

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

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15

16 **Abstract**

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

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

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Introduction

31 Amongst extant amphibians, frogs are by far the most diverse in terms of species number (7449

32 vs. 767 Caudata and 215 Gymnophiona, Amphibia Web 2022) and have a global distribution across

33 both temperate and tropical regions. However, as for all lissamphibians, the early fossil record of

34 frogs is limited and our knowledge of their evolutionary history remains incomplete. The earliest

35 known salientians (Anura + stem taxa) are known from the Early Triassic of Madagascar

36 (*Triadobatrachus massinoti*; Piveteau, 1936) and southern Poland (*Czatkobatrachus polonicus*;

37 Evans and Borsuk-Białynicka, 1998). Furthermore, more derived, stem-anurans are known from the

38 Jurassic of North America (Arizona: *Prosalirus bitis*; Shubin and Jenkins, 1995) and South America

39 (Argentina: *Vieraella herbsti*, *Notobatrachus digiustoi*, Baez and Basso, 1996; Baez and Nicoli,

40 2004). The earliest recognized crown anurans (Discoglossoidea, Rhinophryinae, possible

41 Pelobatidae) are from the Jurassic of Europe (Discoglossoidea: *Eodiscoglossus*, Hecht, 1970) and

42 North America (Morrison Formation: *Enneabatrachus* [Discoglossoidea], and unnamed pelobatid-

43 like taxon, Evans and Milner 1993; the rhinophrynid *Rhadinosteus*, Henrici 1998). Records of

44 Jurassic anurans from Asia are rare. The Daohugou Biota of northeastern China is one of the best-

45 known Asian Jurassic deposits, and has yielded an impression of a metamorphosing tadpole (Yuan *et*

46 *al.*, 2004). However, this specimen lacks evidence of an ossified skeleton and its identification has

47 been questioned (Sullivan *et al.*, 2014). Therefore, certain records of Jurassic anurans from Asia are

48 limited to an isolated atlas from **Western** Siberia (Skutschas *et al.*, 2016). However, the anuran

49 record improves significantly in the Early Cretaceous, with taxa recorded from North and South

50 America, Africa, the Middle East, Europe, and Asia (e.g. Roček, 2008). Several articulated anuran

51 specimens have been reported from the Yixian and Jiufotang formations (Barremian–Aptian) of the

52 Jehol Group, China, and many of these frogs are now attributed to species of the genus

53 *Liaobatrachus* (Dong et al., 2013). A second frog genus, *Genibatrachus* (Gao and Chen, 2017; Xi et
54 al., 2019), has been recovered from the Guanghai Formation, Inner Mongolia (Barremian–Aptian).

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

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

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Geological Setting

73 The Mesozoic (Middle Jurassic to Early Cretaceous) marine and freshwater deposits of the
74 Tetori Group are widely distributed within the Inner Zone of central Japan (Fukui, Gifu, Ishikawa,
75 and Toyama prefectures). The Tetori Group has traditionally been divided into three subgroups; the
76 Kuzuryu, Itoshiro, and Akaiwa Subgroups in ascending order (Maeda, 1961). The fossil material
77 described in this paper was collected from the upper part of the Kuwajima Formation, Itoshiro
78 Subgroup, at the “Kaseki-kabe” locality (Fossil-Bluff) in Kuwajima district, Hakusan City, Ishikawa

79 Prefecture, Japan (Figure 1). A detailed distribution of the Tetori Group in the Shiramine area has
80 been presented in previous papers (e.g. Kusuhashi, 2008) and is not repeated here.

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

88 The Kuwajima Formation is composed of thick, coarse-grained sandstone and alternating beds of
89 fine-grained sandstone and mudstone. Three facies have been identified in the sequence; Facies I,
90 carbonaceous swamp; Facies II, shallow lake; Facies III, vegetated swamp (Isaji *et al.*, 2005). Facies
91 I contains isolated vertebrate fossils and mollusks that are poorly preserved. Facies II consists of
92 silty matrix mixed with angular fine-grained quartz sands and contains fractured leaves and stems,
93 numerous viviparid gastropods and unionid bivalves. Facies III consists of well-sorted silty dark
94 greenish-grey mudstones and occasional angular very fine-grained quartz sands and contains *in situ*
95 plant remains, terrestrial vertebrates and rare aquatic species (Isaji *et al.*, 2005). Together, the three
96 facies have yielded a wide range of vertebrates, dominated by aquatic-semiaquatic taxa, including
97 fish (Yabumoto 2005, 2014; Yabumoto *et al.*, 2006), choristoderes (Matsumoto *et al.*, 2007;
98 Matsumoto *et al.*, 2014), and turtles (Hirayama *et al.*, 2012), but also including terrestrial lizards
99 (Evans and Manabe, 2008; Evans and Matsumoto, 2015), dinosaurs (Barrett *et al.*, 2002; Ohashi and
100 Barrett, 2009), pterosaurs (Unwin and Matsuoka, 2000), mammals (Rougier *et al.*, 2007; Kusuhashi,
101 2008), and tritylodonts (Setoguchi *et al.*, 1999; Matsuoka and Setoguchi, 2000; Matsuoka *et al.*,
102 2016), as well as eggshells (Isaji *et al.*, 2006). However, the locality is unusual in that lissamphibians
103 are rare and limited to frogs (Evans and Manabe, 1998; Matsuoka, 2000) and albanerpetontids
104 (Matsumoto and Evans, 2018), with currently no record of salamanders. All lissamphibian remains,
105 including the material described herein, were recovered from Facies III.

