

1 The first choristoderan record from the Upper Cretaceous of Asia, Tamagawa Formation, Kuji
2 Group, Japan
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19

20 **Abstract**

21 Choristoderes are freshwater diapsid reptiles that are distributed through Laurasia in Jurassic–

22 Miocene deposits. The group shows great diversity in the Early Cretaceous of Asia, with all

23 recognized morphotypes recorded from that region. However, there is then a substantial gap in

24 the Asian record until choristoderes are reported from the Paleocene of Kazakhstan. This gap

25 has raised questions as to whether the group became extinct in Asia during the Late

26 Cretaceous, with subsequent reinvasion from either North America or Europe. Here we report

27 the discovery of vertebrae attributable to Choristodera indet. from the lower Upper Cretaceous

28 (Turonian) of the Tamagawa Formation, Kuji City, Iwate Prefecture, Japan. This is the first

29 record of Choristodera from the Upper Cretaceous of Asia, and may imply that the group

30 persisted in this region from the Jurassic to the Paleocene. The challenge for the future will be

31 to recover a more complete record of Choristodera in the Upper Cretaceous of Asia.

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33 Key words: Choristodera, Diapsida, Late Cretaceous, Kuji Group, Japan

34

35 1. Introduction

36 Choristoderes are an extinct group of amphibious freshwater reptiles that were
37 widely distributed through Laurasia (Dong et al., 2020; Matsumoto and Evans, 2010; Matsumoto
38 et al., 2019ab), and possibly parts of Gondwana (Haddoumi et al. 2016), from the Jurassic to
39 the Miocene (Evans, 1990; Averianov et al. 2006; Evans and Klembara, 2005).

40 By far the greatest diversity of choristoderes is reported from the Lower Cretaceous
41 of eastern Asia, with records from Japan, China, Russia (Transbaikalia, Western and Eastern
42 Siberia), and Mongolia (e.g. Brinkman and Dong, 1993; Efimov, 1975; Evans and Manabe,
43 1999; Gao et al., 2000; Ksepka et al., 2005; Matsumoto et al., 2007, 2014; Skutschas, 2008;
44 Skutschas and Vitenko, 2015). Moreover, between them, these Early Cretaceous Asian
45 choristoderes display an degree of morphological disparity found in no other place or time
46 period, with taxa ranging from brevirostrine and short-necked (e.g. *Monjurosuchus*,
47 *Philydrosaurus*), through brevirostrine and long-necked (e.g. *Hyphalosaurus*), to the derived
48 longirostrine, short-necked neochoristoderes (e.g. *Tchoiria*, *Ikechosaurus*); the lower temporal

49 fenestra may also be open (e.g. *Tchoiria*, *Ikechosaurus*) or closed (*Monjurosuchus*,
50 *Philydrosaurus*). The long-necked morphotype, represented by *Shokawa*, *Hyphalosaurus*, and
51 *Khurendukhosaurus* (Evans and Manabe, 1999; Gao et al., 1999; Sigogneau-Russell and
52 Efimov, 1984; Matsumoto et al., 2019a), is unique to the Early Cretaceous of Asia; the others
53 are more widespread. Given this Early Cretaceous Asian diversity, the complete absence of a
54 Late Cretaceous Asian record has been a frustration. It raised questions as to whether
55 choristoderes survived in the Late Cretaceous of Asia but were unrecorded due to a lack of
56 suitable/ sampled depositional environments, or became extinct in Asia and re-entered
57 (Kazakhstan, Averianov, 2005) during the Paleocene from Europe or North America where the
58 Cretaceous record is more complete (Averianov, 2005; Matsumoto and Evans, 2010).

59 Since 2012, researchers from Waseda University and the Kuji Amber Museum have
60 been jointly excavating a new Upper Cretaceous locality in the Tamagawa Formation (Kuji
61 Group), Iwate Prefecture, northeast Japan. This formation was already well known for amber,
62 but has recently yielded a diversity of vertebrates including fishes, crocodylians, turtles,
63 dinosaurs, and pterosaurs (Hirayama, et al., 2010; Miyata, et al., 2019). Here we report the

64 discovery of isolated choristoderan vertebrae from this locality, representing the first
65 choristoderan record from the lower Upper Cretaceous of Asia.

