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A three-dimensionally preserved frog (Amphibia, Anura) from the Lower Cretaceous Kuwajima Formation, Tetori Group, Ishikawa Prefecture, Japan

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Abstract. The Early Cretaceous Kuwajima Formation, Tetori Group, Japan has yielded various aquatic and terrestrial vertebrates, but lissamphibian records are limited to albanerpetontids and an isolated longbone of a frog. Here we provide the first report of an associated frog specimen from the Tetori Group. The specimen is composed of a few skull elements and several postcranial bones, including the femur, ilium, and vertebrae. This new Tetori frog is distinguished from the previously reported Early Cretaceous Asian genera, *Liaobatrachus* from China, and *Hyogobatrachus* and *Tambabatrachus* from Japan, in having hatchet-shaped sacral diapophyses and a posteriorly tapering urostyle with a weakly developed dorsal crest. Phylogenetic analysis of this new material places it as a non-neobatrachian frog that may be related to previously described Chinese and Japanese taxa, but more complete material would be needed to establish its affinities with confidence.

Keywords: Amphibia, Asia, Early Cretaceous, Frog, Tetori Group

Introduction

Amongst extant amphibians, frogs are by far the most diverse in terms of species number (7449 vs. 767 Caudata and 215 Gymnophiona, Amphibia Web 2022) and have a global distribution across both temperate and tropical regions. However, as for all lissamphibians, the early fossil record of frogs is limited and our knowledge of their evolutionary history remains incomplete. The earliest known salientians (Anura + stem taxa) are known from the Early Triassic of Madagascar (*Triadobatrachus massinoti*; Piveteau, 1936) and southern Poland (*Czatkobatrachus polonicus*; Evans and Borsuk-Białynicka, 1998). Furthermore, more derived, stem-anurans are known from the Jurassic of North America (Arizona: *Prosalirus bitis*; Shubin and Jenkins, 1995) and South America (Argentina: *Vieraella herbsti*, *Notobatrachus digiustoi*, Baez and Basso, 1996; Baez and Nicoli, 2004). The earliest recognized crown anurans (Discoglossoidea, Rhinophrynidae, possible Pelobatidae) are from the Jurassic of Europe (Discoglossoidea: *Eodiscoglossus*, Hecht, 1970) and North America (Morrison Formation: *Enneabatrachus* [Discoglossoidea], and an unnamed pelobatid-like taxon, Evans and Milner, 1993; the rhinophrynid *Rhadinosteus*, Henrici, 1998). Records of Jurassic anurans from Asia are rare. The Daohugou Biota of northeastern China is one of the best-known Asian Jurassic deposits, and has yielded an impression of a metamorphosing tadpole (Yuan *et al.*, 2004). However, this specimen lacks evidence of an ossified skeleton, and its identification has been questioned (Sullivan *et al.*, 2014). Therefore, certain records of Jurassic anurans from Asia are limited to an isolated atlas from Western Siberia (Skutschas *et al.*, 2016). However, the anuran record improves significantly in the Early Cretaceous, with taxa recorded from North and South America, Africa, the Middle East, Europe, and Asia (e.g. Roçek, 2008). Several articulated anuran specimens have been reported from the Yixian and Jiufotang formations (Barremian–Aptian) of the Jehol Group, China, and many of these frogs are now attributed to species of the genus *Liaobatrachus* (Dong *et al.*, 2013). A second frog genus, *Genibatrachus* (Gao and Chen, 2017), has been recovered from the Guanghua Formation, Inner Mongolia (Barremian–Aptian).

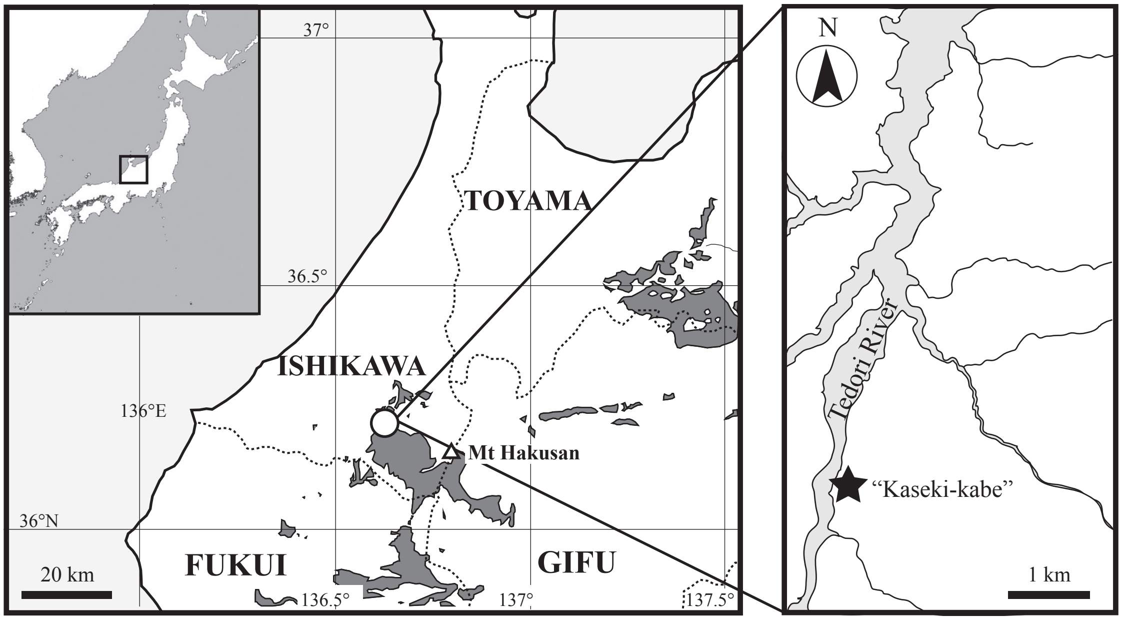

Figure 1. Distribution of the Tetori Group (shaded areas) in central Japan and location of the "Kaseki-kabe" in the Shiramine (Hakusan City, Ishikawa Prefecture) area (asterisk).

In Japan, Cretaceous frog remains are much rarer. The Tetori Group of western Honshu (Barremian–Aptian) comprises a series of well-known Japanese Mesozoic deposits that includes the fossil-rich Okurodani and Kuwajima formations. These formations have yielded a diversity of vertebrate remains. However, amphibian fossils are very rare. They include two specimens of the enigmatic salamander-like Albanerpetontidae (Matsumoto and Evans, 2018) and isolated frog postcranial elements. The latter includes an ilium and a vertebra from the Okurodani Formation (Barremian–Aptian; Evans and Manabe, 1998), and an isolated left tibiofibula from the Kuwajima Formation (Barremian–Aptian: Matsuoka, 2000). In addition, articulated specimens of two named frog genera, *Hyogobatrachus* and *Tambabatrachus*, were described from the slightly younger (Aptian) Sasayama Group, Hyogo Prefecture, Japan (Ikeda *et al.*, 2016).

Here we report on an anuran specimen (SBEI 1778) from the Kuwajima Formation containing an association of skull and postcranial elements representing a single individual. Three-dimensional preservation of individual elements, as revealed through Micro-Computed Tomography, provides new information on little-known Tetori frogs and extends our knowledge of Asian anurans from the Jurassic and Cretaceous.

Geological setting

The Mesozoic (Middle Jurassic to Early Cretaceous) marine and freshwater deposits of the Tetori Group are widely distributed within the Inner Zone of central Japan (Fukui, Gifu, Ishikawa, and Toyama prefectures). The Tetori Group has traditionally been divided into three subgroups; the Kuzuryu, Itoshiro, and Akaiwa Subgroups in ascending order (Maeda, 1961). The fossil material described in this paper was collected from the upper part of the Kuwajima Formation, Itoshiro Subgroup, at the "Kaseki-kabe" locality (Fossil-Bluff) in Kuwajima district, Hakusan City, Ishikawa Prefecture, Japan (Figure 1). A detailed distribution of the Tetori Group in the Shiramine area has been presented in previous papers (e.g. Kusuhashi, 2008) and is not repeated here.

The rock wall behind the "Kaseki-kabe" was excavated between 1997 and 2000 for the construction of a road tunnel. The upper part of the Kuwajima Formation was drilled out during construction and blocks of material were set aside for study by scientists. Since then, these blocks have been processed by researchers and volunteers, and have yielded a large number of fossils, including the specimen described in this paper (SBEI 1778). However, as the rock was removed by heavy machinery and then put aside for study, it is impossible to know precisely where in the formation each specimen was found, other than roughly by facies type.

The Kuwajima Formation is composed of thick, coarse-grained sandstone and alternating beds of fine-grained sandstone and mudstone. Three facies have been identified in the sequence; Facies I, carbonaceous swamp;

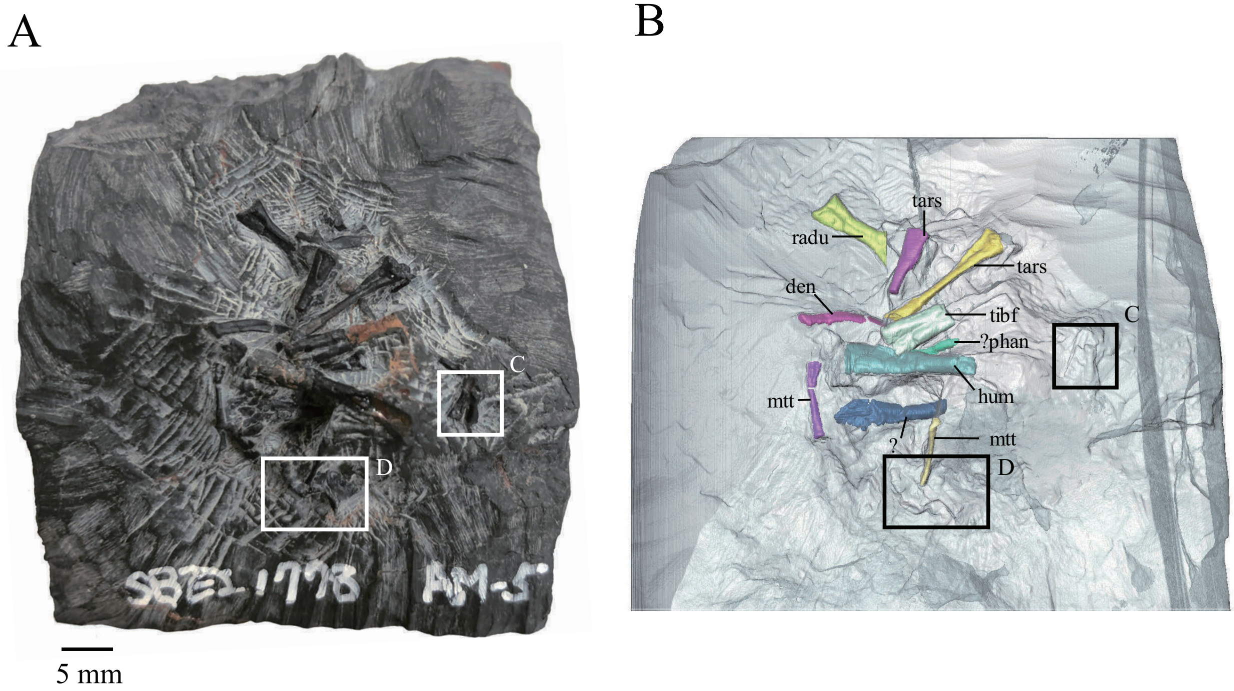

Figure 2. Digital photograph of SBEI 1778 (A) and rendered view of the surface from µCT data with identification of exposed elements (B). The two squares (C and D) on B indicate locations where elements were not registered by the µCT "Toscaner 30000 micro CN" are located.

