The choristoderan reptile *Monjurosuchus* from the Early Cretaceous of Japan

RYOKO MATSUMOTO, SUSAN E. EVANS, and MAKOTO MANABE

The choristoderan reptile *Monjurosuchus* is described from the Lower Cretaceous Tetori Group of Japan on the basis of an associated specimen from the Kuwajima Formation, Ishikawa Prefecture, and more fragmentary remains from the contemporaneous Okurodani Formation, Gifu Prefecture. This is the first report of *Monjurosuchus* from Japan, but a long-necked choristodere, *Shokawa*, has already been recorded from these deposits. *Monjurosuchus* was first described from the Lower Cretaceous Jehol Biota of China, although it has only recently been recognised as a choristodere. As reconstructed, the Japanese *Monjurosuchus* differs from the type species, *Monjurosuchus splendens*, in the structure of the postorbital region, reduction of the quadratojugal, a slender parietal with a deep groove along the interparietal suture, and elongation of the jugal. As in *M. splendens*, the lower temporal fenestrae are closed. A cladistic analysis was performed in order to place Japanese and Chinese taxa, including the incompletely described Chinese long-necked *Hyphalosaurus lingyanensis*, into choristoderan phylogeny. The results support the monophyly of Neochoristodera and of a Sino-Japanese clade of long necked choristoderes. The placement of the European Tertiary *Lazarussuchus* remains problematic, but the analysis supports its placement within Choristodera rather than on the stem. The identification of *Monjurosuchus* from Japan provides an additional link between the fossil assemblages of the Tetori Group and those of the slightly younger Jehol Biota of China.

Key words: Reptilia, Choristodera, *Monjurosuchus*, Cretaceous, Tetori Group, Kuwajima Formation, Japan.

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Introduction

Japan has a number of terrestrial deposits yielding fossils of Early Cretaceous age (Matsukawa and Obata 1994). Among these, the rocks of the Tetori group of central Honshu are particularly important and have produced many well-preserved vertebrate fossils. Within the Tetori Group, the Berriasian–Hauterivian Okurodani Formation (Shokawa, Gifu Prefecture) is the lateral equivalent of the Kuwajima Formation (Kuwajima, Ishikawa Prefecture; Maeda 1961). Both formations are known for microvertebrate assemblages that represent a diverse terrestrial/non-marine aquatic fauna, including fishes, anurans, turtles, dinosaurs, pterosaurs, lizards, birds, tritylodontid synapsids (Kuwajima Formation only), and mammals (Hasegawa et al. 1995; Evans et al. 1998, 2006; Cook et al. 1998; Manabe et al. 2000; Barrett et al. 2002; Isaji et al. 2005). The choristodere *Shokawa*, described from the Okurodani Formation (Evans and Manabe 1999), differed significantly from any choristodere then known in having a long neck with at least 16 cervical vertebrae. However, another long-necked choristodere, *Hyphalosaurus*, was subsequently reported from the slightly younger horizons of the Jehol Group (Yixian and Jiufotang formations) in China

(Gao et al. 1999, 2000). *Hyphalosaurus* has 19–26 cervical vertebrae and a short, pointed snout. Reinterpretation of the enigmatic *Monjurosuchus* (Endo 1940) added a second choristodere to the Jehol Biota (Gao et al. 2000).

Monjurosuchus is characterized by a relatively short neck (cervical vertebral count of eight, not the usual nine) and a rounded snout. *Shokawa*, *Hyphalosaurus*, and *Monjurosuchus* are rather unusual for choristoderes, but two more derived taxa, *Ikechosaurus* and *Tchoiria*, have also been reported from Lower Cretaceous formations in China and Mongolia (Efimov 1975, 1979; Sigogneau-Russell and Efimov 1984; Brinkman and Dong 1993; Efimov and Storrs 2000; Ksepka et al. 2005). These genera show typical choristoderan characteristics, such as an elongated snout and relatively small orbits, like those of the Late Cretaceous–Early Paleogene Euramerican genera *Simoedosaurus* and *Champsosaurus* (Cope 1876; Brown 1905; Erickson 1972, 1985; Sigogneau-Russell and Russell 1978). Most recently (Gao and Fox 2005), another new small choristodere, *Philydrosaurus*, has been described from the Aptian age Jiufotang Formation (Jehol Group) of China. Early Cretaceous Asian choristoderes thus demonstrate an unexpected degree of diversity.
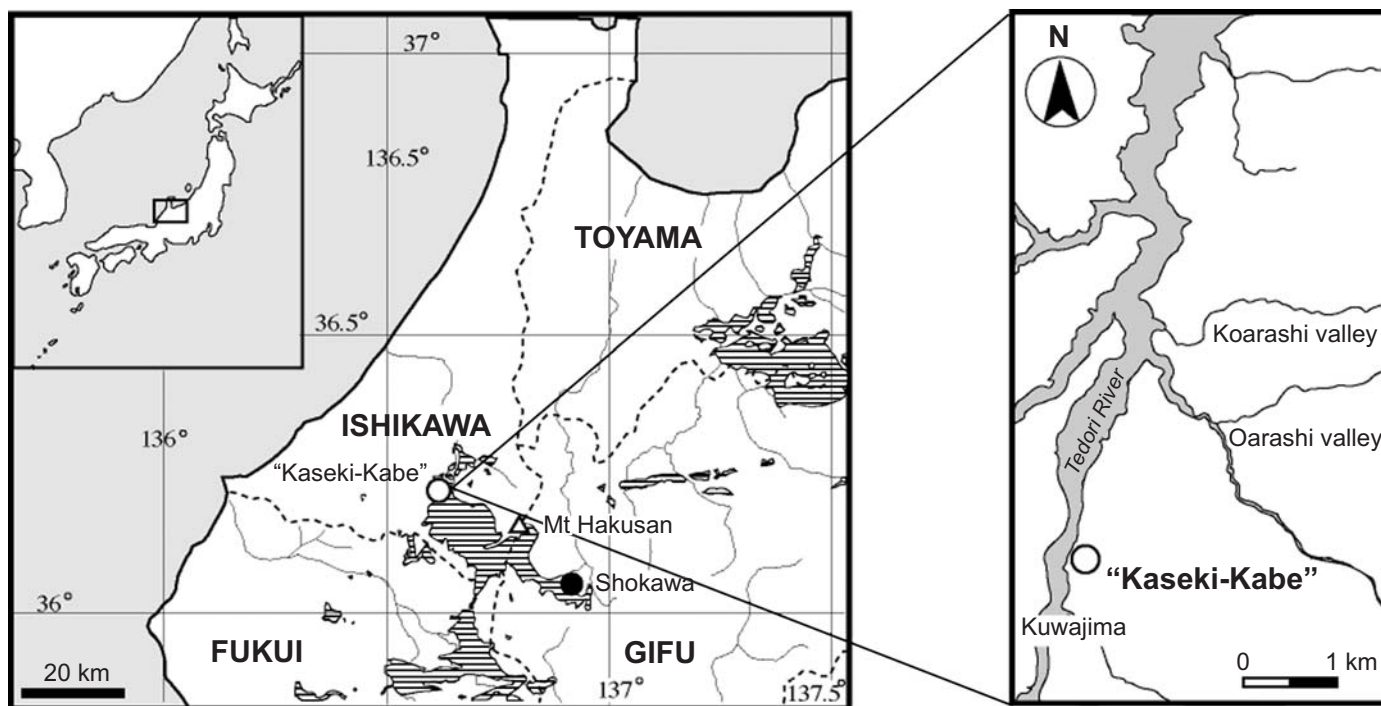
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Fig. 1. Map of north-central Honshu, Japan, showing the "Kaseki-Kabe" locality (Kuwajima Formation) and the Shokawa locality (Okurodani Formation). The hatched area indicates the distribution of the Tetori Group (after Maeda 1961).

New material of *Monjurosuchus* has now been recovered from the Japanese Kuwajima and Okurodani formations, Tetori Group (Matsumoto 2005). This material consists of one association and many disarticulated elements, but they are well preserved without severe deformation. The specimens reveal new anatomical information for *Monjurosuchus* and provide the first record of the genus in Japan. This is the first tetrapod genus to be recorded from both the Jehol and Tetori groups, although the fish *Sinamia* (Stensio 1935) is also known from both (Yabumoto 2005).

The phylogenetic position of Choristodera within Diapsida has been difficult to resolve because of the specialized skull features, including a long snout, a posteriorly expanded skull roof, and a dorsoventrally flattened skull. Romer (1956) classified Choristodera within the paraphyletic diapsid stem group Eosuchia, but most recent works have placed Choristodera within the Archosauromorpha (Currie 1981; Erickson 1985; Evans 1990; Jalil 1997) or as the sister group of Neodiapsida (Gao and Fox 1998). Within Choristodera, the late Oligocene–early Miocene *Lazarussuchus* is particularly problematic. Several analyses have placed it at the base of Choristodera (e.g., Hecht 1992; Evans and Hecht 1993; Evans and Klembara 2005), although these workers also suggested that *Lazarussuchus* might be a derived taxon with some size-linked character reversals (Evans and Hecht 1993; Evans and Klembara 2005). On the other hand, Gao and Fox (1998, 2005) excluded *Lazarussuchus* from Choristodera on the basis that it lacked key choristoderan synapomorphies.

These debates are due in part to the incomplete fossil record of small choristoderes such as *Cteniogenys*, *Hyphalo-*

saurus, *Lazarussuchus*, *Monjurosuchus*, and *Shokawa* (Evans and Hecht 1993; Evans and Klembara 2005; Gao and Fox 2005). The recovery and further study of small choristoderes such as *Monjurosuchus* are therefore important to an understanding of choristoderan evolution. The purpose of this paper is to describe new *Monjurosuchus* material from the Lower Cretaceous of Japan, and to reassess phylogenetic relationships amongst basal choristoderan taxa.

Institutional abbreviations.—DR, Dalian Natural History Museum, China; GMV, National Geological Museum of China, Beijing, China; IBEF VP, Izumi Board of Education, Fukui Prefecture, Japan; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NMM, National Museum of Manchoukuo, China; SBEG, Shokawa Board of Education, Gifu Prefecture, Japan; SBEI, Shiramine Board of Education, Ishikawa Prefecture, Japan.

Other abbreviations.—CI, Consistency Index; MPT, Maximum Parsimony Tree; OTU, Operational Taxonomic Unit; RC, Rescaled Consistency Index.

Geology and materials

Deposits of the Tetori Group are distributed in central Japan (Fukui, Gifu, Ishikawa, and Toyama prefectures; Fig. 1). They are composed of alternating beds of sandstone, mudstone, and conglomerates of Middle Jurassic–Early Cretaceous age, and show a characteristic transition from marine to freshwater

through brackish water environments (Maeda 1961). The Tetori Group is divided into three subgroups: the Middle–Upper Jurassic Kuzuryu Subgroup (Bathonian–Kimmeridgian), the Upper Jurassic–Lower Cretaceous Itoshiro Subgroup (Tithonian–Hauterivian) and Akaiwa Subgroup (Barremian–Albian; Maeda 1961, Matsukawa and Obata 1994). Terrestrial and freshwater vertebrate fossils are known from all subgroups (Azuma and Tomida 1995; Kusuhashi et al. 2002).

In the upper part of the Itoshiro Subgroup, diverse fossil faunas are known from the Kuwajima Formation (Kuwajima [formerly Shiramine], Ishikawa Prefecture) and its lateral equivalent, the Okurodani Formation (Shokawa, Gifu Prefecture). The section spanning the Okurodani and overlying Bessandani formations (Akaiwa Subgroup) has been dated as between 140–120 Ma based on fission-track and K-Ar dating (Gifu-Ken Dinosaur Research Committee 1993). Furthermore, the Kitadani Formation (Akaiwa Subgroup) is considered as late Hauterivian to Aptian on the basis of non-marine molluscs and pollen assemblages (Matsukawa 1977; Matsumoto et al. 1982; Isaji 1993; Umetsu and Matsuoka 2003). These data limit the age of both the Okurodani and Kuwajima formations to Berriasian–Hauterivian.

The uppermost part of the Itoshiro Subgroup, the Kuwajima Formation, and the lowermost part of the Akaiwa Subgroup, the Akaiwa Formation, are distributed in Kuwajima District, Hakusan City (formerly Shiramine Village), Ishikawa Prefecture. Here they form a large bluff known as the "Kaseki-Kabe" along the Tedori River (36°12'N, 136°38'E; Fig. 1). The Kuwajima Formation is overlain conformably by the Akaiwa Formation and consists of massive, medium- to fine-grained sandstone and alternating beds of siltstone and fine-grained sandstone with fossil plants, molluscs, and vertebrates. Several bone-bearing beds lie in the upper part of the formation and a diverse assemblage of vertebrate fossils have been collected from the "Kaseki-Kabe" locality.

At the "Kaseki-Kabe" locality, the bone-bearing beds represent three facies: facies I, carbonaceous sandstones; facies II, dark grey fine-grained silty sandstones; and facies III, dark greenish-grey mudstones (Isaji et al. 2005). The grain size and the fossils (plants and molluscs) indicate that facies I represents a peat marsh, facies II a shallow lake, and facies III a vegetated swamp (Isaji et al. 2005). Each facies preserves a variety of vertebrate remains and most specimens are disarticulated, although some articulated skeletons occur in facies III (Isaji et al. 2005). Fossils show little evidence of abrasion, suggesting they have not travelled over a long distance. Facies II commonly preserves aquatic vertebrates, such as fishes and turtles, whereas facies III is characterized mainly (but not exclusively) by terrestrial vertebrates, such as tritylodontid synapsids, mammals, and lizards.

From 1997 to 2000, a road tunnel was constructed behind the "Kaseki-Kabe". The rocks drilled out during construction were from the upper part of the Kuwajima Formation. This material was preserved and set aside for study and includes four of the specimens described in this paper (SBEI 1223, 1496, 1792, and 2230). It is impossible to give a precise original location for these specimens. The material from the Kuwajima Formation is supplemented by a further specimen from the Okurodani Formation at Shokawa (SBEG 045).

Systematic palaeontology

Diapsida Osborn, 1903
Choristodera Cope, 1884
Monjurosuchus Endo, 1940

Type species: *Monjurosuchus splendens* Endo, 1940; Tanankou, China; Yixian Formation Lower Cretaceous (Hauterivian–Barremian).

Emended diagnosis.—Choristoderan genus characterised by the combination of paired nasals that intervene posteriorly between anterior tips of prefrontals; frontals fused, postero-laterally expanded but markedly narrow and constricted between orbits; prefrontal equal to frontal in length; lachrymal facet on prefrontal longer than maxillary facet; supratemporal fenestra roughly equal to orbital length; postorbitofrontal fused; squamosal square, laterally expanded; infratemporal fenestra closed mainly by the enlarged jugal; interclavicle "T" shaped with straight stem; and fore- and hind feet webbed, with only the claws projecting.