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67

68 **2. Geological setting**

69 The Upper Cretaceous deposits of the main part of the Kuji Group are distributed
70 along a band running from northwest to southeast of Japan (Fig 1). The Kuji Group is composed
71 of three parts, the Tamagawa, Kunitan, and Sawayama formations (e.g. Terui and Nagayama.,
72 1995; Umezu and Kurita, 2007). The lower component of the Tamagawa Formation is formed
73 by shallow marine or terrestrial deposits, about 180 m in maximum thickness (Hirayama et al.,
74 2010). It consists of conglomerate in the lower part, and sandstone and carbonaceous
75 mudstone in the middle to upper parts that have yielded amber and phytolites. Moreover, the
76 middle part also contains oyster shell beds. The Kunitan Formation represents shallow marine
77 deposits, 170 m in thickness. The fine-grained sandstone of the lower to middle parts yields
78 ammonites such as *Polyptychoceras* and the inoceramid *Inoceramus naumanni* (Terui and
79 Nagahama, 1995), and teeth of the marine reptilian mosasauroids (Kawakami et al., 1985). The

80 Sawayama Formation comprises terrestrial deposits which have yielded fossil plants, and it is
81 mainly composed of conglomerate and sandstone. The layer is only 70 m in depth, thinner than
82 the other two layers.

83 The joint Kuji Amber Museum and Waseda University research project has
84 excavated the uppermost part of the Tamagawa Formation which is exposed on the east side of
85 the Kuji Amber Museum, Iwate Prefecture, and is roughly 4 m in thickness. It is composed of
86 carbonaceous silt, greenish-white tuff, and greenish-gray medium-grained sandstones. The
87 depositional environment has been reconstructed as a river – river mouth, based on
88 sedimentological studies by Terui and Nagahama (1995). This locality has yielded various
89 terrestrial and aquatic vertebrates, including isolated elements of turtle, crocodylians, dinosaurs,
90 and pterosaurs (Hirayama et al., 2010, 2021), amounting to roughly 2200 specimens by 2020
91 (unpublished data). In 2014, 2015 and 2017, two relatively well preserved isolated
92 choristoderan vertebrae, and another vertebra, possibly attributable to choristoderes, were
93 recovered from the sandstone bed lying above the tuff layer.

94 The lower part of the Kunitan Formation, overlying the Tamagawa Formation, yields
95 ammonites including *Texanites collignoni*, *T. (Ptesiotexanites) pacificus*, and inoceramids

96 *Sphenocerasmus naumanni*, which are considered to indicate a Santonian age in the northwest
97 Pacific region (e.g. Ando, 1997; Futakami et al., 1987; Toshimitsu et al., 1995, 2007). Although
98 triprojectate pollen is rare, two genera (*Fibulapollis* and *Aquillapollenites*) are known from the
99 upper part of the Tamagawa Formation, as well as from the upper layer of the Sawayama
100 Formation (Umezu and Kurita, 2007). The age of these two layers has been placed as no
101 younger than the Coniacian/ Santonian boundary, at which triprojectate pollen was starting to
102 diversify (Umezu and Kurita, 2007). On the other hand, carbon isotope stratigraphy, based on
103 detrital woods with U-Pb radiometric dating, indicated the depositional age of the bone-bed in
104 the Kuji Group to be the early-middle Santonian (Arimoto et al., 2018). However, more recent
105 studies (Hirayama, et al., 2021; Uno et al., 2018) have suggested that the upper part of the
106 Tamagawa Formation, interbedded in the bone bed, can be dated as 90.51 ± 0.54 Ma based on
107 U-Pb in volcanic ash. In addition, an analysis of the pollen composition in outcrops of the bone
108 bed did not find triprojectate pollen, but other pollens and spores that are consistent with
109 Turonian Flora (Legrand et al., 2019). Overall, the age of the bone bed of the Tamagawa
110 Formation is considered to be between the Turonian and Santonian, but a Turonian age is more
111 (Hirayama et al., 2021).