133 **Institutional abbreviations**

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

136

137 **Anatomical abbreviations**

138 ang, angulosplenic; cp, coronoid process; crv, crista ventralis; dc, dorsal crest; den, dentary; fem,
139 femur; gr, groove; hum, humerus; il, ilium; sd, shallow depression; mg, Meckelian groove; mtt,
140 metatarsals; mx f, maxilla foramen; phan, phalanx; ptg, pterygoid; radu, radioulna; sacd, sacral
141 diapophysis; tars, tarsal; tibf, tibiofibula; uro, urostyle; vert, vertebra.

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143

144 **Systematic Palaeontology**

145

146 Amphibia Linnaeus, 1758

147 Lissamphibia Haeckel, 1866

148 Salientia Laurenti, 1768

149 Anura Rafinesque, 1815

150 Genus and species indet.

151

152 **Description**

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154 SBEI 1778 is a block of grey mudstone on which several anuran bones are visible on the
155 surface of the matrix: a left dentary, a left humerus, two metatarsals, fragments of tibiofibula, a right
156 radioulna, two tarsals, three vertebrae (Figures 2A, B; 3C, D). The μ CT images revealed additional
157 skeletal materials under the matrix, including a left pterygoid, left and right angulosplenials, a femur
158 (side undetermined), two metatarsi, two phalanges, six vertebral centra, and a right ilium. Although
159 all elements are disarticulated, there is no replication of elements and the size of individual bones is

160 consistent with the remains being those of a single individual. In total, thirty-four elements are
161 preserved in SBEI 1778, of which twenty-seven are identifiable and seven are too fragmentary for
162 identification.

163 The postcranial morphology of anurans changes through ontogeny (e.g., Vera and Ponssa,
164 2014). The centra of early post-metamorphic juveniles have a wide notochordal canal, which is at
165 least partially closed mid-centrum in adults (Roček *et al.*, 2012). In SBEI 1778, the notochordal
166 canal is closed in all preserved centra (Figure 5C), which suggests that this was a young-adult or
167 adult individual.

168

169 **Skull**

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

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

182 The right angulosplenic is nearly complete (Figures 4H–K), but only the anterior part of the
183 left bone is preserved. The angulosplenic measures 12.3 mm along its long axis, and tapers
184 anteriorly, forming a sharp tip. The ventral margin is rounded (Figure 4K), whereas the dorsal
185 margin forms a thin edge (Figure 4J). This dorsal margin bears a coronoid process that is longer than

186 wide and is concave in its central part (Figure 4I). The Meckelian groove extends the length of the
187 bone (Figure 4H, I).

188

189 **Vertebral column**

190 SBEI 1778 preserves at least nine vertebrae (Figure 3A, B, D, F, G), as well as an isolated left
191 sacral diapophysis (Figure 5D) and the urostyle (Figure 3A, B).

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

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

212

213 **Forelimb**

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

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

224

225 **Pelvic girdle and hindlimb**

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

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

235 A single femur is preserved on the block. As it lies close to the ilium, it is probably the
236 femur of the right side but this remains uncertain as the bone lacks distinctive features and is missing
237 its proximal and distal heads (Figure 7D, E). The femoral shaft is slender (~13 mm in length), almost
238 straight (Figure 7D, E), and ovoid in cross-section at the mid-shaft (width: 1.26 mm; Figure 7F). A
239 femoral crest is partially preserved on the proximal part of the shaft (Figure 7D).

240 Left and right tibiofibulae are preserved on SBEI 1778 (Figure 8A–C). The left tibiofibula is
241 exposed on the matrix surface and only preserves the distal end (Figure 8A). The right tibiofibula
242 lies under the matrix, and its proximal and its distal ends are incomplete (Figure 8 B, C). The shaft of
243 the right bone is slender and waisted in the mid-section. On each bone, the lateral margin of the shaft
244 is thicker than the medial one in posterior view (Figure 8). A distinct groove marks the boundary
245 between the tibia and fibula on the proximal and distal parts of the mid-shaft.

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

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

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

259

260 **Comparisons**

261 Most recent phylogenetic analyses of Anura based on molecular and/or combined evidence data
262 recognize two major ‘groupings’ among living taxa, namely a monophyletic Neobatrachia and a
263 paraphyletic assemblage of anurans including *Ascaphus*, *Leiopelma*, Costata (Discoglossidae,
264 Alytidae, Bombinatoridae), Xenoanura (Pipidae, Rhinophrynidae) and Anomocoela (Scaphiopodidae,
265 Pelobatidae, Pelodytidae and Megophryidae) (e.g. Pyron and Wiens, 2011). SBEI 1778 has
266 amphicoelous vertebrae, a primitive character state shared with the extant genera *Ascaphus* (North

