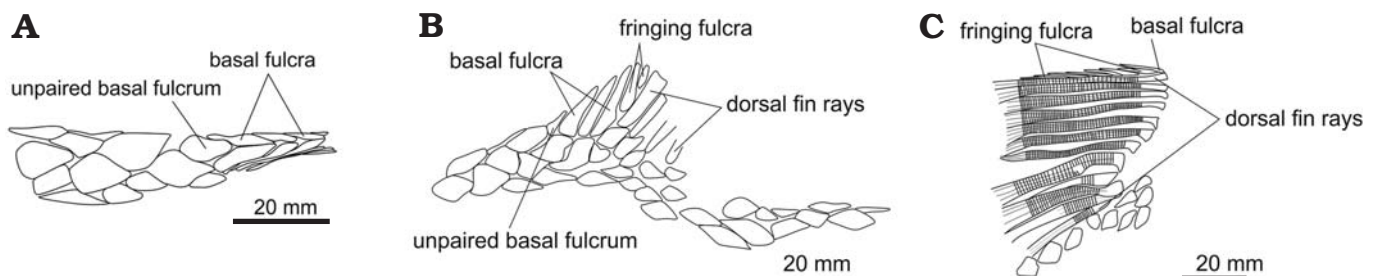


Fig. 16. Ginglymodian fish *Isanichthys lertboosi* sp. nov.; Phu Kradung Formation, Late Jurassic; Kalasin Province, Northeastern Thailand. **A.** KS36-2, dorsal fin in dorsal view. **B.** KS36-2, dorsal fin in lateral view. **C.** KS36-3, dorsal fin in lateral view. All branchings and segmentations of the rays are not drawn, although present, because they are hardly visible on the specimen.

Isanichthys palustris Cavin and Suteethorn, 2006

Holotype: TF 7764, a nearly complete individual, only known specimen.

Type locality: Phu Nam Jun, Thailand.

Type horizon: Upper part of the Phu Kradung Formation, probably Berriasian.

Emended diagnosis.—*Isanichthys* with the body elongated and slender, with the total length 5.5 times the estimated maximum depth, and 4.5 times the head length (including the opercular series); 8–9 suborbitals arranged in a mosaic pattern; no dermal component of the sphenotic; infraorbital and suborbital bones strongly ornamented; median dorsal row of scales without posterior spine; two pairs of extrascapulars; toothed maxilla; dentary bearing approximately 12 small cylindrical teeth.

Remarks.—*Isanichthys palustris* Cavin and Suteethorn, 2006 was identified on the basis of a single specimen from the Phu Nam Jun locality, Thailand. Although from the same formation, i.e., the Phu Kradung Formation, the Phu Nam Jun locality is stratigraphically higher in the formation, close to its top, and consequently the fish assemblage of this locality is likely younger than the assemblage from the Phu Noi locality. The description of *I. lertboosi* led to a re-examination of the specific characters of the type species.

Isanichthys latifrons (Woodward, 1893)

Material.—BMNH P.6838, subcomplete individual; BMNH P.6840, isolated skull bones; BMNH P. 6841 (holotype) isolated but articulated skull bones and scales; BMNH P. 45620, head; from Middle Jurassic of the United Kingdom (for details see Cavin 2010).

Emended diagnosis.—*Isanichthys* with most of the dermal ossifications of the skull ornamented with tubercles of ganoin; skull roof proportionally short, being approximately 1.5 times longer than wide; parietals asymmetrical; preorbital region reduced; ca. 12 suborbitals arranged in a mosaic pattern; semi-tritorial dentition; two pairs of extrascapulars; toothed maxilla.

Remarks.—*Isanichthys latifrons* (Woodward, 1893) was originally described as *Lepidotes latifrons* by Woodward (1893) on the basis of material from the Oxford Clay of Northamptonshire, UK. Woodward (1893) compared the skull of this

species to the Early Jurassic “*Dapedius*” (= *Dapedium*), to which it was thought to be closely related. Later, Jain (1983) discussed some characters of this species.