Facies II, shallow lake; Facies III, vegetated swamp (Isaji *et al.*, 2005). Facies I contains isolated vertebrate fossils and mollusks that are poorly preserved. Facies II consists of silty matrix mixed with angular fine-grained quartz sands and contains fractured leaves and stems, numerous viviparid gastropods and unionid bivalves. Facies III consists of well-sorted silty dark greenish-grey mudstones and occasional angular very fine-grained quartz sands and contains *in situ* plant remains, terrestrial vertebrates and rare aquatic species (Isaji *et al.*, 2005). Together, the three facies have yielded a wide range of vertebrates, dominated by aquatic-semiaquatic taxa, including fish (Yabumoto, 2005, 2014; Yabumoto *et al.*, 2006), choristoderes (Matsumoto *et al.*, 2007, 2014), and turtles (Hirayama *et al.*, 2012), but also including terrestrial lizards (Evans and Manabe, 2008; Evans and Matsumoto, 2015), dinosaurs (Barrett *et al.*, 2002; Ohashi and Barrett, 2009), pterosaurs (Unwin and Matsuoka, 2000), mammals (Rougier *et al.*, 2007; Kusuhashi, 2008), and tritylodonts (Setoguchi *et al.*, 1999; Matsuoka and Setoguchi, 2000; Matsuoka *et al.*, 2016), as well as eggshells (Isaji *et al.*, 2006). However, the locality is unusual in that lissamphibians are rare and limited to frogs (Evans and Manabe, 1998; Matsuoka, 2000) and albanerpetontids (Matsumoto and Evans, 2018), with currently no record of salamanders. All lissamphibian remains, including the material described herein, were recovered from Facies III.

The age of the Kuwajima Formation is generally agreed to be Early Cretaceous. Analysis of zircon U-Pb from a tuff bed in the lower part of the Kuwajima Formation yielded a date of 130.7 ± 0.8 (2 SE) Ma (Matsumoto *et al.*, 2006). Supporting evidence of this date comes from the Okurodani Formation in Gifu Prefecture, the lateral equivalent of the Kuwajima Formation (Maeda, 1952), where zircon U-Pb analysis gave ages of 130.2 ± 1.7 and 117.5 ± 0.7 (2 SE) Ma (Kusuhashi *et al.*, 2006). These two formations share faunal components: e.g., the lizard *Sakurasaurus*, and the choristodere, *Monjurosuchus*. The most recent study, combining these data, dated the Kuwajima Formation as Barremian to early Aptian (Sano, 2015).

Material and methods

Manual preparation of the block SBEI 17785 (50 × 45 × 20 mm) revealed several associated limb bones and partially exposed vertebrae (Figure 2A, B). These elements overlapped one another, and it seemed likely that further elements were hidden in the matrix. However, this specimen was designated as a natural treasure of Ishikawa Prefecture in 2006, and further preparation of the block was not permitted, especially with the risk of damaging surface elements. The specimen was therefore scanned using micro-computed tomography (µCT Toscaner

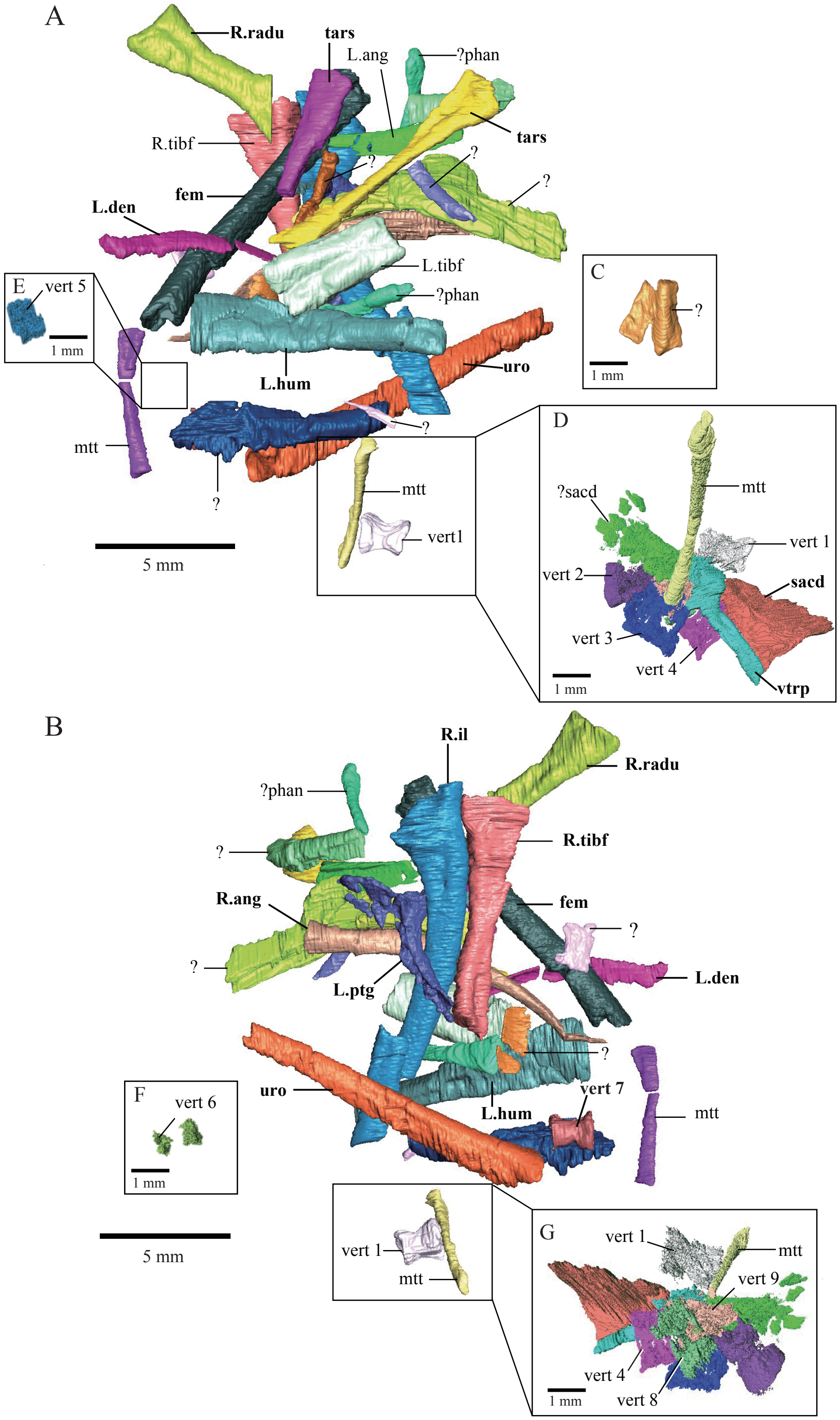

Figure 3. Elements segmented from µCT slice data of SBEI 1778. **A**, exposed side; **B**, the other side of A. C–G, segmented elements from rescanned data by µCT XTH-255 XT. The two squares, C and D, correspond to the squares marked in Figure 2 B. The elements shown in Figures 4–8 are labelled in bold.

30000 micro CN) at the Tokyo Metropolitan Industrial Technology Research Institute of Tokyo, Japan. The slice distance was 0.034003 mm (100 kv, 30 μA). However, several exposed elements on the matrix were not visible on the resulting μCT image, as shown by the black square in Figure 2 (C and D). The specimen was therefore rescanned courtesy of the Nikon XTH-255 XT at a slice thickness of 0.02100804 mm (175 kV, 166 μA) and the resulting scan provided clearer and more informative images. Additional elements are shown within the black square in Figure 3 (C–E). In all cases, image reconstructions were made using AVIZO v.8 software. Elements exposed on the surface of the matrix were studied under the microscope (Nikon SMZ-10), but bones hidden under the matrix were examined and described from the 3D images reconstructed from μCT data. Individual elements were measured by using a caliper (Mitutoyo CD-S20M).

Institutional abbreviations

IBEF: Izumi Board of Education, Fukui, Japan; **IVPP**: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **SBEI**: Shiramine Board of Education, Ishikawa, Japan.

Anatomical abbreviations

ac, acetabular; ang, angulosplenial; cp, coronoid process; crv, crista ventralis; dc, dorsal crest; den, dentary; fe cr, femoral crest; fem, femur; gr, groove; hum, humerus; il, ilium; L, left; sym, symphysis; mg, Meckelian groove; mtt, metatarsals; mx f, maxilla facet; phan, phalanx; ptg, pterygoid; R, right; ra, radius; radu, radioulna; sacd, sacral diapophysis; sd, shallow depression; tars, tarsal; tibf, tibiofibula; u, ulna; uro, urostyle; vert, vertebra; vtrp, vertebral transverse process.

Systematic palaeontology

Amphibia Linnaeus, 1758
Lissamphibia Haeckel, 1866
Salientia Laurenti, 1768
Anura Rafinesque, 1815
Genus and species indet.

Description

SBEI 1778 is a block of grey mudstone on which several anuran bones are visible on the surface of the matrix: a left dentary, a left humerus, two metatarsals, fragments of tibiofibula, a right radioulna, two tarsals, a left sacral diapophysis, a left vertebral transverse process, three vertebrae (Figures 2A, B; 3C, D). The μCT images revealed additional skeletal materials under the matrix, including a left pterygoid, left and right angulosplenials, a femur (side undetermined), two phalanges, six vertebral centra, the urostyle, and a right ilium. Although all elements are disarticulated, there is no replication of elements, and the size of individual bones is consistent with the remains being those of a single individual. In total, thirty-four elements are preserved in SBEI 1778, of which twenty-eight are identifiable and six are too fragmentary for identification.