267 America) and *Leiopelma* (New Zealand), the Jurassic frogs *Prosalirus* (North America), *Vieraella*
268 (South America) and *Notobatrachus* (Argentina), the Jurassic-Cretaceous “*Eodiscoglossus*” (Europe
269 and possibly Siberian Russia), and several Cretaceous Asian genera, as listed on Figure 9. Of these
270 non-neobatrachian taxa, SBEI 1778 is distinguished from the extant *Ascaphus*, *Leiopelma*,
271 *Discoglossus*, *Pelobates* and *Pipa*, and the Jurassic/ Cretaceous genera *Prosalirus*, *Vieraella*,
272 *Notobatrachus*, and *Eodiscoglossus santonjae* in the following character states: closed notochordal
273 canal in amphicoelous vertebrae (vs. open in *Ascaphus*, *Leiopelma*, *Prosalirus*, *Vieraella*,
274 *Notobatrachus*, Middle Jurassic “*Eodiscoglossus*” *oxoniensis*; opisthocoelous vertebrae in
275 *Discoglossus*, *Pipa*; procoelous vertebrae in *Pelobates*); hatchet-shaped sacral diapophysis (vs. rod-
276 like in *Vieraella* and *Prosalirus*; slender in *Leiopelma*, *Notobatrachus*; fan-like in *Pelobates*, *Pipa*),
277 iliac blade lacking a dorsal crest (vs. crest present in *Discoglossus*, *Eodiscoglossus santonjae*, *Pipa*,
278 *Prosalirus*,) and iliac blade ovoid in cross-section (vs. circular in *Ascaphus*, *Leiopelma*).

279

280 Japanese Cretaceous frogs

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

292 The Japanese Cretaceous species *Hyogobatrachus wadai* and *Tambabatrachus kawazu* from the
293 Sasayama Group are each represented by a single articulated specimen (Ikeda *et al.*, 2016). *H. wadai*

294 is largely complete, with both skull and postcranial skeleton preserved; *Tambabatrachus kawazu*
295 lacks most of the skull, parts of the pectoral girdle, and the manus and pes. According to Ikeda *et al.*
296 (2016), the two species differ from one another in several ways, including the orientation of the
297 vertebral transverse processes and of the sacral diapophyses; the presence (*Hyogobatrachus*) or
298 absence (*Tambabatrachus*) of transverse processes on the urostyle; the size of the olecranon process
299 on the radioulna; and the robusticity of the iliac shaft. Both of the Sasayama species share the
300 following similarities with SBEI 1778: amphicoelous vertebrae without a patent notochordal canal;
301 hatchet-shaped sacral diapophyses; an ilium lacking a dorsal crest or dorsal protuberance; hind limb
302 elements of similar relative proportions; and (probably in SBEI 1778) unfused proximal tarsal bones.
303 SBEI1778 differs from *Hyogobatrachus* in characters of the urostyle: low dorsal crest (vs. absent),
304 monocondylar sacro-urostylar articulation (vs. bicondylar sacro-urostylar articulation), absence of
305 transverse processes on the urostyle (vs. transverse processes present), and urostyle tapering
306 posteriorly (vs. extending with similar width toward the distal end). SBEI 1778 resembles
307 *Tambabatrachus* in the absence of transverse processes on the urostyle, but differs in lacking any
308 waisting between the iliac blade and acetabular region (vs. slight waisting in *Tambabatrachus*, Ikeda
309 *et al.* 2016), and having a monocondylar (vs. bicondylar) sacro-urostylar articulation and a slight
310 midline urostylar crest (vs. none). There is also a marked size difference between the Sasayama
311 frogs and SBEI 1778. *Hyogobatrachus* and *Tambabatrachus* are small frogs with a snout-vent length
312 of 26.8 mm in *Hyogobatrachus wadai* and 26.0 mm in *Tambabatrachus kawazu* at maturity (Ikeda *et*
313 *al.*, 2016). Although most elements of SBEI 1778 are incomplete, the urostyle is relatively well-
314 preserved (13.2 mm in length), and this is 150% larger than that of *Hyogobatrachus wadai* (8.9 mm
315 in length). However, size characters should be treated with caution in frogs, as there is often a
316 considerable size disparity between males and females of the same species (e.g. Woolbright, 1983),
317 with females often being the larger morph (e.g. Shine, 1979). Larger animals also have a greater
318 muscle volume, resulting in more marked crests and ridges at attachment sites. Nonetheless, SBEI
319 1778 is distinct from the Sasayama frogs in having a mono- vs. bicondylar sacro-urostylar joint.
320

321 Other Cretaceous Asian frogs

322 Early Cretaceous frogs have been recorded from several other localities across Asia, most
323 notably within the Jehol Biota of China, but also in Mongolia and other parts of China (Figure 9).
324 SBEI 1778 resembles the Chinese frog genus *Liaobatrachus* (including *L. grabaui*, *L. beipiaoensis*,
325 *L. macilentus*, and *L. zhaoi*, Dong *et al.*, 2013) from the Yixian Formation in the absence of both a
326 dorsal crest and dorsal protuberance on the ilium, and in the primitive presence of a monocondylar
327 sacro-urostylar joint, but it is distinguished from all referred species of *Liaobatrachus* in having
328 hatchet-shaped sacral diapophyses (vs. broadly dilated, fan-like diapophyses; Dong *et al.*, 2013), in
329 having a shorter coronoid process of the angulosplenial, 25% of the long axis (vs. long; Dong *et al.*,
330 2013; pars. obs. RM [34% of the length]), and in lacking transverse processes on the urostyle (vs.
331 processes present). In addition, the dentary is distinguished from that of *Liaobatrachus beipiaoensis*
332 (Gao and Wang, 2001) in the presence of sharp dorsal and ventral margins (vs. a thin edentate dorsal
333 crest). SBEI 1778 also differs from an unnamed specimen from the Jiufotang Formation, IVPP
334 V13235 (Wang *et al.*, 2007; Dong *et al.*, 2013), in having amphicoelous vertebrae without a patent
335 notochordal canal (vs. fully notochordal), more expanded sacral diapophyses (vs. unexpanded), a
336 monocondylar sacro-urostylar joint (vs. bicondylar), and lacking transverse processes on the urostyle
337 (vs. transverse processes present). Late Cretaceous species of the group Gobiidae (Mongolia,
338 Uzbekistan, Kazakhstan) (e.g. Spinar and Tatarinov, 1986; Gubin, 1999; Roček, 2008; Skutschas
339 and Kolchanov, 2017) are also differentiated from SBEI 1778 in having bicondylar sacro-urostylar
340 joints and at least one pair of transverse processes on the urostyle (Roček, 2008).

