1 **Manuscript version without figures**

2 **A new choristodere (Reptilia, Choristodera) from an Aptian-Albian**

3 **coal deposit in China**

4 Liping Dong[1,2], Ryoko Matsumoto[3*], Nao Kusuhashi[4], Yuanqing Wang[1,2,5], Yuan

5 Wang[1,2], Susan E. Evans[6]

6

7 [1]Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese

8 Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology,

9 Chinese Academy of Sciences, Beijing, 100044, China

10 [2]CAS Center for Excellence in Life and Paleoenvironment, Beijing, 100044, China

11 [3]Kanagawa Prefectural Museum of Natural History, Odawara, Kanagawa, 250-0031,

12 Japan

13 [4]Department of Earth's Evolution and Environment, Graduate School of Science and

14 Engineering, Ehime University, Ehime, 790-8577, Japan

15 [5] College of Earth and Planetary Sciences, University of Chinese Academy of

16 Sciences, Beijing, 100049, China

17 [6]Department of Cell & Developmental Biology, Biosciences, University College

18 London, Gower Street, London, WC1E 6BT, UK

19 [*]Corresponding author: r-matsumoto@nh.kanagawa-museum.jp

Abstract

Choristoderes are a small clade of freshwater aquatic reptiles known from deposits of Jurassic to Miocene age. They show their greatest diversity in the Early Cretaceous of Asia, with seven recorded genera including longirostrine and brevirostine taxa, long- and short-necked taxa, and representatives of both neochoristoderes and non-neochoristoderes. The latter, informal grouping, comprising *Monjurosuchus*, *Philydrosaurus*, *Hyphalosaurus*, *Khurendukhosaurus*, and, probably, *Shokawa*, is distinguished by the closure of the lower temporal fenestra. This differentiates them from typically diapsid stem choristoderes like the Jurassic Euramerican *Cteniogenys* and from all neochoristoderes like *Champsosaurus* and *Simoeodosaurus*. The recent description of *Coeruleodraco jurassicus* from the Callovian/Oxfordian of China provided the first example of an Asian non-neochoristodere with an open lower temporal fenestra. Herein we describe a second, geologically younger, genus and species from the Shahai Formation of Badaohao locality in western Liaoning, considered to be Aptian-Albian in age. This adds the eighth genus of choristoderes to the Early Cretaceous Asian record. The new species shares the diapsid skull morphology of *C. jurassicus*, demonstrating that a lineage of small, brevirostrine choristoderes with fully diapsid skulls persisted in Asia until the latter part of the Early Cretaceous.

Keywords

45

Introduction

46 **Introduction**

47   Choristoderes form a small, enigmatic clade of freshwater aquatic reptiles that

48 are recorded from deposits of Middle Jurassic (Evans 1990; Averianov *et al.* 2006) to

49 Miocene age (Evans & Klembara 2005). They range from the size of a small lizard

50 (e.g. *Cteniogenys*, Evans 1990) to that of large crocodiles (e.g. *Champsosaurus*,

51 Brown 1905; Erickson 1972; *Simoedosaurus*, Sigogneau-Russell & Russell 1978;

52 Erickson 1987), from brevirostrine to longirostrine, and from short-necked to long-

53 necked (see Matsumoto & Evans 2010). Over the last two decades, a series of

54 discoveries have revealed that the group underwent an important radiation in Asia

55 during the Early Cretaceous, with records from Japan, China, Russia (eastern and

56 western Siberia), and Mongolia (Matsumoto & Evans 2010; Zhang & Gao 2013;

57 Skutschas & Vitenko 2017). These Asian genera include the short-necked,

58 brevirostrine *Monjurosuchus,* total length up to 300 mm (Endo 1940; Endo &

59 Shikama 1940; Gao *et al.* 2000; Gao & Li, 2007; Matsumoto *et al.* 2007) and

60 *Philydrosaurus* (Gao & Fox 2005, Gao *et al.* 2007, 2013), up to 300 mm; the long-

61 necked brevirostrine *Khurendukhosaurus*, ~1 m (Sigogneau-Russell & Efimov 1984;

62 Skutschas 2008; Matsumoto *et al.* 2009, 2019a; Skutschas & Vitenko 2017),

63 *Hyphalosaurus*, up to 1 m (Gao *et al.* 1999; Gao & Ksepka 2008) and *Shokawa* ~

64 400 mm (Evans & Manabe 1999); and the longirostrine, short-necked *Ikechosaurus*

65 ~ 2 m (Sigogneau-Russell 1981; Brinkman & Dong 1993; Liu 2004) and *Tchoiria* ~ 2

66 m(Efimov 1975; Ksepka *et al.* 2005). The latter two are the earliest known members

67 of the Neochoristodera (sensu Evans & Hecht 1993, also including the Cretaceous-

68 Paleogene *Champsosaurus* and *Simoedosaurus*). Gao *et al.* (2005) described and

69 named an additional longirostrine taxon (*Liaoxisaurus*) from the Lower Cretaceous

70   Jiufotang Formation of China. However, the specimen on which the new genus was

71   based is closely similar to *Ikechosaurus pijiagouensis* (Liu 2004) from the same

72   horizon. Matsumoto *et al.* (2015) also reported, but did not name, a longirostrine

73   neochoristodere from the Early Cretaceous of Japan.

74   Neochoristoderes are consistently recovered as a monophyletic clade in

75   phylogenetic analyses (e.g. Matsumoto *et al.* 2013, 2019a, b). The relationships of

76   the brevirostrine taxa have proved more controversial, but they consistently fall

77   outside Neochoristodera. Significantly, although the earliest known unquestionable

78   choristodere (the Middle-Late Jurassic *Cteniogenys*) is fully diapsid, all other 'non-

79   neochoristoderes' for which the skull is known (i.e. *Lazarussuchus* Hecht 1993*,*

80   *Monjurosuchus, Philydrosaurus, Hyphalosaurus, Khurendukhosaurus*) had

81   completely closed the lower temporal fenestrae by expansion of surrounding bones.

82   This observation raised questions as to the ancestry of the earliest known

83   neochoristoderes (*Ikechosaurus*, *Tchoiria*) as these classically diapsid taxa are

84   unlikely to have arisen from a lineage with a closed lower fenestra.

85   More recently, however, we (Matsumoto *et al.* 2019b) described a new

86   brevirostrine choristodere, *Coeruleodraco jurassicus*, from the Late Jurassic of

87   China. This species differs from other Asian brevirostrine species in the presence of

88   an open lower temporal fenestra. Our phylogenetic analysis of *C. jurassicus* placed

89   it, with weak support, as the sister taxon of a clade comprising all Asian brevirostrine

90   choristoderes as well as the European Paleocene-Miocene *Lazarussuchus*.

91   *Cteniogenys* was consistently placed on the choristoderan stem.

92   Here we describe new choristoderan material from the Aptian-Albian Shahai

93   Formation of Badaohao locality, Liaoning Province, China. Although only a few

94   bones are visible at the surface of the relevant blocks, CT scans revealed many

95   other cranial and postcranial elements within the matrix, including a partial skull.

96   These specimens show that, like *Cteniogenys* and *Coeruleodraco jurassicus*, the

97   Badaohao choristodere combined a brevirostrine skull with an open lower temporal

98   fenestra. Thus, a lineage of fully diapsid non-neochoristoderes persisted in Asia until

99   the latter part of the Early Cretaceous.

100

Geological Background

102   The choristodere specimens reported here, IVPP V 25322, 25323 and 25324 were

103   collected from coaly siltstone in the middle part of the Shahai Formation, at the

104   Badaohao locality, in Heishan County, Liaoning Province, China (Fig. 1). The Shahai

105   Formation is generally considered to overlie the Jiufotang Formation conformably

106   and to be overlain conformably by the Fuxin Formation (Wang 1989; Jin 1996),

107   although there are debates as to the conformity between the Shahai and Jiufotang

108   formations (Chen *et al*. 1988). Moreover, there have been suggestions that the

109   Shahai Formation is a synonym of the Fuxin Formation (based on bivalves), or that

110   the Shahai Formation is equivalent to the Jiufotang Formation (based on pollen)

111   (Jiang *et al*. 2010). The age of Shahai Formation has not been ascertained by either

112   radiometric dating or index fossils, but is considered to be of Aptian-Albian age

113   based on the underlying Jiufotang Formation that has a radiometric age of 120 Ma

114   (He *et al*. 2004; Kusuhashi *et al*. 2009a, b, 2010).

115

116   [insert Fig. 1 here]

117

118   The Fuxin flora, represented by the plant fossils from the Shahai and Fuxin

119   formations, consists of over 300 species, dominated by Filicopsida, Ginkgopsida and

120   Coniferopsida. The flora is divided into three assemblages, of which the Shahai

121   Formation is represented by the *Acanthopteris-Ginkgo coriacea* Assemblage (Deng

122   *et al.* 2012). The Fuxin flora is considered indicative of a humid, temperate climate,

123   comparable with the Early Cretaceous floras of Siberia and Canada, and the Tetori

124   flora of Japan (Deng *et al.* 2012).

125   Several mammals, including eutriconodontans, spalacotheriids,

126   multituberculates, stem zatherian and eutherians (Hu *et al.* 2005; Li *et al.* 2005;

127   Kusuhashi *et al.* 2009a, b, 2010, 2016), have been reported from the Badaohao

128   locality, as well as some dinosaur teeth and eggs (Xu *et al.* 1998; Zhao & Zhao

129   1999; Amiot *et al.* 2010), and fishes (Jin 1996). Other fossil vertebrates, including

130   lizards and frogs, have been recovered from the locality and are currently under

131   study.

132

Material and methods

134   There are three blocks (IVPP V 25322, 25323, 25324) (Fig. 2), all collected by Dr.

135   Qian Li on the 23rd September, 2003, at the Badaohao locality, and housed in the

136   collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP),

137   Beijing, China. The surface of IVPP V 25323 bears the impression of a dentary that

138   is preserved on the surface of IVPP V 25322, and the two blocks fit together showing

139   they were originally one piece. However, based on the embedded elements (see

140   below; one right surangular in IVPP V 25323, and a right and a left surangulars in

141   IVPP V 25322), separate catalogue numbers were given to the blocks in case two

142   different individuals are represented between these blocks. The only elements

143   exposed on the surface of the blocks are a left dentary on IVPP V 25322, its

144   impression on IVPP V 25323, and a right jugal on IVPP V 25323.