112

113 **3. Systematic paleontology**

114 Reptilia Linnaeus, 1748

115 Diapsida Osborn, 1903

116 Choristodera Cope, 1884

117 Choristodera gen. et sp. indet.

118

119 **Institutional abbreviations**

120 **AMNH**, American Museum Natural History, New York, USA; **IVPP**, Institute of Vertebrate

121 Paleontology and Paleoanthropology, Beijing, China; **OSD**, Osawada River, Kuji Amber

122 Museum, Iwate Prefecture, Japan; **RTMP**, Royal Tyrrell Museum of Palaeontology, Drumheller,

123 Canada; **SMM**, The Science Museum Minnesota, St. Paul, Minnesota, USA.

124

125 **4. Materials**

126 Two isolated vertebrae found in the Tamagawa Formation as exposed along the

127 Osawada River on the eastern side of the Kuji Amber Museum (OSD), Iwate Prefecture, Japan:

128 cervical vertebra (OSD 586); and dorsal or sacral vertebra (OSD 844). Another very worn
129 cervical vertebra (OSD 1600; similar to OSD 586 in having a midventral keel) were also found
130 from this locality but it is too fragmentary for description. These specimens are housed in Kuji
131 Amber Museum.

132

133 **5. Description**

134 OSD 586 is a vertebra with an amphiplatyan centrum in which the notochordal canal
135 is closed, and the neurocentral articular surface is clearly preserved, demonstrating that the
136 neurocentral suture remained open (Fig. 2A–F). The centrum is short (length 10.99 mm; height
137 10.71 mm; width 10.86 mm) and the articular surface of the centrum is circular (Fig. 2A, C), and
138 spool-like as in neochoristoderes (Matsumoto et al., 2019b, Appendix 2). The centrum is slightly
139 worn, but the rib parapophyses are weakly visible on the anteroventral margin of the centrum
140 (Fig. 2D–F), and a strong midventral keel is developed (Fig. 2A, C, E). These features suggest
141 that OSD 586 is a cervical vertebra. In most neochoristoderes (e.g. *Ikechosaurus*
142 *Champsosaurus*, *Simoedosaurus*), the parapophysis is first seen from the level of vertebra (v)3-
143 –4, but it is first developed on v 5 in *Champsosaurus albertensis* [RTMP 86.12.11], *C. gigas*

144 [SMM 77.33.24] and *C. natator* (Matsumoto, 2011). The parapophyses of these taxa project
145 laterally from v5 or v6 (e.g. *C. gigas* [SMM 77.33.24], *C. ambulator* [AMNH 983], *C. laramiensis*
146 [AMNH 982]). The anterior-most parapophysis is located on the anteroventral margin of the
147 centrum and it gradually moves dorsally along the cervical series, until it merges with the
148 diapophysis in posterior cervical vertebrae (Russell 1956; Matsumoto, 2011). *Ikechosaurus* is
149 the earliest known neochoristodere from Asia, and several specimens preserve nearly complete
150 cervical vertebrae (e.g. IVPP V 9611-1, 9611-3, 13283). In *Ikechosaurus*, the ventral keel
151 becomes strong on v3, and the parapophysis is located ventrally, near the ventral keel. In v4,
152 the parapophysis is placed at the middle of the centrum in lateral view. By comparison with
153 *Ikechosaurus* and *Champsosaurus*, OSD 586 was probably from the anterior or middle portion
154 of the neck, somewhere between v3–v5.