Isanichthys latifrons possesses characters of the genus *Isanichthys* such as the strongly ornamented bones of the skull roof, the frontal only slightly narrower anteriorly than posteriorly, the frontal less than 2.5 times longer than the parietal, two supraorbitals, the cheek region completely covered by bones, the preopercle slightly curved, the maxilla forming a thin blade with a posterior rounded plate-like part, a posttemporal fossa and an oral sensory canal, ratio of skull length to orbit length greater than 6, and the quadrate situated below the orbit. Moreover, based on the proportions of the skull and the reconstruction figured by Jain (1983), the anterior infraorbital would have been deep, and the anterior supraorbital would have closed the orbit anteriorly and should have contacted two infraorbitals, three other characters diagnostic of *Isanichthys*. In contrast to the other *Isanichthys* species, *I. latifrons* bears small tubercles of ganoin of its dermal skull bones, and other specific characters mentioned in the diagnosis above.

Isanichthys luchowensis (Wang, 1974)

Fig. 18.

Holotype: CDUT cv 002, a nearly complete individual, only known specimen.

Type locality: Upper Shaximiao Formation, Sichuan, China.

Type horizon: Early to Middle Jurassic.

Emended diagnosis.—*Isanichthys* with preorbital region reduced; no tritorial dentition; few infraorbitals (7) and few suborbitals (6) arranged in one row; dentary and premaxilla bearing strong teeth with vertical shaft and conical cap; no conspicuous dorsal median ridge scale.

Remarks.—“*Lepidotes*” *luchowensis* was described by Wang (1974) from the Upper Shaximiao Formation in Sichuan, a series of continental Early to Middle Jurassic deposits (Chang and Jin 1996). We have studied the only known specimen

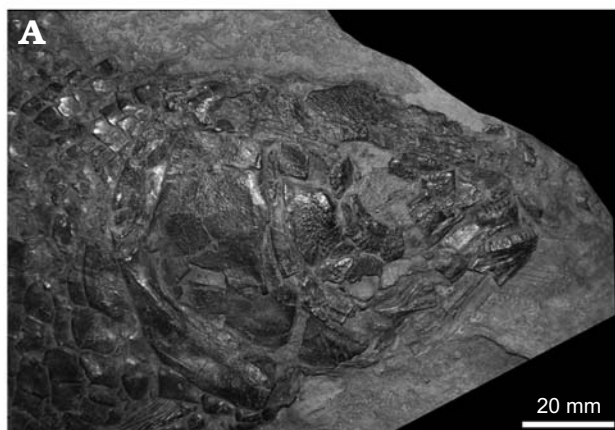


Fig. 18. Skull of ginglymodian fish *Isanichthys luchowensis* sp. nov., cv 002; Early or middle Jurassic of Sichuan, China. **A.** Photograph. **B.** Semi-interpretative line drawing.

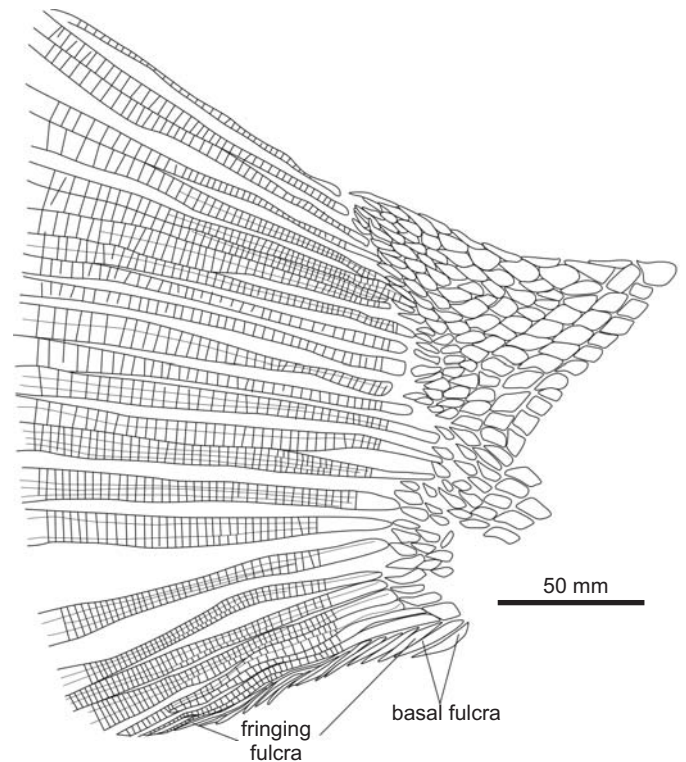
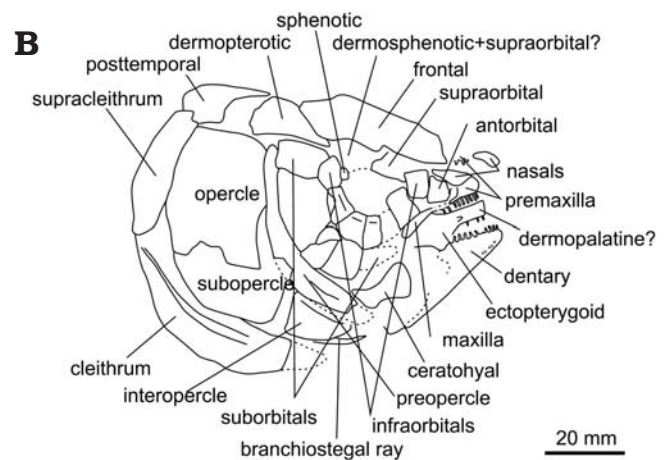