The postcranial morphology of anurans changes through ontogeny (e.g. Vera and Ponssa, 2014). The centra of early post-metamorphic juveniles have a wide notochordal canal, which is at least partially closed mid-centrum in adults (Roçek *et al.*, 2012). In SBEI 1778, the notochordal canal is closed in all preserved centra (Figure 5C), which suggests that this was a young-adult or adult individual.

Skull

Four skull elements are preserved in SBEI 1778: left pterygoid, left dentary, and left and right angulosplenial. The pterygoid is triradiate, and the anterior ramus is longer than the posterior and medial rami (Figure 4A, B). A groove along the lateral margin of the anterior ramus is a facet for the maxilla (Figure 4C, mx f). The tip of the anterior ramus may have attached to the palatine, but there is no clear facet on the CT image, and this part may be broken. The posterior ramus forms a dorsoventrally expanded flange that is articulated with the quadratojugal. The medial ramus is slightly dorsally inclined and forms a shallow process for the pro-otic (Figure 4C).

The dentary is missing its mid-section, but both anterior and posterior ends are nearly complete (Figure 4D–E). The dentary is a slender, mediolaterally compressed element, with a shaft that is weakly curved in dorsal view (Figure 4E). Both dorsal and ventral margins are sharp-edged. The dentary symphysis is expanded dorsoventrally with a smooth articular surface, and the mentomeckelian bone is obviously fused to the dentary (Figure 4G).

The right angulosplenial is nearly complete (Figures 4H–K), but only the anterior part of the left bone is preserved. The angulosplenial measures 12.3 mm along its long axis, and tapers anteriorly, forming a sharp tip. The ventral margin is rounded (Figure 4K), whereas the dorsal margin forms a thin edge (Figure 4J). This dorsal margin bears a coronoid process that is longer than wide and is concave in its central part (Figure 4I). The Meckelian groove extends the length of the bone (Figure 4H, I).

Vertebral column

SBEI 1778 preserves at least nine vertebrae (Figure 3A, B, D, F, G), as well as a left vertebral transverse process, an isolated left sacral diapophysis (Figure 5D, E) and the urostyle (Figure 3A, B, 5F–I).

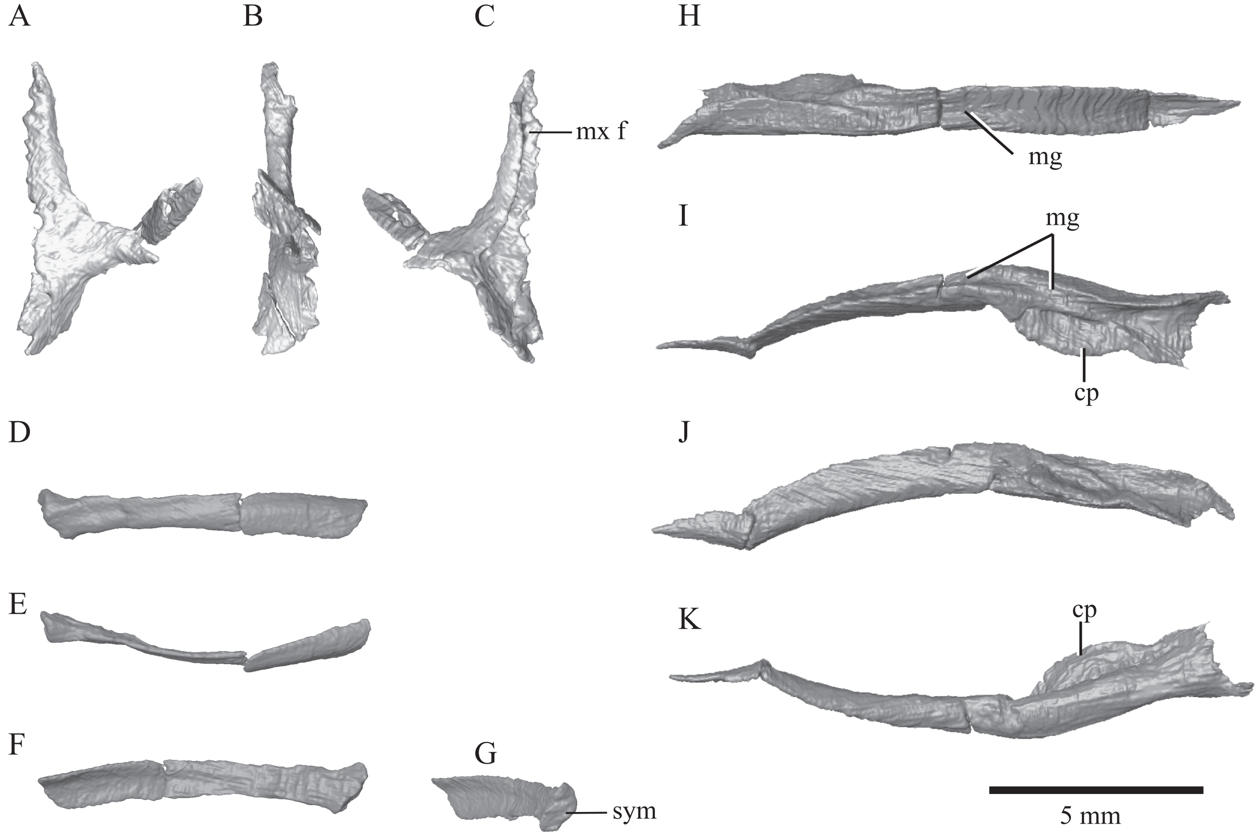

Figure 4. Left pterygoid (A–C), Left dentary (D–G) and right angulosplenial (H–K) of SBEI 1778. Left pterygoid in dorsal (A); lateral (B); ventral (C) views. Left dentary in lateral (D); dorsal (E); medial (F); and anteromedial (G) views. Right angulosplenial in lateral (H); dorsal (I); medial (J) and in ventral (K) views.

The vertebral centra are longer than high (1.8 mm in mid-ventral length; 0.86 mm in mid-central height; vert. 1 in Figures 3A, 5A–C). The articular surface of each centrum is oval and dorsoventrally compressed (Figure 5C). All preserved centra are amphicoelous with a notochordal canal that is closed in the mid-centrum (Figure 5A–C). Transverse processes and neural spines are broken in most vertebrae, except for a few transverse processes that are partially exposed on the matrix surface (Figures 3D, 5D). One of the transverse processes (Figure 5D) is flat and is shaped like an elongated rectangle, with a slightly waisted proximal end. In dorsal view, the process is posteriorly inclined at roughly 10°. An isolated sacral diapophysis is exposed on the surface of the matrix (Figure 3D). It is moderately dilated and is hatchet-shaped in dorsal view (Figure 5E). Vertebrae 4, 8 and 9 are closely associated with the detached sacral diapophysis, and one of these elements may therefore represent the body of the sacral vertebra (Figure 3G). However, as the detailed morphology of these vertebrae, including the position of rib attachments, is not clear from the μCT data, the sacral vertebra cannot be identified with any confidence.

The urostyle is nearly complete and is 13.2 mm along its long axis (Figure 5F–H). In lateral view, the proximal end of the urostyle is dorsoventrally expanded, but it tapers gradually toward the posterior end (Figure 5H). The condylar fossa is dorsoventrally compressed and elliptical, forming a shallow monocondylar articulation (Figure 5I). The canalis coccygeus is obscured on this specimen, due to the poor preservation state. A shallow groove extends along the lateral surface of the urostyle shaft, and the dorsal margin bears a weakly developed crest (Figure 5F, H). There are no transverse processes.

Forelimb

Most of the proximal part of the left humerus is preserved (up to 9.8 mm in length, Figure 6A–C), except the articular head. It is slightly expanded. Although the midshaft of the humerus is dorsoventrally compressed, the crista ventralis is partially preserved as a low keel (Figure 6A, B), and the shaft is oval in cross-section.