The combination of narrow, fused frontals, a short neck of only eight cervicals, a short rounded preorbital region, and closed lower temporal fenestrae differentiates *Monjurosuchus* from all other described choristoderes (modified from Gao et al. 2000).

Distribution.—Lower Cretaceous (Berriasian–Barremian), Japan and China.

Monjurosuchus splendens Endo, 1940

1940 *Monjurosuchus splendens* sp. nov.; Endo 1940: 1–14, pls. 1, 2.
1942 *Rhynchosaurus orientalis* sp. nov.; Endo and Shikama 1942: 2–6, pls. 1–3.

Holotype: NMM 3671 (reportedly lost during World War II). Tanankou, approximately 10.5 km southwest of Lingyuan, western Liaoning, China. Yixian Formation, Lower Cretaceous (Hauterivian–Barremian; Wang and Zhou 2003).

Neotype: GMV216, an adult individual (Gao et al. 2000). Niuyingzi, Lingyuan, western Liaoning, China; Lower Cretaceous (Hauterivian–Barremian) Yixian Formation (Zhou et al. 2003).

Referred specimens.—IVPP V13273, 13279, 13866, 14269, small juvenile individuals; IVPP V3673, sub-adult individual with skin impressions (originally attributed to *Rhynchosaurus orientalis* by Endo and Shikama, 1942); DR0003C, complete adult individual.

Monjurosuchus sp.
Figs. 2–15.

Material.—SBEI 1223 (dorsal vertebra), SBEI 1496 (left squamosal), SBEI 1792 (block bearing an association of bones), and SBEI 2230 (left squamosal); SBEG 045 (association of right squamosal, jugal, quadratojugal, and quadrate).
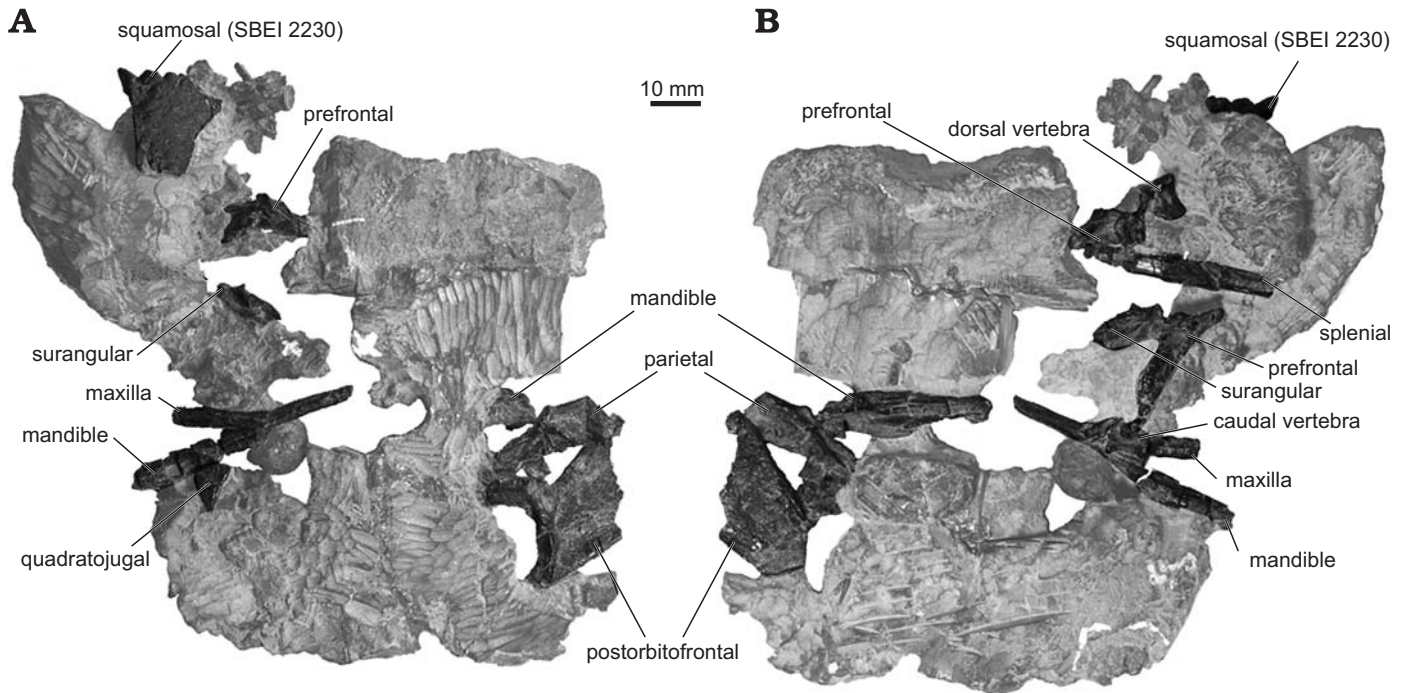
Fig. 2. Choristoderan reptile *Monjurosuchus* sp. (SBEI 1792), Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. Photograph of main block of the holotype. **A** and **B** show alternate sides of the block.

Description.—SBEI 1792 is a block of dark greenish-grey mudstone preserving 25 choristoderan bones including: cervical, dorsal, and caudal vertebrae; right and left prefrontals; right and left dentaries (associated angular); an articulated left maxilla and the anterior part of a jugal; a left surangular; a left splenial; an articulated left squamosal, jugal and quadratojugal; a right quadratojugal; an associated right surangular, prearticular, articular, and angular; an articulated right parietal, the lateral part of the right squamosal, and the posterior part of the right frontal; and an articulated right postorbitofrontal, the anterior part of the right squamosal, the lateral part of the right frontal, and the posterior part of the right jugal. The smaller, more fragile cranial elements and most of the postcranium are not preserved. The bones on SBEI 1792 form an association within a small area of 110 mm × 140 mm × 20 mm (Fig. 2). Most of the bones are at least partly articulated, but four skull elements, the left splenial, surangular, squamosal, and right dentary are isolated, as are the vertebrae. With one exception (see below) there are never more than two examples of each skull element on the block (allowing for the fact that some bones are broken and their parts attached to neighbouring bones), these are always left and right, and they are always of matching size. It is therefore highly probable that the bones on SBEI 1792 constitute the remains of a single individual. Many other associations of this type are known from the same deposit. However, an additional left squamosal, SBEI 2230, is also found on the block (Fig. 2A). It is morphologically identical to the other squamosals, but smaller, and clearly came from a second individual. The presence of this second individual renders SBEI 1792 problematic as a potential holotype, and although the Japanese *Monjurosuchus* is probably specifically distinct from the Chinese *Monjurosuchus splendens*, it is not formally named herein.

Skull (Figs. 3–12).—In Choristodera, the upper surface of the skull is composed of eleven or twelve pairs of bones: nasals, prefrontals, premaxillae, maxillae, lachrymals, frontals, parietals, postorbitals, postfrontals (or combined postorbitofrontal), jugals, squamosals, quadratojugals, and quadrates. Only four elements, the lachrymal, premaxilla, nasal, and quadrate, are not identified in SBEI 1792, but parts of the quadrate are preserved on SBEG 045.

The skull is reconstructed on the basis of SBEI 1792 and isolated specimens (SBEI 1496, SBEG 045; Fig. 3). A skull of *M. splendens* (DR0003C) is shown for comparison (Fig. 4). In SBEI 1792, the partly articulated postorbital elements are preserved, but some preorbital elements are not. As a result, the postorbital skull length can be reconstructed with some confidence, but the preorbital region is more difficult. However, SBEI 1792 preserves a nearly complete right dentary and a left dentary with an associated angular. In addition, a nearly complete right surangular is associated with the angular and a small part of the dentary. From these elements, the length of the mandible can be reconstructed as approximately 70 mm. As reconstructed, the skull preserved on SBEI 1792 is 80 mm in length and about 50 mm wide. The difference between jaw and skull length can be explained by the fact that the quadrate-articular joint lies forward of the posterior limit of the skull. The dermal bones are ornamented with a pattern of anteroposterior striae. As seen in dorsal
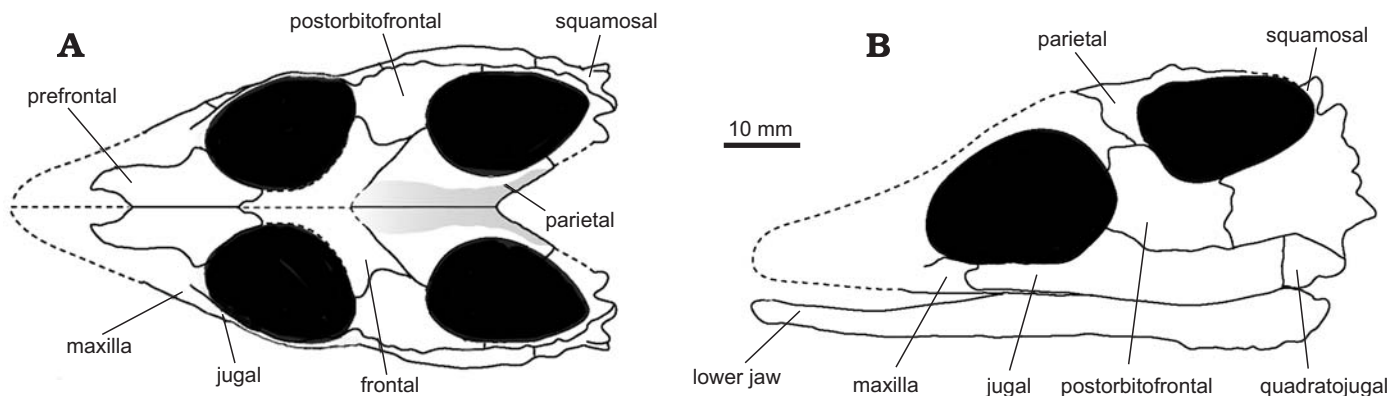
Fig. 3. Choristoderan reptile *Monjurosuchus* sp., Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. Partial reconstruction of the skull in dorsal (**A**) and lateral (**B**) views.
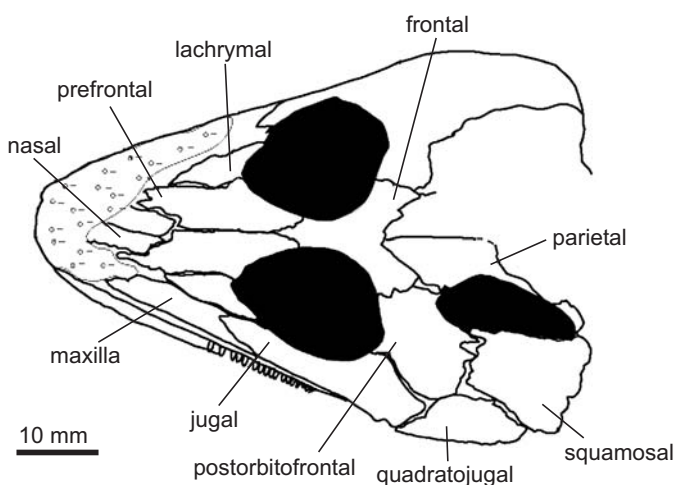

Fig. 4. Choristoderan reptile *Monjurosuchus splendens* (DR0003C), Yixian Formation, Liaoning Province, China. Skull in dorsal view. Circle and dash pattern indicates matrix.
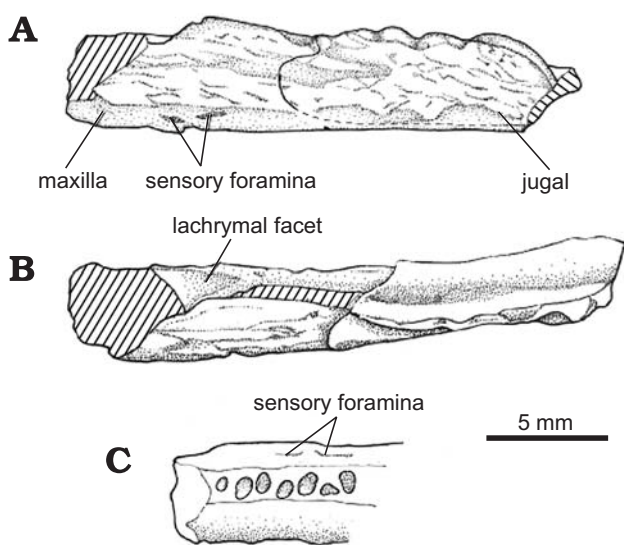

Fig. 5. Choristoderan reptile *Monjurosuchus* sp. (SBEI 1792), Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. Left maxilla and jugal, in lateral (**A**), dorsal (**B**), and partial ventral (**C**) views.

view (Fig. 3A), the orbits are large and dorsally directed and the upper temporal fenestrae are anterolaterally expanded. In SBEI 1792, the squamosal lacks the process for the parietal so the length of parietal process was inferred from an isolated complete squamosal (SBEI 1496). The squamosal process on the parietal is complete, and suggests that the suture between the squamosal and parietal lay half way along the postero-medial border of the upper temporal fenestra. As reconstructed, the length of the upper temporal fenestra is similar to that of the orbit.

The squamosal, quadratojugal, jugal, and part of the post-orbitofrontal lie vertically and form the lateral side of the skull (Fig. 3B). The quadrate is located behind the squamosal/post-orbitofrontal suture so that the lower jaw is posteriorly elongated in comparison to that of *Monjurosuchus splendens*.

An incomplete left maxilla is preserved in SBEI 1792, missing the regions for articulation with the premaxilla and prefrontal but with part of the jugal in association (Fig. 5). The maxilla is mediolaterally narrow and dorsoventrally flattened, with its lateral surface ornamented with a pattern of fine anteroposterior striae and sensory foramina (Fig. 5A). In dorsal view (Fig. 5B), an anteroposterior flange is seen to bear a medially inflected notch-like facet for the lachrymal. Posteriorly, the flange articulates with the orbital ramus of the jugal. At least seven tooth sockets are visible on the maxilla, but all teeth have been lost (Fig. 5C). The implantation is subthecodont and tooth sockets are ovoid.