341 *Genibatrachus* from the Lower Cretaceous Guanghai Formation in Inner Mongolia (Gao
342 and Chen, 2017) is distinguished from all the Japanese taxa in having procoelous vertebrae and
343 unexpanded sacral diapophyses. Isolated frog remains (maxilla, urostyle, tibiofibula, proximal
344 tarsals) from the Early Cretaceous Khilok Formation of Transbaikalian Russia were attributed
345 to ?Discoglossidae (Skutschas, 2003), but without opisthocoelous vertebral centra this attribution
346 cannot be confirmed. Nonetheless, if the Russian specimens belong to a single taxon, it differs from

347 SBEI 1778 in having a bicondylar sacro-urostyler joint, and proximal and distal fusion of the tibiale
348 and fibulare.

349

350 **Phylogenetic analysis**

351 In order to examine the phylogenetic position of SBEI 1778 among other Asian frogs, SBEI 1778
352 was coded into the morphological data matrix of Ikeda *et al.* (2016), with the addition of three early-
353 branching neobatrachian species (*Hadromophryne natalensis*, *Heleophryne purcelli*, *Sooglossus*
354 *sechellensis*, Pyron and Wiens, 2011) to provide an additional outgroup. The analysis was run using
355 TNT (version1; Goloboff *et al.*, 2008) with the New Technology search option with Ratchet (1000
356 random addition sequences: 20 iterations). Caudata was the designated outgroup taxon. The resulting
357 trees were re-analysed by using a Traditional search mode to fully explore all possible topologies.
358 The bootstrap consensus tree was analyzed with 5000 replicated resampling. This analysis yielded
359 the four most parsimonious trees (MPTs, Length 200), and the strict consensus tree placed SBEI
360 1778 as the sister taxon of the Chinese *Liaobatrachus* rather than the Japanese taxa, *Hyogobatrachus*
361 and *Tambatrachus*. However, when character traits were mapped on the tree, SBEI 1778 and
362 *Liaobatrachus* were found to share a single character state, monocondylar sacro-urostyler
363 articulation (character no. 45) (Figure 10), a trait generally considered primitive. When the analysis
364 was re-run with character 45 de-activated, the analysis yielded 31 MPTs (Length 193). In the Strict
365 Consensus tree from this second analysis, SBEI 1778 was placed on the stem of a clade comprising
366 the Chinese *Liaobatrachus* and the Japanese *Hyogobatrachus* and *Tambatrachus*. This instability in
367 the position of SBEI 1778 is probably due to the large amount of missing data (88%), especially for
368 elements with diagnostic characters (e.g. premaxilla, frontoparietal, prefrontal). SBEI 1778 thus
369 represents a non-neobatrachian grade frog of uncertain affinity. It may be related to one or more of
370 the previously named Early Cretaceous frogs from China and Japan, but further material is needed
371 for comparison, particularly from the skull.

372

373 **Discussion**

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

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

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

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

414

415

416 **Conclusions**

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

426

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440

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618

619 **Figure captions**

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

622

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

626

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

631

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

636

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

642

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

646

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

649

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

655

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

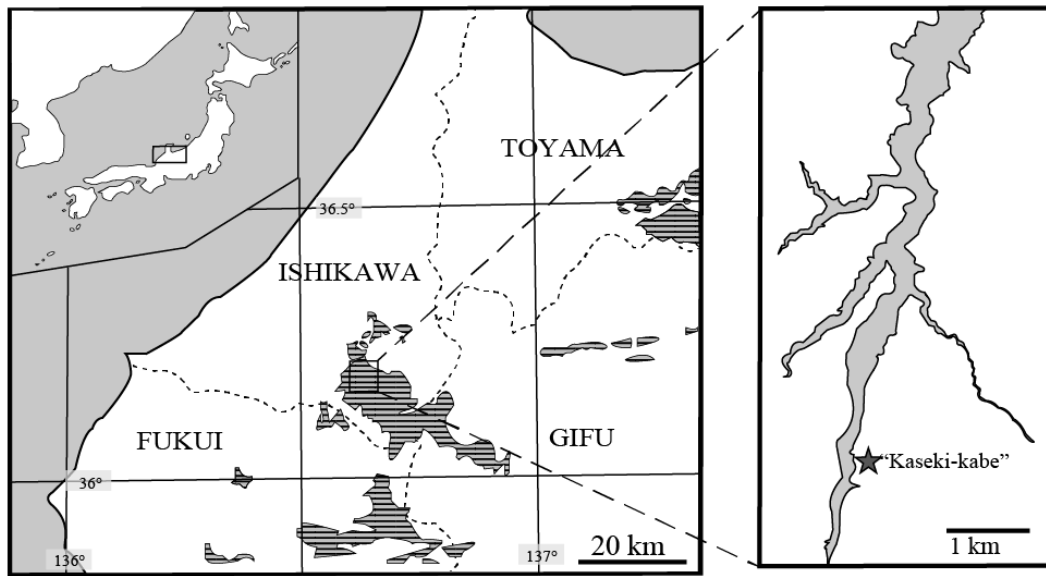
658

659 **Figure 10.** Phylogenetic relationships of SBEI 1778 within Mesozoic anurans. **A**, strict consensus of
660 the four most parsimonious trees (MPTs) obtained by TNT analysis of the matrix of Ikeda *et al.*
661 (2016) with three additional neobatrachian species (*Hadromophryne natalensis*, *Heleophryne*
662 *purcelli*, *Sooglossus sechellensis*); **B**, bootstrap consensus tree, examined by 5000 replicated
663 resampling analysis, numbers on tree B indicate bootstrap values.