The right radioulna is preserved. The proximal head is

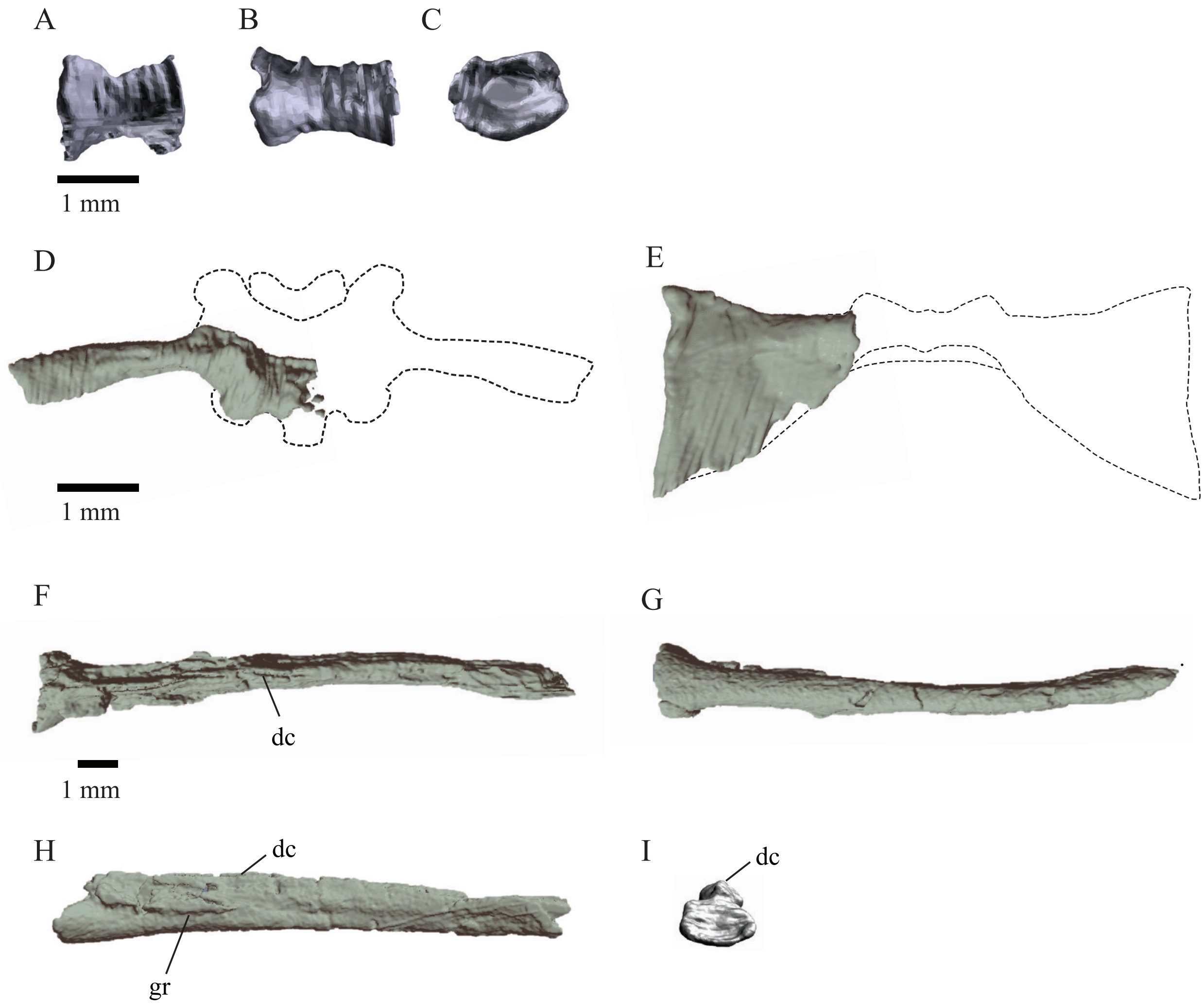

Figure 5. Vertebra (A–C) shown as No. 7 in Figure 3, part of left transverse process (D), left sacral diapophysis (E), urostyle (F–I) of SBEI 1778. Vertebra in ventral (A); lateral (B); anterior (C) views. Part of transverse processes in dorsal view (D), missing part indicated by a dotted line (extant species used for these models; *Discoglossus* and *Conraua*), sacral diapophysis in dorsal view (E). Urostyle in dorsal (F); ventral (G); left lateral (H); and anterior (I) views.

nearly complete, but the distal head is damaged (Figure 6D–G). The shaft is dorsoventrally compressed, giving its cross-section the shape of a flattened disk. The middle portion of the shaft is waisted and slightly curved along the radial margin (Figure 6E, G). A shallow groove runs along the midline of the shaft, marking the border between the ulna and radius (Figure 6E), but there is no clear division of these two parts on the proximal head (Figure 6D). The distal end is damaged.

Pelvic girdle and hindlimb

The right ilium, femur, fragments of tibiofibulae (two pieces, unlikely to be a single bone), two tarsals, two metatarsi, two possible phalanges are preserved in SBEI 1778.

The ilium is in two pieces and is damaged at both ends (~14.2 mm along the long axis of the blade; Figure 7A–C). Although the acetabular region is damaged, a remnant of the acetabular surface is visible as a shallow depression (Figure 7A, B). There is no trace of a dorsal tubercle. The iliac blade is slender and curves dorsally at the posterior end (Figure 7A). It is mediolaterally compressed, with an ovoid cross-section and no development of a dorsal crest (Figure 7B). The medial surface of the blade bears a groove along most of its length, whereas the lateral surface is smooth (Figure 7A, C).

A single femur is preserved on the block. As it lies close to the ilium, it is probably the femur of the right side, but

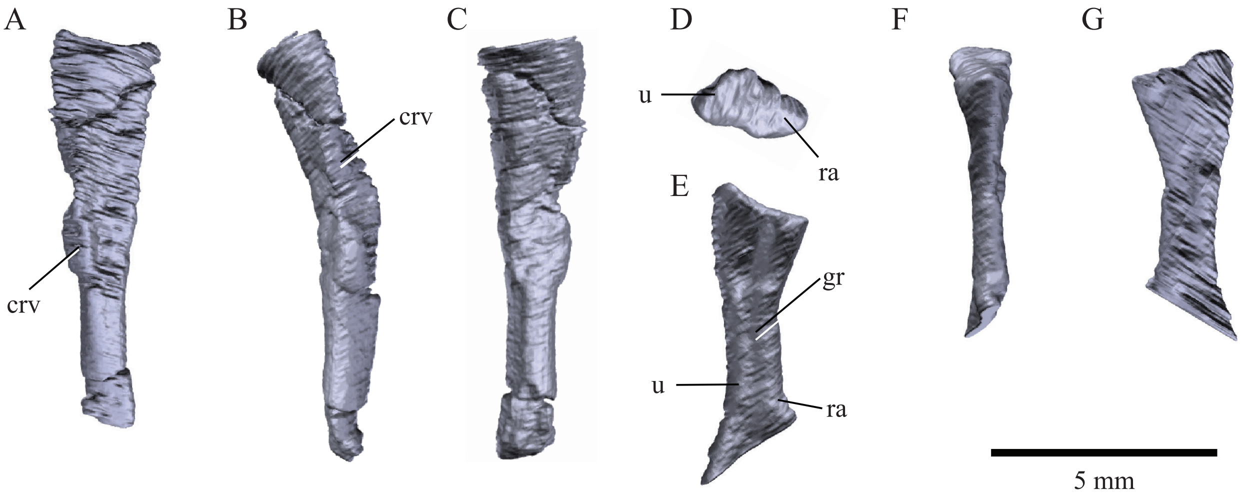

Figure 6. Left humerus (A–C) and right radioulna (D–G) of SBEI 1778. Left humerus in dorsal (A); anterior (B); and ventral (C) views. Right radioulna in proximal (D); dorsal (E); medial (F); and ventral (G) views.

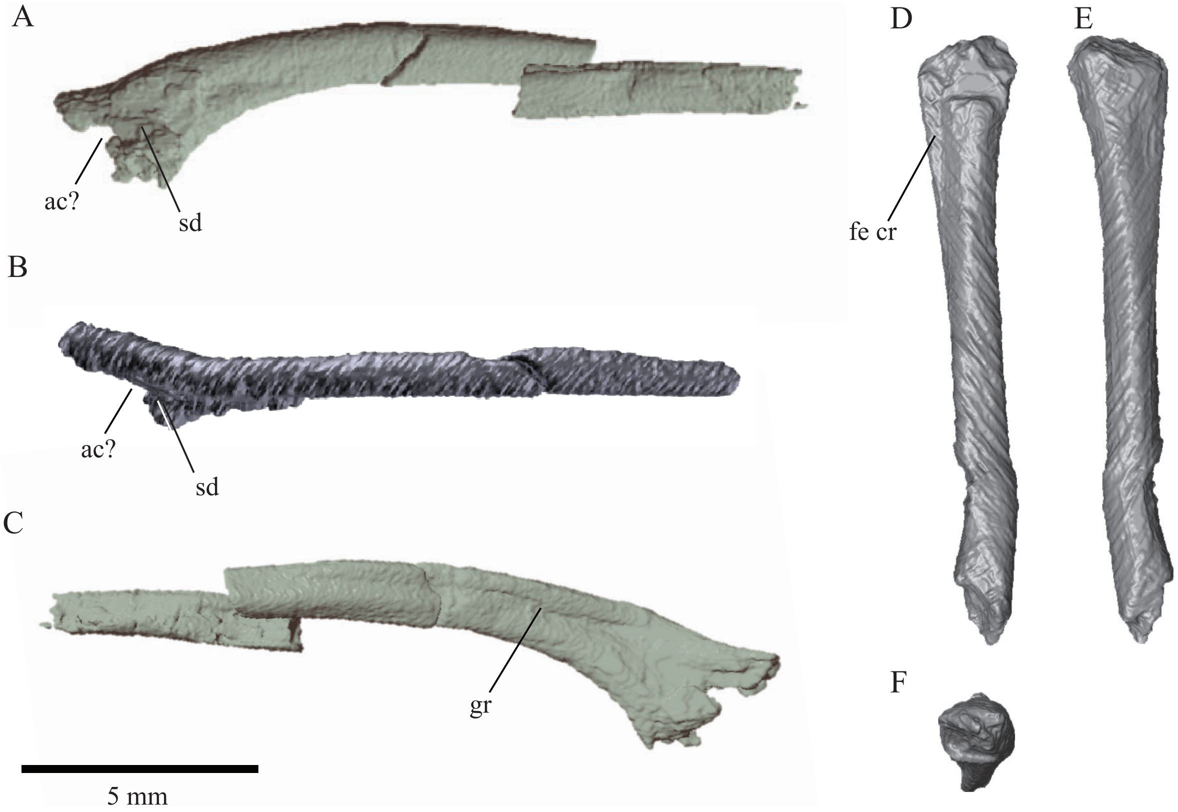

Figure 7. Right ilium (A–C) and femur (D–F) of SBEI1778. Right ilium in lateral (A), dorsal (B), and medial (C) views. Femur (side indeterminate) in anterior (D), posterior (E), and distal (F) views.