The elongated right and left prefrontals are both preserved in SBEI 1792 (Fig. 6). The right bone is nearly complete, but the ventral side is covered by matrix (Fig. 6A). The left bone is of equal size but has a crack in the middle, and is partly lacking the frontal process (Fig. 6B). The dorsal surface is horizontal and sculptured, with a well-developed orbital flange bearing weak tubercles (Fig. 6). The straight medial edge bears a deep suture for the opposite prefrontal. The prefrontal tapers posteriorly, and its narrow frontal process enters the rim of the large, dorsolaterally directed orbits. Anterodorsally, there is a small recess for the nasals (Fig. 6A). This is limited to the anterior tip of the bone, and covers
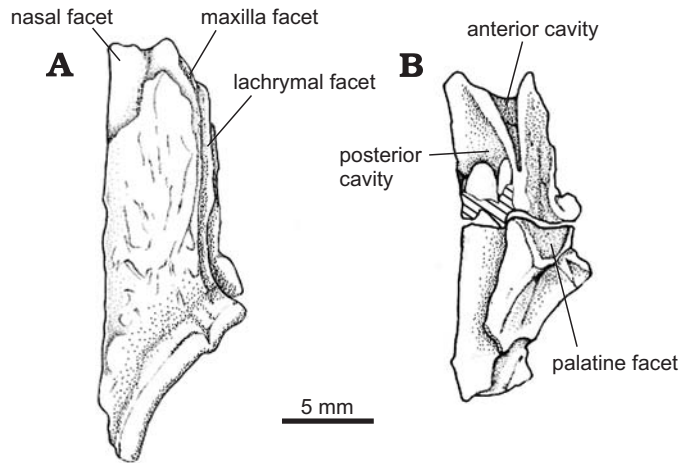
Fig. 6. Choristoderan reptile *Monjurosuchus* sp. (SBEI 1792), Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. **A**. Right prefrontal in dorsal view. **B**. Left prefrontal, in ventral view.
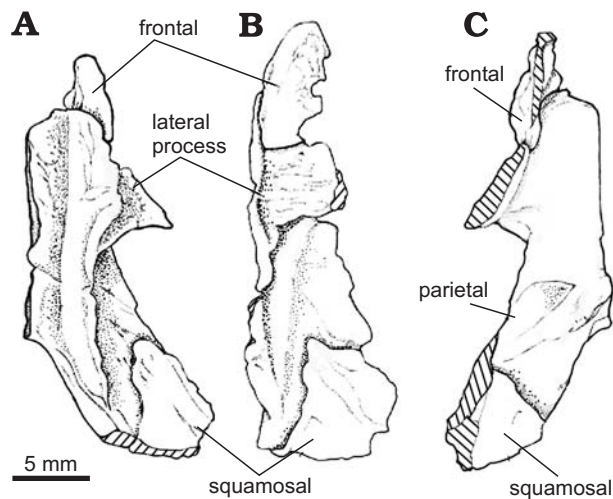

Fig. 7. Choristoderan reptile *Monjurosuchus* sp. (SBEI 1792), Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. Right frontal, parietal, and squamosal, in dorsal (**A**), lateral (**B**), and ventral (**C**) views.

only one fifth of the entire prefrontal length. Laterally, there are anterior and posterior facets for the maxilla and lachrymal respectively (Fig. 6A). The maxillary facet is extremely reduced, and is limited by the anterior part of an elongated lachrymal facet that lies parallel to the interprefrontal suture. Below the lachrymal facet lies the palatine process (Fig. 6B). The anterior nasal cavity terminates in the middle of the palatine process, separated from the posterior nasal cavity by the medial edge of the palatine process (Fig. 6B). Anteroposteriorly, the medial edge forms the margin of a channel leading forward from the frontal into the posterior nasal cavity (Fig. 6B).

SBEI 1792 preserves the right parietal in association with parts of the frontal, and squamosal (Fig. 7). It lacks the tip of the frontal facet and the neomorph process, but is otherwise nearly complete. The bone is anteroposteriorly elongate. As

in all known choristoderes, the parietals are paired and lack a parietal foramen (Fig. 7A). A deep concavity runs parallel to the midline (Fig. 7A). Anterior and lateral processes met the frontal and postorbitofrontal respectively (Fig. 7A, B). Posterolaterally, the parietal is drawn into an expanded squamosal wing that has a strong overlapping facet with the squamosal (Fig. 7A, C).

As in all choristoderes except *Champsosaurus* and *Cteniogenys*, the postorbital and postfrontal are fused without trace of a suture (Fig. 8). The resulting postorbitofrontal is divided into two parts. The main body of the bone contacts the squamosal and jugal and forms the posterior margin of the orbit and the anteroventral margin of the supratemporal fenestra (Fig. 8A). A dorsally expanded wing meets the frontal and parietal and contributes to the posterodorsal margin of the orbit and the anterior margin of the supratemporal fenestra (Figs. 3, 8A). The external surface of the postorbitofrontal is sculptured and the dorsolateral edges are tuberculate (Fig. 8A). The jugal facet is anteroventrally expanded, and is longer than the squamosal facet in lateral view (Fig. 8A). As seen in medial view, the anterior orbital rim is strengthened by buttresses but behind this the bone becomes very thin (Fig. 8B).

The left and right jugals are preserved in SBEI 1792 (Figs. 8, 9), but are fragmented. The anterior part of the left jugal is associated with the maxilla and the posterior part is associated with the quadratojugal and squamosal, but the middle section with facets for the maxilla and postorbitofrontal is missing (Figs. 5A, 9A). The right jugal is better preserved and is associated with the postorbitofrontal and squamosal, but its orbital flange and quadratojugal facet are missing (Fig. 8). Overall, the jugal is anteroposteriorly elongated
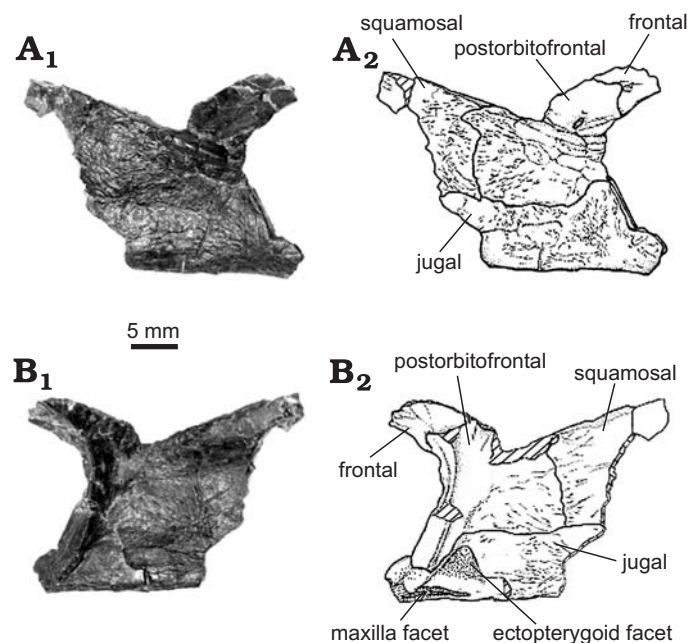

Fig. 8. Choristoderan reptile *Monjurosuchus* sp. (SBEI 1792), Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. Right frontal, jugal, postorbitofrontal, and squamosal, in lateral (**A**) and medial (**B**) views. A_1, B_1, photographs; A_2, B_2, interpretive drawings.
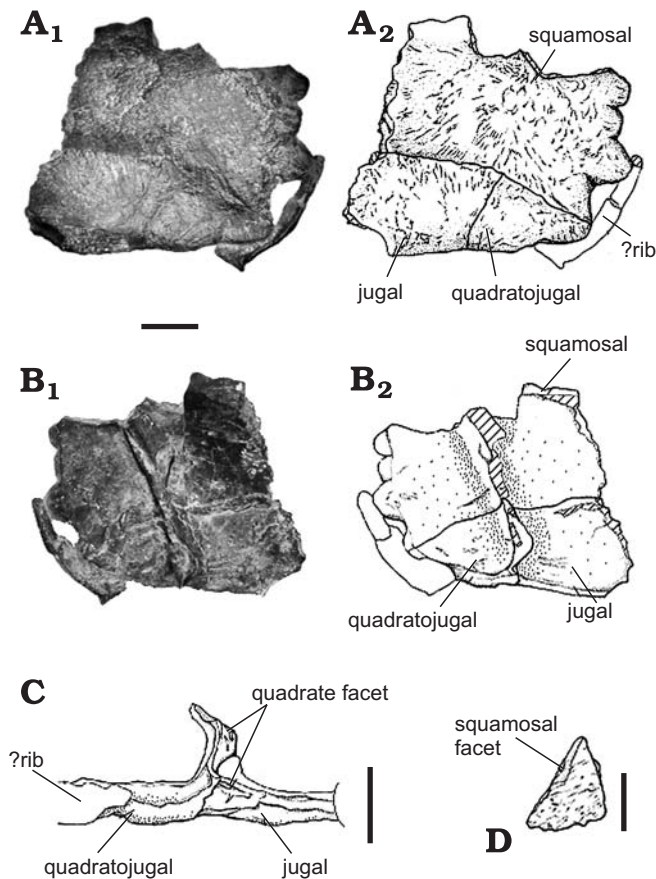
Fig. 9. Choristoderan reptile *Monjurosuchus* sp. (SBEI 1792), Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. **A–C**. Left squamosal, quadratojugal, and jugal, in lateral (**A**), medial (**B**), and ventral (**C**) views. **D**. Drawing of right quadratojugal in lateral view. A_1, B_1, photographs; A_2, B_2, C, interpretive drawings. Scale bars 5 mm.

with a strongly sculptured lateral surface (Figs. 8A, 9A–C). The anterior process is dorsoventrally flattened with a triangular cross-section (Fig. 5A, B). It gives rise to a dorsally expanded flange that forms the curved orbital margin (Fig. 8). In the postorbital region, the jugal is mediolaterally flattened and dorsally expanded, forming the vertical lateral skull margin. Its dorsal and ventral margins run almost in parallel, but the ventral edge is much thicker. The jugal bears a number of distinct facets. The ventromedial maxillary facet lies along the ventral margin, terminating just behind the level of the orbital rim (Fig. 8B). The medial ectopterygoid facet lies above the maxillary facet as a weak notch (Fig. 8B). Dorsolaterally, the jugal overlies the postorbitofrontal, while posteriorly it meets the squamosal and quadratojugal to close the lower temporal fenestra, the squamosal facet being roughly equal in length to the quadratojugal facet (Fig. 9A, D). The quadrate facet is weakly striated and is located just above the junction of the jugal and quadratojugal (Fig. 9C).

The quadratojugals are preserved on SBEI 1792 (Fig. 9) and SBEG 045 (Fig. 10B). On SBEI 1792, the left bone is complete and has an expanded medial surface (Fig. 9A–C); the right bone is detached, and its medial side is covered with

matrix (Fig. 9D). The quadratojugal is reduced to a small triangular plate, ornamented with the characteristic sculpture pattern and a tuberculate ventral margin (Fig. 9A, B). It articulates with the jugal, the quadrate, and the squamosal but does not contact the postorbitofrontal. In lateral view, the quadratojugal-jugal suture is a straight line, subequal in length to the quadratojugal-squamosal suture (Fig. 9A). A medially expanded flange gives the bone an "L" shape in ventral view (Fig. 9C). This flange meets the squamosal dorsally and the quadrate posteriorly, forming a deep quadrate recess (Fig. 9C).

Both squamosals are preserved on SBEI 1792 (Figs. 8, 9A–C), although the right bone is split, with its anteromedial process attached to the parietal (Fig. 7) and its lateral wing associated with the jugal and postorbitofrontal (Fig. 8). The left squamosal is articulated with a jugal and a quadratojugal (Fig. 9A, B). It lacks the dorsal margin and the parietal process. SBEI 2230, the smaller left bone on the same block, is isolated, and it is also missing the parietal process, but SBEI 1496 (Fig. 10A) and SBEG 045 (Fig. 10B) are almost complete. The squamosal is made up of lateral and medial plates. The dorsoventrally expanded lateral plate forms the side of the skull and the lateral margin of the supratemporal fenestra (Figs. 9A, $10A_1$, A_2, B_1, B_2). From anterodorsal to posteroventral, the plate has sutures with the postorbitofrontal, jugal, and quadratojugal (Fig. $10A_2$, B_1, B_2). The medial plate forms the posterior rim of the supratemporal fenestra and extends to meet the parietal (Fig. $10A_5$, B_3, B_4). This parietal process is well-preserved in SBEI 1496, and is seen to be rather square in dorsal view, with an uneven surface (Fig. $10A_3$). Anteriorly, as shown in SBEG 045 (Fig. $10B_3$–B_6), this parietal process bears a small concavity for the quadrate and the quadratojugal. The medial and lateral squamosal plates contact each other vertically (Fig. $10B_5$), although the medial plate is inclined posterodorsally at 45 degrees (Fig. 9B, $10B_4$). The squamosal has a strongly sculptured lateral surface, with spike-like tubercles ornamenting the dorsal and posterior rims (Figs. 9A, 10).