155 OSD 844 (Fig. 2G–L) is smaller than the cervical vertebra (OSD 586). The centrum
156 length and height are almost equal (length 8.44 mm; height 7.3 mm; width 8.09 mm). As in OSD
157 586, the centrum is amphiplatyan with a closed notochordal canal (Fig. 2G, I). The articular
158 surface of the centrum has a horizontal dorsal margin in anterior and posterior views (Fig. 2G,
159 I), giving the centrum a subcylindrical morphology. The ventral surface of the vertebra is smooth

160 (Fig. 2K). In OSD 844 the parapophyses have merged with the diapophyses at the border of the
161 neurocentral articulation (Fig. 2J, L). These rib facets do not have a strong lateral projection, a
162 feature that is often shown in neochoristodere sacral vertebra where the sacral ribs are unfused
163 (RM pers obs). Thus, OSD 844 might be a dorsal or sacral vertebra but this cannot be
164 confirmed without further material showing the range of vertebral morphology in this taxon.

165

166

167 **6. Comparison**

168 The Tamagawa Formation has yielded vertebrae of several different vertebrates,
169 including fishes, turtles, squamates and neosuchian crocodylians (Hirayama et al., 2015). OSD
170 586 and OSD 844 are distinguished from those of other reptiles by the following characters:
171 amphiplatyan centra, closed notochordal canal, and open neurocentral suture. Some early
172 crocodyliformes have broadly similar amphicoelous centra (the transition from amphicoelous to
173 procoelous vertebrae occurred in Crocodylia: Salisbury et al., 2006). However, OSD 586 and
174 844 are distinguished from vertebrae of crocodyliforms in the morphology of the articular
175 surface for the neural arch. On the dorsal surface of the centrum in these specimens, a ridge is

176 weakly developed along the midline and it is flanked by shallow grooves forming an hourglass
177 shape. The sutural surfaces for the neural arch pedicels are shallow and relatively smooth, with
178 the surfaces widest anteriorly and narrowing posterolaterally. These are characteristic features
179 of choristoderan centra (e.g. Evans, 1991).

180 The two vertebrae (OSD 586, 844) resemble those of neochoristoderes (e.g.
181 Matsumoto et al., 2019b, Appendix 2) in having a short spool-like centrum (centrum height and
182 length almost equal), unlike the more elongated centra seen in most non-neochoristoderes. In
183 addition, the articular surfaces of the Tamagawa Formation centra are subcylindrical (OSD 586)
184 or cylindrical (OSD 844), unlike those of the long-necked choristoderes
185 (*Hyphalosaurus*, *Shokawa*, *Khurendukhosaurus*), whose articular surfaces form a dorsoventrally
186 elongated oval (Matsumoto, 2011). Although most known Neochoristodera have a relatively
187 larger body size than other choristoderes, *Ikechosaurus sunailinae* (IVPPV 9611-1) from the
188 Lower Cretaceous Laohongdong Formation is small and may be a juvenile (snout-vent length;
189 0.32 m). This small *Ikechosaurus* (IVPPV 9611-1) has cervical centra ~7 mm in length
190 (Brinkman and Dong, 1993) and dorsal vertebrae that are slightly smaller than either OSD 586
191 or 844 (pers. obs. RM). Although the body proportions of the Tamagawa choristodere are

192 unknown, the individual would have been relatively small (< 1m in snout-vent length). Here we
193 refer these vertebrae from the Tamagawa Formation to Choristodera indet. A more precise
194 taxonomic identification is not possible due to a lack of diagnostic characters in isolated
195 choristoderan centra, but the Tamagawa vertebrae more closely resemble those of known
196 neochoristoderes than those of non-neochoristoderan genera.

197

198 **7. Discussion**

199 Two vertebrae from the Tamagawa Formation (Turonian), Iwate Prefecture have
200 been identified as those of choristoderes, and are thus the first record of choristoderes from the
201 Upper Cretaceous of Asia. Although fragmentary, these specimens are important in filling a gap
202 in the Asian choristodere record between the Early Cretaceous and the Paleocene (Fig. 3).
203 They support the suggestion (Matsumoto and Evans 2010) that the apparent absence of
204 choristoderes in the Late Cretaceous might be an artefact caused by a lack of suitable
205 depositional environments for the preservation of warm, temperate fresh-water reptiles. As
206 outlined above, the depositional environment of the uppermost part of the Tamagawa Formation
207 has been reconstructed as a fluvial (Legrand et al., 2019), and the locality has yielded both