Fig. 17. Ginglymodian fish *Isanichthys lertboosi* sp. nov., KS36-2 (holotype); Phu Kradung Formation, Late Jurassic; Kalasin Province, North-eastern Thailand. Caudal fin in right view. All branchings and segmentations of the rays are not drawn, although present, because they are hardly visible on the specimen.

(CDUT cv 002), and we review only those osteological characters which are important in the comparison with the Thai material, or characters for which we disagree with the original description by Wang (1974). The dermal bones, especially the circumorbital ossifications, bear strong, densely arranged tubercles. The frontal is almost complete, except the anterior extremity and the medial border, which are broken. It is roughly rectangular and only slightly narrower anteriorly than posteriorly. The parietal and extrascapular are not preserved.



The dorsal margin of the orbit is bordered by a supraorbital anteriorly, which contacts an infraorbital. Posterior to the anterior supraorbital is a large impression in the matrix, which is deeper posteriorly than anteriorly and has curved dorsal and ventral margins. This impression would have contained the dermosphenotic, and possibly a posterior supraorbital as figured by Wang (1974), but this arrangement is uncertain. The infraorbital series consists of seven infraorbitals with the anteriormost one not contacting the orbit. There are six suborbitals arranged in one row (with two small ossifications arranged transversely to the row, but the whole pattern cannot be regarded as a mosaic pattern). The oral process of the premaxilla is well developed and bears at least six strong conical teeth with a bulbous cap. The nasal process of the premaxilla is covered by the nasal. Posteriorly to the series of premaxillary teeth, two more teeth are visible, and these are borne on a poorly preserved ossification. We identify this bone as the maxilla. Posterior to this element is a better preserved elongated rod of bone, which was interpreted as a supramaxilla by Wang (1974), and that we identify as the continuation of the maxilla. Ventral to the premaxilla is a broad ossification, with a quadrangular anterior extremity and a broadened posterior part that Wang identified as a maxilla. Four, widely spaced teeth are present in the anterior half of the bone. Because of its shape and position—the ossification extends ventrally to the premaxilla, and it extends posteriorly beneath the maxilla and coronoid process—we consider that this element represents part of the suspensorium, probably the anterior extremity of the ectopterygoid and the dermopalatine (but no suture is visible in this element). The anterior part of the dentary bears ten conical teeth with a bulbous cap on its anterior rim. The anterior part of a deep coronoid process, probably formed by the dentary, is preserved. The imprints of the posterior part of the mandible show the limit of the dentary, which develops an elongated posterior process that does not reach the posterior margin of the lower jaw, and shows a deep impression corresponding to the sensory canal that runs along the centre of the bone and opens with three large pores at its anterior part. The preopercle is narrow and gently curved. The anterior part of the horizontal limb is missing, but we can estimate the shape from the trace of bone. The opercle is approximately rectangular in shape and deeper than long. The subopercle is well developed with a vertical limb reaching half the depth of the opercle, and the interopercle is visible as a large triangular bone. The posttemporal, supracleithrum, cleithrum, and postcleithrum are preserved. The cleithrum has a narrow vertical limb and a broader horizontal limb. The anterior end is missing but we can determine the limit of the bone from the imprint. A portion of the branchial lamina extending under the subopercle is visible dorsally. A band of denticles extends along the ridge that separates the branchial from the lateral surface of the cleithrum. This band is broader than in *Semionotus elegans* (Newberry, 1888) (Olsen and McCune 1991), *Propterus* Agassiz, 1834 (Bartram 1977) but reminiscent of the eight to ten parallel bands of denticles in *Lepidotes glorioae* Thies, 1989.