The quadrate is not preserved in SBEI 1792, but supplementary information is available from SBEG 045, an association of the right quadrate, squamosal, quadratojugal, and posterior part of the jugal (Fig. $10B_3$–B_6). SBEG 045 matches SBEI 1792 in the shape and the size of the component elements. The quadrate is triangular, with a narrow dorsal apex capped by a small cephalic condyle (Fig. $10B_3$–B_6). The condyle is located near the lateral surface of the skull and has a smooth surface, but the surrounding facets indicate that no movement could have occurred. The bone is attached to the quadratojugal posterolaterally, the squamosal dorsally, and the jugal laterally (Fig. $10B_3$–B_6). Its medial face is broad and bears a series of interlinked facets for the opisthotic, pterygoid, and neomorph, each separated by grooves (Fig. $10B_3$, B_4). The large, posteroventral pterygoid facet extends about half way up the medial edge, with the deep, anteroventral neomorph facet running beside it (Fig. $10B_3$, B_4). Above these two facets there is a shallower surface for the opisthotic.
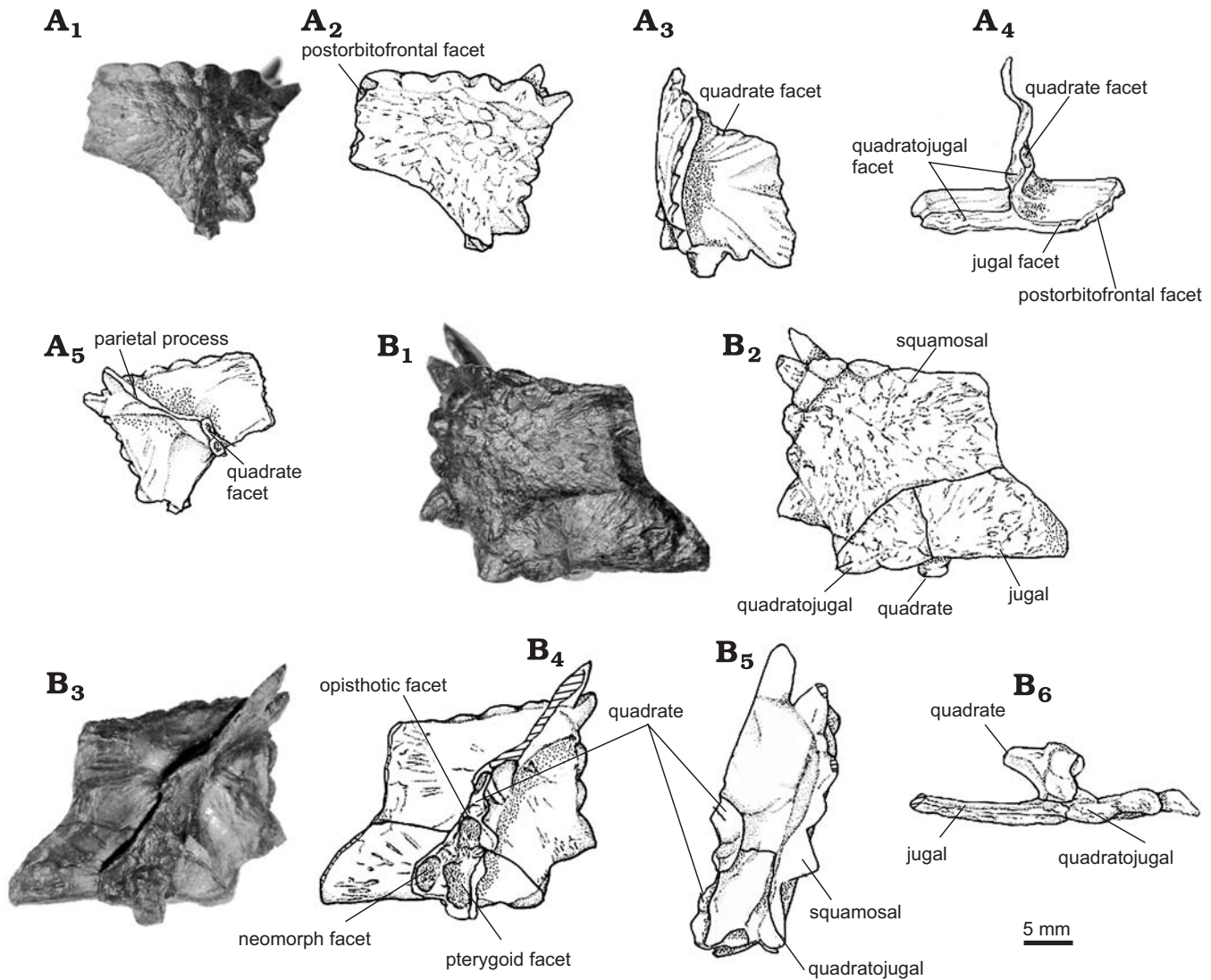
Fig. 10. Choristoderan reptile *Monjurosuchus* sp. **A**. Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. Left squamosal (SBEI 1496), in lateral (A_1, A_2), dorsal (A_3), ventral (A_4), and medial (A_5) views. **B**. Okurodani Formation, Shokawa, Gifu Prefecture, Japan. Right squamosal, jugal, quadratojugal, and quadrate (SBEG 045), in lateral (B_1, B_2), medial (B_3, B_4), posterior (B_5), and ventral (B_6) views. A_1, B_1, B_3, photographs; A_2–A_5, B_2, B_4–B_6, interpretive drawings.

Lower jaw.—In choristoderes the lower jaw is made up of seven bones: dentary, splenial, coronoid, angular, surangular, prearticular, and articular. Of these, six (the dentary, splenial, angular, articular, prearticular, and surangular) have been identified in SBEI 1792.

SBEI 1792 preserves a nearly complete right dentary, and a partial left dentary articulated with an angular (Fig. 11). The dentary is a slender element with the anterior end slightly upturned. The depth gradually increases posteriorly (Fig. 11A). The external surface is finely striated, with a line of sensory nerve foramina, each of which opens into a short groove (Fig. 11A₁). In medial view, the symphysial surface is short by comparison with that of neochoristoderes and *Lazarussuchus* (Fig. 11A₂). The Meckelian fossa is enclosed at the symphysis. Its dorsal and ventral margins run in parallel, but the subdental shelf is thicker than the lower edge (Fig. 11A₂). This resembles the condition in the Jurassic *Cteniogenys*.

Facets for the splenial are clearest on the lower border of Meckelian fossa and show that the splenial was excluded from the symphysis, leaving the anterior part of the fossa open (Fig. 11A₂). The entry foramen of the inferior alveolar canal is not preserved. Towards the rear of the tooth row, the subdental ridge and the lower border of the Meckelian fossa narrow abruptly (Fig. 11A₂). Here the splenial facets end and are replaced by the angular facet in the floor of the Meckelian fossa (Fig. 11A₂). On the left dentary, part of the angular is associated (Fig. 11B). The tooth implantation is subthecodont as in all Choristodera. Most of the teeth have been lost, but four are preserved within the alveoli (Fig. 11A₁). They are conical with a smooth base, as seen in *Cteniogenys*, *Hyphalosaurus*, and *Lazarussuchus*.

The left splenial is preserved, but is lacking its anterior and posterior parts (Fig. 11C). The bone is flat and thin with straight dorsal and ventral margins, and a smooth surface.
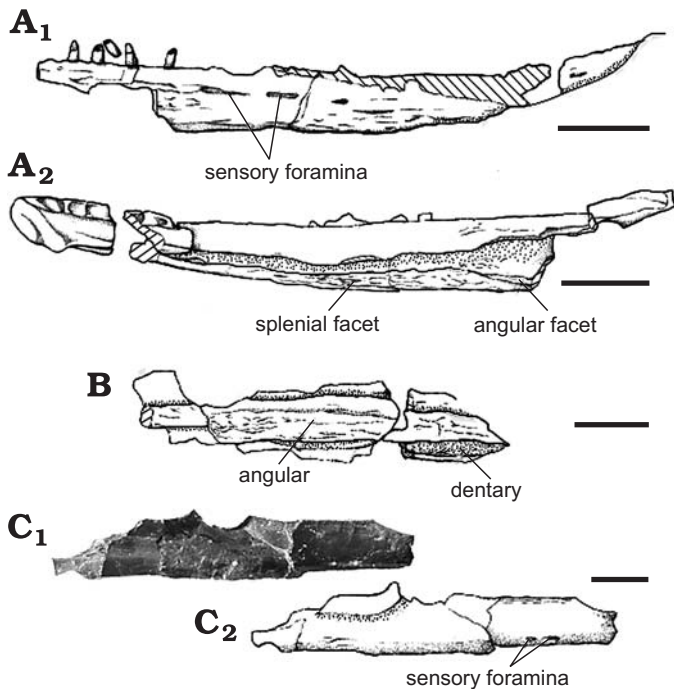
Fig. 11. Choristoderan reptile *Monjurosuchus* sp. (SBEI 1792), Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. **A**. Right dentary in lateral (A_1) and medial (A_2) views. **B**. Left dentary in medial view. **C**. Left splenial in lateral view. C_1, photograph; C_2, interpretive drawing. Scale bars 5 mm.

Two lingual sensory foramina open anteroventrally (Fig. 11C_2). The dorsal margin bears a slight posteromedial inflection, probably to accommodate the coronoid (Fig. 11C).

SBEI 1792 also preserves the left and right surangular. The right bone is nearly complete, and is associated with the dentary, angular, articular, and prearticular (Fig. 12A). The left bone is isolated, and is missing its anterior part (Fig. 12B). The surangular is a robust element that lies along the posterodorsal edge of the mandible. It is almost rectangular with parallel dorsal and ventral margins, and lateral sculpture (Fig. 12A_1, B_1). The bone bears a deep anterodorsal coronoid facet and a broad, ventrolateral angular facet (Fig. 12A_1, B_1). Posteriorly, the latter facet angles dorsally and is bordered by a raised, tuberculate rim. In medial view, the anterior adductor chamber is separated from the posterior articular region by a smoothly curved crest (Fig. 12B_2, B_3), the base of which is robust. The dorsal border of the adductor compartment is thick and posteriorly rounded, whereas the ventral border is incurved (Fig. 12A_2, B_2, B_3). There is a narrow groove facet for the prearticular. Just above it, posteriorly, is the facet for the articular (Fig. 12B_2). The articular fossa is relatively shallow, occupying only the upper half of the surangular (Fig. 12B_2, B_3). This resembles the condition in *Cteniogenys*, *Hyphalosaurus*, and *Lazarussuchus*. In neochoristoderes, such as *Champsosaurus*, *Ikechosaurus*, *Simoedosaurus*, and *Tchoiria*, the articular fossa extends over a larger area and fills almost the entire depth of the surangular. There are no nerve foramina on the medial surface.

The right angular articulates with the surangular and prearticular (Fig. 12A); the left is more fragmentary, but its midsection is preserved in association with the dentary (Fig. 11B). The angular is a long, robust element that contributes to the posteroventral border of the mandible, covering the ventral margin of the surangular. It is therefore exposed both medially and laterally (Fig. 12A). Both surfaces are sculptured, and the posteroventral margin is also tuberculate. The angular runs parallel to the prearticular and narrows posteriorly (Fig. 12A_2). Anteriorly it meets the dentary, extending medially into the Meckelian fossa (Fig. 11B).

The right prearticular is associated with the articular (Fig. 12A_2). It runs above the angular and is anteroposteriorly elongate and slender, with a weakly sculptured medial surface (Fig. 12A_2). The articular (Fig. 12A_2) is robust and posteriorly expanded, lying above the posterior part of the prearticular, and mostly internal to both it and the surangular (Fig. 12A_2).

Postcranial skeleton (Figs. 13, 14).—The only postcranial elements that can be attributed with confidence to the Japanese *Monjurosuchus* are vertebrae.

Fig. 12. Choristoderan reptile *Monjurosuchus* sp. (SBEI 1792), Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. **A**. Right surangular, angular, and prearticular, in lateral (A_1) and medial (A_2) views. **B**. Left surangular, in lateral (B_1), medial (B_2), and dorsal (B_3) views. Circle and dash pattern in A_1 indicates matrix.
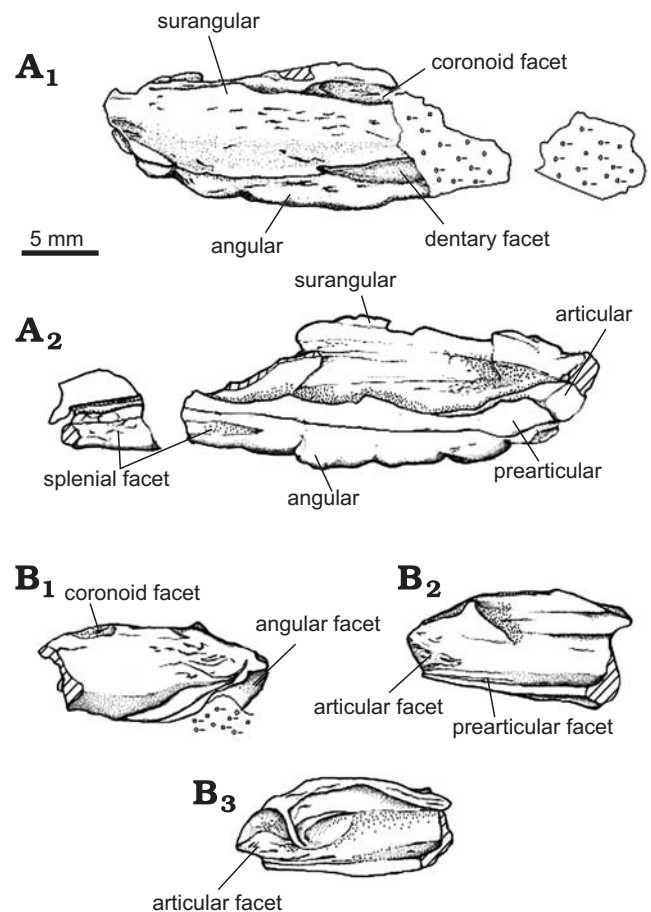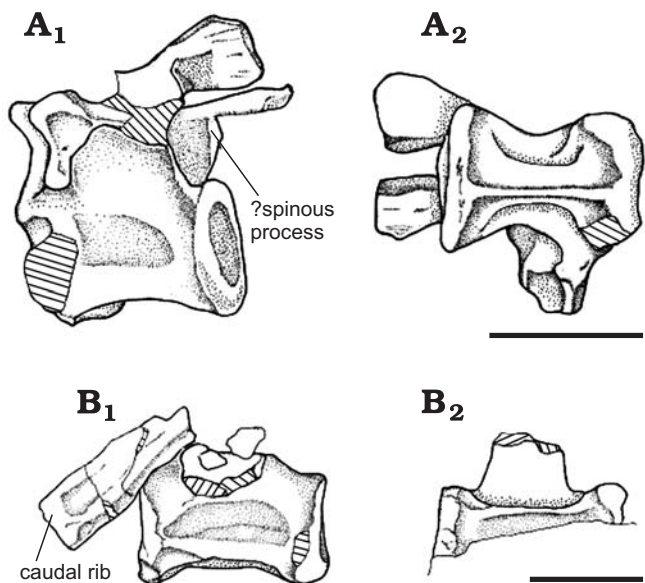
Fig. 13. Choristoderan reptile *Monjurosuchus* sp. (SBEI 1792), Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. **A**. Cervical vertebra, in left lateral (A_1), and ventral (A_2) views. **B**. Partial caudal vertebra, in lateral (B_1) and ventral (B_2) views. Scale bars 5 mm.
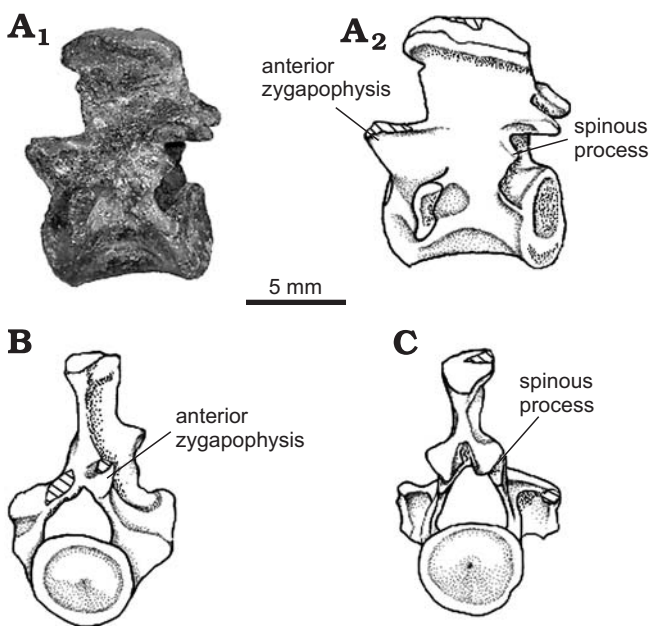

Fig. 14. Choristoderan reptile *Monjurosuchus* sp. (SBEI 1223), Lower Cretaceous Kuwajima Formation, Kuwajima, Ishikawa Prefecture, Japan. Dorsal vertebra, in left lateral (**A**), anterior (**B**), and posterior (**C**) views. A_1, photograph, A_2, interpretive drawing.