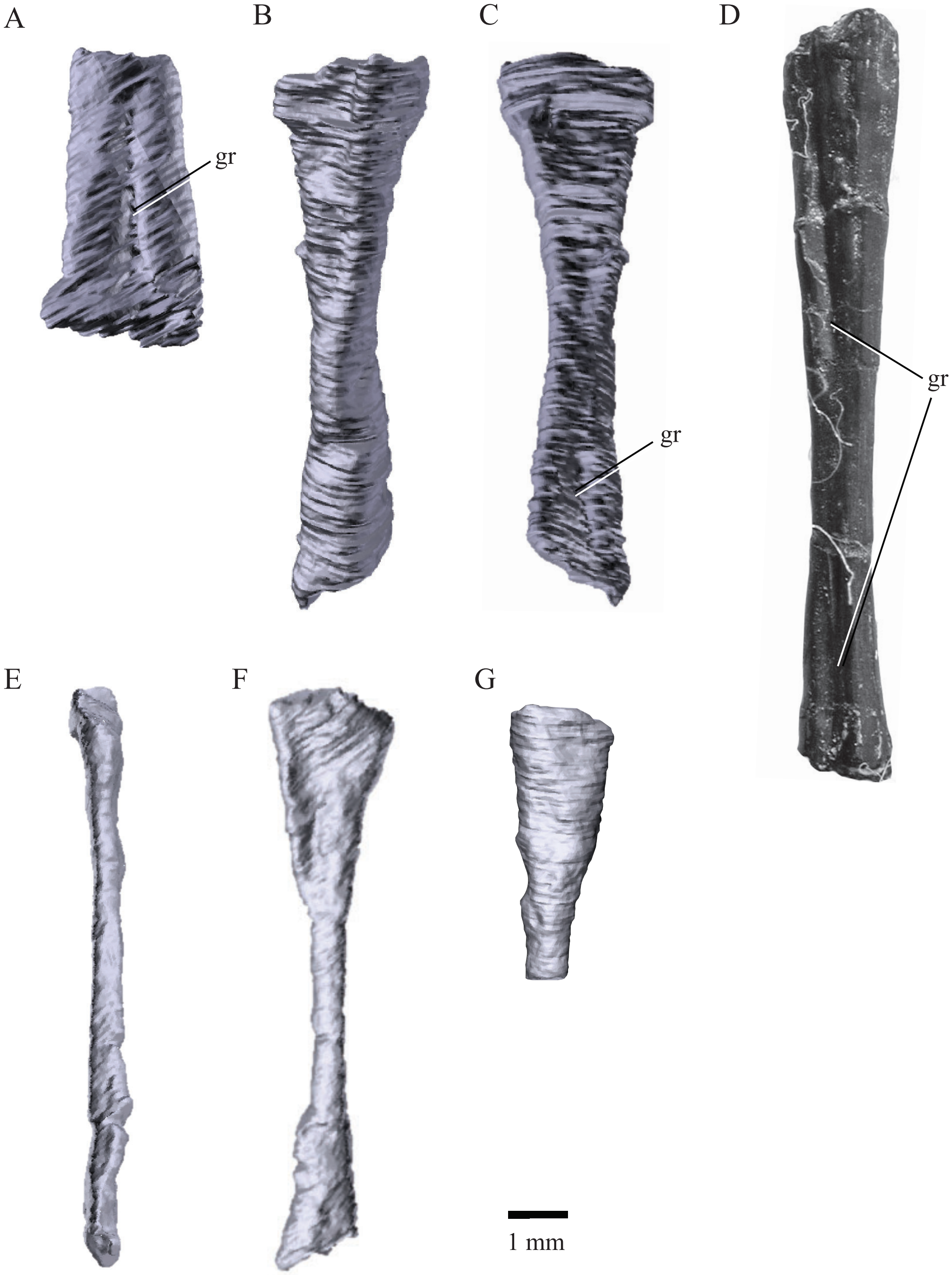

Figure 8. Two tibiofibulae (A–C) of SBEI 1778, isolated tibiofibula, SBEI 1222 (D), and two tarsals (E–G) of SBEI 1778; distal end of left tibiofibula in posterior view (A), mid-shaft of right tibiofibula in anterior (B), posterior (C) views; the left tibiofibula of SBEI 1222 in anterior view (D); relatively well-preserved proximal tarsal in lateral (E) and dorsal (F) views, and proximal half of second proximal tarsal in dorsal (G) view.

this remains uncertain as the bone lacks distinctive features and is missing its proximal and distal heads (Figure 7D, E). The femoral shaft is slender (~13 mm in length), almost straight (Figure 7D, E), and ovoid in cross-section at the mid-shaft (width: 1.26 mm; Figure 7F). A femoral crest is partially preserved on the proximal part of the shaft (Figure 7D).

Left and right tibiofibulae are preserved on SBEI 1778

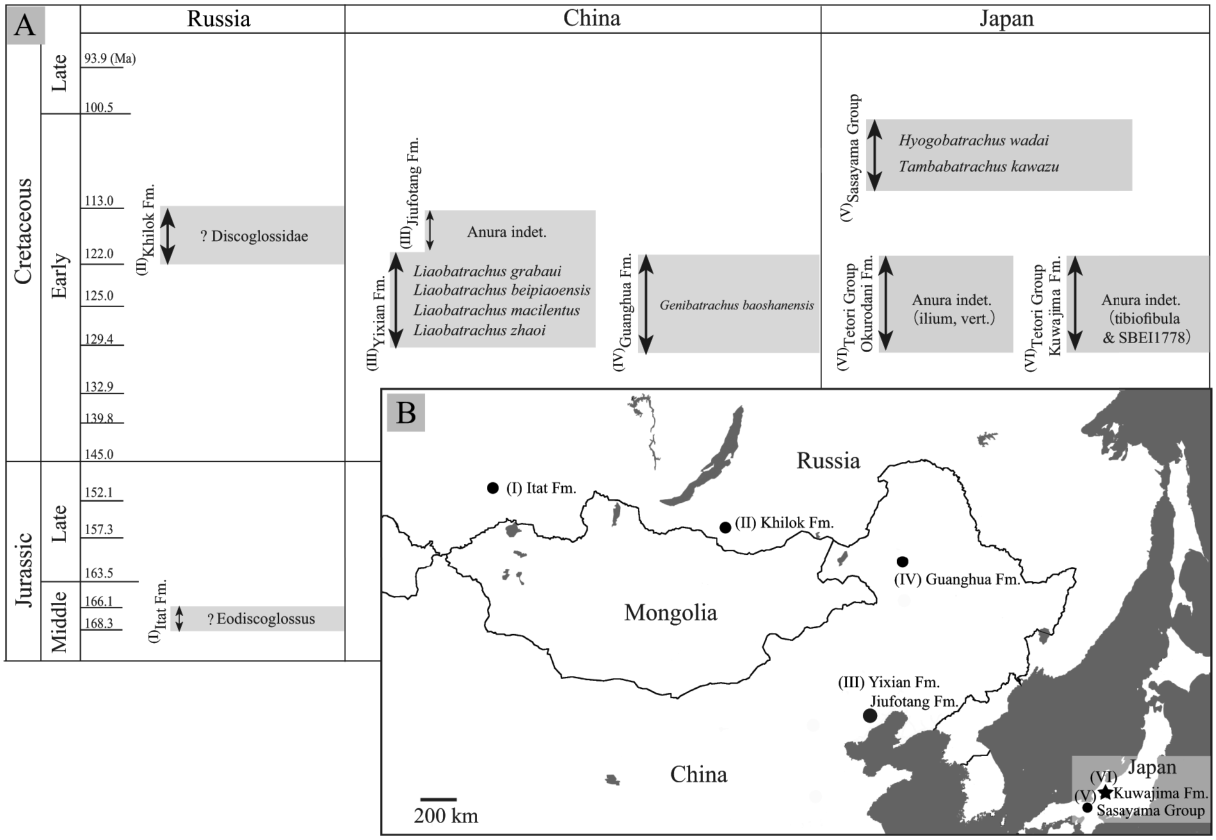

Figure 9. Occurrences of Anura through time during the Jurassic-Cretaceous of Asia (A) and map of Asia (B). Black spots indicate occurrence horizons.

(Figure 8A–C). The left tibiofibula is exposed on the matrix surface and only preserves the distal end (Figure 8A). The right tibiofibula lies under the matrix, and its proximal and its distal ends are incomplete (Figure 8 B, C). The shaft of the right bone is slender and waisted in the mid-section. On each bone, the lateral margin of the shaft is thicker than the medial one in posterior view (Figure 8A). A distinct groove marks the boundary between the tibia and fibula on the proximal and distal parts of the mid-shaft.

Matsuoka (2000) reported an isolated tibiofibula (SBEI1222: Figure 8D) from the same locality as SBEI 1778 (12.76 mm in length). The long shaft is waisted in the distal half, and the proximal head is wider than the distal one. The mid-shaft and the distal end are relatively narrower than those of SBEI 1778 (Figure 8A, C). Whether SBEI 1778 and 1222 represent the same species at different ontogenetic stages, or different species, is uncertain.

Two proximal tarsals (?tibiale and fibulare) are exposed on the matrix (Figure 2); one is nearly complete (Figure 8E, F), and the other one has only the proximal head preserved (Figure 8G). The well-preserved proximal tarsal (Figure 8E, F) is slender (9.6 mm in length) and straight, but it is strongly waisted at the mid-shaft, and both ends are mediolaterally compressed. As both the proximal and distal heads are damaged, we cannot be certain whether or not the proximal tarsals were originally fused, but it seems unlikely given that one is almost complete.

Two metatarsi are also visible on the matrix surface (Figures 2, 3A). These are both of similar lengths (5.1 mm and 5.2 mm), and are roughly half the length of the proximal tarsals.

Comparisons

Most recent phylogenetic analyses of Anura based on molecular and/or combined evidence data recognize two major 'groupings' among living taxa, namely a monophyletic Neobatrachia and a paraphyletic assemblage of anurans including *Ascaphus*, *Leiopelma*, Costata (Discoglossidae, Alytidae, Bombinatoridae), Xenoanura (Pipidae, Rhinophrynidae) and Anomocoela (Scaphiopodidae, Pelobatidae, Pelodytidae and Megophryidae) (e.g. Pyron and Wiens, 2011). SBEI 1778 has amphicoelous vertebrae, a primitive character state shared with the extant genera *Ascaphus* (North America) and *Leiopelma* (New Zealand), the Jurassic frogs *Prosalirus* (North America), *Vieraella* (South America) and *Notobatrachus* (Argentina), the Jurassic–Cretaceous "*Eodiscoglossus*" (Europe and possibly Siberian Russia), and several Cretaceous Asian genera, as listed on Figure 9. Of these non-neobatrachian taxa, SBEI 1778 is distinguished from the extant *Ascaphus*, *Leiopelma*, *Discoglossus*, *Pelobates* and *Pipa*, and the Jurassic/ Cretaceous genera *Prosalirus*, *Vieraella*, *Notobatrachus*, and *Eodiscoglossus santonjae* in the following character states: closed notochordal canal in amphicoelous vertebrae (vs. open in *Ascaphus*, *Leiopelma*, *Prosalirus*, *Vieraella*, *Notobatrachus*, Middle Jurassic "*Eodiscoglossus*" *oxoniensis*; opisthocoelous vertebrae in *Discoglossus*, *Pipa*; procoelous vertebrae in *Pelobates*); hatchet-shaped sacral diapophysis (vs. rod-like in *Vieraella* and *Prosalirus*; slender in *Leiopelma*, *Notobatrachus*; fan-like in *Pelobates*, *Pipa*), iliac blade lacking a dorsal crest (vs. crest present in *Discoglossus*, *Eodiscoglossus santonjae*, *Pipa*, *Prosalirus*,) and iliac blade ovoid in cross-section (vs. circular in *Ascaphus*, *Leiopelma*).

Japanese Cretaceous frogs

The Okurodani Formation, Tetori Group, is considered to be a lateral equivalent of the Kuwajima Formation (Maeda, 1952) (Figure 9). Two isolated unnamed anuran bones, a left ilium (IBEF VP 28) and a dorsal vertebra (IBEF VP29), are known from these deposits (Evans and Manabe, 1998). The ilia of SBEI 1778 and IBEF VP28 are roughly similar in length (~12–14 mm), and both have iliac blades that are ovoid in cross-section, with a weakly developed supracetabular region. However, whereas the Okurodani frog has a low dorsal tubercle and a slight iliac crest, the iliac blade of SBEI 1778 seems to lack both. Unfortunately, further comparison is difficult due to the lack of a complete acetabulum in SBEI 1778. The vertebral centra of both SBEI1778 and IBEF VP29 are amphicoelous, but the transverse processes are broken off in both. SBEI 1778 could belong to the same taxon as the Okurodani Formation frog (e.g. IBEF 28, 29) or represent a distinct taxon of similar morphological grade. Without further specimens, this remains undetermined.