664

665 Appendix 1: Data matrix

666 Fig.1



667

668

669 Fig.2

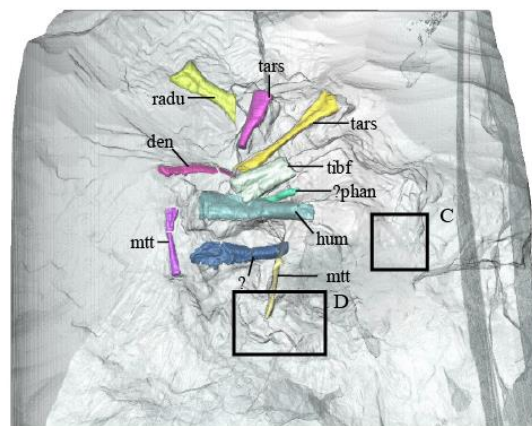
A

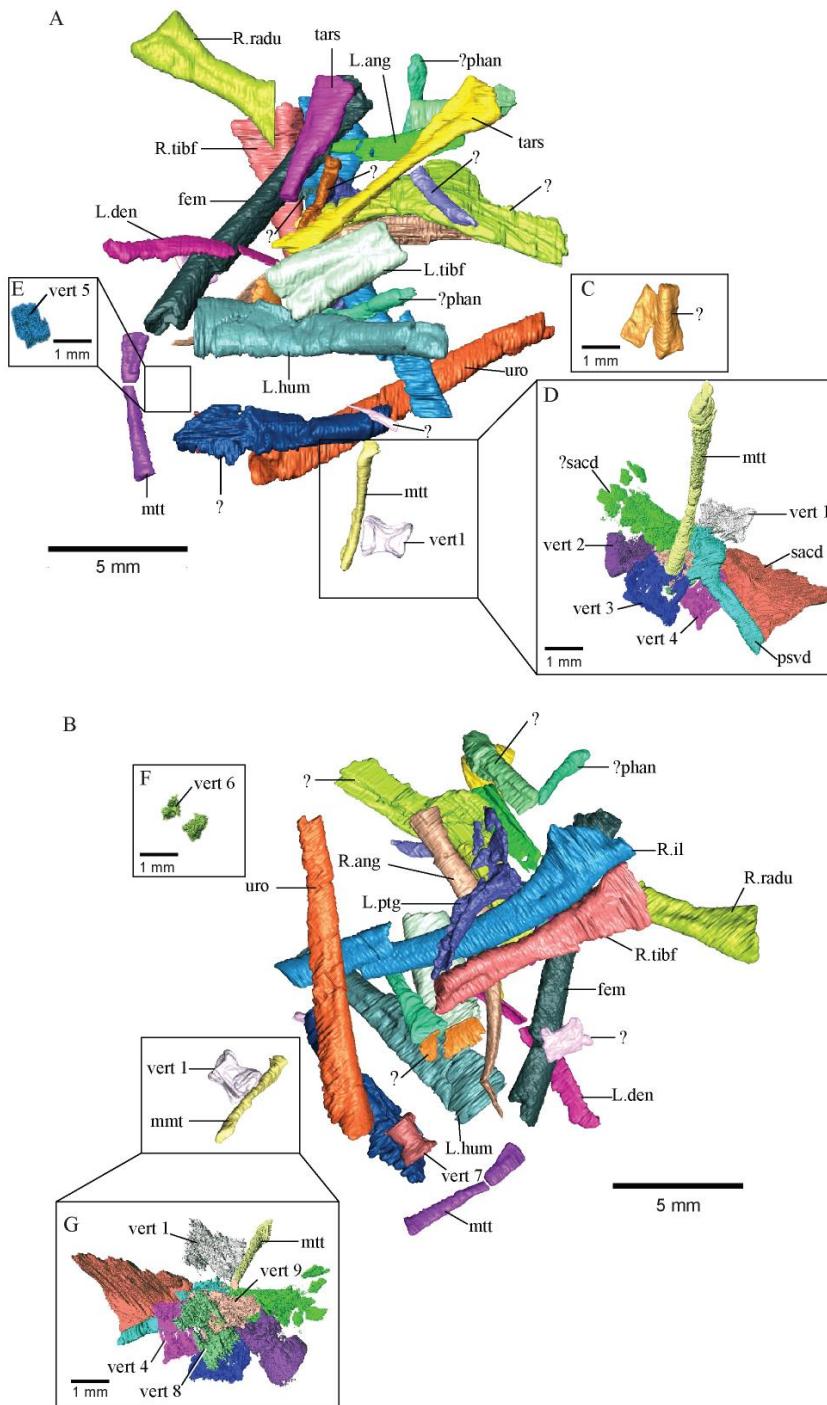


670

5 mm

B





671

672 **Fig.3**

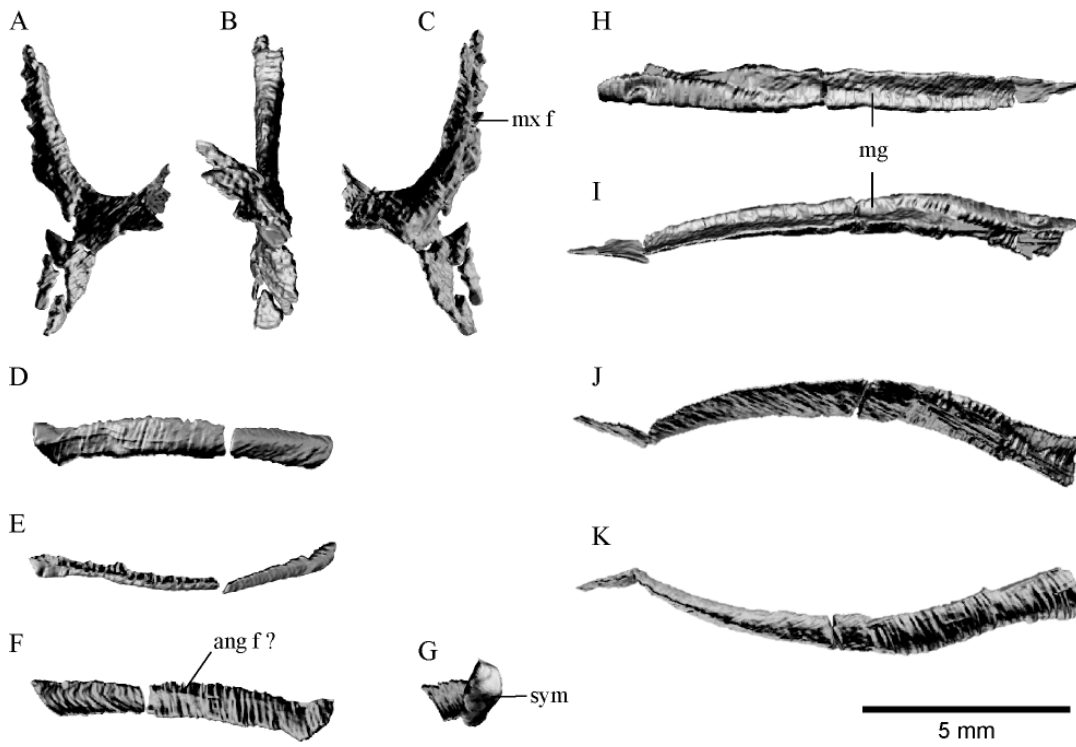
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674