A single cervical vertebra is preserved on SBEI 1792, with both the neural spine and anterior zygapophyses broken (Fig. 13A). The neural arch is fused to the centrum, with no trace of the neurocentral suture (Fig. 13A_1). The posterior zygapophysis is a broad, rectangular plate (Fig. 13A_2), and is orientated at 45° to the horizontal. Below it on the right side is a small expansion that may be equivalent to the spinous

process of the dorsal vertebrae (Fig. 13A_1). The transverse process is positioned above the centrum (Fig. 13A_1). Its tip is vertically expanded and bears a posteriorly concave rib facet (Fig. 13A_2). The parapophysis is shorter and is horizontal in orientation. The centrum has a strong midventral keel (Fig. 13A_2), flanked on either side by lateral concavities.

Although two fragmentary dorsal vertebrae are preserved on SBEI 1792, by far the most complete specimen is SBEI 1223 (Fig. 14). This is slightly larger than the vertebrae on SBEI 1792, but has the same morphology. The anterior and posterior zygapophyses are roughly equal in length (Fig. 14A), with the posterior zygapophysis orientated at 45° to the horizontal plane (Fig. 14C). The neural spine has an apex with a smooth surface. There is a small spinous process below the postzygapophyses (Fig. 14A, C), and it bears accessory facets. The transverse process is expanded and single-headed, positioned just above the level of the neurocentral suture, although this is closed without a trace (Fig. 14A). The centrum is platycoelous and is excavated by a shallow concavity on each side of the midline.

A partial anterior caudal vertebra is preserved on SBEI 1792 (Fig. 13B). It is longer than the cervical and dorsal vertebrae. The centrum is concave in lateral view (Fig. 13B_1) and bears a midventral groove for caudal blood vessels (Fig. 13B_2). Part of the caudal rib is fused to the centrum, just above the level of the neurocentral suture (Fig. 13B_1). This rib is rectangular in cross-section and, as preserved, is long and robust although it is broken in the middle (Fig. 13B_1).

Remarks.—SBEI 1792 presents the following choristoderan synapomorphies: median contact of prefrontals along entire length of elements; elongated postorbitofrontal; coarse external sculpture, striated on maxillae; mandibular foramina open into anteroposteriorly oriented grooves; flared posterior temporal region that extends posteriorly; parietal foramen absent; conical subthecodont teeth; slender dentary; and platycoelous vertebral centrum (Evans and Klembara 2005). Furthermore, SBEI 1792 is distinguished from all neochoristoderes (*Champsosaurus*, *Ikechosaurus*, *Simoedosaurus*, and *Tchoiria*) and the Jurassic *Cteniogenys,* in the closure of the lower temporal fenestra and a posterior constriction of the prefrontal that is associated with medially expanded orbits. However, in these two characters SBEI 1792 shows similarities to the Oligocene to Miocene European *Lazarussuchus* (Hecht 1992; Evans and Klembara 2005); the Early Cretaceous Chinese *Hyphalosaurus* (Gao et al. 1999; RM personal observation); and the Early Cretaceous Chinese *Monjurosuchus* (Gao et al. 2000; Evans and Klembara 2005; Gao and Fox 2005), and *Philydrosaurus* (Gao and Fox 2005). SBEI 1792 differs from *Lazarussuchus* in having the following characters states: amphiplatyan vertebral centrum with a closed notochordal canal; posteriorly constricted prefrontal with a much shorter maxillary facet; a shorter mandibular symphysis, limited to one or two tooth positions; and margin of lower jaw anteroposteriorly straight. SBEI 1792 differs from *Hyphalosaurus* in the following characters: the cervical neural arch is taller; the dorsal

neurocentral sutures are closed; the squamosal is more slender in its posterior part; the dentary is more slender; and the prefrontal has a broader maxillary contact.

SBEI 1792 differs from the new *Philydrosaurus* in lacking distinct ridges on the prefrontal and postfrontal, in having distinct ornamentation on the squamosal, and in lacking the distinct supratemporal trough (Gao and Fox 2005).

Apart from attributed jaws, no skull material is yet available for the Early Cretaceous Japanese *Shokawa* (Evans and Manabe 1999). However, SBEI 1792 can be distinguished from *Shokawa* based on characters of the postcranial skeleton: the cervical neural arch is taller; dorsal neurocentral sutures are closed (open in *Shokawa* with centra that are nearly equal in size); centra of caudal vertebra bear a shallow ventral groove for caudal blood vessels (deep ventral flanges flank grooves in *Shokawa*); posterior zygapophyses expand in parallel with each side, as seen in a dorsal view of the cervical vertebra (laterally expanded in *Shokawa*); and cervical diapophysis orientated vertically and above neurocentral suture (horizontally and just on the neurocentral suture in *Shokawa*).

The new Japanese choristodere is very similar to *Monjurosuchus splendens* (Fig. 4). The following comparison is based partly on the description of *Monjurosuchus splendens* by Gao et al. (2000) and Evans and Klembara (2005), but mainly on a study of new complete material in DR (DR0003C, Fig. 4), and IVPP (IVPP V 3673, 13273, 13279, 13866, 14269). The prefrontal of SBEI 1792 matches that of *Monjurosuchus splendens,* but not other choristoderes, in size and shape. Both share a prefrontal with a single facet for the maxilla that is limited to the anterior region between the nasal and lachrymal facets. The latter is extremely long and extends along the lateral margin of the prefrontal. At the anterior tip of the prefrontal, the interprefrontal suture is invaded by the nasal to about one quarter or one fifth of its length. The nasal facets are wedge-shaped. Posteriorly, the process for the frontal is markedly narrow and constricted. However, the prefrontal of SBEI 1792 differs slightly from that of *M. splendens* in the structure of the orbital margin, which bears a steep dorsally directed flange. In *M. splendens,* the orbital margin lacks this flange and is strongly tuberculate instead.

The parietal of SBEI 1792 resembles that of *Cteniogenys* (Evans 1990), *Hyphalosaurus* (RM personal observation), *Lazarussuchus* (Hecht 1992; Evans and Klembara 2005), and *M. splendens* (RM personal observation), and differs from *Philydrosaurus* (Gao and Fox 2005) in having an anterolateral expansion that forms most of the skull roof. The parietal of SBEI 1792 has a broad facet for the squamosal, matching the condition in *M. splendens*. However, there are several differences between the parietal of SBEI 1792 and that of *M. splendens*. In SBEI 1792, the parietal is longer anteroposteriorly and more slender, and the postorbitofrontal and frontal facets are borne on a dorsolateral flange that lies above the level of the interparietal suture. In contrast, the parietal of *M. splendens* is anteroposteriorly short, and the dor-

sal surface of the parietal is flatter, so that the postorbitofrontal and frontal facets lie on the same level as the interparietal suture.

The quadrates of the Japanese choristodere and *Monjurosuchus splendens* differ from those of neochoristoderans in that the lateral part of the quadrate mandibular condyle attaches to the skull margin. The quadrate of the Japanese reptile differs from that of *Cteniogenys* in the position of the neomorph and quadratojugal, having the facets parallel to each other. In *Cteniogenys,* the neomorph facet lies between the pterygoid and opisthotic, and the quadratojugal facet is limited to the posteroventral edge.

In the new Japanese choristodere, the lower temporal fenestra is closed by the elongated jugal and expanded postorbitofrontal and squamosal. *Monjurosuchus splendens* also had a closed lower temporal fenestra (Gao et al. 2000). In both taxa, the compound postorbitofrontal met the frontal anteromedially and the parietal posteromedially. In lateral view, the postorbitofrontal contacts the squamosal anterior to the mid-point of the supratemporal fenestra. The squamosal and postorbitofrontal of both taxa are of similar shape, but the posterior part of the jugal and the quadratojugal of the Japanese choristodere differ from those of *M. splendens* in shape and length. In *M. splendens,* the length of the quadratojugal is roughly one half that of the jugal, whereas an elongated jugal meets the squamosal in the Japanese choristodere but not in *M. splendens*. The jugal meets the quadratojugal anterior to the squamosal/postorbitofrontal junction in *M. splendens,* but behind it in the Japanese choristodere. The squamosal of the Japanese choristodere matches that of *M. splendens* in its shape and in the anteroposterior expansion of the parietal process.

The mandible of *Monjurosuchus splendens* is partially preserved in IVPP V13279, and preserves a terminal symphysis, spanning the length of 1–2 tooth positions, as in SBEI 1792. This is shorter than that of *Lazarussuchus* (roughly six tooth positions; Hecht 1992; Evans and Klembara 2005). Furthermore, the posterior dentary of *M. splendens* (IVPP V13279) is dorsoventrally expanded, as in SBEI 1792. The surangular of SBEI 1792 resembles that of *Cteniogenys*, *Hyphalosaurus*, and *Lazarussuchus* in general shape. In these taxa, the dorsal and ventral margins of the surangular are subparallel, and the articular flange and symphysis lie on the same horizontal plane. In Neochoristodera, the surangular is posteroventrally deflected and the articular flange lies below the level of the symphysis. However, in SBEI 1792, the ventral margin of the surangular is robust and curves medially, unlike that of *Cteniogenys*, *Hyphalosaurus*, and *Lazarussuchus*.

The only postcranial elements known for the Japanese choristodere are vertebrae. The dorsal vertebrae have vertically expanded single-headed transverse processes, and platycoelous cervical, dorsal, and caudal centra with fully closed neurocentral sutures and no notochordal pit. This combination of characters matches only *Monjurosuchus splendens*. However, *M. splendens* and the Japanese choristodere differ in some characters. In the Japanese form, there is a small spinous
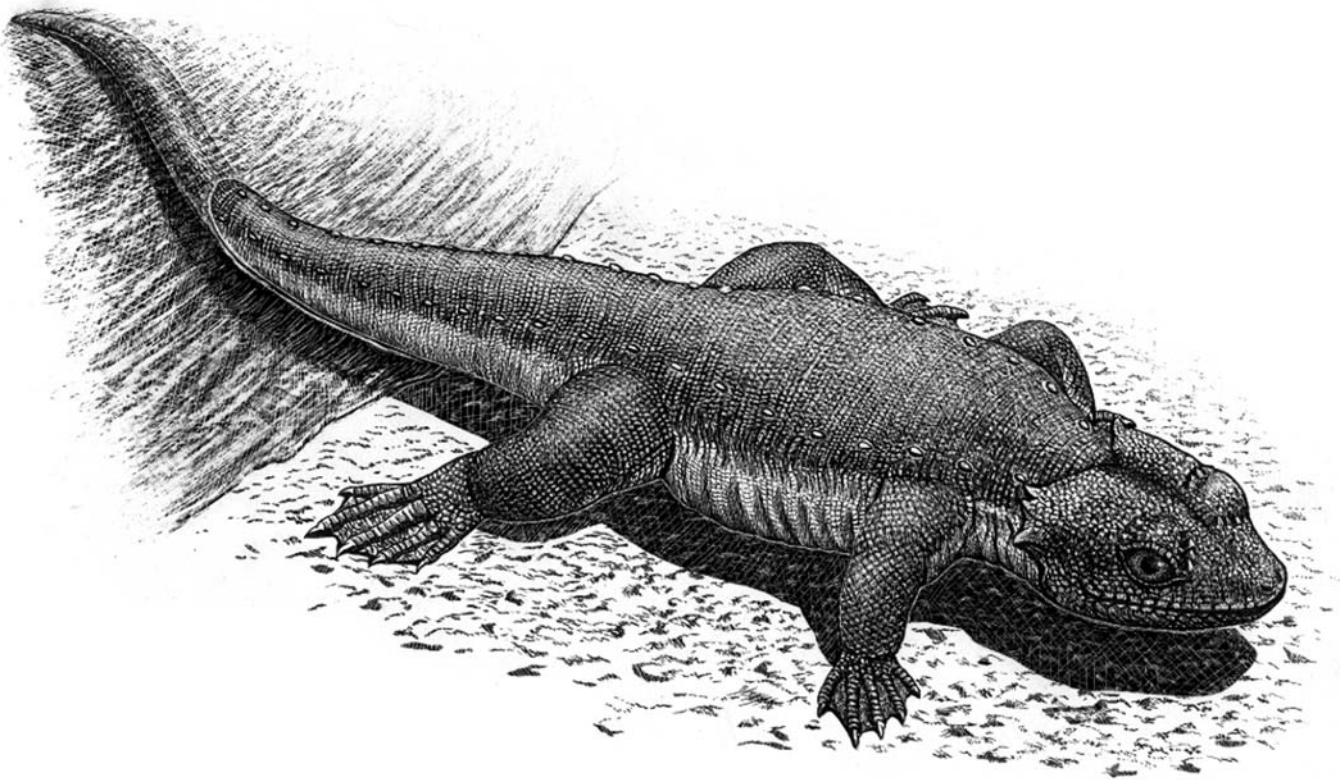
Fig. 15. Life reconstruction of the Japanese *Monjurosuchus*.

process on the rear margin of the neural arch pedicel, just below the postzygapophyses. In *M. splendens*, this spinous process is absent (Evans and Klembara 2005; RM personal observation).

In summary, *Monjurosuchus splendens* and the Japanese choristodere share a unique combination of character states: closure of the lower temporal fenestra and corresponding modification of the jugal, quadratojugal, squamosal, and postorbitofrontal (also closed in *Hyphalosaurus*, *Lazarus-suchus*, and *Philydrosaurus*); a short medial symphysis extending over 1–2 tooth positions; a posteriorly constricted prefrontal that contributes to large medially expanded orbits; steeply sloping, but strongly tuberculate or spike-like projections on the posterior margin of the squamosal (also *Lazarus-suchus*); an anteriorly elongated lachrymal; a prefrontal contacting the maxilla anteriorly through an extremely short facet; and closure of the vertebral neurocentral sutures in the adult. These similarities permit attribution of the Japanese choristodere to *Monjurosuchus*. However, the Japanese *Monjurosuchus* differs from *M. splendens* in the length and width of the parietal and the relative proportions of the postorbitofrontal and frontal facets; the level of the postorbitofrontal and frontal facets in relation to the midline of the skull; the length and ornamentation of the quadratojugal; the presence or absence of a jugal/squamosal contact, and the position of the jugal/quadratojugal contact in relation to the postorbitofrontal/squamosal suture; the level of ornamenta-

tion on the posterior edge of the squamosal; and the presence or absence of a facetted spinous process on the presacral vertebrae. These differences probably distinguish the Japanese *Monjurosuchus* from *M. splendens* at the species level but additional material and associated specimens (frontal, premaxilla and postcranial bones) would make the relationship clearer.

A life reconstruction of the Japanese *Monjurosuchus* is shown in Fig. 15, using *M. splendens* (Gao et al. 2000) to reconstruct the postcranial skeleton and soft tissue.