The Japanese Cretaceous species *Hyogobatrachus wadai* and *Tambabatrachus kawazu* from the Sasayama Group are each represented by a single articulated specimen (Ikeda *et al.*, 2016). *H. wadai* is largely complete, with both skull and postcranial skeleton preserved; *Tambabatrachus kawazu* lacks most of the skull, parts of the pectoral girdle, and the manus and pes. According to Ikeda *et al.* (2016), the two species differ from one another in several ways, including the orientation of the vertebral transverse processes and of the sacral diapophyses; the presence (*Hyogobatrachus*) or absence (*Tambabatrachus*) of transverse processes on the urostyle; the size of the olecranon process on the radioulna; and the robusticity of the iliac shaft. Both of the Sasayama species share the following similarities with SBEI 1778: amphicoelous vertebrae without a patent notochordal canal; hatchet-shaped sacral diapophyses; an ilium lacking a dorsal crest or dorsal protuberance; hind limb elements of similar relative proportions; and (probably in SBEI 1778) unfused proximal tarsal bones. SBEI1778 differs from *Hyogobatrachus* in characters of the urostyle: low dorsal crest (vs. absent), monocondylar sacro-urostylar articulation (vs. bicondylar sacro-urostylar articulation), absence of transverse processes on the urostyle (vs. transverse processes present), and urostyle tapering posteriorly (vs. extending with similar width toward the distal end). SBEI 1778 resembles *Tambabatrachus* in the absence of transverse processes on the urostyle, but differs in lacking any waisting between the iliac blade and acetabular region (vs. slight waisting in *Tambabatrachus*, Ikeda *et al.*, 2016), and having a monocondylar (vs. bicondylar) sacro-urostylar articulation and a slight midline urostylar crest (vs. none). There is also a marked size difference between the Sasayama frogs and SBEI 1778. *Hyogobatrachus* and *Tambabatrachus* are small frogs with a snout-vent length of 26.8 mm in *Hyogobatrachus wadai* and 26.0 mm in *Tambabatrachus kawazu* at maturity (Ikeda *et al.*, 2016). Although most elements of SBEI 1778 are incomplete, the urostyle is relatively well-preserved (13.2 mm in length), and this is 150% larger than that of *Hyogobatrachus wadai* (8.9 mm in length). However, size characters should be treated with caution in frogs, as there is often a considerable size disparity between males and females of the same species (e.g. Woolbright, 1983), with females often being the larger morph (e.g. Shine, 1979). Larger animals also have a greater muscle volume, resulting in more marked crests and ridges at attachment sites. Nonetheless, SBEI 1778 is distinct from the Sasayama frogs in having a mono- vs. bicondylar sacro-urostylar joint.

Other Cretaceous Asian frogs

Early Cretaceous frogs have been recorded from several other localities across Asia, most notably within the Jehol Biota of China, but also in Mongolia and other parts of China (Figure 9). SBEI 1778 resembles the Chinese frog genus *Liaobatrachus* (including *L. grabaui*, *L. beipiaoensis*, *L. macilentus*, and *L. zhaoi*, Dong *et al.*, 2013) from the Yixian Formation in the absence of both a dorsal crest and dorsal protuberance on the ilium, and in the primitive presence of a monocondylar sacro-urostylar joint, but it is distinguished from all referred species of *Liaobatrachus* in having hatchet-shaped sacral diapophyses (vs. broadly

Figure 10. Phylogenetic relationships of SBEI 1778 within Mesozoic anurans. **A,** strict consensus of the four most parsimonious trees (MPTs) obtained by TNT analysis of the matrix of Ikeda *et al.* (2016) with three additional neobatrachian species (*Hadromophryne natalensis*, *Heleophryne purcelli*, *Sooglossus sechellensis*); **B,** bootstrap consensus tree, examined by 5000 replicated resampling analysis, numbers on tree B indicate bootstrap values. Asterisk symbols indicate fossil taxa.

dilated, fan-like diapophyses; Dong *et al.*, 2013), in having a shorter coronoid process on the angulosplenial, extending along 25% of the long axis (vs. long; Dong *et al.*, 2013; pars. obs. RM [34% of the length]), and in lacking transverse processes on the urostyle (vs. processes present). In addition, the dentary is distinguished from that of *Liaobatrachus beipiaoensis* (Gao and Wang, 2001) in the presence of sharp dorsal and ventral margins (vs. a thin edentate dorsal crest). SBEI 1778 also differs from an unnamed specimen from the Jiufotang Formation, IVPP V13235 (Wang *et al.*, 2007; Dong *et al.*, 2013), in having amphicoelous vertebrae without a patent notochordal canal (vs. fully notochordal), more expanded sacral diapophyses (vs. unexpanded), a monocondylar sacro-urostylar joint (vs. bicondylar), and lacking transverse processes on the urostyle (vs. transverse processes present). Late Cretaceous species of the group Gobiatidae (Mongolia, Uzbekistan, Kazakhstan) (e.g. Spinar and Tatarinov, 1986; Gubin, 1999; Roçek, 2008; Skutschas and Kolchanov, 2017) are also differentiated from SBEI 1778 in having bicondylar sacro-urostylar joints and at least one pair of transverse processes on the urostyle (Roçek, 2008).

Genibatrachus from the Lower Cretaceous Guanghua Formation in Inner Mongolia (Gao and Chen, 2017) is distinguished from all the Japanese taxa in having procoelous vertebrae and unexpanded sacral diapophyses. Isolated frog remains (maxilla, urostyle, tibiofibula, proximal tarsals) from the Early Cretaceous Khilok Formation of Transbaikalian Russia were attributed to ?Discoglossidae (Skutschas, 2003), but without opisthocoelous vertebral centra this attribution cannot be confirmed. Nonetheless, if the Russian specimens belong to a single taxon, it differs from SBEI 1778 in having a bicondylar sacro-urostylar joint, and proximal and distal fusion of the tibiale and fibulare.

Phylogenetic analysis

In order to examine the phylogenetic position of SBEI 1778 among other Asian frogs, SBEI 1778 was coded into the morphological data matrix of Ikeda *et al.* (2016), with the addition of three early-branching neobatrachian species (*Hadromophryne natalensis*, *Heleophryne purcelli*, *Sooglossus sechellensis*, Pyron and Wiens, 2011) to provide further outgroup comparison. The analysis was run using TNT (version1; Goloboff *et al.*, 2008) with the New Technology search option with Ratchet (1000 random addition sequences: 20 iterations). Caudata was the designated outgroup taxon. The resulting trees were re-analysed by using a Traditional search mode to fully explore all possible topologies. The bootstrap consensus tree was analyzed with 5000 replicated resampling. This analysis yielded the four most parsimonious trees (MPTs, Length 200), and the strict consensus tree placed SBEI 1778 as the sister taxon of the Chinese *Liaobatrachus* rather than the Japanese taxa, *Hyogobatrachus* and *Tambatrachus*. However, when character traits were mapped on the tree, SBEI 1778 and *Liaobatrachus* were found to share a single character state, monocondylar sacro-urostylar articulation (character no. 45) (Figure 10), a trait generally considered primitive. When the analysis was re-run with character 45 de-activated, the analysis yielded 31 MPTs (Length 193). In the Strict Consensus tree from this second analysis, SBEI 1778 was placed on the stem of a clade comprising the Chinese *Liaobatrachus* and the Japanese *Hyogobatrachus* and *Tambatrachus*. This instability in the position of SBEI 1778 is probably due to the large amount of missing data (88%), especially for elements with diagnostic characters (e.g. premaxilla, frontoparietal, prefrontal). SBEI 1778 thus represents a non-neobatrachian grade frog of uncertain affinity. It may be related to one or more of the previously named Early Cretaceous frogs from China and Japan, but further material is needed for comparison, particularly from the skull.

Discussion

SBEI 1778 is the first associated anuran specimen combining both postcranial and skull elements (e.g. pterygoid, dentary and angulosplenial) from the Kuwajima Formation, Tetori Group, of Japan. The Kuwajima Formation has yielded a diversity of small vertebrates, but amphibian records are very rare (Isaji *et al.*, 2005; Matsumoto and Evans, 2018). This is unlikely to be a sampling bias, because the 'Kaseki-kabe' locality has been well studied for more than twenty years, and several thousand specimens, both associations and individual elements, have been collected over that time. There may be several reasons for the lack of amphibian records in this area, including palaeoenvironmental conditions and sedimentary environment.

The average annual temperature during deposition of the Kuwajima Formation may have been relatively low, 10 ± 4°C (Amiot *et al.*, 2011), but similar temperatures were estimated for the Jehol Biota of China (Amiot *et al.*, 2011), where frog fossils are more abundant. Moreover, although many extant neobatrachian frogs are distributed within the tropics (Wiens, 2007), others (e.g. Ranidae, Bufonidae) occur in temperate regions, as do many non-neobatrachians. Ambient temperature is therefore unlikely to have been a factor.

Although the Jehol Biota has yielded several frog specimens, salamanders are far more common. This reflects habitat differences. The Jehol sediments represent a lake environment (e.g. Pan *et al.*, 2012) and the remains of aquatic-semiaquatic vertebrates (fish, salamanders, choristoderes) are more likely to be preserved than those of predominantly terrestrial taxa, including adult frogs (Wang *et al.*, 2010). This may also explain, at least in part, why small terrestrial animals are rarer in the floodplain environment of the Kuwajima Formation (Isaji *et al.*, 2005). However, this does not explain the absence of aquatic salamander fossils. The fine-grain deposits of the Yixian and Jiufotang formations are certainly more suitable for the preservation of fragile vertebrates like amphibians, but this seems an unsatisfactory explanation for the absence of salamanders in the Kuwajima Formation. Thus, the reason for the rarity of amphibian fossils in the Kuwajima Formation, and particularly the absence of salamanders, remains unresolved.