145

146   [insert Fig. 2 here]

147

148   We scanned the specimens using Micro-computerized tomography (developed

149   by the Institute of High Energy Physics, Chinese Academy of Sciences [CAS]) at the

150   Key Laboratory of Vertebrate Evolution and Human Origins, IVPP, CAS, Beijing. All

151   three blocks were scanned with a beam energy of 140 kV and a flux of 120 µA, using

152   a detector resolution of 63.05 µm per pixel for IVPP V 25322, of 61.90 µm per pixel

153   for IVPP V 25323; and of 63 µm per pixel for IVPP V 25324. A 360° rotation with a

154   step size of 0.5° and an unfiltered aluminium reflection target was adopted for each

155   scan. A total of 720 transmission images were reconstructed in a 2048*2048 matrix

156   of 1536 slices using a two-dimensional reconstruction software developed by the

157   Institute of High Energy Physics, CAS. The slice data revealed that the blocks

158   contained many more elements than were visible on the surface (Fig. 2). Each

159   element from each block was segmented out and visualized using the software Avizo

160   8.1 and 9.0 to display detailed anatomical information. The cranial elements,

161   mirrored as necessary, were then 3D printed to assemble into a reconstruction (Fig.

162   3). The 3D printing was carried out using an Objet 260 Connex3, at three times the

163   original size. The elements from IVPP V 25322 and 25323 were then scaled with

164   those on IVPP V 25324 based on the length of squamosal and jugal to give a

165   uniform scale.

166   IVPP V 25322 was found to contain several skull bones including a left

167   squamosal, jugal, prefrontal, and lachrymal, a right ectopterygoid, and the right and

168   left dentaries and surangulars. It also bears a scatter of vertebrae (cervical, caudal),

169   ribs, and phalanges, as well as some unidentified elements. IVPP V 25323 contains

170   further vertebrae (cervical, dorsal, caudal), ribs, gastralia, and phalanges, as well as

171   a clavicle, a possible tibia, a right surangular, and some unidentified bones including

172   what may be fragments of braincase. IVPP V 25324 (Fig. 2E, F) contains the

173   remains of a second individual including a partial skull (left parietal, postorbital, jugal,

174   quadratojugal and squamosal); further disarticulated skull elements including right

175   and left quadrates, a right premaxilla, a right jugal, a left ectopterygoid, a left

176   coronoid, prearticular and splenial, a right palatine, and a few postcranial elements

177   including a rib, a vertebra, phalanges, and possible carpals. We have designated

178   IVPP V 25324 as the holotype due to the partial articulated skull that is certainly from

179   a single individual.

180   The close similarity in the morphology of bones such as the jugals,

181   squamosals, and prearticulars between the blocks supports the conclusion that the

182   bones on all three blocks represent individuals of a single species.

183

184   **Institutional abbreviations**

185   **BMNHC**, Beijing Museum of Natural History, Beijing, China; **CAGS-IG**, Institute of

186   Geology, Chinese Academy of Geological Sciences, Beijing, China; **CAS**, Chinese

187   Academy of Sciences; **CNMM**, former Central National Museum of Manchoukuo, in

188   Hsinking (now Changcun); **DR**, Dalian Natural History Museum, Dalian, China;

189   **GMC**, Geological Museum of China, Beijing, China; **GMV**, the Geological Museum of

190   China, vertebrate fossil collections, Beijing, China; **IGM**, Geological Institute of the

191 Mongolian Academy of Sciences, Ulan Bataar, Mongolia; **IVPP**, Institute of

192 Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science,

193 Beijing, China; **LPMC**, Liaoning Paleontological Museum of China, Shenyang, China;

194 **MNHN,** Muséum National d'Histoire Naturelle, Paris, France; **PIN**,

195 Paleontologicheski Institut Rossiiskoi Akademii Nauk, Moscow, Russia; **PKUP**,

196 Peking University Paleontological collections, Beijing, China; **RTMP,** Royal Tyrrell

197 Museum of Palaeontology, Drumheller, Alberta, Canada; **SMM,** The Science

198 Museum Minnesota, St. Paul, Minnesota, U.S.A.

199

200

201 **Systematic Palaeontology**

202

203

204   **Reptilia** Linnaeus, 1758

205   **Choristodera** Cope, 1884

206   Genus *Heishanosaurus* gen.nov*.*

207

208 **Etymology.** Heishan is the name of the county in which the type locality for the

209 choristoderan material is located.

210 **Type species.** *Heishanosaurus pygmaeus*.

211 **Diagnosis.** As for type and only species.

212

213

214   ***Heishanosaurus pygmaeus* sp. nov**

215   (Figs 2, 3, 5–12)

216 **Etymology.** Pygmaeus (Latin), meaning dwarf. The species name recognizes the

217 small size of this taxon compared to many other Cretaceous species.

218 **Holotype.** IVPP V 25324, partial skull with some disarticulated cranial and post

219 cranial elements (Fig. 2E, F).

220 **Type Locality and horizon.** Badaohao locality, Heishan County, Liaoning Province,

221 China. Shahai Formation, of Aptian-Albian (Early Cretaceous) age.

222 **Differential diagnosis.** A small choristodere that resembles *Cteniogenys* and

223 *Coeruleodraco*, and differs from all other described choristoderes, in combining the

224 possession of a small lower temporal fenestra with a short rostrum, a small

225 lachrymal limited to the orbital margin, separate postfrontal and postorbital bones,

226 and a short mandibular symphysis. It resembles *Cteniogenys* and differs from

227 *Coeruleodraco* in having a lachrymal canal that perforates the lachrymal bone

228 (passes between lachrymal and prefrontal in *Coeruleodraco*). *Heishanosaurus* differs

229 from *Cteniogenys* in having a more slender postorbital process of the squamosal; a

230 narrower, more tapered dorsal process of the jugal; a prefrontal that is pentagonal

231 rather than rectangular in dorsal view; a parietal that is more massive in its build with

232 deeper postparietal processes; a coronoid that, although small, has a distinct

233 coronoid process (rounded dorsal margin in *Cteniogenys*); and a skull outline that is

234 proportionally shorter and wider (narrow and tapering in *Cteniogenys*). It resembles

235 *Coeruleodraco* and differs from *Cteniogenys* in having tubercular sculpture along the

236 posterior margin of the squamosal. *Heishanosaurus* also resembles *Coeruleodraco*

237 in having ungual phalanges without a tubercle, but differs in having a squamosal with

238 a postorbital process longer than quadratojugal process (shorter/equal in

239 *Coeruleodraco*); a square lateral plate of the squamosal (anteroposteriorly elongated

240 in *Coeruleodraco*); a median parietal suture that is longer than the parietal

squamosal process (shorter/equal in *C. jurassicus*); distinct dorsal and posterior

processes of the jugal (processes short in *Coeruleodraco*); a sickle-shaped

quadratojugal (narrow rectangle in *Coeruleodraco*); a postorbital with a weakly

concave (vs strongly concave) ventral margin; a shorter mandible with fewer dentary

teeth (27 in *Heishanosaurus pygmaeus* vs 37–38 in *Coeruleodraco*); and caudal

transverse processes that are not expanded (expanded caudal ribs are a diagnostic

character of *Coeruleodraco*).

Referred specimens. IVPP V 25322 and IVPP 25323 (originally part of a single

block), also from Shahai Formation at the type locality.

Remarks. This newly discovered small reptile is identified as a choristodere based

on the combination of the following characteristic features: paired prefrontals

meeting in the midline, forming anterior margin of orbits; a long shallow dentary

ramus with labial neurovascular foramina opening into longitudinal grooves; conical

subthecodont teeth; well sculptured parietal and squamosal forming cordiform skull.

Heishanosaurus most closely resembles *Coeruleodraco* in general skull features, but

a majority of these are either primitive (short rostrum, lower temporal fenestra,

separate postorbital and postfrontal) or common in non-neochoristoderes crownward

of *Cteniogenys* (tubercular sculpture). In the phylogenetic analyses run for this work

(see below), *Heishanosaurus* and *Coeruleodraco* were not found to be sister taxa

and were consistently placed as consecutive or unresolved outgroups to all other

choristoderes except *Cteniogenys*. This separate placement could be due to missing

data (e.g. for the palate, braincase, and limb skeletons of *Heishanosaurus*) but,

given the age difference (Aptian/Albian vs Callovian/Oxfordian), and the striking

266 differences between *Heishanosaurus* and contemporary Asian choristoderes, it

267 seems preferable to place the Badaohao choristodere in a new genus pending the

268 recovery of further material. To aid comparison, new comparative figures of

269 *Coeruleodraco* are provided in Supplementary data files.

270

271 **Description.**

272 Fig. 3 shows a reconstruction of the skull (Fig. 3A) and lower jaw (Fig. 3B) based on

273 the individual elements on the three blocks, with comparable elements scaled to the

274 same size and 3D printed. Overall skull length is constrained by dentary and

275 surangular length, but we cannot be certain of the shapes or relative proportions of

276 the nasals (absent), prefrontals (possibly breakage), and frontals (absent). The

277 cranial bones and their articular surfaces are fully formed and seem therefore to be

278 those of adult and/or sub-adult individuals. This is supported by the complete closure

279 of the neurocentral sutures, the absence of a patent notochordal canal in the

280 vertebrae, and the ossification of tarsal and carpal elements scattered through the

281 blocks.

282

283 [insert Fig. 3 here]

284

285 As reconstructed, the skull is dorsoventrally compressed with preorbital and

286 postorbital regions of roughly equal length, although snout length remains somewhat

287 uncertain (as is coded as such in the data matrix). As in all choristoderes, the

288 prefrontals met in the midline between the nasals and frontals, and contributed to the

289 preorbital skull roof, and there is a large, posteriorly expanded upper temporal

290 fenestra. As in neochoristoderes, *Cteniogenys*, and *Coeruleodraco jurassicus* (Fig.