Discussion

Phylogenetic position.—*Monjurosuchus* sp. from the Lower Cretaceous Tetori Group contributes new information on cranial morphology and also extends the geographic range of the genus. This requires some changes to the character codings for the genus in recent data matrices, such as those of Evans and Klembara (2005) and Gao and Fox (2005). Of the characters used in the analysis, numbers 1–73 were taken from Evans and Klembara (modified from Evans 1990; Hecht 1992; Gao and Fox 1998). The character of "Interclavicle shape" (character number 63) was combined with another character "Clavicular facets on interclavicle" (character number 65; Evans and Klembara 2005). Four new char-
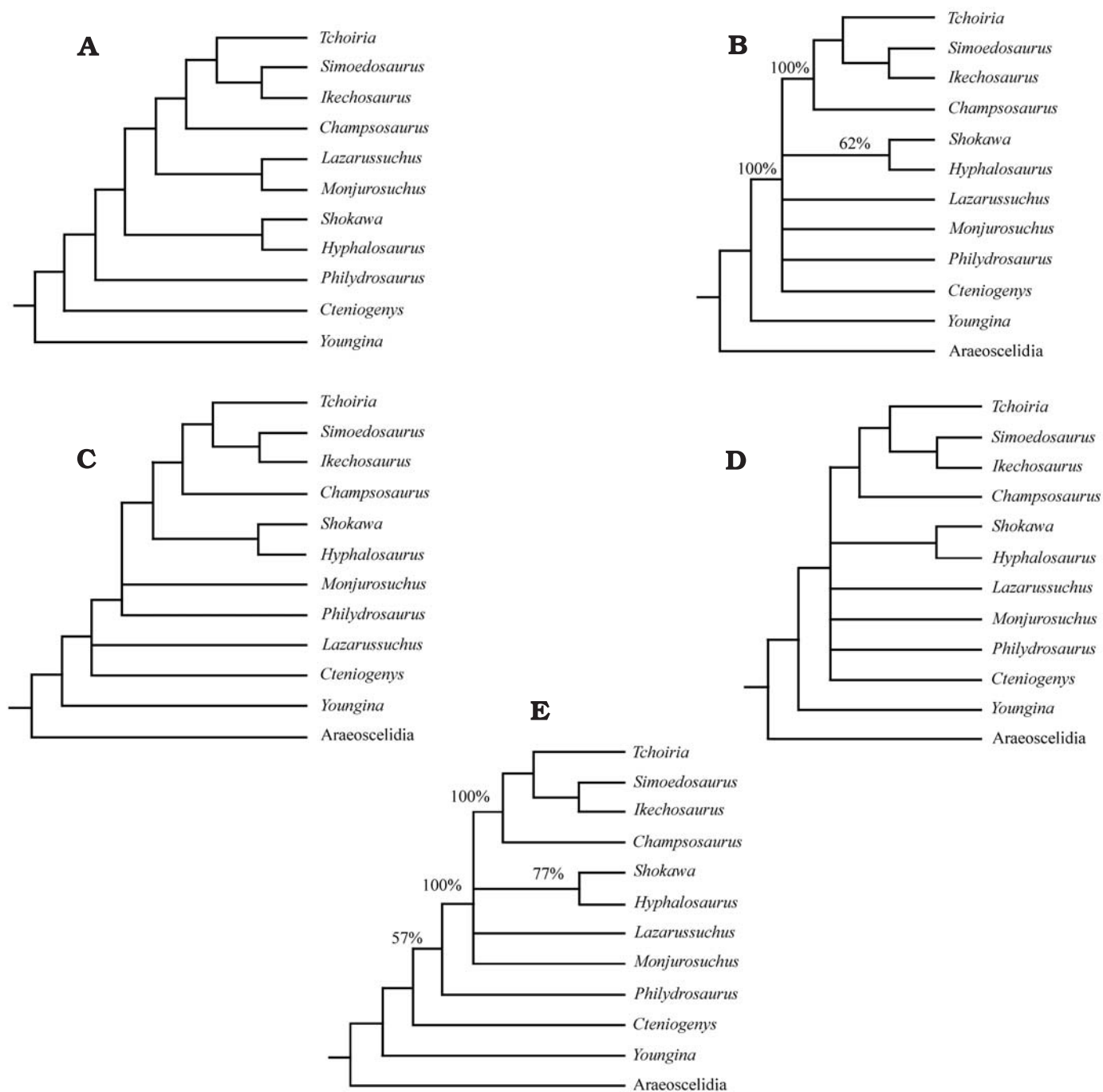
Fig. 16. Cladograms showing alternative hypotheses of relationship for Choristodera based on a sequence of analyses described in the text. **A**. Cladogram obtained using the characters and matrix in Appendices 1 and 2. **B**. Cladogram obtained using the characters and matrix of Gao and Fox (2005) unchanged. **C**. Strict consensus of three most-parsimonious trees obtained after updating character codings (matrix of Gao and Fox 2005) for non-neochoristoderan taxa. **D**. Strict consensus of four most-parsimonious trees obtained after adding codings for four new characters to the matrix used under C. **E**. Strict consensus of three most-parsimonious trees obtained after adding three new characters (from Gao and Fox 2005) to the matrix in Appendix 2.

acters (character numbers 74–77) were added (Appendix 1). For *Monjurosuchus*, the Japanese material provided data for six missing entries in the original matrix (character numbers 11, 25, 38, 41, 42, and 45) and required changes in two characters (character numbers 15, 67). New *Monjurosuchus splendens* specimens from the Yixian Formation (examined by the authors) also added six missing data points (character numbers 1, 53, 56, 60, 63, and 64) and corrected the coding in three more characters (character numbers 14, 67, 72). This study thus changed codings in 17 characters for *Monjurosuchus*. The poorly known long-necked Chinese choristodere, *Hyphalosaurus lingyuanensis,* has been included in the

phylogenetic analysis based partly on the description by Gao et al. (1999) and also on personal observation of new specimens by the senior author. The poorly known *Pachystropheus* was excluded because it is too fragmentary and its status as a choristodere is unconfirmed.

The relationships of the Lower Cretaceous Asian choristoderes were analysed using PAUP 4.0b10 (Swofford 2002) and the exhaustive search mode. All characters were equally weighted and the tree rooted by outgroup (*Youngina*). A maximum-parsimony analysis including all attributed choristoderan taxa (except the problematic *Pachystropheus*) yielded a single shortest tree (length = 134; consistency index = 0.776; rescaled consistency index = 0.579; Fig. 16A). This tree confirms the monophyly of Neochoristodera (Evans and Hecht 1993) including *Champsosaurus*, *Ikechosaurus*, *Simoedosaurus*, and *Tchoiria*. Neochoristoderans share 12 synapomorphies: elongated and fused nasals (8); nasal/premaxilla contact (9); large, dorsally directed orbits (10); upper temporal fenestra posteriorly flared and substantially larger than orbit (13); palatal foramen preserved between pterygoid and palatine, without contribution from vomer (19); quadratojugal bears a cotyle meeting a rounded quadrate process (24); pterygoid process of quadrate low, slender and horizontal, with a reduced pterygoid facet (25); tooth enamel infolded at base (35); pterygoquadrate foramen present and enclosed by neomorph and quadrate (39); cervical neurocentral sutures open (62); prefrontal and frontal equal in length (72); articular level lower than mandibular symphysis level (74). Within Neochoristodera, *Champsosaurus*, and then *Tchoiria* were consistently placed as consecutive sister taxa of the *Simoedosaurus–Ikechosaurus* clade. These placements agree with those of other recent studies (e.g., Gao and Fox 1998, 2005; Ksepka et al. 2005).

The relationships of the non-neochoristoderan taxa have been more controversial (e.g., Gao and Fox 1998, 2005; Evans and Klembara 2005; Ksepka et al. 2005). In our analysis, the Jurassic *Cteniogenys* retains a basal position, with the Chinese *Philydrosaurus* (Gao and Fox 2005) one node above it. The Japanese and Chinese long-necked taxa (*Shokawa* and *Hyphalosaurus*, respectively) form a small clade characterised by five synapomorphies: number of ossified carpal elements reduced to, at most, seven (58); cervical vertebra count more than 16 (65); caudal neural spines long and narrow (70); cervical neural spine much lower than dorsal neural spine (75); cervical postzygapophyses horizontal with broad facets (76). The problematic *Lazarussuchus* emerged as the sister taxon of *Monjurosuchus* in a clade that is the sister group of Neochoristodera. The more crownward position of *Lazarussuchus* in this cladogram contrasts with that of previous studies where it is basal (e.g., Gao and Fox 1998, 2005), albeit sometimes with caveats (Evans and Hecht 1993; Evans and Klembara 2005). Running the analysis again but permitting one extra step had little effect, resulting in three additional trees in which the only difference was in the relative positions of *Monjurosuchus* and *Lazarusuchus*. However, bootstrap analysis of our original tree shows only

weak support (58%) for the clade encompassing all choristoderes other than *Cteniogenys*. Four characters (16, 29, 30, and 72) notionally support the relationship among *Lazarussuchus*, *Monjurosuchus*, and neochoristoderes, but of these one (16, prefrontal-nasal contact) is difficult to code on crushed skulls; two (29, 30) are uncoded in *Lazarussuchus*; and the last (72) shows state 2 in *Lazarussuchus* but state 1 in *Monjurosuchus* and neochoristoderes. Of seven characters (7, 11–13, 36, 69, 77) supporting the position of *Lazarussuchus* above *Cteniogenys* and *Philydrosaurus*, only two (7, 11) are unequivocal. Finally, of the 10 characters linking all choristoderes except *Cteniogenys*, only two (61, 73) are unequivocal for *Lazarussuchus*. Thus, in total, four or five characters firmly support a crownward placement of *Lazarussuchus* in relation to *Cteniogenys*.

Gao and Fox (2005) also ran an analysis of Choristodera to assess the position of their new genus. Their trees, like ours, found a monophyletic Neochoristodera and a small clade of long-necked choristoderes (*Hyphalosaurus* + *Shokawa*) that Gao and Fox (2005) named Hyphalosauridae. Their two most-parsimonious trees differed only in the positions of *Monjurosuchus* and Hyphalosauridae in relation to one another and to Neochoristodera. However, there were two major differences between their phylogeny and ours, the positions of *Lazarussuchus* and *Philydrosaurus*. In their trees, *Lazarussuchus* retains a basal position on the stem of Choristodera, while *Philydrosaurus* is the sister taxon of *Monjurosuchus*. When we reran their analysis (using their matrix), we obtained the same topology (Fig. 16B). Removing their additional outgroup (Araeoscelidia) had no effect. Similarly, although Gao and Fox (2005) included the problematic *Pachystropheus* in their data matrix (omitted by us), they did not run it in an analysis. We ran a bootstrap analysis on their consensus tree and found only 56% bootstrap support for the clade excluding *Lazarussuchus* and only 59% bootstrap support for the clade linking *Philydrosaurus* with *Monjurosuchus*.

Both matrices and character lists share a common ancestry (Evans 1990; Hecht 1992; Gao and Fox 1998), and many of the characters and codings are the same (see Appendix 2 for details). However, there are a number of important differences. The first is that although Gao and Fox (2005) cite a new description and phylogenetic analysis of *Lazarussuchus* (Evans and Klembara 2005) that appeared as their manuscript was in revision, they did not incorporate the new data in their matrix nor discuss the phylogenetic conclusions. Consequently, 18/75 characters in their analysis are miscoded for *Lazarussuchus*. A second difference is that we have coded more characters for *Hyphalosaurus*, based on examination of original material in the collections of the IVPP (resulting in a difference of 31/75 codings for this taxon). A third difference is that while most of the characters are congruent between the two analyses, a few characters differ (four new characters in the matrix of Gao and Fox [2005], and four in ours), two characters were combined in our tree, one deleted in theirs, and five common characters have addi-
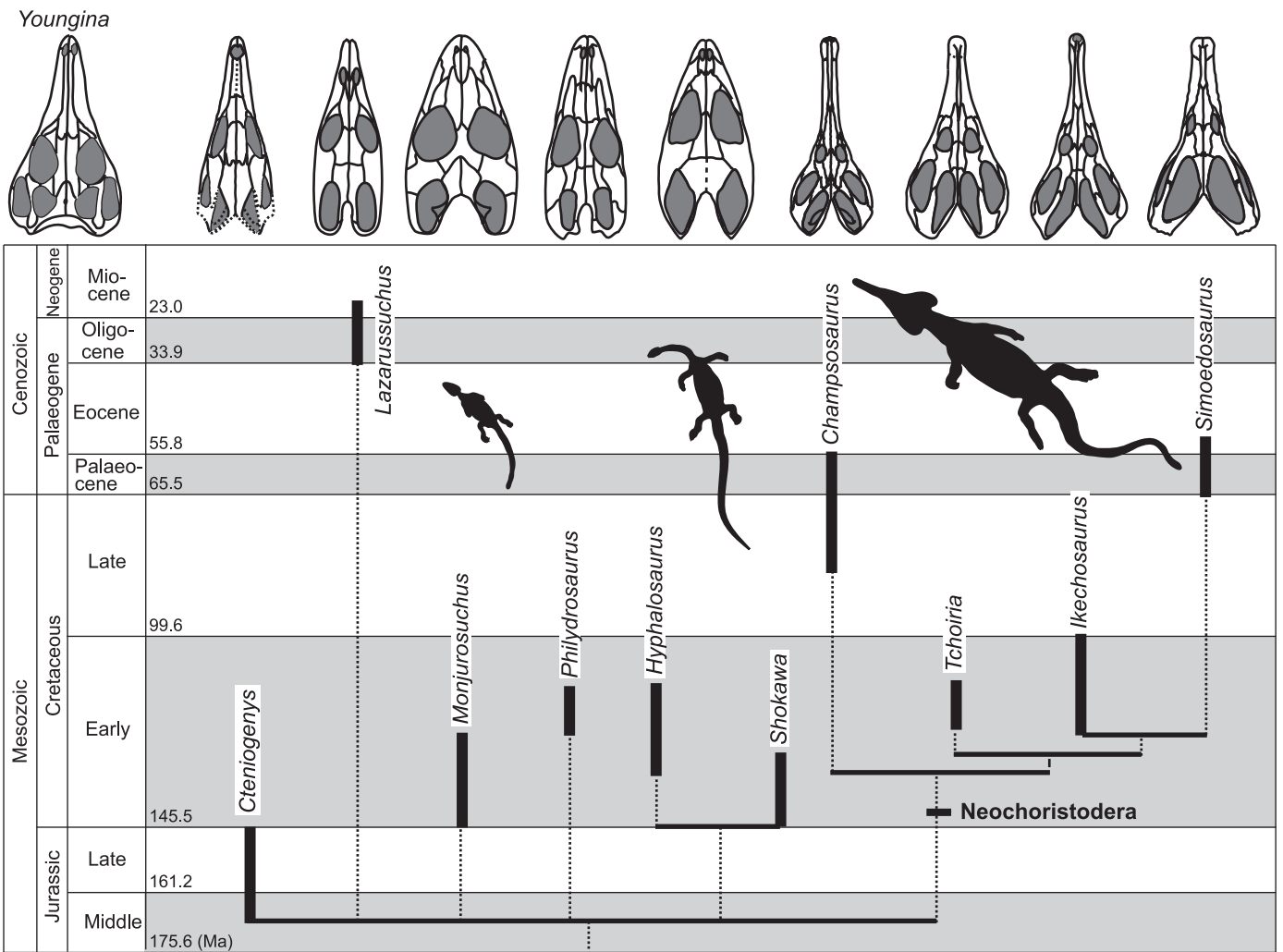
Fig. 17. Phylogenetic tree for Choristodera plotted against time.

tional or slightly altered states. Finally there were several instances, particularly for those taxa outside of Neochoristodera, where there is disagreement on the coding of character states (see Appendix 3).