208 terrestrial and aquatic vertebrates, including turtles, crocodylians, dinosaurs, and pterosaurs
209 (Hirayama et al., 2010). A paleovegetational study based on fossil pollen and spore indicates
210 that the Tamagawa Formation represents a humid environment (Legrand et al., 2019). Thus,
211 recent field work in the Tamagawa Formation and the new discoveries have confirmed that
212 choristoderes persisted in Asia from at least the Jurassic to the Paleocene, and in freshwater
213 localities with humid and warm-temperate environments. There are several other Late
214 Cretaceous vertebrate assemblages from Middle and Central Asia (Averianov and Sues, 2012).
215 Of these localities, the Zhirkindek Formation in Kazakhstan is similar to the Tamagawa
216 Formation, with several horizons that mark marine transgressions and yield vertebrates such as
217 fish, squamates, turtles, salamanders, crocodylians, pterosaurs, and dinosaurs (Averianov, et
218 al., 2016). Some of these vertebrates are shared with the Tamagawa Formation, such as adacid
219 turtles (Hirayama et al., 2010; 2021), and the marine-to-brackish-water shark *Scapanorhynchus*
220 (Miyata et al., 2019). In addition, the age of Zhirkindek Formation is considered to be Turonian
221 (Nesov, 1993), similar to that of the Tamagawa Formation. The last record of choristoderes in
222 Asia is also from Kazakhstan (Averianov, 2005), and the Zhirkindek Formation may therefore
223 have the potential to yield choristoderes.

224 The choristodere material from the Tamagawa Formation is too fragmentary to
225 determine the morphotype (e.g. rostral length) of the taxon represented. However, although
226 vertebral morphology changes along the trunk, short, spool-like cervical centra of the kind found
227 in the Tamagawa Formation are characteristic of those found in short-necked neochoristoderes
228 (Matsumoto et al., 2019b, Appendix 1,2). Neochoristoderes are known to have diversified in the
229 Late Cretaceous of North America and Europe. These Euramerican neochoristoderes are
230 known from deposits representing low-lying river channels and deltaic deposits, whereas small
231 non-neochoristoderes have generally been recovered from continental lake environments
232 (Matsumoto and Evans, 2010). The Tamagawa Formation has been reconstructed as
233 representing a river (Legrand et al., 2019), whereas Lower Cretaceous Japanese choristoderan
234 localities in the Okurodani and Kuwajima formations of the Tetori Groups are considered to
235 represent floodplain environments (Isaji et al., 2005). In addition, the Tamagawa Formation
236 differs from that typically associated with Early Cretaceous choristoderes (Matsumoto and
237 Evans, 2010) in the presence of crocodylians. The crocodylians from the Tamagawa Formation
238 were tentatively identified as Neosuchia based on vertebrae, osteoderms and isolated teeth
239 (Hirayama et al., 2015). The maximum total adult length is estimated to be roughly ~3 m, based

240 on comparisons with extant crocodylian species (pers. obs. RH). Under this interpretation, the
241 young crocodylians from the Tamagawa Formation could possibly compete with the
242 choristoderes, in terms of their size.

243 There may have been a transition in the choristoderan fauna between the Early and
244 the Late Cretaceous, with neochoristoderan genera gradually replacing the smaller non-
245 neochoristoderan taxa. Further discoveries from the Tamagawa Formation will be important to
246 our understanding of the evolutionary history and diversification of choristoderes in Asia.

247

248 **8. Conclusions**

249 Two isolated vertebrae from the Upper Cretaceous (Turonian) Tamagawa Formation,
250 Iwate Prefecture, Japan, are attributed to the Choristodera (and probably Neochoristodera)
251 based on amphiplatyan centra; a closed notochordal canal; open neurocentral sutures; shallow
252 facets for neural arch pedicels, widest anteriorly, narrowing posteriorly, bearing hourglass-
253 shaped grooves along the midline; and a short spool-like centrum. These new specimens, albeit
254 fragmentary, provide the first record of Choristodera from the Upper Cretaceous of Asia and fill
255 a gap in the Asian fossil record of the group between the Lower Cretaceous and Paleocene.