Only a few characters visible in the type specimen of *Isanichthys luchowensis* are diagnostic for the genus *Isanichthys*. These are: the strongly ornamented bones of skull roof, the frontal only slightly narrower anteriorly than posteriorly, the cheek region completely covered by bones, the slightly curved preopercle, the ratio of skull length to orbit length greater than 6, the quadrate situated below the orbit. The grouping of *I. luchowensis* with the other species of that genus also rests on the optimization of some characters, which are unknown in the Chinese species, and consequently this identification should be regarded as tentative (see phylogenetic analysis below). Characters distinguishing this species are mentioned in the diagnosis above.

Discussion

The material from the Phu Noi locality is referred to *Isanichthys* because it shares with the type species the absence of continuous ganoin cover on the strongly ornamented skull roof bones; the frontals only slightly narrower anteriorly than posteriorly; ratio of frontal length to parietal length less than 2.5; two anterior infraorbitals not in contact with the orbit, the anteriormost infraorbital deeper than long; two supraorbitals, the anterior one generally elongated with its anterior margin contacting the first or second infraorbital; cheek region completely covered by bones; preopercle slightly curved; the maxilla formed by a posterior rounded plate-like part, a thin anterior part and an inwardly articular process; one supra-maxilla; epiotic with a short and simple posteriorly directed process; the orbital ring closed; the ratio of skull length by orbit length more than 6; quadrate below the orbit. However it differs from the type species by the occurrence of three extrascapulars (versus four in *I. palustris*), the number and arrangement of suborbitals (4–6 suborbitals arranged in a single row in *I. lertboosi*, versus numerous plates arranged in a mosaic pattern in *I. palustris*), an edentulous anterior portion of maxilla in *I. lertboosi* while few cylindrical teeth are present in *I. palustris*, the cheek bears weak ornamentation in *I. lertboosi*, versus coarse radiating ornamentation from centres of ossification in *I. palustris*, the number of branchiostegal rays (six elongated branchiostegal rays in *I. lertboosi*, at least ten in *I. palustris*) and the presence of conspicuous dorsal ridge scales (scales on the mid dorsal with a posterior spine in *I. lertboosi* and none in *I. palustris*).

KS34-281 shows differences from the holotype (KS36-2) such as a lower number of infraorbitals and suborbitals (8 infraorbitals in the holotype and 6 in KS34-281, with the last infraorbital almost twice deeper than long in KS34-281 and longer than deep in the holotype; 6 suborbitals in the holotype and 4 in KS34-281), the shape of the anteriormost supraorbital (in the holotype it extends more anteriorly than in KS34-281), a difference in the shape of the preopercle (it is slightly curved in the holotype whereas it is more angled in KS34-281), the shape of the ventral margin of the opercle is curved in KS34-281 and straight in the holotype, and the obvious difference in

the shape of the teeth. However, the cheek pattern is usually polymorphic in fossil species of ginglymodians known from large samples. For instance, in *Thaichthys buddhabutrensis* (Cavin et al. 2013), a species described on the basis of more than 200 specimens, the number of infraorbitals and their pattern show differences between specimens, and even between both sides of a single specimen. Because of the small available sample of specimens of *Isanichthys lertboosi*, it is difficult to decide at present if the differences between the holotype and KS34-281 correspond to polymorphism or to specific characters. We prefer to keep both specimens in the same species pending the discovery of new material.

Cladistic analysis.—In order to test the monophyly of the genus *Isanichthys* and to assess its phylogenetic relationships with other ginglymodians, we included the characters of the new taxon in the data matrix used in Cavin et al. (2013). The list of examined specimens is available in the electronic supplementary material of Cavin (2010). Because of new data, we added one character, the anterior supraorbital bone contacts one infraorbital versus more than one (character 90), and we altered the states of character 31 dealing with the supraorbital(s): supraorbital absent (state 0), one (state 1), two (state 2), or more than 2 (state 3) (versus supraorbital absent/present in Cavin et al. 2013). We also included new data from a recent description of new ginglymodians by Schröder et al. (2012) from the Late Jurassic of Europe. On the basis of this study, we included in the analysis a new taxon from the Solnhofen locality, *Macrosemimimus fegeerti*, we altered the coding of some characters of *Macrosemimimus lennieri* (previously referred to “*Lepidotes*” *lennieri*, with “*L.*” *toomb-si* as a junior synonym), and we added a new state for a character discussed in Schröder et al. (2012) concerning the arrangement of suborbital ossifications: “two suborbitals, the ventral one much larger than the dorsal one” (character 29). We also completed the data matrix from Cavin et al. (2013) for *Isanichthys latifrons* with information from Woodward (1893). Several states of characters for this species are based on the specimen NHMUK P.6841. It consists of a completely disarticulated skull and postcranial elements. The dermal ossifications of the skull are well preserved and fit to each other, which permitted its reconstruction in 3D. The coding of some of the characters is based on this reconstruction. We altered the names of some of the terminal taxa used in the analysis of Cavin et al. (2013) following the recent phylogenetic analysis by López-Arbarello (2012). Finally, we added to the previous analysis *Lepidotes luchowensis*, from the Early or Middle Jurassic of Sichuan, on the basis of direct examination of the single known specimen. We are aware that other Chinese species of ginglymodians represent interesting candidates for this analysis, but a review of all this material is beyond the scope of this paper. Supplementary Online Material at http://app.pan.pl/SOM/app59-Deesri_etal_SOM.pdf shows the list of characters and the data matrix.