The new Kuwajima frog specimen, SBEI 1778, preserves a limited number of postcranial elements for comparison with other Early Cretaceous Asian frogs (sacral diapophyses, ilium, urostyle and vertebrae). SBEI 1778 shares some similarities with the Early Cretaceous Chinese *Liaobatrachus* and Japanese *Hyogobatrachus* and *Tambabatrachus*, but is distinct from them, based on the combination of hatchet-shaped sacral diapophyses; a monocondylar sacro-urostylar joint; absence of transverse processes on the urostyle; posteriorly tapering urostyle with weakly developed dorsal crest. However, there are too few diagnostic characters in SBEI 1778 to designate it as the type of a new species. The phylogenetic analysis places SBEI 1778 as a non-neobatrachian frog that may be related to *Liaobatrachus*, which is chronologically close to the Kuwajima Formation, and/or to *Hyogobatrachus* and *Tambabatrachus* which come from a slightly younger deposit (Figure 9). However, this hypothesis of relationship is weakly supported due to the large amount of missing data. Additional material of the Tetori frog (or frogs) is needed, especially the discovery of cranial elements and a complete ilium, in order to understand how it fits into the evolutionary history and distribution pattern of Early Cretaceous Asian frogs.

Conclusions

A rare frog specimen from the Early Cretaceous Kuwajima Formation, Ishikawa Prefecture, Japan, containing 28 identified elements of a single individual within a block of matrix, is attributed to a non-neobatrachian grade frog based on the combination of amphicoelous vertebrae and a monocondylar sacro-urostylar joint. This new Tetori frog is distinguished from other Asian species of similar grade, such as the Japanese *Hyogobatrachus* and *Tambabatrachus*, and the Chinese *Liaobatrachus* by a combination of iliac, sacral and urostylar characters. This new specimen, which is not complete enough to be named, provides additional information on the diversity of anurans in the Early Cretaceous of East Asia, but more material is needed to understand its relationships and evolutionary history.

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References

Amiot, R., Wang, X., Zhou, Z., Wang, X., Buffetaut, E., Lecuyer, C. *et al.*, 2011: Oxygen isotopes of East Asian dinosaurs reveal exceptionally cold Early Cretaceous climates. *Proceedings of the National Academy of Sciences of the United States of America*, vol. 108, p. 5179–5183.

Amphibia Web: *Browse by Family* [online]. [Cited 6 February 2022]. Available from: https://amphibiaweb.org/lists/index.shtml.

Baez, A. M. and Basso, N., 1996: The earliest known frogs of the Jurassic of South America: review and cladistic analysis. *Münchner Geowissenschaftliche Abhandlungen, Reihe A (Geologie Paläontologie)*, vol. 30, p. 131–158.

Baez, A. M. and Nicoli, L., 2004: A new look at an old frog: the Jurassic *Notobatrachus* Reig from Patagonia. *Ameghiniana*, vol. 41, p. 257–270.

Barrett, P. M., Hasegawa, Y., Manabe, M., Isaji, S. and Matsuoka, H., 2002: Sauropod dinosaurs from the Lower Cretaceous of Eastern Asia: taxonomic and biogeographical implications. *Palaeontology*, vol. 45, p. 1197–1217.

Dong, L., Roçek, Z., Wang, Y. and Jones, M. E. H., 2013: Anurans from the Lower Cretaceous Jehol Group of Western Liaoning, China. *PLOS ONE*, doi: /10.1371/journal.pone.0069723.

Evans, S. E. and Borsuk-Białynicka, M., 1998: A stem group frog the Early Triassic of Poland. *Acta Paleontologica Polonica*, vol. 43, p. 573–580.

Evans, S. E. and Manabe, M., 1998: Early Cretaceous frog remains from the Okurodani Formation, Tetori Group, Japan. *Paleontological Research*, vol. 2, p. 275–278.

Evans, S. E. and Manabe, M., 2008: A herbivorous lizard from the Early Cretaceous of Japan. *Palaeontology*, vol. 51, p. 487–498.

Evans, S. E. and Matsumoto, R., 2015: An assemblage of lizards from the Early Cretaceous of Japan. *Palaeontologia Electronica*, 18. 2, 36A, p. 1–36.

Evans, S. E. and Milner, A. R., 1993: Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America. *Journal of Vertebrate Paleontology*, vol. 13, p. 24–30.

Evans, S. E., Milner, A. R. and Mussett, F., 1990: A discoglossid frog from the Middle Jurassic of England. *Palaeontology*, vol. 33, p. 299–311.

Gao, K. Q. and Chen, J., 2017: A new crown-group frog (Amphibia: Anura) from the Early Cretaceous of northeastern Inner Mongolia, China. *American Museum Novitates*, no. 3876, p. 1–40.

Gao, K. Q. and Wang, Y., 2001: Mesozoic anurans from Liaoning Province, China, and phylogenetic relationships of archaeobatrachian anuran clades. *Journal of Vertebrate Paleontology*, vol. 21, p. 460–476.

Goloboff, P., Farris, J. and Nixon, K., 2008: TNT, a free program for phylogenetic analysis. *Cladistics*, vol. 24, p. 774–786.

Gubin, Y. M., 1999: Gobiatids (Anura) from the Upper Cretaceous locality Khermeen-Tsav (Gobi Desert, Mongolia). *Paleontological Journal*, vol. 33, p. 77–87.

Haeckel, E., 1866: *Generelle Morphologie der Organismen: allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie*, 462 p. G. Reimer, Berlin.

Hecht, M. K., 1970: The morphology of *Eodiscoglossus*, a complete Jurassic frog. *American Museum Novitates*, no. 2424, p. 1–17.

Henrici, A. C., 1998: A new pipoid anuran from the Late Jurassic Morrison Formation at Dinosaur National Monument, Utah. *Journal of Vertebrate Paleontology*, vol. 18, p. 321–332.

Hirayama, R., Isaji, S. and Hibino, T., 2012: *Kappachelys okurai* gen. et. sp. nov., a new stem soft-shelled turtle from the Early Cretaceous of Japan. *In*, Brinkman, D. G., Holroyd, P. A. and Graner, J. D. *eds*., *Morphology and Evolution of Turtles*, *Vertebrate Paleobiology and Paleoanthropology*, p. 179–185. Springer Science + Business Media, Dordrecht.

Ikeda, T., Ota, H. and Matsui, M., 2016: New fossil anurans from the Lower Cretaceous Sasayama Group of Hyogo Prefecture, Western Honshu, Japan. *Cretaceous Research*, vol. 61, p. 108–123.

Isaji, S., Matsushita, A. and Hirayama, R., 2006: Chelonian eggshells from the Lower Cretaceous Kuwajima Formation of the Tetori Group, central Japan. *Paleontological Research*, vol. 10. p. 29–36.

Isaji, S., Okazaki, H., Hirayama, R., Matsuoka, H., Barrett, P. M., Tsubamoto, T. *et al.*, 2005: Depositional environments and taphonomy of the bone-bearing beds of the Lower Cretaceous Kuwajima Formation, Tetori Group, Japan. *Bulletin of the Kitakyushu Museum National History and Human History*, *Series A*, vol. 3, p. 123–133.

Kusuhashi, N., 2008: Early Cretaceous multituberculate mammals from the Kuwajima Formation (Tetori Group), central Japan. *Acta Palaeontologica Polonica*, vol. 53, p. 379–390.

Kusuhashi, N., Matsumoto, A., Murakami, M., Tagami, T., Hirata, T., Iizuka, T. *et al.*, 2006: Zircon U-Pb ages from tuff beds of the upper Mesozoic Tetori Group in the Shokawa district, Gifu Prefecture, central Japan. *Island Arc*, vol. 15, p. 378–390.

Laurenti, J. N., 1768: *Specimen medicum, exhibens synopsin Reptilium emendatam cum experimentis circa venena et antidota Reptilium austriacorum*, 215 p. Typis Joan. Thomae nob. de Trattnern, Viennae.

Linnaeus, C., 1758: *Systema naturae, per regna tria naturae: secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*, 824 p. Laurentii Salvaii, Holmiae.

Maeda, S., 1952: A stratigraphical study on the Tetori Series in the upper Shiokawa district in Gifu Prefecture. *Journal of the Geological Society of Japan*, vol. 58, p. 145–153. (*in Japanese with English abstract*)

Maeda, S., 1961: On the geological history of the Mesozoic Tetori Group in Japan. *Journal of the Collections of Arts and Science*, *Chiba University*, vol. 3, p. 369–426.

Matsumoto, R. and Evans, S. E., 2018: The first record of albanerpetontid amphibians (Amphibia: Albanerpetontidae) from East Asia. *PLOS ONE*, doi: 10.1371/journal.pone.0189767.

Matsumoto, R., Evans, S. E. and Manabe, M., 2007: The choristoderan reptile *Monjurosuchus* from the Early Cretaceous of Japan. *Acta Palaeontologica Polonica*, vol. 52, p. 329–350.

Matsumoto, R., Evans, S. E. and Manabe, M., 2014: The first record of a long-snouted choristodere (Reptilia, Diapsida) from the Early Cretaceous of Ishikawa Prefecture, Japan. *Historical Biology*, vol. 27, p. 583–594.

Matsumoto, A., Kusuhashi, N., Murakami, M., Tagami, T., Hirata, T., Iizuka, T. *et al.*, 2006: LA-ICPMS U-Pb zircon dating of tuff beds of the upper Mesozoic Tetori Group. *Abstracts with Programs of the 155th Regular Meeting of the Palaeontological Society of Japan*, p. 110. (*in Japanese*)

Matsuoka, H., 2000: A fossil frog. *In*, Matsuoka, H. *ed*., *Fossil of the Kuwajima* “Kaseki-kabe” *(Fossil-bluff), Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan*, p. 50–52. Shiramine Village Board of Education, Hakusan. (*in Japanese*)

Matsuoka, H., Kusuhashi, N. and Corfe, I. J., 2016: A new Early Cretaceous tritylodontid (Synapsida, Cynodontia, Mammaliamorpha) from the Kuwajima Formation (Tetori Group) of central Japan. *Journal of Vertebrate Paleontology*, vol. 36, doi: 10.1080/02724634.2016.1112289.

Matsuoka, H. and Setoguchi, T., 2000: Significance of Chinese tritylodonts (Synapsida, Cynodontia) for the systematic study of Japanese materials from the Lower Cretaceous Kuwajima Formation, Tetori Group of Shiramine, Ishikawa, Japan. *Asian Paleoprimatology*, vol. 1, p. 161–176.

Ohashi, T. and Barrett, P. M., 2009: A new ornithischian dinosaur from the Lower Cretaceous Kuwajima Formation of Japan. *Journal of Vertebrate Paleontology*, vol. 29. p. 748–757.

Pan, Y., Sha, J., Fuersich, F. T., Wang, Y., Zhang, X. and Yao, X., 2012: Dynamics of the lacustrine fauna from the Early Cretaceous Yixian Formation, China: implications of volcanic and climatic factors. *Lethaia Foundation*, vol. 45, p. 299–314.