256 They demonstrate that choristoderes may have persisted in this region from the Jurassic to the
257 Paleocene, and highlight the importance of searching other Upper Cretaceous Asian deposits
258 for choristodere remains. Additional specimens, especially of the skull, are required in order to
259 identify the Tamagawa Formation choristoderes.

260

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398

399 **Figure Captions**

400 Figure 1. Map showing the position of the fossil locality and the distribution of the Tamagawa
401 Formation Kuji Group within Japan. The geological map is modified from Umezu et al. (2013).

402

403 Figure 2. Vertebrae of *Choristodera* indet. from the Tamagawa Formation, Kuji Group, Upper
404 Cretaceous, northeast Japan. A–F OSD 586, cervical centrum, in anterior (A), dorsal (B),
405 posterior (C), left lateral (D), ventral (E), and right lateral (F) views. G–L, OSD 844, dorsal or
406 sacral centrum, in anterior (G), dorsal (H), posterior (I), left lateral (J), ventral (K), and right
407 lateral (L) views. Abbreviations; kl, keel; n.a facet, neural arch pedicel; pa, parapophysis. Scale
408 bars are 5 mm.

409

410 Figure 3. Provisional stratigraphic correlation of the occurrence of choristoderes through the
411 Jurassic to Paleocene in Asia. Black squares (1–13) indicating localities where choristoderes
412 are known, and grey squares (14–21) showing localities where choristoderes are not yet known
413 (Averianov and Sues, 2012), but have a faunal composition or palaeoenvironment similar to that
414 of choristodere bearing localities elsewhere. 1, Balabansai Svita (Kyrgyzstan), Choristodera
415 indet. (Averianov, 2005); 2, Dzhylyga (Kazakhstan), *Simoedosaurus* indet. (Averianov, 2006); 3,
416 Murtoi Formation, *Khurendukhosaurus* sp. (Skutschas, 2008)/ Khilok Formation, Choristodera
417 indet. (Skutschas and Vitenko, 2017); 4, Ilek Formation, ?Neochoristodera indet. (Skutschas
418 and Vitenko, 2017); 5, Laohongdong Formation (Inner Mongolia), *Ikechosaurus sunailinae*
419 (Brinkman and Dong, 1993); 6, Two Volcanoes (Gobi Desert of Mongolia), *Tchoiria klauseni*
420 (Ksepka et al., 2005); 7, Khuren Dukh Formation (Mongolia), *Tchoiria namsarai* (Efimov, 1975),
421 *Khurendukhosaurus orlovi* (Sigogneau-Russell and Efimov, 1984; Matsumoto et al., 2009,
422 2019a); 8, Tiaojishan Formation, *Coeruleodraco jurassicus* (Matsumoto et al., 2019b)/ Qigu
423 Formation, Choristodera indet. (Richter et al., 2010); 9, Yixian Formation, *Monjurosuchus*
424 *splendens* (Endo, 1940; Gao et al., 2000), *Hyphalosaurus lingyuanensis* (Gao et al., 1999), *H.*
425 *bitaigouensis* (Ji et al., 2004); 10, Jiufotang Formation, *Philydrosaurus proseilus* (Gao and Fox,

426 2005), *Ikechosaurusu pijiagouensis* (Liu 2004); 11, Shapai Formation, *Heishanosaurus*
427 *pygmaeus* (Dong et al., 2020); 12, Kuwajima Formation, *Monjurosuchus* sp., *Neochoristodera*
428 indet. (Matsumoto et al., 2014); 13. Okurodani Formation, *Shokawa ikoi* (Evans and Manabe,
429 1999), *Monjurosuchus* sp. (Matsumoto et al., 2007); 14, Zhirkindek Formation; 15, Bostobe/
430 Syuk Shuk formations; 16, Darbasa Formation; 17, Lower Bayn Shire Formation; 18, Upper
431 Bayn Shire Formation; 19, Djadokhta Formation; 20, Barun Goyot Formation; 21, Nemegt
432 Formation (14–21, Averianov and Sues, 2012).
433
434
435