In order to determine the effect of the coding differences on the resulting trees, we performed a series of separate analyses on the Gao and Fox (2005) matrix: after updating the codings for *Hyphalosaurus*; for *Monjurosuchus*; for *Lazarussuchus*; for all non-neochoristoderes (Fig. 16C); for all non-neochoristoderes and *Tchoiria*; and after adding our four new characters to their recoded matrix (Fig. 16D). We also reran our analysis after adding their additional characters (Fig. 16E). The results of these analyses are described in more detail in Appendix 3.

The phylogenetic position of the Oligocene–Miocene *Lazarussuchus* is problematic. In all recent studies, *Lazarussuchus* has been placed at the base of the choristoderan tree (Hecht 1992; Gao and Fox 1998; Evans and Manabe 1999; Evans and Klembara 2005), although Evans and Hecht (1993) also offered an alternative hypothesis that *Lazarussuchus*

might be a derived taxon with some size-linked character reversals. Similarly, Evans and Klembara (2005) showed that one extra step was enough to yield a subset of trees that moved *Lazarussuchus* from the basal position. On the other hand, Gao and Fox (1998, 2005) placed *Lazarussuchus* as the sister taxon of Choristodera, because *Lazarussuchus* seemed to have none of the derived characters diagnosing the group (but see Evans and Klembara 2005).

The overriding conclusion from the set of analyses presented here is that while the position of *Lazarussuchus* in relation to other choristoderes remains unresolved, such is the ambiguity of its position (moving up or down the tree as characters are added and codings changed) that it cannot be excluded from Choristodera (*contra* Gao and Fox 2005). In Gao and Fox (1998), the relationship between *Lazarussuchus* and other choristoderes was supported by two characters; prefrontal elongated with median contact (2); and absence of the parietal foramen (3). This study, however, suggests that *Lazarussuchus* shares at least three synapomorphies with all other choristoderes: absence of the parietal fo-

ramen (3); dorsal flange of maxilla low, with dorsal border inflected medially (5); and vomer-maxilla contact present (17). When the matrix of Gao and Fox (2005) is updated, four independent and unequivocal characters (their characters 8, 11, 12, and 63) support a placement of *Lazarussuchus* above *Cteniogenys*; five unequivocal characters (2, 51, 52, 57, 61) support the reversed position, although characters relating to fusion of the neurocentral sutures, fusion of the sacral and caudal ribs to their vertebrae, and greater development of the flexor tubercle of the unguals could be linked to more terrestrial habits.

Support for a monjurosuchid clade incorporating both *Monjurosuchus* and *Philydrosaurus* is weak, and the latter taxon tends to plot in a more basal position. Only one character (Gao and Fox 2005, 75: the presence of a distinct process on the ischium) supports the relationship. A second purported synapomorphy (Gao and Fox 2005, 3: interorbital contriction of the frontals) is problematic since it is intimately related to eye size, itself a character and depends on the width of the posterior part of the frontal. *Philydrosaurus* (coded as 1), actually has a broader interorbital frontal (interorbital width divided by the posterior width, 0.67) than does *Lazarussuchus* (0.56, coded at 0). The monophyly of Hyphalosauridae and of Neochoristodera is strongly supported by both studies, with the caveat that the nothing is known of the skull of the Japanese *Shokawa*, so that the relationship is based solely on postcranial characters.

It is very obvious that additional data are needed for all non-neochoristoderan taxa, particularly with respect to palatal and braincase characters, and such is the instability of the lower part of the tree that new data may well support alternative hypotheses of relationship. Recovery of a Mesozoic representative of the *Lazarussuchus* lineage would be illuminating.

Implications.—The choristoderan skull shows many unique features amongst Reptilia and is particularly characterized by dorsoventral compression and posteriorly expanded supratemporal fenestrae. However, even within Choristodera, skull morphology is diverse and can be classified into three types. One is characterized by a long-snout, small dorsally directed orbits, and an open lower temporal fenestra. This type is found in Neochoristodera (*Champsosaurus*, *Ikechosaurus*, *Simoedosaurus*, and *Tchoiria*). The second skull type is characterized by closed lower temporal fenestrae, a shorter snout, large dorsally directed orbits, and an upper temporal fenestra that is equal in size to the orbit. This type is shown by *Hyphalosaurus*, *Lazarussuchus*, and *Monjurosuchus*. The third type is characterized by a short snout, and by elongated and more laterally facing orbits. This is known only in the basal *Cteniogenys* and may represent the ancestral morphology for Choristodera. *Philydrosaurus* has a skull intermediate between the second and third types in that the skull shape is similar to that of *Cteniogenys* but it shares the closed temporal fenestrae of the other taxa. If the tree is correct, then closure of the lower temporal fenestrae is an enigmatic character. Assuming the choristoderan ancestor to

have been fully diapsid, the lower fenestra either closed independently in *Philydrosaurus*, *Monjurosuchus*, *Lazarussuchus*, and the ancestor of a clade containing *Hyphalosaurus* and *Shokawa* (assuming the latter shows this feature), or it closed in the ancestry of post-*Cteniogenys* choristoderans and reopened early in neochoristoderan history. In terms of the number of required changes, the latter hypothesis is more parsimonious but it will be tested by subsequent finds. A more radical alternative would be that the lower temporal fenestra was closed in the ancestor of choristoderes and opened in *Cteniogenys* and neochoristoderes. This needs to be tested with a broader analysis of diapsid relationships.

Conclusions

Choristoderan bones from the Lower Cretaceous Kuwajima Formation, Ishikawa Prefecture and the Okurodani Formation, Gifu Prefecture, Japan, may be attributed to the Jehol genus *Monjurosuchus*, and probably represent a new species, based mainly on differences in the morphology of the vertebrae, squamosal, quadratojugal, parietal, and jugal. Previously, *Monjurosuchus* was known only from the Yixian Formation (Upper Hauterivian–Barremian) of northeastern China. The new *Monjurosuchus* from the Kuwajima and Okurodani formations (Berriasian–Hauterivian) of Japan extends both the geographic and temporal range of the group and also our knowledge of its morphological variation.

Our cladistic analysis supports the monophyly of Neochoristodera and of the Hyphalosauridae of Gao and Fox (2005). However, the basal position of the Oligocene–Miocene *Lazarussuchus* is not confirmed, nor is a relationship between *Philydrosaurus* and *Monjurosuchus*.

Acknowledgements

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Appendix 1

The characters used in the analysis are taken mainly from Evans and Klembara (2005) and Ksepka et al. (2005) and modified from Evans (1990), Hecht (1992), Gao and Fox (1998), and Evans and Manabe (1999), but character 64 has been modified and four new characters (74–77) are added. Character codings for Monjurosuchus have been changed in several places to reflect new observations and interpretations of the authors. One new taxon, *Hyphalosaurus*, is added.

1. **External nares:** paired, oval, nearly terminal (0); paired, elongate and dorsally placed (1); terminal and confluent (2).
2. **Prefrontals:** anterolateral and separated by frontals (0); median contact limited to posterior two-thirds of length (1); median contact long, through entire length of element (2).
3. **Parietal foramen:** present (0); absent (1).
4. **Preorbital skull proportions:** moderately short and rounded (0); elongate but less than 50% of skull length (1); more than 50% of skull length (2).
5. **Dorsal flange of maxilla:** high and vertical (0); low, with dorsal border inflected medially (1).
6. **Lachrymal:** enters external narial opening (0); retracted posteriorly from the opening, but remains elongate (1); further reduced as a small triangular bone (2).
7. **Lachrymal perforation:** perforated by one or two foramina (0); lachrymal foramen between lachrymal and prefrontal (1)
8. **Nasals:** short and paired (0); elongate and paired (1); elongate and fused (2).
9. **Nasal/premaxilla contact:** nasals contact but do not intervene between premaxillae (0); nasals intervene between premaxillae (1); nasals do not contact premaxillae (2).
10. **Orbits:** large and laterally directed (0); small and dorsally directed (1); large and dorsally directed (2).
11. **Postfrontal/postorbital fusion:** bones discrete and both enter orbital margin (0); bones discrete but postorbital excluded from orbital margin (1); postfrontal and postorbital fused (2).
12. **Dorsal process of squamosal:** broad and short (0); slender and elongate to middle level of inferior temporal opening (1); Evans and Klembara (2005) code *Monjurosuchus* (0) for this character,
13. **Upper temporal fenestra:** shorter than orbit (0); roughly equal in length to orbit (1); posteriorly flared and substantially longer than orbit (2); Gao et al. (2000) code *Monjurosuchus* (0) for this character, but in the well-preserved *M. splendens* (DR0003C) and *Monjurosuchus* sp., the upper temporal fenestra is roughly equal in size to the orbit (1).
14. **Parietal:** having broad contact with the postorbital/postfrontal complex (0) having reduced contact (1).
15. **Squamosal/parietal suture in occiput:** near posterior end of superior temporal fenestra (0); half way along fenestra (1).
16. **Nasal/prefrontal contact:** straight line contact dorsolaterally on snout (0); broad V-shaped contact at dorsal midline (1); long, narrow wedge (2).
17. **Vomer-maxilla contact:** absent (0); present (1).
18. **Location of choana:** anterior, close to the premaxilla (0); retracted close to the midpoint of the marginal tooth row (1); displaced far back (2).
19. **Palatal foramen:** absent with vomer, palatine and pterygoid meeting at a closed three-point suture (0); opening at the junction between the three palatal bones (1); between pterygoid and palatine, without contribution from vomer (2).
20. **Internarial:** absent (0); present (1).
21. **Pterygoid flange:** consisting of pterygoid only and ventrally directed (0); consisting of pterygoid and ectopterygoid and having a horizontal overlap (1).
22. **Basipterygoid/pterygoid joint:** basipterygoid process articulates with pterygoid cotyle as part of a metakinetic joint (0); process and cotyle are reduced and the two bones are sutured (1); the two bones are fused (2).
23. **Parasphenoid/pterygoid contact:** no contact (0); clear sutural contact (1); tight contact or fusion (2)
24. **Quadratojugal/quadrate articulation:** having a simple overlapping facet for the quadrate (0); quadratojugal bears a cotyle meeting a rounded quadrate process (1).
25. **Pterygoid process of quadrate:** broad, vertically oriented with a large pterygoid facet (0); low, slender, and horizontal, with a reduced pterygoid facet (1); the process is oriented vertically in *Monjurosuchus* sp. (0).
26. **Dorsal process of jugal:** as prominent as anteroventral process (0); prominent but much shorter than anteroventral process (1); little or no process (2).
27. **Nasopalatal trough:** absent (0); present (1).
28. **Palatal teeth:** palate covered by shagreen of small teeth (0); paired pterygoid tooth batteries separated by nasopalatal trough (1); narrow rows of palatal teeth separated by nasopalatal trough (2).
29. **Midline contact of pterygoids:** separate or just touching in the midline anteriorly (0); long midline suture (1).
30. **Size and location of interpterygoid vacuity:** large and extends anterior to suborbital fenestra (0); small and near posterior border of the fenestra (1).
31. **Enclosure of interpterygoid vacuity:** enclosed anteriorly by pterygoids, but open posteriorly (0); enclosed anteriorly by pterygoid and posteriorly by parasphenoid (1); enclosed both anteriorly and posteriorly by pterygoids (2).
32. **Shape of parasphenoid:** isosceles triangle with long rostrum (0); broader anteriorly with short rostrum, moderate posterolateral expansion (1); slender anteriorly with long rostrum and strong posterolateral wing-like expansion (2).
33. **Basal tubera of braincase:** weakly developed (0); moderately expanded laterally (1); strongly expanded posterolaterally and wing-like (2).
34. **Marginal tooth sockets:** circular (0); transverse expansion occurs in anterior part of tooth row (1).
35. **Basal infolding of tooth enamel:** absent (0); present (1); absent in *Monjurosuchus* sp. (SBEI 1792) and *M. splendens* (DR0003C) (0).
36. **Location of craniomandibular joint:** roughly on a level with the occipital condyle (0); anterior to the condyle (1); posterior to the condyle (2).
37. **Shape of suborbital fenestra:** narrow, elongate (0); subtriangular with straight medial edge (1); short, kidney-shaped (2).
38. **Neomorph** (*sensu* Fox 1968) **in braincase:** absent (0); present as part of external wall of braincase and medial wall of temporal

fossa (1); *Monjurosuchus* sp. (SBEI 1792) has a facet for the neomorph on the quadrate (1).

39. **Pterygoquadrate foramen:** absent (0); present and enclosed by neomorph and quadrate (1).

40. **Paroccipital process/quadrate contact:** only tip of process meets quadrate (0); elongated process lies in a trough formed by the quadrate and neomorph (1); elongated process lies in a trough of the quadrate that is lined by a thin sheet of the neomorph (2).

41. **Mandibular symphysis:** small and terminal (0); moderate elongation equalling length of one third or less of the tooth row with little inclusion of splenial (1); strongly elongate, equalling at least half the length of the tooth row with longer inclusion of splenial (2); the symphysis is small and terminal in *Monjurosuchus* sp. (SBEI 1792) and *M. splendens* (IVPP V13279).

42. **Lateral exposure of splenial:** splenial confined to medial side of mandible (0); exposed on ventrolateral surface of mandible (1); splenial confined to medial side in *Monjurosuchus* sp., SBEI 1792 (0).

43. **Orientation of paroccipital processes:** horizontal (0); slightly depressed (1); strongly deflected ventrally (2).

44. **Supraoccipital/parietal contact:** free from parietal (0); supraoccipital lightly arched, with sutural surfaces for parietal placed anteriorly (1); supraoccipital keeled, and parietal facets extend to posterior margin (2).

45. **Posttemporal fenestra:** present (0); absent through loss (1); the fenestra is absent in *Monjurosuchus* sp. (1).

46. **Pila antotica:** remains unossified (0); ossified as part of the sphenoid (1).

47. **Posterior opening of internal carotid artery:** does not penetrate parasphenoid and opens ventrolaterally (0); penetrates parasphenoid and opens ventrally (1).