675

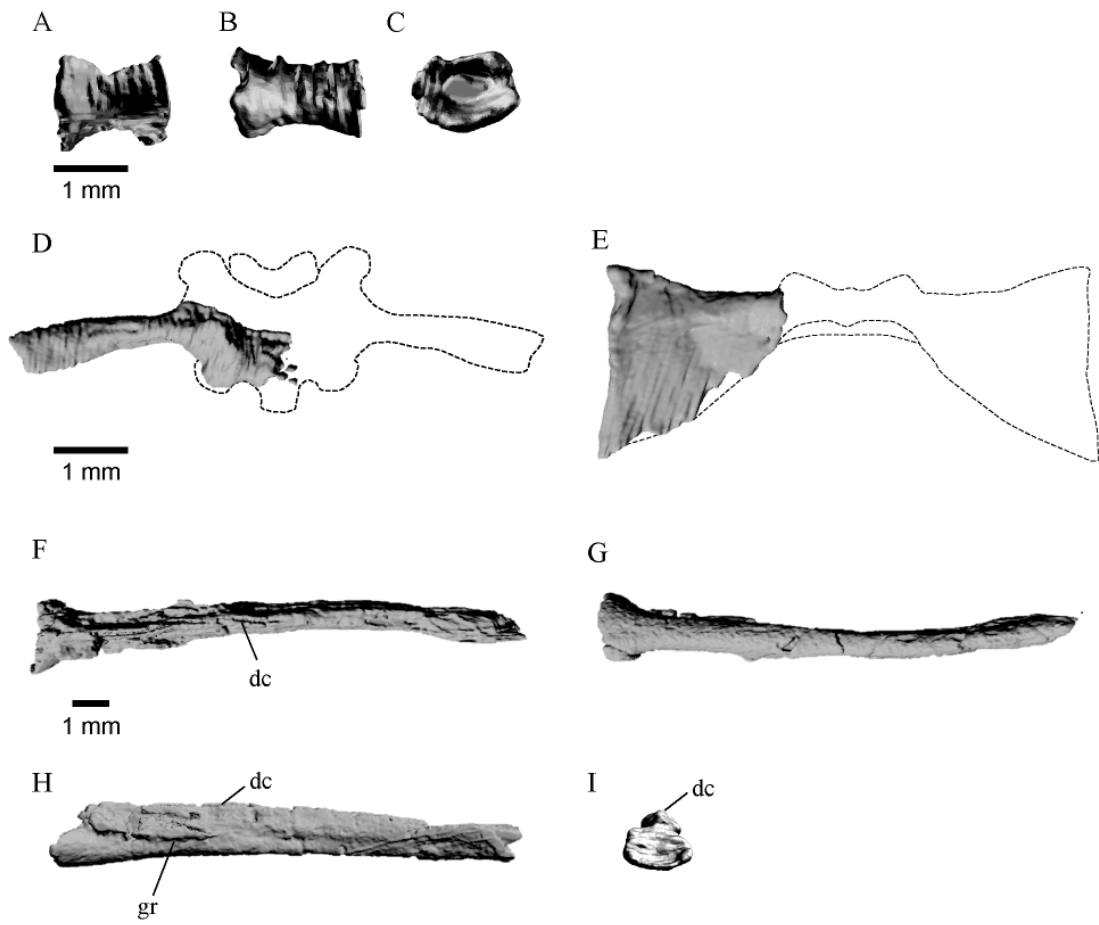
676 Fig.4

677



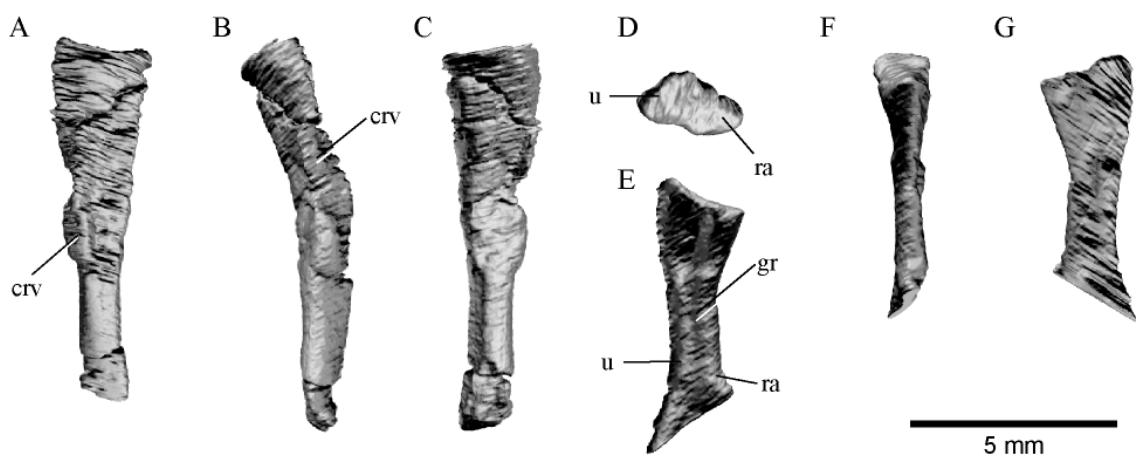
678