Figure 1

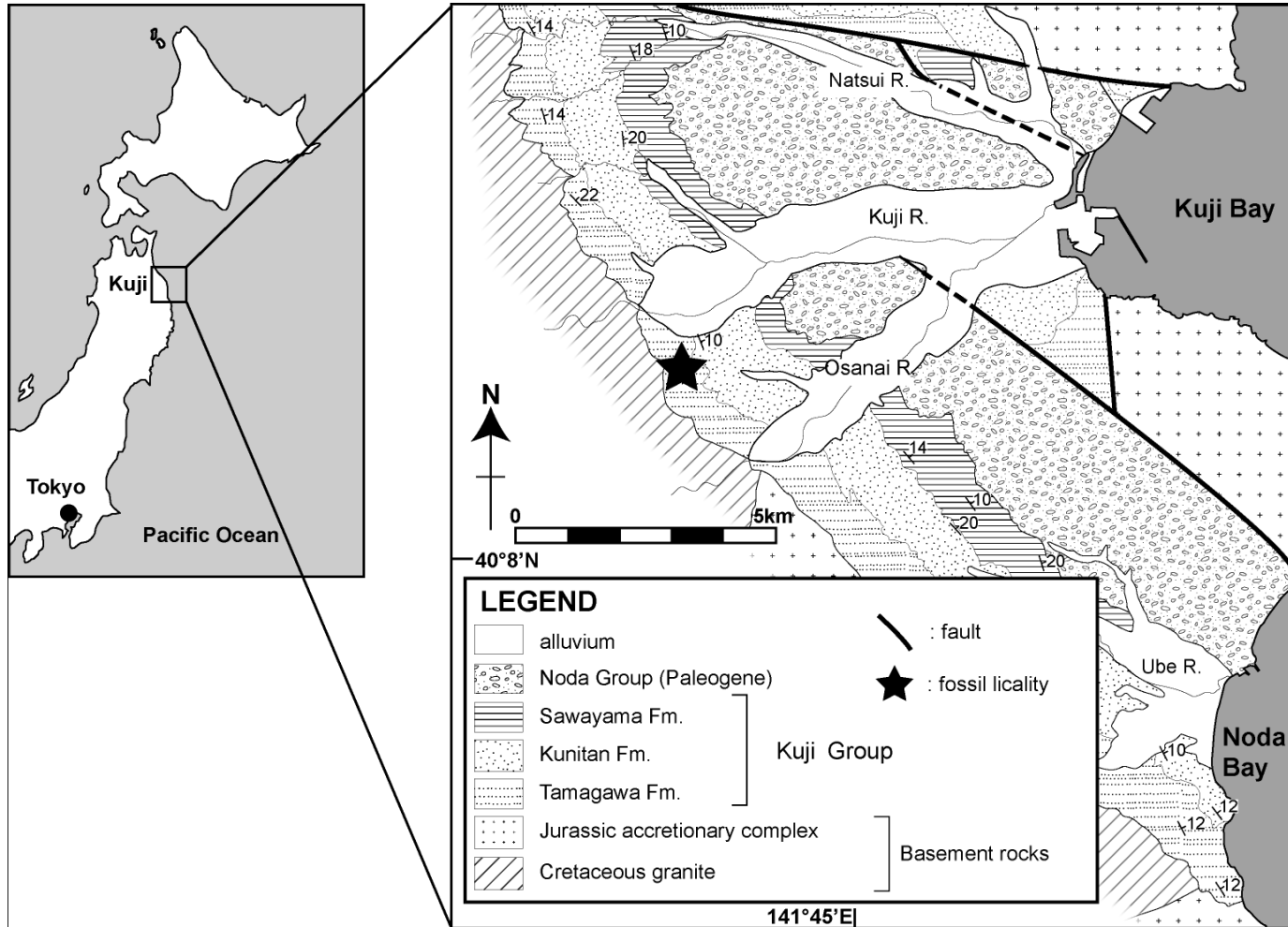


Figure 2

What do you mean
by the grooves
described in the text?
Label them?