291   4, and Supplementary Information), there is also a lower temporal fenestra. All

292   median skull bones are paired, and the parietals and squamosals are strongly

293   sculptured with bony tubercles and spikes.

294

295   [insert Fig. 4 here]

296

297   **The skull of IVPP V 25324**

298   The designated holotype (IVPP V 25324) contains the partial left half of a skull with

299   the parietal, squamosal, postorbital, jugal, and quadratojugal in close association

300   (Fig. 3C). Other cranial (right jugal, right prearticular, right coronoid, both quadrates,

301   left ectopterygoid, left palatine, left premaxilla) and postcranial elements (phalanges,

302   possible carpals, a rib, a caudal vertebra) in proximity to the association are probably

303   part of the same individual, based on size and the consistency of morphological

304   features.

305   The parietals were originally paired (Fig. 5A, B). As preserved, the left parietal

306   is formed by two distinct plates, the dorsal skull table and a posteroventrolaterally

307   expanded squamosal wing, with the former slightly longer than the latter (almost

308   equal in *Coeruleodraco*). The median parietal suture is relatively shallow for a

309   choristodere, although it deepens slightly at the posterior end. As in all

310   choristoderes, there was no medial parietal foramen (Fig. 5A). The dorsal plate of

311   the parietal is heavily sculptured with a strong lateral crest that runs parallel to the

312   midline and forms the dorsomedial margin of the upper temporal fenestra. The crest

313   separates the horizontal rectangular skull table from a sloping ventrolateral flange

314   that would have accommodated adductor muscles. As delimited by the crests, the

315   skull table is narrower than that of *Coeruleodraco.* The forked anterior margin of the

13

316   skull table bears an interdigitating suture for the frontal. Further laterally, the angled

317   margin of the adductor flange bears a facet for the postorbital. Posterolaterally, the

318   parietal expands into a broad wing that met the squamosal to form the posteromedial

319   margin of the upper temporal fenestra. However, the posterior 20% of this wing lies

320   at a slightly different level to the rest and could be the anterior edge of the

321   squamosal. Clearly, the squamosal has a strong articulation with the parietal. The

322   ventral margin of the posterior wing is damaged, but it probably attached to the

323   opisthotic, whereas the posteromedial edges of the parietal table met the

324   supraoccipital.

325   The left squamosal on IVPP V 25324 (Fig. 5C, D) is almost complete but it is

326   supplemented by the squamosal on IVPP V 25322 (Fig. 5E–H). The squamosal is

327   formed by lateral and posteromedial plates that meet at 30°, and together formed the

328   posterolateral border of the upper temporal fenestra. The lateral plate is square

329   (roughly equal in length and height), strongly ornamented, and has ventral and

330   posterior margins bearing strong spikes (Fig. 5C, E). The plate bifurcates anteriorly

331   into dorsal and ventral processes. The narrow dorsal process is mediolaterally

332   compressed and is roughly one and a half times the length of the ventral process

333   (almost equal in *Coeruleodraco*). The dorsal process is damaged at the tip but bears

334   part of a slot facet for the postorbital (Fig. 5E). Together the squamosal and

335   postorbital formed the upper temporal bar, between upper and lower temporal

336   fenestrae. The shorter, ventral process of the lateral plate met the quadratojugal, and

337   bears a sloping facet for that bone at its anteroventral tip. The squamosal thus

338   provided the posterodorsal and posteroventral borders of the small lower temporal

339   fenestra. The medial lamina of the squamosal met the parietal anterodorsally, as

340   described above. Below the parietal facet, the medial lamina bears a deep groove

14

341   that expands dorsoventrally and accommodated the dorsolateral margin of the

342   quadrate (Fig. 5D, 5C). At the junction of the parietal and quadrate facets, there is a

343   small notch facet for the neomorph (Fig. 5D, 5F–G).

344

345   [insert Fig. 5 here]

346

347   The associated left jugal on IVPP V 25324 is in two parts, with its suborbital

348   process slightly displaced (reconstructed in Fig. 6A, B). It is supplemented by a

349   disarticulated right jugal on the same block, and by a well-preserved left jugal on

350   IVPP V 25322 (Fig. 6C–E). The jugal is strongly triradiate with anterior, dorsal and

351   posterior processes. The dorsal process is slightly shorter than the posterior process

352   and has a small anterolateral postorbital facet at its tip. The shallow anterior

353   suborbital process is the longest and bears a narrow, ventromedial facet for the

354   maxilla (Fig 6B, D, E). The narrow posterior process bears a distinct posteromedial

355   facet for the quadratojugal (Fig. 6B, D), the two bones forming most of the ventral

356   margin of the open lower temporal fenestra. This slender posterior process is

357   markedly different from the jugal of *Monjurosuchus*, *Philydrosaurus*, and

358   *Hyphalosaurus*, where the deep posterior flange of the jugal contributes to the

359   closure of the lower temporal fenestra. The medial surface of the jugal is generally

360   smooth, but it bears a facet for the ectopterygoid at the medial junction of the three

361   processes. At its anterior tip, the ectopterygoid facet lies adjacent to the posterior

362   part of the maxillary facet (Fig. 6B, D), and it is possible that these bones were in

363   contact.

364   The left quadratojugal is preserved only on IVPP V 25324 (Fig. 6F–I). It has a

365   scythe-like shape in lateral view, tapering anteriorly but with a slight dorsal concavity.

366   The anterior process forms the posterior half of the lower temporal bar. Its anterior

367   tip is somewhat dorsoventrally compressed, and bears a shallow dorsolateral facet

368   for the jugal (Fig. 6F). The thicker posterior end of the bone bears a medial slot facet

369   that accommodated the lateral process of the quadrate (Fig. 6G, I), and a

370   posterodorsal overlap facet for the ventrolateral process of the squamosal (Fig. 6H,

371   I).

372   The left postorbital completes the associated skull part on IVPP V 25324 (Fig.

373   6J–N). It is a robust bone with a thick, ornamented, orbital rim that supports the

374   postfrontal facet dorsally and an interlocking jugal facet ventrally. A broad temporal

375   lamina extends posteriorly from the orbital margin, divided into dorsal and ventral

376   parts by a strong ridge that formed the anterolateral margin of the upper temporal

377   fenestra (Fig. 6K). The lamina tapers posteriorly into the ventral squamosal process

378   that bears a mediolaterally compressed, interdigitating facet for the squamosal at its

379   tip (Fig. 6K, M–N). The facet for the postfrontal excavates the dorsal surface of the

380   dorsal temporal lamina anteriorly, whereas the anteromedial border bears an

381   interdigitating surface for articulation with the parietal (Fig. 6K, M–N). As articulated,

382   it seems unlikely that the postfrontal met the parietal, unlike *Coeruleodraco* where

383   there is a small contact. The posteromedial edge enters the margin of the upper

384   temporal fenestra. The ventrolateral margin of the temporal lamina borders the lower

385   temporal fenestra.

386

387   [insert Fig. 6 here]

388

389   Both right and left quadrates lie in association with the partial skull on IVPP V

390   25324 although they are not in articulation (Fig. 7A–F). Each resembles a flattened

391   triangle, with a narrow dorsal apex, a slightly expanded lateral flange and a more

392   strongly expanded medial one separated by a dorsoventral crest (Fig. 7B, E). This

393   crest, absent in *Coeruleodraco*, supports a small rounded dorsal condyle, and an

394   anteroposteriorly compressed, bilobed, ventral mandibular condyle (Fig. 7F). The

395   anterior surface of the quadrate is slightly concave at the junction between the

396   mandibular condyle and the medial flange (Fig. 7A, D). The lateral margin of the

397   bone bears two facets. The longer, dorsal one is a narrow facet that extends up to

398   the dorsal condyle, and which inserted into the slit on the medial surface of the

399   squamosal. The smaller ventral facet inserted into the shallow groove on the

400   posteromedial margin of the quadratojugal (Fig. 7C). The medial flange of the

401   quadrate is expanded into a pterygoid lappet that has a deep pterygoid facet along

402   the ventral margin (Fig. 7B, E). Dorsal to the pterygoid facet, the medial border of the

403   bone bears an overlapping facet for the opisthotic, whereas a more dorsal facet,

404   close to the apex, may be for a neomorph (Fig. 7B, E).

405   Three other cranial bones are preserved on IVPP V 25324, a right premaxilla, a

406   right partial palatine, and a left ectopterygoid. Given their proximity to the associated

407   skull region, they probably belong to the same individual.

408   The premaxilla is small and may not be complete (Fig. 7G–J). The vertical

409   medial margin met the contralateral premaxilla in a short anterior suture. The lateral

410   margin is deeper and notched, possibly for articulation with the maxilla (not

411   preserved on any specimen). From medial to lateral, the anterodorsal margin is

412   curved. No median nasal process is preserved, suggesting the nares may have been

413   confluent, but this is coded as uncertain in the data matrix as the bone may be

414   damaged. Two conical teeth are preserved in situ, with space for an additional tooth

415   medially (Fig. 7H). On the posterodorsal surface, a shallow depression may

416   represent an articular facet for the vomer (not identified; Fig. 7G).

417   A small triangular bone lying close to the left jugal seems to be part of the

418   palatine, but it may not be complete (Fig. 7K, L). It has processes for the maxilla and

419   vomer (Fig. 7K). The maxillary process is short and broad-based, and seems to have

420   abutted the medial surface of the maxilla (Fig. 7K). The vomerine process may be

421   broken, but its tip has part of a slot facet for the vomer. Between the maxillary and

422   vomerine processes, the concave anterior margin formed the posterior border of the

423   choana. Posterolateral to the vomerine facet, the palatine would have articulated

424   with the pterygoid, but this part of the bone is damaged (Fig. 7K). A single, slightly

425   curved, palatal tooth row extends along the maxillary border, with conical denticles

426   (Fig. 7K). On the dorsal surface, there are several features, including a ridge that

427   crosses the bone parallel to the choanal margin before curving posteriorly (Fig. 7L).