48. **Atlas-axis complex:** little or no development of anterior odontoid prominence of axis (0); free odontoid process unfused to axis (1).

49. **Dorsal neurocentral sutures:** closed in adult (0); remain open in adult (1).

50. **Vertebral centrum:** amphicoelous and notochordal (0); amphiplatyan with notochordal canal closed (1).

51. **Presacral vertebral centra:** longer than wide (0); short and spool-like (1).

52. **Ventromedial crest of dorsal vertebra:** anterior dorsal vertebrae are strongly keeled like the cervicals (0); low or no keels (1).

53. **Small spinous processes below the presacral postzygapophyses:** absent (0); present but without accessory facets (1); present and bear accessory facets (2); *Monjurosuchus* sp. (SBEI 1223, 1792) has small processes, but *M. splendens* (DR0003C) does not have the process (0/1).

54. **Number of sacral vertebrae:** two sacrals (0); three sacrals (1); four sacrals (2).

55. **Sacral and caudal ribs:** fused to the vertebra in the adult (0); sacral ribs free, caudal ribs fused (1); sacral and caudal ribs free (2).

56. **Caudal zygapophyses:** lie at a small angle to the horizontal (0); nearly vertical (1); they are vertical in *Monjurosuchus splendens*.

57. **Centra of caudal vertebrae:** bears shallow ventral groove for caudal blood vessels (0); groove is flanked by deep ventral flanges (1).

58. **Number of ossified carpal elements:** at least nine (0); number reduced to, at most, seven (1).

59. **Flexor tubercle or process on the ventral surface of the ungual:** distinct and well developed (0); flexor tubercle low and reduced (1).

60. **Bone structure:** cancellous (0); having reduced medullary cavity (1); pachyostotic in adult (2); in *M. splendens*, the femur has been sectioned and the bone structure is cancellous (0).

61. **Iliac blade, dorsal margin:** essentially vertical or at a steep angle to the horizontal in adults (0); dorsal margin essentially horizontal, blade expanded, often triangular (1).

62. **Cervical neurocentral sutures:** closed (0); open (1).

63. **Interclavicle shape and clavicular facets on interclavicle:** interclavicle shape is rhomboid and clavicles meet at an angle in the midline (0); T-shaped and clavicle facets continue across the midline (1); in *Monjurosuchus*, the interclavicle is T-shaped and the clavicular facets continue across the midline (1). Character 65 (in Evans and Klembara 2005) was combined with character 63 (in Evans and Klembara 2005).

64. **Interclavicle stem:** long, slender and essentially parallel-sided (0); flask-shaped, broad in anterior and central portions, tapering distally (1); stem shorter than lateral processes (2); interclavicle stem is long and slender in *Monjurosuchus* (0).

65. **Cervical vertebral count:** eight or nine (0); more than 16 (1).

66. **Cervical vertebral centra length:** longer than high (0); shorter than high (1).

67. **Dorsal vertebral centrum shape:** subcylindrical (0); cylindrical (circular cross-section) (1); *Monjurosuchus* has cylindrical centra (1).

68. **Fibula shape:** proximal and distal ends of similar width, or proximally wider (0); proximal end narrow, distal end flared (1).

69. **Gastralia thickness:** thin, lightly built (0); robust, almost as thick as axial ribs and pachyostotic (1).

70. **Caudal neural spines:** low (0); long and narrow (1).

71. **Naso-maxillary contact:** nasals contact maxillae laterally (0); nasals reduced and separated from maxillae by prefrontals (1).

72. **Prefrontal-frontal lengths:** prefrontal shorter than frontal (0); longer than frontal (1); equal in length to frontal (2); in *Monjurosuchus* (DR0003C) and *Lazarussuchus*, the prefrontals are longer (1).

73. **Lower temporal fenestra:** open, with complete or incomplete boundaries (0); closed by apposition of jugal, squamosal, postorbitofrontal, and quadratojugal (1); derived condition in *Hyphalosaurus, Lazarussuchus* and *Monjurosuchus* (1).

74. **Articular and mandibular symphysis level:** roughly equal level (0); articular level is lower than mandibular symphysis (1); derived condition in Neochoristodera.

75. **Cervical neural spine:** equal in height to dorsal neural spine (0); much lower than dorsal neural spine (1); *Shokawa and Hyphalosaurus* have an exceptionally low neural spine.

76. **Cervical zygapophyses:** project dorsolaterally with narrow facets (0); horizontal with broad facets (1); in *Shokawa and Hyphalosaurus,* these cervical zygapophyses have expanded facets (1).

77. **Frontal:** prefrontal and parietal facets are equal, or nearly equal, in width (0); parietal facet is wider than prefrontal facet (1); in *Lazarussuchus, Hyphalosaurus* and *Monjurosuchus*, the parietal facet is wider than the prefrontal facet.

Appendix 2

A = 0/1; B = 1/2; C = 0/2

	5	10	15	20	25	30	35	40
Youngina	00000	00000	00000	00000	00000	00000	00000	00000
Lazarussuchus	11111	21002	2?100	211?0	???0?	1????	??00	?0???
Cteniogenys	22111	10A20	0?A00	?1110	11100	10000	10000	?01??
Shokawa	????1	?????	?????	?????	?????	?????	??0?	?????
Champsosaurus	22121	21211	B1200	21221	12211	11211	22201	12112
Tchoiria	221B1	112?1	B1210	21120	11111	11111	11111	2111?
Ikechosaurus	22111	1?211	21211	1?120	11111	21111	11111	2111?
Simoedosaurus	22111	11211	21211	11120	11111	21111	11111	2111?
Hyphalosaurus	02101	1?002	2?10?	011B0	?????	B??00	??00	1????
Monjurosuchus	02101	1?002	220A0	1????	??B00	11111	1??00	1?100
Philydrosaurus	1?111	10002	00000	0????	?????	1????	??00	01???

	45	50	55	60	65	70	75	77
Youngina	00000	00000	00000	00000	00000	00000	00000	00
Lazarussuchus	11???	??00	00A20	11000	101?0	00100	12100	01
Cteniogenys	000??	00111	00012	11?11	00???	00?00	0000?	?0
Shokawa	00???	??11	0?011	1111B	00001	01111	????1	1?
Champsosaurus	21210	00111	01012	11?11	11110	A1110	01010	00
Tchoiria	20111	?1111	0111?	?1??B	11110	011?0	?101?	?0
Ikechosaurus	10121	11?11	11112	?0?1?	11100	0A110	?1010	00
Simoedosaurus	10121	11111	11112	00??2	11110	11110	01010	00
Hyphalosaurus	?????	????1	01?12	?110B	10011	01111	00101	11
Monjurosuchus	00???	???01	0?A10	10010	10100	01100	02100	01
Philydrosaurus	0????	??101	01011	11???	10100	??100	0010?	?0

Appendix 3

Basic data

The matrix in Appendix 2 has 77 characters, the matrix of Gao and Fox (2005) has 75. Of these, 66 are exactly the same. Five characters are almost the same with slight changes in character states. Two further characters are the same but were combined in our matrix. Four characters are new in each matrix.

Differences in coding of character states

Key: in each line, the first number is the character number in the matrix of Gao and Fox (2005); the second number in the square bracket is the equivalent character number in Appendix 1; the third number or symbol represents the code for that character in Gao and Fox's matrix; the fourth, again in square brackets, represents the code in our matrix. An asterisk marks where an additional state has been added or a state changed. The final figure in bold shows the total number of character codings that differ for that taxon or group of taxa.

Neochoristodera

Tchoiria: 33 [31] 1 [1/2]; 34 [32] 1 [1/2]; 38 [36] 2 [0/2]; 53 [51] 1 [0]; 58 [56] 1 [0] [?]; 59 [57] 1 [0]

Ikechosaurus: 43 [41] 2 [1]; 57* [55] 1 [2]

Simoedosaurus: 42 [40] 1 [?]; 57* [55] 1 [2]; 60 [58] 1 [?]

Champsosaurus: 12 [11] 1 [1/2]; 53 [51] 1 [0]; 57* [55] 1 [2]; 59 [57] 0 [1]; 60 [58] 1 [?] 62 [60] 2 [1] **(17/300)**

Other choristoderes

Shokawa: 51 [49] ? [1]; 58 [56] ? [1]; 60 [58] ? [1]; 61 [59] ? [1]; 70 [68] 0 [1] **(5/75)**

Cteniogenys: 19 [17] 0 [1]; 43 [41] 1 [0]; 51 [49] ? [1]; 57* [55] 1 [2] **(4/75)**

Lazarussuchus: 8 [7] 0 [1]; 9 [8] 1 [0]; 11 [10] 0 [1]; 19 [17] ? [1]; 20 [18] 0 [1]; 26 [24] ? [0]; 28 [26] ? [1]; 30 [28] 0 [?]; 31 [29] 0 [?]; 34 [32] 0 [?]; 35 [33] 0 [?]; 38 [36] 0 [?]; 44 [42] 0 [1]; 55 [53] 0 [0/1]; 59 [57] 0 [1]; 63 [61] 0 [1]; 64* [63] ? [1] **(18/75)**

Monjurosuchus: 8 [7] 0 [?]; 9 [8] ? [0]; 12 [11] 0 [2]; 13 [12] 2 [0]; 16 [14] 0 [0/1]; 17 [15] ? [0]; 18 [16] 0 [1]; 22 [20] 0 [?]; 25 [23] ? [1/2]; 26 [24] ? [0]; 27 [25] ? [0]; 29 [27] ? [1]; 30 [28] ? [1]; 31 [29] ? [1]; 32 [30] ? [1]; 33 [31] ? [1]; 38 [36] 0 [1]; 40 [38] ? [1]; 41 [39] ? [0]; 42 [40] ? [0]; 47 [45] 1 [?]; 53 [51] ? [0]; 55 [53] 0 [0/1]; 57 [55] 1 [0]; 59 [57] ? [0]; 61 [59] ? [1]; 62 [60] ? [0]; 63 [61] 0 [1]; 64 [62] ? [1]; 65 [64] ? [0]; 68 [66] ? [0]; 69 [67] ? [1] **(32/75)**

Philydrosaurus: 8 [7] ? [0] (state description differs in original text); 9 [8] 1 [0] (proportional); 13 [12] 2 [0]; 17 [15] ? [0]; 22 [20] 0 [?]; 44 [42] 0 [?]; 47 [45] 1 [?]; 50 [48] ? [1]; 53 [51] ? [0]; 63 [61] 0 [1]; 65 [64] ? [0] **(12/75)**

Hyphalosaurus: 1 [1] ? [0]; 2 [2] ? [2]; 7 [6] ? [1]; 9 [8] ? [0]; 10 [9] ? [0]; 12 [11] ? [2]; 15 [73] ? [1]; 16 [14] ? [0]; 18 [16] ? [0]; 19 [17] ? [1]; 20 [18] ? [1]; 21 [19] ? [1/2]; 22 [20] ? [0]; 28 [26] ? [1/2]; 31 [29] ? [0]; 32 [30] ? [0]; 38 [36] 0 [1]; 43 [41] 0 [?]; 51 [49] 0 [?]; 53 [51] ? [0]; 54 [52] ? [1]; 57* [55] 1 [2]; 59 [57] ? [1]; 60 [58] 0 [1] (put as ?); 61 [59] ? [0]; 62 [60] ? [1/2]; 63* [61] 0 [1]; 64 [63] ? [0]; 65 [64] ? [1]; 68 [66] ? [0]; 69 [67] ? [1] **(31/75)**

Total difference (101/450)

Analyses

The following maximum-parsimony analyses were performed in order to understand the effect of modifying the character state codings between the two matrices.

(1) We updated only the codings for *Hyphalosaurus* (31/75) in Gao and Fox's (2005) matrix. The result was a single shortest tree (length [L] = 126; consistency index [CI] = 0.825; rescaled consistency index [RC] = 0.707) with a topology essentially unchanged from that of Gao and Fox (2005); that is, *Lazarussuchus* in a basal position, Hyphalosauridae as the sister group of Neochoristodera, and *Monjurosuchus* and *Philydrosaurus* forming a clade).

(2) We updated only the codings of *Monjurosuchus* (32/75) in Gao and Fox's (2005) matrix and obtained a single shortest tree (L = 128; CI = 0.812; RC = 0.684) in which *Lazarussuchus*, *Cteniogenys*, *Hyphalosauridae*, *Philydrosaurus*, and finally *Monjurosuchus* formed consecutive sister taxa to Neochoristodera (i.e., the relationship between *Philydrosaurus* and *Monjurosaurus* was not supported).

(3) Updating only the codings for *Lazarussuchus* in Gao and Fox's matrix (18/75) had a greater effect. We obtained four shortest trees (L = 127; CI = 0.819; RC = 0.69), each with a very different topology from that in Gao and Fox (2005). In all cases, either *Monjurosuchus* alone or *Monjurosuchus* + *Philydrosaurus* were the most basal choristoderes; above them *Cteniogenys*, *Lazarussuchus*, and the Hyphalosauridae changed position in relation to Neochoristodera. However, the strict consensus tree (Fig. 16C) supports only Neochoristodera and Hyphalosauridae as clades, in a polytomy with remaining taxa. In a 50% majority rule consensus tree, Gao and Fox's (2005) Monjurosuchidae (*Monjurosuchus* + *Philydrosaurus*) is supported (75%) and lies at the base of Choristodera, forming the sister group to a second, larger, clade comprising all remaining taxa (75%).

(4) We then updated codings for all non-neochoristoderan taxa in the matrix of Gao and Fox (2005) and reran the analysis. This resulted in three shortest trees (L = 136; CI = 0.757; RC = 0.605), two of which had *Lazarussuchus* in the basal position, and the third placed *Lazarussuchus* above *Cteniogenys*. The strict consensus tree (Fig. 16D) has *Lazarussuchus* and *Cteniogenys* unresolved at the base of Choristodera. Updating the codings for *Tchoiria* (based mainly on Ksepka et al. 2005) had little effect, except to weaken bootstrap support in the non-neochoristoderan part of the tree.

(5) In the final analysis on Gao and Fox's (2005) matrix, we added in our four new characters. This resulted in four shortest trees (L = 147; CI = 0.748; RC = 0.589), in which *Lazarussuchus* and *Cteniogenys* were each basal in two. Again, only one of the four supported a relationship between *Monjurosuchus* and *Philydrosaurus*. The strict consensus tree (Fig. 16E) has a polytomy of *Cteniogenys*, *Lazarussuchus*, *Monjurosuchus*, and *Philydrosaurus*, with Hyphalosauridae and Neochoristodera in the crown.

(6) The last analysis was a rerun of our matrix incorporating three of Gao and Fox's new characters. The fourth, their character 3, was omitted as it is problematic. The reanalysis resulted in three shortest trees (L = 142; CI = 0.754; RC = 0.541) with relatively little difference from our original tree, except in breaking the weak relationship between *Monjurosuchus* and *Lazarussuchus*.