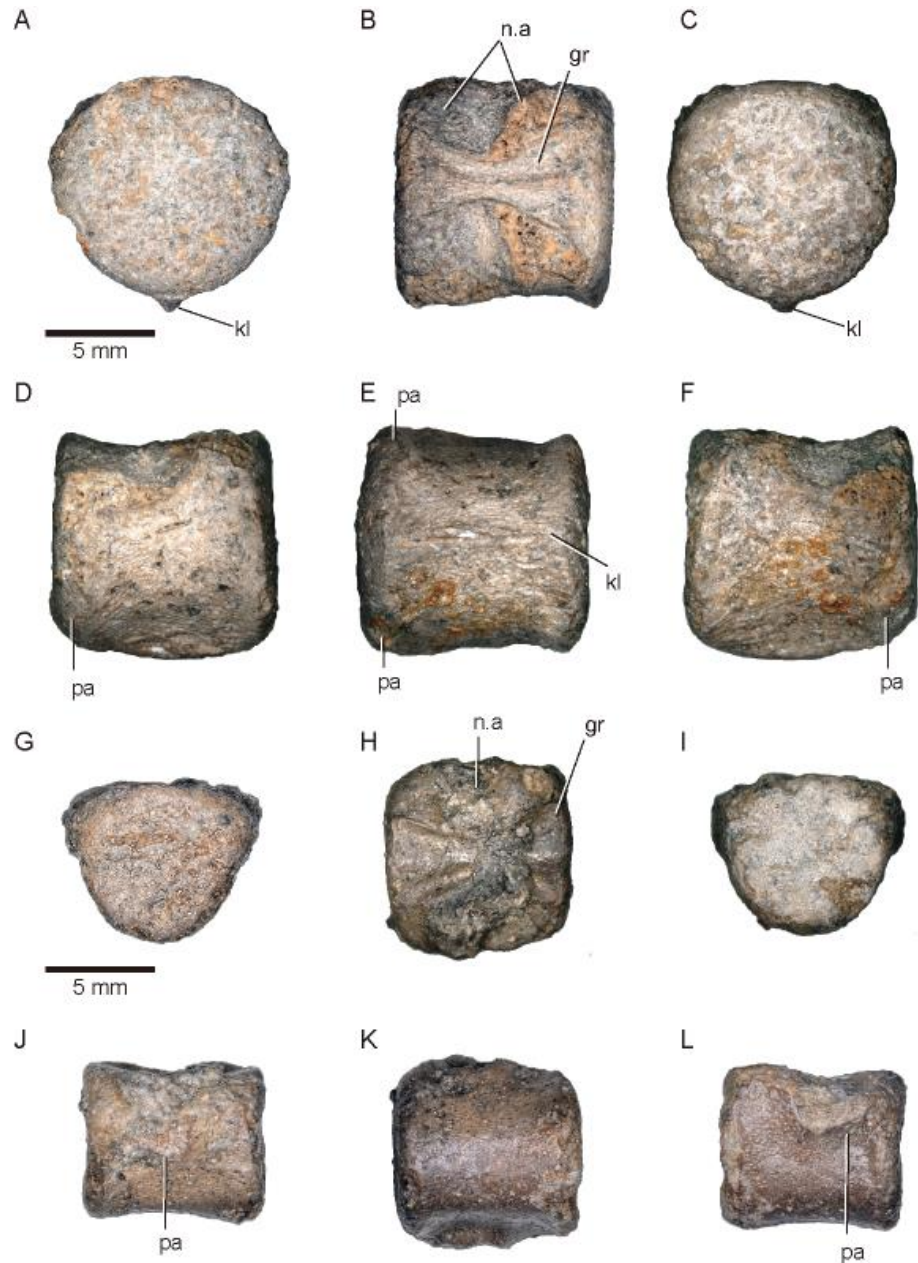


Figure 3

Kyrgyzstan