428   Small grooves cross the dorsal surface of the palatine in *Cteniogenys* (Evans, 1990),

429   but it is not clear whether this ridge is a part of a similar groove arrangement, or

430   some other structure. The ridge is flanked posteriorly by what appears to be a facet.

431   However, without either the maxilla or pterygoid, it is difficult to estimate how far

432   anteriorly the palatine was placed and how it was related to the other rostral skull

433   elements.

434   The ectopterygoid is a small hammer-shaped element, composed of a short,

435   wide lateral head, and a slender, horizontally orientated, pterygoid process (Fig. 7M–

436   O). The lateral head bears a smooth triangular surface (Fig. 7O), apex anterior, that

437   fits into a recess on the medial surface of the jugal. The anteroventral part of this

438   surface has a small, narrow facet for the maxilla (Fig. 7N). The pterygoid process

439   has a slightly expanded medial end that lies at 90° to the jugal surface. The facet for

440   the pterygoid is probably not complete. A right ectopterygoid is preserved on IVPP V

441   25322, but provides no additional details.

442   A coronoid and prearticular associated with IVPP V 25324 are described below

443   with the lower jaw elements.

444

445   **Additional skull elements on IVPP V 25322 and 25323**

446   The prefrontal is preserved only on IVPP V 25322 (Fig. 8A–E). As in other

447   choristoderes, it comprises a horizontal dorsal lamina, and a ventrolateral lamina that

448   contributed to the orbital margin and the preorbital skull wall (Fig. 3A). The dorsal

449   lamina met the contralateral prefrontal in the midline to form the anterior part of

450   interorbital skull roof and to contribute to the rostrum between the nasals and

451   frontals. The reconstruction in Fig. 3 is based on the assumption that the median

452   suture is fully preserved, but this area is thin and the surface lacks detail. The main

453   body of the bone is trapezoid with a slight ornamentation (Fig. 8A). Its posterodorsal

454   surface bears an anteriorly tapering concavity that represents the frontal facet (Fig.

455   8A). The ventrolaterally expanded lamina met the lachrymal along the orbital margin.

456   Anterior to the lachrymal facet, the lamina bears a narrow shelf that was overlapped

457   by the maxilla (Fig. 8A, E). On the ventral surface, an L-shaped ridge met the

458   palatine (Fig. 8B). When the skull is reconstructed, the prefrontal as preserved

459   seems to be too short and it is possible that part of the bone is missing anteriorly.

460   The shallow descending lamina also suggests that the rostrum was depressed.

461   IVPP V 25322 also preserves a small wedge-shaped lachrymal that lay in the

462   orbital margin between the jugal posteroventrally, the maxilla anteroventrally, and the

463   prefrontal anterodorsally (Fig. 8F–J). The concave orbital margin is perforated by a

464   foramen (probably two merged foramina) that would have led into a nasolachrymal

465   canal, but this canal could not be traced through the bone on the CT scan data due

466   to the difficulty of distinguishing between cracks and canals. The dorsolateral surface

467   of the bone is triangular with a long tapering posterior process and a short curved

468   anterior border (Fig. 8F). The lateral surface is slightly concave, and it is perforated

469   by a small foramen that leads into a recess on the ventromedial surface (Fig. 8G).

470   This foramen is likely to have carried a sensory branch of the maxillary (trigeminal)

471   nerve. The ventral border of the bone bears a deep groove that accommodated the

472   maxilla anteriorly and the jugal posteriorly (Fig. 8G, H). The maxillary facet extends a

473   short distance up the anterior margin of the bone (Fig. 8I). Further dorsally, this

474   anterior margin would also have met the prefrontal but the articular surface is not

475   clearly demarcated on the specimen except at the dorsal tip (Fig. 8F). This may be a

476   resolution problem or due to damage.

477   Other fragmentary elements on the blocks may be parts of the braincase or

478   rostrum, but we were not able to identify any of these with confidence.

479

480   [insert Fig. 8 here]

481

482   **Lower jaws**

483   Both dentaries are preserved on IVPP V 25322, the right bone exposed on the

484   surface and the left within the block and revealed by CT scan. They are ~ 28 mm in

485   length and show typical choristoderan features including a long shallow dentary

486   ramus with fine lateral striations and two rows of labial neurovascular foramina with

487   many of these foramina opening into longitudinal grooves on the lateral surface (Fig.

488   9A, E). However, the dentaries differ from those of most choristoderes in being

489   relatively short, and in being significantly deeper (by three times) at the posterior end

than the symphysial end (twice the depth in *Coeruleodraco*), with a slightly curved

ventral margin (Fig. 9B). The bone is bifurcated at its posterior tip, with the upper

ramus much longer than the lower one. Seen in medial view (Fig. 9B), the meckelian

fossa is open the full length of the bone, and divides the short (3–4 tooth positions)

symphysial surface into dorsal and ventral parts (Fig. 9B, C). The subdental ridge

and the ventral border of the bone are smooth, so that the presence or absence of a

splenial cannot be confirmed (Fig. 9B, D). At the posterior end of the tooth row there

is a shallow facet for the small coronoid and, below this, a larger facet for the

surangular that slots into the posterior end of the dentary (Fig. 9B). There is no

obvious angular facet. The right dentary bears 26 conical homodont teeth with a

subthecodont implantation in shallow circular alveoli (Fig. 9C). With 3–4 positions

missing the teeth, the total tooth count is around 30. A tooth count is more difficult on

the left, but appears to be roughly the same. These teeth are simple and conical

throughout the tooth row, with no basal labyrinthine folding and enamel extending

only over the upper two-thirds of the crown. The anterior ten teeth are somewhat

smaller and narrower than those in the middle and posterior end of the jaw (Fig. 9B).

Empty tooth positions suggest that active replacement was ongoing.

[insert Fig. 9 here]

The left and right surangulars are also preserved in IVPP V 25322 (Fig. 10A–

E), with the right element more complete (Fig. 10C–E). There is also an additional,

partial surangular on IVPP V 25323. The bone is deep posteriorly and tapers

anteroventrally. The lateral surface of the surangular shows a similar ornamentation

to that seen on the dentary (Fig. 10A, C). The anterior tip inserts into the posterior

515 end of the Meckelian canal of the dentary, as shown by the deep forked grooves

516 along almost two thirds of the dorsolateral margin (Fig. 3B, 10C). Posterior to the

517 dentary facet, the ventral margin bears a shallow angular facet (Fig. 10A, C). In

518 medial view, the dorsal border of the adductor region is thick and rounded, with an

519 incised facet for the coronoid along the anterior edge (Fig. 10B, D). The ventral

520 border is thinner, especially anteriorly (Fig. 10E). There are no obvious facets for the

521 prearticular, and it is likely that this was supported ventrally by the angular.

522 Posteromedially, a sharp crest separates the adductor chamber from the articular

523 region (Fig. 10B, D). The articular compartment has a roughened surface for the

524 attachment of the articular (Fig. 10B, D), but neither this element, not the angular,

525 are preserved on any of the blocks.

526

527   [insert Fig. 10 here]

528

529   The coronoid is a small, needle-like element preserved on the holotype block

530 (IVPP V 25324; Fig. 11A–D). As seen in medial view, the bone comprises a small

531 coronoid process, a short, thick, posterior surangular process, and a long slender

532 anterior dentary process (Fig. 11A). Just anterior to the coronoid process, the bone

533 also expands medially into a small hook-shaped process that forms the curved

534 anterior margin of the adductor fossa (Fig. 11B). The inferior surface of this medial

535 shelf must have contacted the prearticular, although there is no obvious facet (Fig.

536 11D).

537   A prearticular is preserved on IVPP V 25324 (Fig. 11E–G) and IVPP V 25323

538 (Fig. 11H), both from the left side. The bone on IVPP V 25323 is better preserved

539 (Fig. 11E–G). It forms a smooth, slender plate with a keel running along the

540 ventromedial margin and delimiting the dorsal margin of a large angular facet. The

541 prearticular expands posteriorly, creating a gently curved dorsal margin (Fig. 11E,

542 H). In lateral view, this dorsal margin appears thick and rounded, forming the medial

543 edge of the adductor fossa (Fig. 11F). The expanded posterior end of the bone is

544 slightly inflated dorsally and ventrally bears a recess that may have supported the

545 articular (Fig. 11F, G).

546

547   [insert Fig.11 here]

548

549   Although the angular is not preserved, the facets on the surangular and

550 prearticular suggest that it would have been a substantial, trough-like bone forming

551 the posteroventral margin of the mandible and linking the surangular laterally with

552 the prearticular medially.

553

554 **Axial skeleton**

555 Isolated vertebrae are preserved on each of the blocks. All vertebrae are

556 amphicoelous but with a closed notochordal canal and closed neurocentral sutures

557 (Fig. 12A–T).

558   A single cervical is preserved on IVPP V 25323 (Fig. 12A–E). It is almost

559 complete, with only slight damage to the slightly tapering neural spine that is set

560 towards the posterior end of the vertebra (Fig. 12B). The centrum is short, its length

561 almost equal to its height (Fig. 12B). The anterior and posterior joint surfaces contain

562 a small notochordal pit (Fig. 12A, C). The centrum bears a strong midventral keel,

563 flanked by concavities on either side of the centrum (Fig. 12A). The transverse

564 process is positioned at the junction of the centrum and neural arch, but the

565   parapophysis is damaged and not visible (Fig. 12B). The anterior and posterior

566   zygapophyses are broad (Fig. 12A, C), with the anterior joint surfaces almost

567   horizontal and the posterior one slightly inclined (~30° to the horizontal).

568   Three complete dorsal vertebrae are preserved on IVPP V 25322 (Fig. 12F–J)

569   and V 25323 (Fig. 12K–N). That on IVPP V 25322 has a shorter centrum (1.5 times

570   longer than high) than those on IVPP 25323 (~twice as long as high; Fig. 12L), and

571   is probably from a more anterior position along the vertebral column. The centra

572   have a rounded, rather than sharp, midventral ridge (Fig. 12J, N), and are flanked by

573   shallower concavities. The neural spine is square in lateral view rather than tapering

574   (Fig. 12G, L), becoming more rectangular in profile in the more posterior dorsals, and

575   the dorsal edge of the spine (the spine table) is slightly expanded (Fig. 12F, K).