The parsimony analysis was run in PAUP* 4.0b10 (Swofford 2001). A heuristic search (using random addition

sequence, 2000 replications, 10 trees held at each iteration, and tree bisection and reconnection branch swapping) was carried out to try to avoid the “islands of trees” problem (Maddison 1991). Figure 19 shows the strict consensus tree of the 24 most parsimonious trees produced by PAUP (83 characters informative; consistency index 0.38; retention index 0.65). The main pattern of the consensus tree is similar to that obtained by Cavin et al. (2013), except for the position of the genus *Sangiorgioichthys*, which is located in a slightly more derived position than in the former cladogram, and some other minor differences, such as the position of *Lepidotes gloriae*, which was resolved in a broad polytomy gathering several taxa and the Lepisosteiformes, while it is here resolved as the sister-group of this large clade. Although based on different sets of characters, López-Arbarello’s phylogenetic analysis (2012) and the present one show similar relationships for the genus *Isan-*

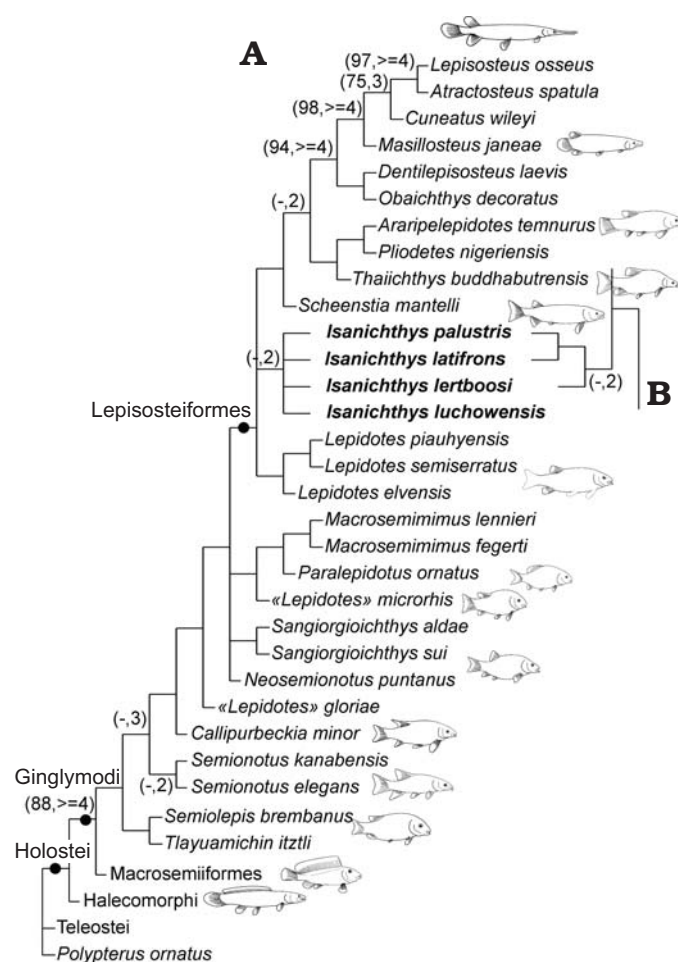


Fig. 19. Phylogenetic hypothesis of ginglymodians interrelationships. A. Strict consensus tree of the 24 most parsimonious tree (305 steps; consistency index = 0.38; retention index = 0.65). All characters are unordered and have equal weight. In brackets are the bootstrap values of the nodes if superior to 50 (3840 replicates) and the Bremer supports if superior to 1. B. Relationships between the species of *Isanichthys* if *I. luchowensis* is removed from the analysis (strict consensus of three trees, 303 steps, CI = 0.38, RI = 0.65). The rest of the cladogram is similar to A.