679 Fig.5



680

681 Fig.6

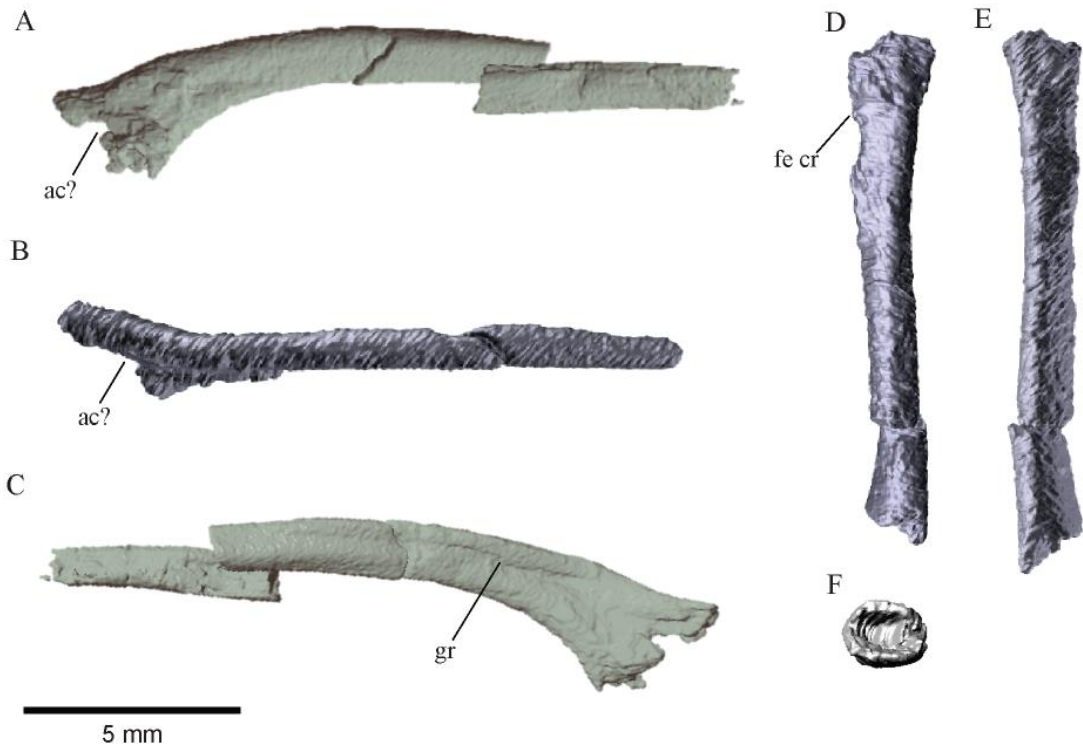


682

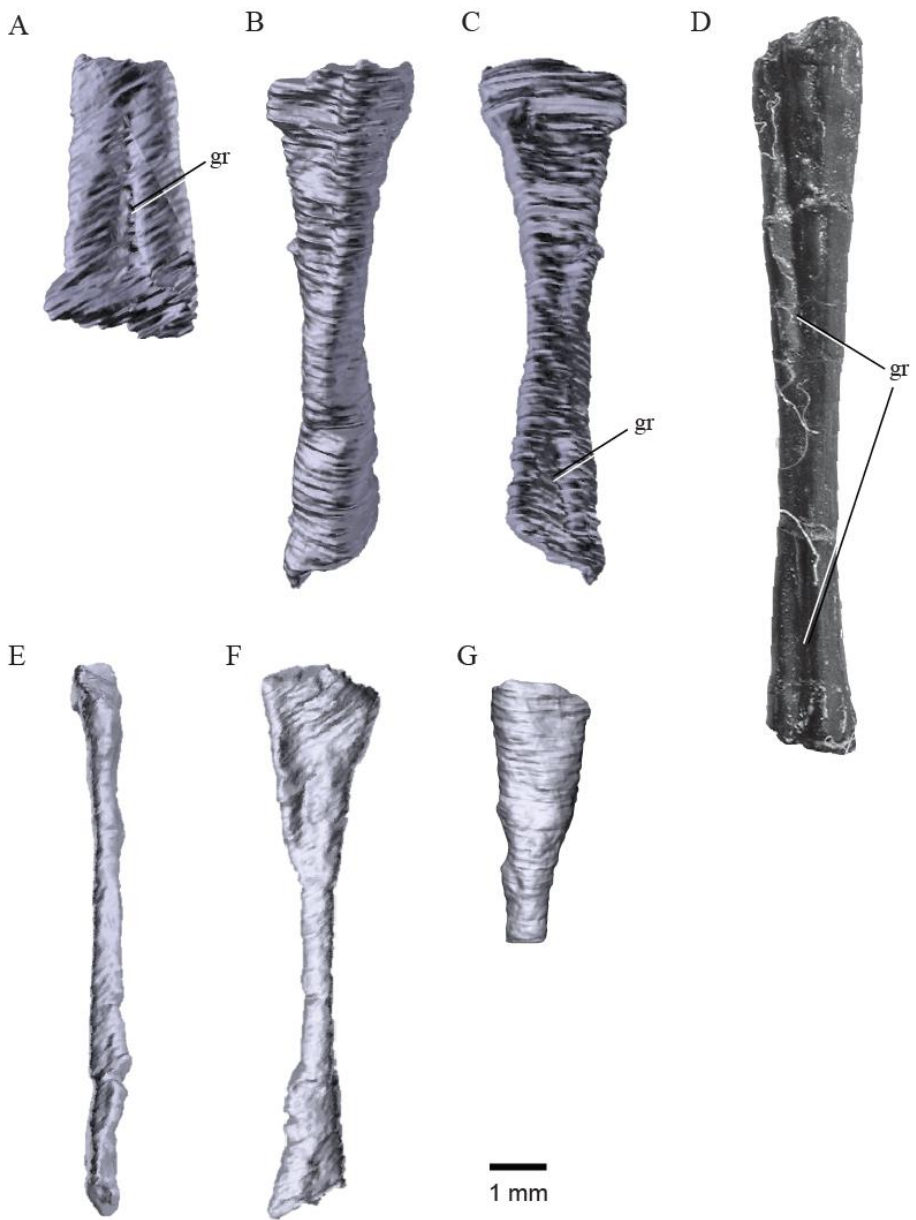
683