576   Unlike those of cervical vertebra, the zygapophyses of the dorsal vertebra are

577   narrow and lie closer to the midline (Fig. 12F, H, K, M). The zygapophysial surfaces

578   change in orientation from almost horizontal (anterior; Fig. 12F) to more strongly

579   inclined dorsally (posterior; Fig. 12K). There is no accessory spinous process below

580   the posterior zygapophysis (Fig. 12G, L). The transverse processes are posteriorly

581   inclined at about 20° to the vertical plane, and lie across the level of the neurocentral

582   junction (Fig. 12G, L). They are dorsoventrally deepest in the more anterodorsal part,

583   perhaps reflecting the fusion of parapophysis and diapophysis, and they become

584   narrower posteriorly.

585

586   [insert Fig. 12 here]

587

588   No sacral vertebrae are preserved, but there are several caudals (2: IVPP V

589   25322; 4: IVPP V 25323; ?1: IVPP 25324), including elements from the anterior,

590 middle, and posterior ends of the tail. The caudal centra are cylindrical,

591 amphicoelous, and more than three times longer than high (Fig. 12P). The

592 zygapophyses are small with joint surfaces that are almost vertical (Fig. 12O, Q). In

593 the anterior and middle portions of the tail, the centra bear a midventral groove

594 flanked by paired parallel crests (Fig. 12R, T), but these are missing on the more

595 posterior caudals. Some anterior caudals bear a neural spine, but this is lost in more

596 posterior vertebrae. Anterior caudals also bear caudal ribs that are fused to the

597 centrum. These ribs are mostly slender, with rounded or rectangular ends (Fig. 12R,

598 T). In this respect they differ from the flared caudal ribs of *Coeruleodraco.*

599   Apart from the vertebrae, the axial skeleton is represented by a few single

600 headed ribs (all blocks; Fig. 13A–B) and by a single, slender, gastral element (IVPP

601 V 25323; Fig. 13C).

602

603   [insert Fig. 13 here]

604

605 **Appendicular skeleton**

606 Very little of the appendicular skeleton is preserved across the three blocks, other

607 than scattered metapodials and phalanges (Fig. 13F–H). The exceptions are a right

608 clavicle and a right tibia on IVPP V 25322 (Fig. 13D–E).

609   The clavicle is an L-shaped element with tapering ventromedial and

610 dorsolateral ends (Fig. 13D–E). The medially extended process is slightly wider than

611 the dorsal one, and bears a groove facet for the interclavicle (Fig. 13E). The dorsal

612 process bears a keel on the dorsal edge (Fig. 13E).

613   The tibia is 17 mm in length (Fig. 13I). It is robust with a proximal head of

614 roughly twice the width of the distal one (5.5 mm: 3.7 mm), and a midshaft width of

615 2.1 mm (Fig. 13K–M). The proportions are generally similar to those of *C. jurassicus*,

616 although the proximal head of *Heishanosaurus pygmaeus* is slightly broader relative

617 to the length of the bone.

618   The length of the tibia by comparison with that of the fully articulated skeleton of

619 *Coeruleodraco* (Matsumoto *et al*. 2019b) allows us to make a rough estimate of the

620 size of *Heishanosaurus pygmaeus* individual(s) on IVPP V 25323 (Fig. 13I–M). The

621 type and only specimen of *Coeruleodraco* has a snout-pelvis length (SPL) of 200

622 mm. Given a roughly similar tibia, this would yield a SPL of ~162 mm for

623 *Heishanosaurus pygmaeus*.

624

625 **Phylogenetic analysis**

626 *Heishanosaurus pygmaeus* was coded into the data matrix of Matsumoto *et al*.

627 (2019b) and an analysis was run using TNT (version 1; Goloboff *et al*., 2008) with a

628 New Technology search mode with ratchet (1000 random addition sequences: 50

629 iterations). The diapsid *Petrolacosaurus* was the designated outgroup taxon but, as

630 done previously (e.g. Matsumoto *et al*. 2019b), several other diapsids were included

631 in the ingroup (stem-diapsids *Youngina* and *Araeoscelis*, the archosauromorphs

632 *Prolacerta* and *Mesosuchus*, the lepidosaur *Gephyrosaurus*, and the

633 sauropterygians *Nothosaurus* and *Keichosaurus*) because the diapsid sister taxon of

634 choristoderes remains uncertain. The resulting trees were then reanalysed using a

635 Traditional search option. The bootstrap tree was analysed with 10,000 replicate

636 resampling.

637   Matsumoto *et al*. (2019b) found weak support for the placement of the

638 Jurassic *Coeruleodraco* as the sister taxon of non-neochoristodere genera (other

639 than *Cteniogenys*), despite its retention of a lower temporal fenestra. The process of

640   coding *Heishanosaurus* into the matrix led to a re-assessment of two character state

641   codings for *Coeruleodraco*: character 87 (dorsal vertebral centrum) from 0

642   (subcylindrical) to ? (cylindrical or subcylindrical); and character 96 (caudal centrum)

643   from 1 (amphiplatyan) to ? (amphiplatyan or amphicoelous). These changes, and the

644   combination of character states found in *Heishanosaurus* moved *Coeruleodraco*

645   stemward. A strict consensus of 31 most parsimonious trees (Fig. 14A) placed

646   *Heishanosaurus*, in an unresolved polytomy with *Coeruleodraco*, the

647   Neochoristodera (strongly supported), and a 'parapsid' non-neochoristodere clade

648   made up of those taxa in which the lower temporal fenestra is closed

649   (*Hyphalosaurus*, *Monjurosuchus*, *Philydrosaurus*, *Khurendukhosaurus*,

650   *Lazarussuchus*), or likely to be closed (*Shokawa*) based on its phylogenetic position

651   as sister to *Hyphalosaurus*. This clade has been recovered consistently in recent

652   analyses (e.g. Matsumoto *et al*. 2019a, b), although it is not supported in the

653   Bootstrap tree (Fig. 14B) and only weakly by Bremer Support (Fig. 14A).

654

655   [insert Fig.14 here]

656

657   **Discussion**

658   Based on comparisons of tibial length in *Heishanosaurus* and *Coeruleodraco,* we

659   estimated that the individuals of *Heishanosaurus* were around 160 mm in snout-

660   pelvis length and perhaps 300 mm in total length, which is similar in size to

661   *Cteniogenys* (Evans, 1991). This is relatively small for a Cretaceous choristodere;

662   e.g. long-necked *Hyphalosaurus* (IVPP-V 17705), total length 1036 mm; *Shokawa*,

663   total length ~400 mm (Evans and Manabe, 1999); short-necked *Monjurosuchus,*

664   snout-vent length up to 300 mm (Gao et al., 2000); *Philydrosaurus,* total length up to

665   300 mm (personal observation, RM). Although small size and low tooth count could

666   be juvenile features, the fused neurocentral vertebral sutures suggest the individuals

667   were close to adult size.

668   These new specimens are significant. They not only represent a new genus

669   and species for the latter part of the Early Cretaceous, but also a distinct morphotype

670   for this period. Although distinct in its details, the skull of *Heishanosaurus* most

671   closely resembles that of the Jurassic *Cteniogenys* and *Coeruleodraco*, which

672   represent the likely ancestral choristoderan skull morphology (e.g. open lower

673   temporal fenestra, short mandibular symphysis). The most complete material of

674   *Cteniogenys* comes from the Jurassic of Euramerica (Evans 1990), but

675   *Cteniogenys*-like vertebrae have been recorded from the Middle Jurassic of

676   Kyrgyzstan (Averianov *et al*. 2006), Western Siberia (Averianov *et al*. 2016),

677   European Russia (Pashchenko *et al*. 2018) and eastern Morocco (Haddoumi *et al*.

678   2016), and putative choristodere dental remains were reported from the Late

679   Jurassic (Oxfordian) of Xinjiang (Richter *et al*. 2010). The recovery of the complete

680   skeleton of *Coeruleodraco jurassicus* (Matsumoto *et al*. 2019b) confirmed the

681   presence of relatively conservative small choristoderes in eastern Asia during the

682   Jurassic. The revised position for *Coeruleodraco* recovered in our phylogenetic

683   analysis (Fig. 14A), lying stemward of both Neochoristodera and a clade of non-

684   neochoristoderes with closed lower temporal fenestrae, is more consistent with both

685   its anatomy and its stratigraphic position (Callovian-Oxfordian).

686   The grouping of *Lazarussuchus* (Palaeocene-Miocene, Europe),

687   *Hyphalosaurus*, *Monjurosuchus*, and *Philydrosaurus* (Early Cretaceous, China),

688   *Shokawa* (Early Cretaceous, Japan), and *Khurendukosaurus* (Early Cretaceous,

689   Mongolia and Transbaikalian Russia) has been recovered in several recent

690   phylogenetic analyses, but the clade is always weakly supported (e.g. Matsumoto *et*

691   *al.* 2013, 2019a, b, this paper). All are brevirostrine with a lower temporal fenestra

692   closed by expansion of the postorbital, squamosal, jugal and quadratojugal. All, with

693   the exception of the more recent *Lazarussuchus*, are from Asia. To date, we have

694   refrained from erecting a formal name for this specialized clade of small

695   choristoderes, as the support values are consistently low. However, to distinguish

696   this grouping of derived taxa from more conservative non-neochoristoderes

697   (*Cteniogenys*, *Coeruleodraco*, *Heishanosaurus*) , we suggest the informal name

698   'allochoristoderes' with the potential of formalizing this name should future material

699   and/or analysis provide more robust support. The prefix allo (Greek) means other or

700   different.

701   Until now, all Cretaceous choristoderes recovered from Asia have been either

702   longirostrine neochoristoderes (*Tchoiria* and *Ikechosaurus* from Mongolia and China)

703   or brevirostrine 'allochoristoderes' with a closed lower temporal fenestra. The latter

704   appear too specialized to provide an ancestral stock for Neochoristodera. The

705   recovery of a small choristodere, albeit fragmentary, with an open lower temporal

706   fenestra and a short jaw symphysis, implies the survival of a lineage of small,

707   relatively conservative choristoderes similar to *Cteniogenys* in Asia from the Jurassic

708   through to the latter part of the Early Cretaceous (Aptian/Albian). To date,

709   *Heishanosaurus pygmaeus* is the geologically youngest choristodere from China.