ichthys, which is resolved together with the genera *Scheestia* and *Lepidotes* as stem Lepisosteiformes. The genus *Lepidotes* includes in our cladogram *L. elvensis* (regarded here as a synonym of *L. gigas*) and *L. semiserratus*, as in López-Arbarello's analysis (2012), but also *L. piahyensis*, a taxon not included in the latter study. Other parts of the cladograms differ significantly between both studies. In particular our analysis did not resolve the Semionotiformes and the Callipurbeckiidae as clades. However, it should be mentioned that most branches of this part of our phylogenetic analysis are weakly supported, as also in López-Arbarello's analysis (2012).

The aim of this paper, however, is not to discuss the hypothesis of relationships within the set of ginglymodian taxa, but to focus on the inter- and intrarelationships of the genus *Isanichthys*. *I. palustris* and *I. latifrons* are grouped together, as already noticed by Cavin (2010) and Cavin et al. (2013) (although they did not remove *L. latifrons* from the genus "*Lepidotes*"). To both species are added here two other species, *I. luchowensis* and *I. lertboosi*, but the relationships between the four taxa are not resolved. Because few characters can be coded for *I. luchowensis* in this phylogenetic analysis (40%), we conducted another analysis without this species. The strict consensus tree (Fig. 19B) is similar to the tree with all taxa, except that *Isanichthys* is resolved as the sister group of *Scheenstia mantelli* + *Lepisosteidae* sensu López-Arbarello (2012) (instead in a trichotomy with *Lepidotes*), and the relationships between the three species of *Isanichthys* are now resolved. *Isanichthys lertboosi* is the sister-group of the pair *I. palustris* + *I. latifrons*. In this new analysis, *Isanichthys* is characterized by six homoplasies, with two observed in all three species: the frontal as broad, or almost as broad, anteriorly as posteriorly (character 19) and the ratio of skull length to orbit diameter greater than 6 (character 36). A third character, presence of a moderately tritorial dentition between palate and coronoids (character 47) is present in *I. lertboosi* and *I. latifrons*, but unknown in *I. palustris*. Other characters are known in one of the three species, or show a reversed state in one of the species. Based on our analysis, *I. palustris* and *I. latifrons* share a mosaic pattern of suborbitals (character 29) and the absence of scale with posterior spine along the dorsal midline (character 85).

Conclusions

The ginglymodian specimens from Phu Noi can be referred to a distinctive new species with confidence. However, the absence of completely preserved specimens and the polymorphic condition observed for several of its characters make its assignment to the genus *Isanichthys* still uncertain. In particular, new material will be necessary to assess if there is more than a single species in this assemblage, and if all are referable to the genus *Isanichthys*. The cladistic analysis provides interesting results with the grouping of three

species, Middle Jurassic to basal Cretaceous in age, discovered in freshwater deposits of South-East Asia and South China. The inclusion in this clade of a species, *I. latifrons* from a Middle Jurassic marine assemblage from Europe, is more unexpected. The results obtained here should be interpreted with caution because this clade is weakly supported and might easily be challenged by new discoveries. However, if true, affinities between species from Eastern Asia with one from Europe are not so surprising if we consider the direct connection between both areas along the northern margin of the Tethys during most of the Mesozoic. As early as the Triassic, marine actinopterygian species belonging to same genera are known in Europe and China (for instance Tintori et al. 2008; López-Arbarello et al. 2011; Lombardo et al. 2011).

Isanichthys lertboosi is the third ginglymodian species from the Phu Kradung Formation to be properly characterized. Other material from this formation, still under study, indicates that at least two other ginglymodian taxa are present. Remains of other actinopterygian clades are extremely rare in the Phu Kradung Formation, and the single known recognized taxon is an isolated spine referred to an indeterminate actinopterygian from the Chong Chat locality and fragments of articulated fishes from Khok Sanam referred to cf. *Ptycholepis* (Cavin et al. 2009). The abundance of ginglymodian remains in the Phu Kradung Formation, as well as in the overlying formations of the Khorat Group deposited mostly in freshwater environments, is certainly caused partly by taphonomic biases. Ganoid scales and thick dermal ossifications of the skull are more prone to fossilize than more fragile bones of most other ray-finned fishes, in particular teleosts.

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