684

685 Fig.7

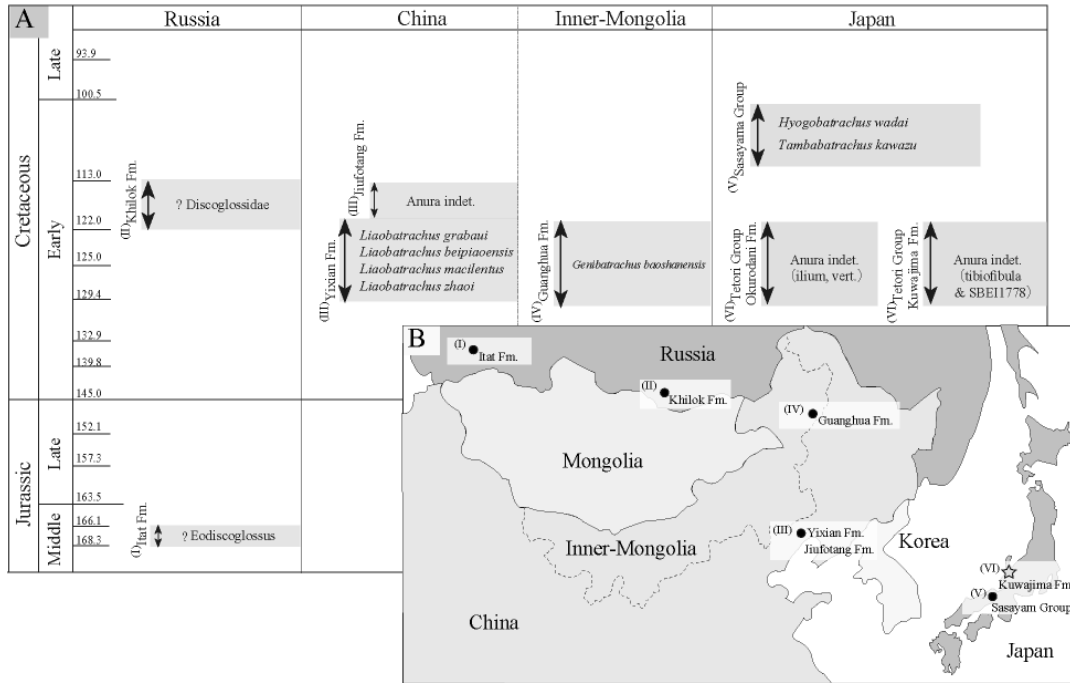


686



687 Fig.8

688 Fig.9



689



690

691 **Fig.10**