710   The coal-bearing deposit of Shahai Formation is considered to represent a

711   lowland swamp environment, very rich in accumulated vegetation (Deng *et al.* 2012).

712   Although most of the taxa recovered are terrestrial (dinosaurs, lizards, mammals),

713   fish remains have also been recovered (Jin 1996) as well as freshwater invertebrates

714   (Jiang *et al.* 2010). In fact, the environment was probably not unlike that of the

715 swampier facies at Shiramine (Tetori Group, Japan) which has also yielded

716 choristoderes (Evans & Manabe 1999; Matsumoto *et al.* 2007; Matsumoto *et al.*

717 2015).

718 Taken in combination with *Coeruleodraco jurassicus* from the Jurassic of

719 Qinglong, the *Heishanosaurus* specimens from the Aptian-Albian add to the

720 remarkable diversity of choristoderes in the Late Jurassic-Early Cretaceous of Asia

721 (China, Japan, Mongolia). Although Choristodera may have originated elsewhere,

722 the waterways of Asia seem to have provided an ideal habitat in which the group

723 thrived and diversified.

724

Acknowledgements

725 **Acknowledgements**

726

737

738

References

739 **References**

740   **Amiot, R, Kusuhashi, N, Xu, X, Wang, Y.** 2010. Isolated dinosaur teeth from the

741   Lower Cretaceous Shahai and Fuxin formations of northeastern China. *Journal of*

742   *Asian Earth Sciences*, **39**, 347–358.

743   **Averianov A. O., Martin, T., Evans, S. E. & Bakirov, A. A.** 2006. First Jurassic

744   Choristodera from Asia. *Naturwissenschaften*, **93**, 46–50.

745   **Averianov A. O., Martin, T., Skutschas, P., Danilov, I., Schultz, J., Schellhorn,**

746   **R., Obraztsova, E., Lopatin, A., Sytchevskaya, E., Kuzmin, I., Krasnolutskii, S. &**

747   **Ivantsov, S.** 2016. Middle Jurassic vertebrate assemblage of Berezovsk coal mine

748   in western Siberia (Russia). *Global Geology*, **19**, 187–204.

749   **Brinkman, D. B., Dong, Z. M.** 1993. New material of *Ikechosaurus sunailinae*

750   (Reptilia: Choristodera) from the Early Cretaceous Langhongdong Formation, Ordos

751   Basin, Inner Mongolia, and the interrelationships of the genus. *Canadian Journal of*

752   *Earth Sciences*, **30**, 2153–2162.

753   **Brown, B.** 1905. The osteology of *Champsosaurus* Cope. *American Museum of*

754   *Natural History Memoirs*, **9**, 1–26.

755   **Chen, F., Meng, X., Ren, S. & Wu, C.** 1988. *The Early Cretaceous flora and the*

756   *coal-bearing strata from the Fuxin and Tiefa Basins of Liaoning*. Geological

757   Publishing House, Beijing, 180 pp.

758   **Cope, E. D.** 1876. On some extinct reptiles and Batrachia from the Judith River and

759   Fox Hills beds Montana. *Proceedings of the Academy of Natural Sciences of*

760   *Philadelphia*, **28**, 340–359.

761   **Deng, S., Lu, Y., Fan, R., Li, X., Fang, L. & Liu, L.** 2012. Cretaceous floras and

762   biostratigraphy of China. *Journal of Stratigraphy*, **36**, 241–265.

763 **Efimov, M. B.** 1975. [Champsosaurs from the Lower Cretaceous of Mongolia]. *Trudy*

764 *Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii*, **2**, 84**–**93. [in

765 Russian].

766 **Endo, R.** 1940. A new genus of Thecodontia from the *Lycoptera* beds in

767 Manchoukou. *Bulletin of the National Central Museum of Manchoukuo*, **2**, 1–14.

768 **Endo, R. & Shikama, T.** 1942. Mesozoic reptilian fauna in the Jehol mountain land,

769 Manchoukuo. *Bulletin of the National Central Museum of Manchoukuo*, **3**, 1–20.

770 **Erickson, B. R.** 1972. The lepidosaurian reptile *Champsosaurus* in North America.

771 *Monograph, Science Museum of Minnesota (Paleontology)*, **1**, 1–91.

772 **Erickson, B. R.** 1987. *Simoedosaurus dakotensis*, new species, a diapsid reptile

773 (Archosauromorpha; Choristodera) from the Paleocene of North America. *Journal of*

774 *Vertebrate Paleontology*, **7**, 237–251.

775 **Evans, S. E.** 1990. The skull of *Cteniogenys*, a choristodere (Reptilia,

776 Archosauromorpha) from the Middle Jurassic of Oxfordshire. *Zoological Journal of*

777 *the Linnean Society*, **99**, 205–237.

778 **Evans, S. E.** 1991. The postcranial skeleton of the choristodere *Cteniogenys*

779 (Reptilia: Diapsoda) from the Middle Jurassic of England. *Geogios*, **24**, 187–199.

780 **Evans, S. E. & Hecht, M. K.** 1993. A history of an extinct reptilian clade, the

781 Choristodera: longevity, Lazarus-taxa, and the fossil record. *Evolutionary Biology*,

782 **27**, 323–338.

783 **Evans, S. E. & Klembara, J.** 2005. A choristoderan reptile (Reptilia; Diapsida) from

784 the Lower Miocene of northwest Bohemia (Czech Republic). *Journal of Vertebrate*

785 *Paleontology*, **25**, 168–181.

786 **Evans, S. E. & Manabe, M.** 1999. A choristoderan reptile from the Lower

787 Cretaceous of Japan. *Special Papers in Paleontology*, **60**, 101–119.

788   **Gao, K. & Fox, R. C.** 2005. A new choristodere (Reptilia: Diapsida) from the Lower

789   Cretaceous of western Liaoning Province, China, and phylogenetic relationships of

790   Monjurosuchidae. *Zoological Journal of the Linnean Society*, **145**, 427**–**444.

791   **Gao, K. & Li, Q.** 2007. Osteology of *Monjurosuchus splendens* (Diapsida,

792   Choristodera) based on a new specimen from the Lower Cretaceous of western

793   Liaoning, China. *Cretaceous Research*, **28**, 261–271.

794   **Gao, K. & Ksepka, D.** 2008. Osteology and taxonomic revision of *Hyphalosaurus*

795   (Diapsida: Choristodera) from the Lower Cretaceous of Liaoning, China. *Journal of*

796   *Anatomy*, **212**, 747–768.

797   **Gao, K., Tang, Z. & Wang, X.** 1999. A long-necked diapsid reptile from the Upper

798   Jurassic/Lower Cretaceous of Liaoning Province, northeastern China. *Vertebrata*

799   *PalAsiatica*, **37**, 1–8.

800   **Gao, K., Ksepka, D., Hou, L., Ye, D. & Hu, D.** 2007. Cranial morphology of an Early

801   Cretaceous monjurosuchid (Reptilia: Diapsida) from Liaoning Province of China and

802   evolution of the choristoderan palate. *Historical Biology*, **19**, 215–224.

803   **Gao, K., Evans, S. E., Ji, Q., Norell, M. & Ji, S.** 2000. Exceptional fossil material of

804   a semi-aquatic reptile from China: the resolution of an enigma. *Journal of Vertebrate*

805   *Paleontology*, **20**, 417**–**421.

806   **Gao, K. Q., Zhou, C. F., Hou, L. H., & Fox, R. C.** 2013. Osteology and ontogeny of

807   Early Cretaceous *Philydrosaurus* (Diapsida; Choristodera) based on new specimens

808   from Liaoning province, China. *Cretaceous Research*, **45,** 91–102.

809   **Gao, C. L., Lu, J. C., Liu, J. Y. & Ji, Q.** 2005. New Choristodera from the Lower

810   Cretaceous Jiufotang Formation in Chaoyang area, Liaoning China (in Chinese).

811   *Geological Review*, **51**, 694–697.

812   **Haddoumi, H., Allain, R., Meslouh, S., Metais, G., Monbaron, M., Pons, D., Rage,**

813 **J-C., Vullo, R., Zouhri, S., & Gheerbrant.** 2016. First continental flora and fauna

814 including mammals from the Middle Jurassic of Africa. *Gondwana Research*, **29**,

815 290–319.

816 **He, H. Y., Wang, X., Zhou, Z. H., Wang, F., Boven, A., Shi, G. H., & Zhu, R. X.**

817 2004. Timing of the Jiufotang Formation (Jehol Group) in Liaoning, northeastern

818 China, and its implication. *Geophysical Research Letter* **31**, L12605.

819 Doi:10.1029/2004GL019790

820 **Hecht, M. K.** 1992. A new choristodere (Reptilia, Diapsida) from the Oligocene of

821 France: an example of the Lazarus effect. *Geobios*, **25**, 115–131.

822 **Hu, Y., Fox, R.C., Wang, Y., & Li, C.** 2005. A new spalacotheriid symmetrodont

823 from the Early Cretaceous of northeastern China. *American Museum Novitates*,

824 **3475**, 1–20.

825 **Huang, D., Cai, C., Xu, X., Wang, X., Su, Y., Liao, H., Jiang, J., & Sha, J**. 2015.

826 Daohugou fossil beds and Daohugou Biota. Pp. 37–70 in D. Huang (ed.) *The*

827 *Daohugou Biota*. Shanghai Scientific & Technical Publishers, Shanghai.

828 **Jiang, B., Yao, X., Niu, Y., Rao, X., & Li, Q**. 2010. *Introduction to the Jurassic and*

829 *cretaceous Systems in Western Liaoning, NE China*. University of Science and

830 Technology of China Press, Hefei, China, 87pp.

831 **Jin, F.** 1996. New advances in the late Mesozoic stratigraphic research of western

832 Liaoning, China. *Vertebrata PalAsiatica*, **34**, 102–122.

833 **Kusuhashi, N., Hu, Y., Wang, Y., Hirasawa, S., & Matsuoka, H.** 2009a. New

834 triconodontids (Mammalia) from the Lower Cretaceous Shahai and Fuxin formations,

835 northeastern China. *Geobios*, **42**, 765–781.