Piveteau, J., 1936: Une forme ancestrale des Amphibiens Anoures dans le Trias inférieur de Madagascar. *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences*, vol. 202, p. 1607–1608. (*in French*)

Pyron, R. A. and Wiens, J. J., 2011: A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution*, vol. 61, p. 543–583.

Rafinesque, C. S., 1815: *Analyse de la nature: or, Tableau de l'univers et des corps organisés*, 224 p. Aux dépens de l'auteur, Palerme. (*in French*)

Roçek, Z., 2008: The Late Cretaceous frog *Gobiates* from Central Asia: its evolutionary status and possible phylogenetic relationships. *Cretaceous Research*, vol. 29, p. 577–591.

Roçek, Z., Wang, Y. and Dong, L., 2012: Post-metamorphic development of Early Cretaceous frogs as a tool for taxonomic comparisons. *Journal of Vertebrate Paleontology*, vol. 32, p. 1285–1292.

Rougier, G. W., Isaji, S. and Manabe, M., 2007: An Early Cretaceous mammal from the Kuwajima Formation (Tetori Group), Japan, and a reassessment of triconodont phylogeny. *Annals of Carnegie Museum*, vol. 76, p. 73–115.

Sano, S., 2015: New view of the stratigraphy of the Tetori Group in Central Japan. *Memoir of Fukui Prefectural Dinosaur Museum*, vol. 14, p. 25–61.

Setoguchi, T., Matsuoka, H. and Matsuda, M., 1999: New discovery of an Early Cretaceous tritylodontid (Replilia. Therapsida) from Japan and the phylogenetic reconstruction of Tritylodontidae based on the dental characters. *In*, Wang, Y. and Deng, T. *eds*., *Proceedings of the 7th annual meeting of the Chinese Society of Vertebrate Paleontology*, p. 117–124. China Ocean Press, Beijing.

Shine, R., 1979: Sexual selection and sexual dimorphism in the Amphibia. *Copeia*, vol. 1979, p. 297–306.

Shubin, N. H. and Jenkins, F. A., Jr., 1995: An Early Jurassic jumping frog. *Nature*, vol. 377, p. 49–52.

Skutschas, P. P., 2003: Anuran remains from the Early Cretaceous of Transbaikalia, Russia. *Russian Journal of Herpetology*, vol. 10, p. 213–216.

Skutschas, P. P. and Kolchanov, V. V., 2017: Anurans (Amphibia: Anura) from the Upper Cretaceous (Santonian–lower Campanian) Bostobe Formation of Northeastern Aral Sea Region, Kazakhstan. *Palaeoworld*, vol. 26, p. 202–208.

Skutschas, P. P., Martin, T. and Krasnnolutskii, A. S., 2016: First Jurassic frog from Siberia, Russia. *Journal of Vertebrate Paleontology*, vol. 36, doi: 10.1080/02724634.2016.1101376.

Spinar, Z. V. and Tatarinov, L. P., 1986: A new genus and species of discoglossid frog from the Upper Cretaceous of the Gobi Desert. *Journal of Vertebrate Paleontology*, vol. 6, p. 113–122.

Sullivan, C., Wang, Y., Hone, D. W., Wang, Y., Xu, X. and Zhang, F., 2014: The vertebrates of the Jurassic Daohugou Biota of northeastern China. *Journal of Vertebrate Paleontology*, vol. 34, p. 243–280.

Unwin, D. M. and Matsuoka, H., 2000: Pterosaurs and birds. *In*, Matsuoka, H. *ed*., *Fossil of the Kuwajima* "*Kaseki-Kabe*" *(Fossil-bluff), Scientific report on a Neocomian (Early Cretaceous) fossil assemblage from the Kuwajima Formation, Tetori Group, Shiramine, Ishikawa, Japan*, p. 99–104. Shiramine Village Board of Education, Hakusan. (*in Japanese*)

Vera, M. C. and Ponssa, M. L., 2014: Skeletogenesis in anurans: cranial and postcranial development inmetamorphic and postmetamorphic stages of *Leptodactylus bufonius* (Anura: Leptodactylidae). *Acta Zoologica*, vol. 95, p. 44–62.

Wang, Y., Dong, L. and Evans, S. E., 2010: Jurassic–Cretaceous herpetofaunas from the Jehol associated strata in NE China: evolutionary and ecological Implications. *Bulletin of the Chinese Academy of Sciences*, vol. 24, p. 76–79.

Wang, Y., Jones, M. E. H. and Evans, S. E., 2007: A juvenile anuran from the Lower Cretaceous Jiufotang Formation, Liaoning, China. *Cretaceous Research*, vol. 28, p. 235–244.

Wiens, J. J., 2007: Global patterns of diversification and species richness in amphibians. *American Naturalist*, vol. 170, p. 86–106.

Woolbright, L. L., 1983: Sexual selection and size dimorphism in anuran Amphibia. *American Naturalist*, vol. 121, p. 110–119.

Yabumoto, Y., 2005: Early Cretaceous freshwater fishes from the Tetori Group, central Japan. *Bulletin of Kitakyushu Museum of Natural History and Human History*, *Series A*, vol. 3, p. 135–143.

Yabumoto, Y., 2014: *Shinamia kukurihime*, a new Early Cretaceous amiiform fish from Ishikawa, Japan. *Paleontological Research*, vol. 18, p. 211–223.

Yabumoto, Y., Yang, S. Y. and Kim, T. W., 2006: Early Cretaceous freshwater fishes from Japan and Korea. *Journal of the Paleontological Society of Korea*, vol. 22, p. 119–312.

Yuan, C.-X., Zhang, H.-B., Li, M. and Ji, X.-X., 2004: [Discovery of a Middle Jurassic fossil tadpole from Daohugou Region, Ningcheng, Inner Mongolia, China]. *Acta Geologica Sinica*, vol. 78, p. 145–149. (*in Chinese; original title translated*)

Author contributions

R. M. performed computerized microtomography; A. M. completed computerized microtomography rendering; A. M. initiated the study and was primarily responsible for the taxonomic aspects; A. M. and R. W. discussed the geological setting and taphonomy of deposits; A. M. and R. M. made figures; A. M., R. M. and S. E. performed the phylogenetic analysis of the data. All authors contributed to the data interpretation and the writing of the paper.

Appendix 1. Matrix of taxa and characters used in phylogenetic analysis. A(0&1); B(1&2); C(0&2); gap = -; ? = missing data or inapplicable. Asterisk symbols indicate fossil taxa.

	5	10	15	20	25	30	35	40	45	50	55	60	65
Caudata	000A0	00000	00000	00000	00000	0--AA	-0000	000?0	?000-	0--0-	-0000	0-?00	00000
*Triadobatrachus**	000??	10000	0????	00000	01??0	?0000	00?10	?0000	00000	000??	01000	10000	?????
*Czatkobatrachus**	?????	?????	?????	?????	?????	?????	?????	?0?0?	?10??	?????	?110?	1?0??	?????
*Prosalirus**	?1???	1??01	??1??	?????	?1???	?0?0?	?0???	?0?0?	?10B?	?10?0	??01?	1?110	????0
Ascaphus	01101	10210	10011	11100	10-01	01100	01012	00122	01120	01111	01111	10?11	01010
Leiopelma	01101	10210	20001	11100	10121	01110	01012	00122	11020	01000	01111	10111	01110
Alytes	01001	10210	21101	20100	11121	11110	10013	01102	11121	01111	12111	11111	01100
Barbourula	01000	11010	21001	20100	11121	11110	20013	01002	11222	01111	12111	10111	01100
Bombina	01000	10210	21AA1	30100	11121	11110	C0013	01002	11222	01112	12111	10111	01100
Discoglossus	01010	10210	21101	20110	11121	11110	20013	01002	11121	01111	12111	11111	01100
*Eodiscoglossus**	01000	1011?	1??0?	20100	1????	?????	?0?13	010?2	1122B	2?1?1	1?111	1?110	?1??0
*Notobatrachus**	00000	10111	10100	11100	10011	00001	00012	?00?1	01010	01000	01010	10110	????0
*Vieraella**	010?0	10110	1?001	??100	11111	?010?	??011	?00?2	0?0??	??0?0	0?01?	1??1?	?????
Pelobates	00000	11-11	21101	10111	11120	11111	20013	02004	11222	11101	0?111	11111	12201
*Eopelobates**	00000	10011	?????	?0111	11???	11111	?0?13	?20?4	11222	1?102	??11?	10111	0????
Megophrys	01000	10011	2?101	?0101	11??1	1111?	20013	02004	11221	11100	0?111	11111	12201
Pelodytes	011A1	10C1?	2?101	10100	11120	11110	10013	12004	11222	0110A	??111	11112	01201
Pipa	A1001	11-10	22010	11300	12??1	02111	201B3	11003	11223	21010	1?111	10011	11201
Xenopus	A1200	11-10	23010	11300	12??1	02110	20113	01023	11223	21122	1?111	10011	11211
Rhinophrynus	11000	11-11	21001	10200	111?1	02102	01123	01004	11221	21111	22111	11111	11201
*Palaeobatrachus**	11000	11-10	21000	1A100	111?1	02100	10013	12023	01121	21110	1111A	1?111	11??1
*Liaobatrachus_grabaui**	01000	102?1	2?001	10100	11101	01??1	?0012	000A2	0122?	01111	01111	10110	?0???
*Liaobatrachus_beipiaoensis**	01000	10211	2?00?	10100	11121	011?1	?0012	00012	01222	00111	01111	10110	?0???
*Liaobatrachus_macilentus**	010?0	10211	2?001	10100	11121	011?1	10012	00012	01222	01111	01111	10110	?0???
*Liaobatrachus_zhaoi**	01000	10211	2?001	10100	11121	01111	10012	00012	01222	01111	01111	10110	?????
*Hyogobatrachus_wadaii**	01000	10110	???0?	211?0	1????	?1111	?0013	000?2	11121	0???1	12111	1?110	?????
*Tambabatrachus_kawazu**	01???	???1?	2????	?1???	?????	?????	????3	00012	01121	2????	?211?	1?110	?????
SBEI1778*	?????	?????	?????	?????	?????	????A	???B?	?0???	??122	?????	?????	1?1??	?????
Hadromophryne_natalensis	01111	10211	11101	20101	111?0	11100	2?013	020A4	?1121	?1001	1?011	11110	112?1
Heleophryne_purcelli	01111	10211	11101	20101	111?0	11100	2?013	020A4	?1121	?1001	1?011	11110	112?1
Sooglossus_sechellensis	11011	10211	21101	20101	111?0	01110	2?013	02014	?1122	?1101	10111	11111	112?1