836 **Kusuhashi, N., Hu, Y., Wang, Y., Setoguchi, T., & Matsuoka, H.** 2009b. Two

837 eobaatarid (Multituberculata; Mammalia) genera from the Lower Cretaceous Shahai

838 and Fuxin Formations, Northeastern China. *Journal of Vertebrate Paleontology*, **29**,

839 1264–1288.

840 **Kusuhashi, N., Hu, Y., Wang, Y., Setoguchi, T., & Matsuoka, H.** 2010. New

841 multituberculate mammals from the Lower Cretaceous (Shahai and Fuxin

842 Formations), northeastern China. *Journal of Vertebrate Paleontology*, **30**, 1501–

843 1514.

844 **Kusuhashi, N., Wang, Y-Q., Li, C-K., & Jin, X.** 2016. Two new species of

845 *Gobiconodon* (Mammalia, Eutriconodonta, Gobiconodontidae) from the Lower

846 Cretaceous Shahai and Fuxin formations, northeastern China. *Historical Biology*, **28**,

847 14–26.

848 **Ksepka, T. D., Gao, K. & Norell, A. M.** 2005. A new choristodere from the

849 Cretaceous of Mongolia. *American Museum Novitates*, **3648**, 1–22.

850 **Li, C., Setoguchi, T., Wang, Y., Hu, Y., & Chang, Z.** 2005. The first record of

851 "Eupantotherian" (Theria, Mammalia) from the late Early Cretaceous of western

852 Liaoning, China. *Vertebrata PalAsiatica*, **43**, 245–255.

853 **Linnaeus, C.** 1758. *Systema Naturae*. L. Salvii, Holmiae, 824 pp.

854 **Liu, J.** 2004. A nearly complete skeleton of *Ikechosaurus pijiagouensis* sp. nov.

855 (Reptilia: Choristodera) from the Jiufotang Formation (Lower Cretaceous) of

856 Liaoning, China. *Vertebrata PalAsiatica*, **42**, 120–129.

857 **Matsumoto, R. & Evans, S. E.** 2010. Choristoderes and the freshwater

858 assemblages of Laurasia. *Iberian Journal of Geology*, **36**, 253–274.

859 **Matsumoto, R., Evans, S. E. & Manabe, M.** 2007. The choristoderan reptile

860 *Monjurosuchus* from the Early Cretaceous of Japan. *Acta Palaeontologica Polonica*,

861 **52**, 329–350.

862   **Matsumoto, R., Buffetaut, E., Escuillie, F., Hervet, S. & Evans, S. E**. 2013. New

863   material of the choristodere *Lazarussuchus* (Diapsida, Choristodera) from the

864   Paleocene of France. *Journal of Vertebrate Paleontology*, **33**, 319–339.

865   **Matsumoto, R., Manabe, M., & Evans, S. E.** 2015. The first record of a long-

866   snouted choristodere (Reptilia, Diapsida) from the Early Cretaceous of Ishikawa

867   Prefecture, Japan. *Historical Biology*, **27**, 583–594.

868   **Matsumoto, R., Suzuki, S., Tsogtbaatar, K. & Evans, S. E.** 2009. New material of

869   the enigmatic reptile *Khurendukhosaurus* (Diapsida: Choristodera) from Mongolia.

870   *Naturwissenschaften*, **96**, 233–242.

871   **Matsumoto, R., Tsogtbaatar, K., Ishigaki, S., Tsogtbaatar, C., Enkhtaivan, Z., &**

872   **Evans, S. E.** 2019a. Revealing body proportions of the enigmatic choristodere reptile

873   *Khurendukhosaurus* from Mongolia. *Acta Palaeontologica Polonica,* **64**, 363–377.

874   **Matsumoto, R., Dong, L., Wang, Y., & Evans, S. E.** 2019b. The first record of a

875   nearly complete choristodere (Reptilia: Diapsida) from the Upper Jurassic of Hebei

876   Province, Peoples' Republic of China. *Journal of Systematic Palaeontology*, **17**,

877   1031–1048.

878   **Pashchenko, D. I., Kuzmin, I. T., Sennikov, A. G., Skutschas, P. P. & Efimov, M**

879   **B.** 2018. On the finding of neosuchians (Neosuchia, Crocodyliformes) in the Middle

880   Jurassic (Bathonian) deposits of the Moscow Region. *Paleontological Journal*, 52,

881   77–90.

882   **Richter, A., Wings, O., Pfretzschner, H-U., & Martin, T.** 2010. Late Jurassic

883   Squamata and possible Choristodera from the Junggar basin, Xinjiang, Northwest

884   China. *Palaeobiodiversity and Palaeoenvironments*, **90**, 275–282.

885 **Sigogneau-Russell, D.** 1981. Présence d'un nouveau Champsosauridé dans le

886 Cretace supérieur de Chine. *Comptes Rendus Académie des Sciences, Paris*, **292**,

887 1–4.

888 **Sigogneau-Russell, D. & Efimov, M.** 1984. Un Choristodera (Eosuchia?) insolité du

889 Crétacé inferieur de Mongolie. *Paläontologische Zeitschrift*, **58**, 279–294.

890 **Sigogneau-Russell, D. & Russell, D. E.** 1978. Etude osteologique du reptile

891 *Simoedosaurus* (Choristodera). *Annales de Paléontologie (Vertébrés)*, **64**, 1–84.

892 **Skutschas, P. P.** 2008. A choristoderan reptile from the Lower Cretaceous of

893 Transbaikalia. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **247**,

894 63–78.

895 **Skutschas, P. P. & Vitenko, D. D.** 2017. Early Cretaceous choristoderes (Diapsida,

896 Choristodera) from Siberia, Russia. *Cretaceous Research*, **77**, 79–92.

897 **Wang, G.** 1989. Jurassic and Cretaceous of Fuxin Basin. *Journal of Stratigraphy*, **13**,

898 98–107.

899 **Xu, K., Li, Y., Li, R., & Wang, R.** 1998. Discovery of the dinosaur fossil in Heishan,

900 Lioaning and its stratigraphical significance. *Journal of Stratigraphy*, **22**, 227−231.

901 **Zhang, W., & Gao, K.** 2013. Early Cretaceous evolution of choristoderes in western

902 Liaoning based on geographic and stratigraphic evidence. *Journal of*

903 *Palaeogeography*, **16**, 205–216.

904 **Zhao, H., & Zhao, Z.** 1999. A new form of elongatoolithid dinosaur eggs from the

905 Lower Cretaceous Shahai Formation of Heishan, Liaoning Province. *Vertebrata*

906 *PalAsiatica*, **37**, 278–284.

907

908

909

910

Figure Captions

Figure 1. Location and horizon of *Heishanosaurus pygmaeus* sp. nov. Map showing

the location of the new specimen and other choristoderes from this region. 1,

Badaohao: *Heishanosaurus pygmaeus* gen. et sp. nov. (IVPP V 25322, IVPP V

25323, IVPP V 25324, this paper); 2, **Pijiagou**: *Ikechosaurus pijiagouensis*

(Holotype, IVPP V 13283, Liu 2004); 3, **Shangheshou**: *Philydrosaurus proseilus*

(Holotype, PKUP V2001, Gao & Fox 2005);4, **Yuanjiawa**: *Philydrosaurus proseilus*

(LPMC 021, Gao *et al.* 2007); **5, Luojiagou**: *Hyphalosaurus* sp. (Zhang *et al.* 2012);

6, **Niuyingzi**: *Monjurosuchus splendens* (Neotype, GMV 2167, Gao *et al.* 2000).

There are three more specimens of *Monjurosuchus* (GMV 2135, 2162, 2166) whose

localities Gao *et al.* (2000) did not record. Based on the rock matrix around these

specimens, they probably came from the neotype locality; 7, **Dawangzhangzi**:

Hyphalosaurus lingyuanensis (Fanzhangzi, IVPP V 11705, Gao *et al.* 1999; PKUP

V1052, GMC juvenile, Gao & Ksepka 2008, see note below); 8, **Danangou**:

Monjurosuchus splendens (Holotype, CNMM 3671, Endo 1940; IVPP V 3673, Endo

& Shikama 1942); 9, **Jingangshan**: *Monjurosuchus splendens* (IVPP V 13761,

Wang *et al.* 2005) (Gao & Fox [2005] thought Caocishan and Jingangshan were the

same locality, see text); 10, **Baitaigou**: *Hyphalosaurus baitaigouensis* (Holotype,

CAGS-IG-03-7-02, Ji *et al.* 2004); 11, **Toutai**: *Monjurosuchus splendens* (BMNHC

V073, Gao *et al.* 2007); 12, **Nanshimen**: *Coeruleodraco jurassicus* (IVPP V 23318,

Matsumoto *et al.*, 2018). Horizon yielding the type and referred specimens of

Heishanosaurus pygmaeus, with the stratigraphic distribution of Chinese

choristoderes found so far. The stratigraphy is modified from Huang *et al.* 2015 and

Wang 1989.

935

936   Figure 2. *Heishanosaurus pygmaeus*, gen. et sp. nov. Specimens IVPP V 25322,

937   IVPP V 25323, and IVPP V 25324 (Holotype). A–B, IVPP V 25322: A. Digital image

938   of the specimen; B. CT model showing the skeletal elements within the block; C–D.

939   IVPP V 25323, C. Digital image of the specimen; D. CT model showing the skeletal

940   elements within the block; E–F. IVPP V 25324 (Holotype), E. Digital image of the

941   specimen; F. CT model showing the skeletal elements within the block. G. left

942   dentary on the surface of IVPP V 25322; H. right jugal on the surface of IVPP V

943   25324 (Holotype). G and H are not to the scale.

944

945   Figure 3. Skull and mandible of *Heishanosaurus pygmaeus*, gen. et sp. nov. A,

946   reconstruction of *Heishanosaurus pygmaeus* skull in dorsal view; B, reconstruction of

947   the left lower jaw in medial view; C, three-dimensional reconstruction of the

948   postorbital region in lateral view.

949

950   Figure 4. Skull and mandible of *Coeruleodraco jurassicus* IVPP V 23318. A, three-

951   dimensional reconstruction of the postorbital region in lateral view. B–C, left lower

952   jaw in medial (B) and in lateral (C) views. Abbreviations: Ang, angular; Ar, articular;

953   Co, coronoid; D, dentary; J, jugal; Pa, parietal; Pf, postfrontal; Po, postorbital; Pra,

954   prearticular; Qj, quadratojugal; Sq, squamosal; Sur, surangular.

955

956   Figure 5. *Heishanosaurus pygmaeus*, gen. et sp. nov. A–B, left parietal (IVPP V

957   25324) in dorsal (A), and ventral (B) views. C–D, left squamosal (IVPP V 25324) in

958   lateral (C) and medial (D) views. E–H, supplementary left squamosal (IVPP V 25322)

959   in lateral (E), medial (F), anterior (G), and posterior (H) views. Abbreviations: fr,

960 frontal facet; ne, neomorph facet; pa, parietal facet; po, postorbital facet; q, quadrate

961 facet; qj, quadratojugal facet; soc, supraoccipital facet; sq, squamosal facet.

962

963 Figure 6. *Heishanosaurus pygmaeus*, gen. et sp. nov. A–B, F–I, J–N, left jugal,

964 quadratojugal, and postorbital (IVPP V 25324). C–E, supplementary left jugal (IVPP

965 V 25322). A–B, left jugal in lateral (A) and medial (B) views; left jugal in lateral (C),

966 medial (D), and ventral (E) views. F–I, left quadratojugal (IVPP V 25324) in lateral

967 (F), dorsal (G), posterior (H), and medial (I) views. J–N, left postorbital in lateral (J),

968 dorsal (K), anterior (L), ventral (M), and medial (N) views. Abbreviations: ecpt,

969 ectopterygoid facet; fr, frontal facet; j, jugal facet; la, lachrymal facet; mx, maxilla

970 facet; pa, parietal facet; pf, postfrontal facet; po, postorbital facet; q, quadrate facet;

971 qj, quadratojugal facet; sq, squamosal facet.

972

973 Figure 7. *Heishanosaurus pygmaeus*, gen. et sp. nov. IVPP V 25322. A–C, right

974 quadrate, in anterior (A), posterior (B), and lateral (C) views. D–F, left quadrate, in

975 anterior (D), posterior (E), and ventral (F) views. G–J, right premaxilla, in dorsal (G),

976 ventral (H), lateral (I), and medial (J) views. K–L, right palatine, in ventral (K) and

977 dorsal (L) views. M–O, right ectopterygoid, in dorsal (M), ventral (N) and lateral (O)

978 views. Abbreviations: ch, choana margin; j, jugal facet; mid, midline facet; mx,

979 maxilla facet; ne, neomorph facet; opi, opisthotic facet; pt, pterygoid facet; qj,

980 quadratojugal facet; sq, squamosal facet; t p, tooth position; v, vomer facet.

981

982 Figure 8. *Heishanosaurus pygmaeus*, gen. et sp. nov. IVPP V 25322. A–E, left

983 prefrontal, in dorsal (A), ventral (B), anterior (C), medial (D), and lateral (E) views. F–

984 J, left lachrymal, in dorsolateral (F), ventromedial (G), ventral (H), anterior (I), and

985 posterior (J) views. Abbreviations: fo, foramen; fr, frontal facet; j, jugal facet; la,

986 lachrymal facet; la f, lachrymal foramen; mid, midline facet; mx, maxilla facet; pal,

987 palatine facet; prf, prefrontal facet.

988

989 Figure 9. *Heishanosaurus pygmaeus*, gen. et sp. nov. IVPP V 25322. A–D, right

990 dentary, in lateral (A), medial (B), dorsal (C) and ventral (D) views. E, left dentary in

991 lateral view. Abbreviations: co, coronoid facet; ne f, neurovascular foramina; sur,

992 surangular facet; sym, symphysis.

993

994 Figure 10. *Heishanosaurus pygmaeus*, gen. et sp. nov. IVPP V 25322. A–B, right

995 surangular in lateral (A), and medial (B) views. C–E, left surangular in lateral (C),

996 medial (D), and dorsal (E) views. Abbreviations: ang, angular facet; ar, articular

997 facet; co, coronoid facet; d, dentary facet.

998

999 Figure 11. *Heishanosaurus pygmaeus*, gen. et sp. nov. A–D, left coronoid (IVPP V

1000 25324) in lateral (A), medial (B), dorsal (C), and ventral (D) views. E–G, right

1001 prearticular (IVPP V 25323), in medial (E), lateral (F), and ventral (G) views; H, right

1002 prearticular (IVPP V 25324) in medial view. Abbreviations: add f, adductor fossa;

1003 ang, angular facet; ar, articular facet; d, dentary facet; sur, surangular facet.

1004

1005 Figure 12. *Heishanosaurus pygmaeus*, gen. et sp. nov. A–E, cervical vertebra (IVPP

1006 V 25323), in anterior (A), lateral (B), posterior (C), dorsal (D), and ventral (E) views.

1007 F–J, dorsal vertebra 1 (IVPP V 25322), in anterior (F), lateral (G), posterior (H),

1008 dorsal (I), and ventral (J) views. K–N, dorsal vertebra 2 (IVPP V 25323), in anterior

1009 (K), lateral (L), posterior (M) and ventral (N) views. O–R, caudal vertebra (IVPP V

1010   25323), in anterior (O), lateral (P), posterior (Q), and ventral (R) views. S–T, caudal

1011   vertebra (IVPP V 25323), in posterior (S), and ventral (T) views. Abbreviations: gr,

1012   groove; sph, synapophysis.

1013

1014   Figure 13. *Heishanosaurus pygmaeus*, gen. et sp. nov. A–B, left dorsal rib (IVPP

1015   V25324) in anterior (A), and posterior (B) views. C, gastral rib (IVPP V 25323) in

1016   anterior view. D–E, left clavicle (IVPP V 25323) in ventral (D) and dorsal (E) views.

1017   F–H, ungual phalanx (IVPP V 25323) in lateral (F), and posterior (G) views. H,

1018   phalanx (IVPP V 25323) in dorsal view. I–M, right tibia (IVPP V 25323) in medial (I),

1019   anterior (J), proximal (K), lateral (L), and distal (M) views. Abbreviations: ri, ridge;

1020   incl, interclavicle facet.

1021

1022   Figure 14. Phylogenetic relationships of *Heishanosaurus pygmaeus*, gen. et sp. nov.

1023   within Choristodera. A, strict consensus of 31 most parsimonious trees (MPTs)

1024   obtained by TNT (tree length = 335). Numbers in brackets indicate Bremer branch

1025   supports. B, bootstrap consensus tree with bootstrap values, as examined by a

1026   10,000 replicate resampling analysis.

1027

1028

1029   Supplementary Information

1030   Sup-Data. Data Matrix for the phylogenetic analyses.

1031

1032   Sup-Fig. 1. Skull of *Coeruleodraco jurassicus* (IVPP V 23318). A, three-dimensional

1033   reconstruction of the skull in dorsal (A), and lateral (B) views. Abbreviations: Fr,

1034   frontal; J, jugal; La, lachrymal; Mx, maxilla; Pa, parietal; Pf, postfrontal; Pmx,

1035 premaxilla; Po, postorbital; Prf, prefrontal; Q, quadrate; Qj, quadratojugal; Sq,

1036 squamosal.

1037

1038 Sup-Fig. 2. *Coeruleodraco jurassicus* (IVPP V 23318). A–B, left parietal in dorsal (A)

1039 and ventral (B) views. C–D, left squamosal in lateral (C) and medial (D) views.

1040 Abbreviations: fr, frontal facet; ne, neomorph facet; pa, parietal facet; pf, postfrontal

1041 facet; po, postorbital facet; q, quadrate facet; qj, quadratojugal facet; soc,

1042 supraoccipital facet.

1043

1044 Sup-Fig. 3. *Coeruleodraco jurassicus* (IVPP V 23318). A–C, left jugal in lateral (A),

1045 medial (B), and ventral (C) views. D–F, left postfrontal in dorsal (D), ventral (E), and

1046 anterior (F) views. G–J, left quadratojugal in lateral (G), dorsal (H), posterior (I), and

1047 medial (J) views. Left postorbital in lateral (K), dorsal (L), anterior (M), ventral (N),

1048 and medial (O) views. Abbreviations: ecpt, ectopterygoid facet; fr, frontal facet; j,

1049 jugal facet; mx, maxilla facet; ne, neomorph facet; pa, parietal facet; pf, postfrontal

1050 facet; po, postorbital facet; q, quadrate facet; qj, quadratojugal facet; sq, squamosal

1051 facet.

1052

1053 Sup-Fig. 4. *Coeruleodraco jurassicus* (IVPP V 23318). A–C, left quadrate, in anterior

1054 (A), posterior (B), lateral (C), and ventral (D) views. E–J, left premaxilla, in dorsal (E),

1055 lateral (F), anterior (G), ventral (H), medial (I), and posterior (J) views. Abbreviations:

1056 mx, maxilla facet; na, nasal facet; opi, opisthotic facet; pt, pterygoid facet; qj,

1057 quadratojugal facet; v, vomer facet.

1058

1059   Sup-Fig. 5. *Coeruleodraco jurassicus* (IVPP V 23318). A–D, left prefrontal, in dorsal

1060   (A), ventral (B), lateral (C), and medial (D) views. I–L, left maxilla in dorsal (I), lateral

1061   (J), medial (K), and ventral (L) views. Abbreviations: fr, frontal facet; j, jugal facet; la,

1062   lachrymal facet; la f, lachrymal foramen; mid, midline facet; mx, maxilla facet; na,

1063   nasal facet; pal, palatine facet; pmx, premaxilla facet; prf, prefrontal facet; v, vomer

1064   facet.