A new basal ichthyosauromorph from the Lower Triassic (Olenekian) of Zhebao, Guangxi Province, South China

Jicheng Ren [1], Haishui Jiang [2], Kunpeng Xiang [3], Corwin Sullivan [4, 5], Yongzhong He [3], Long Cheng [6], Fenglu Han
Corresp. [2]

[1] School of Li Siguang, China University of Geosciences (Wuhan), Wuhan, Hubei Province, China

[2] School of Earth Sciences, China University of Geosciences (Wuhan), Wuhan, Hubei Province, China

[3] Guizhou Geological Survey, Guiyang, Guizhou Province, China

[4] Department of Biological Sciences, University of Alberta, Edmonton, Canada

[5] Philip J. Currie Dinosaur Museum, Wembley, Canada

[6] Wuhan Centre of China Geological Survey, Wuhan 430223, China

Corresponding Author: Fenglu Han
Email address: hanfl@cug.edu.cn

Here we describe a newly discovered basal ichthyosauromorph from the Lower Triassic of South China, *Baisesaurus robustus* gen. et sp. nov. The only known specimen of this new species was collected from the Lower Triassic (Olenekian) Luolou Formation in the Zhebao region of Baise City, on the northwest margin of the Nanpanjiang Basin, and comprises a partial skeleton including the ribs, the gastralia, a limb element, twelve centra, and seven neural arches. Comparisons to a wide variety of Early Triassic marine reptiles show *Baisesaurus robustus* to be a basal ichthyosauromorph based on the following features: neural arches lack transverse processes; dorsal ribs are slender, and not pachyostotic even proximally; and median gastral elements have long, sharp anterior processes. The limb element is long and robust, and is most likely to be a radius. *Baisesaurus robustus* is large (estimated length more than 3 m) relative to early ichthyosauromorphs previously discovered in China, and shares noteworthy morphological similarities with *Utatsusaurus hataii*, particularly with regard to body size and the morphology of the probable radius. *Baisesaurus robustus* also represents the first record of an Early Triassic ichthyosauromorph from Guangxi Province, extending the known geographic distribution of ichthyosauromorphs in South China.

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[1]School of Li Siguang, China University of Geosciences, Wuhan, Hubei Province, China
[2]School of Earth Sciences, China University of Geosciences, Wuhan, Hubei Province, China
[3]Guizhou Geological Survey, Guiyang, Guizhou Province, China
[4]Department of Biological Sciences, University of Alberta, Edmonton, Canada
[5]Philip J. Currie Dinosaur Museum, Wembley, Canada
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*Corresponding Author:
Fenglu Han
Email address: hanfl@cug.edu.cn

Abstract

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42 China, *Baisesaurus robustus* gen. et sp. nov. The only known specimen of this new species was
43 collected from the Lower Triassic (Olenekian) Luolou Formation in the Zhebao region of Baise
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55 ichthyosauromorphs in South China.

Introduction

56

57 Mesozoic marine reptiles first appeared in the Early Triassic, primarily in the form of three main
58 clades: the sauropterygians, the thalattosaurs and the ichthyosauromorphs (Scheyer et al. 2014).
59 Early Triassic sauropterygians include *Corosaurus* from North America (Storrs 1991; Rieppel
60 1998a), *Cymatosaurus* from Europe (Rieppel 2000), and multiple genera from southern China,
61 namely *Kwangsisaurus* (Young 1959; Rieppel 1998b) from Guangxi Province, *Hanosaurus*
62 (Young & Dong 1972a; Rieppel 1998c) and *Lariosaurus* (Li & Liu 2020) from Hubei Province,
63 and *Majiashanosaurus* (Jiang et al. 2014) from Anhui Province. These taxa were coast-dwelling,
64 slender-bodied animals that would have superficially resembled swimming lizards when they
65 were in the water, and were not greatly specialized for marine life. Thalattosaurs are a less
66 diverse group of small to medium-sized secondary marine reptiles (Scheyer et al. 2014). They
67 were modestly adapted to an aquatic lifestyle, and have characteristic anatomical features
68 including a long snout and a small, or even absent, upper temporal fenestra (Müller 2005).
69 Thalattosaurs are mainly known from the Middle and Upper Triassic of Europe (Müller et al.
70 2005), North America (Nicholls 1999) and China (Jiang et al. 2004). A few specimens of
71 *Thalattosaurus*, *Paralonectes* and *Agkistrognathus* have been reported from the Lower to Middle
72 Triassic Sulphur Mountain Formation in Canada, but their exact age is still uncertain (Nicholls &
73 Brinkman 1993b; Scheyer et al. 2014).
74

75 Ichthyosauromorpha (Motani et al. 2015a) is an expansive group that includes the two clades
76 Hupehsuchia (Young & Dong 1972b) and Ichthyosauriformes. Hupehsuchia is a distinctive clade
77 of Early Triassic marine reptiles so far known only from five southern Chinese species, namely
78 *Nanchangosaurus suni* (Wang 1959), *Hupehsuchus nanchangensis* (Carroll & Dong 1991),

79   *Parahupehsuchus longus* (Chen et al. 2014b), *Eohupehsuchus brevicollis* (Chen et al. 2014c) and
80   *Eretmorhipis carrolldongi* (Chen et al. 2015). Ichthyosauriformes includes the Nasorostra,
81   represented by two short-snouted genera (Motani et al. 2015a; Jiang et al. 2016), along with four
82   species of *Chaohusaurus* and the more diverse Ichthyopterygia. Most known ichthyopterygians
83   belong to the derived clade Ichthyosauria, a group of Mesozoic marine reptiles with large eyes,
84   fish-shaped bodies, and numerous other adaptations to the aquatic environment (Sander 2000;
85   Motani 2009). Ichthyosauromorphs first appeared in the Spathian subage of the Early Triassic
86   (Sander 2000; Maisch 2010; Moon 2019), and maintained a cosmopolitan distribution until their
87   extinction in the Cenomanian Age of the Late Cretaceous (Zammit 2012). The origin and early
88   evolution of ichthyosauromorphs are still under study, but many recent discoveries have greatly
89   expanded scientific knowledge of Early Triassic members of the group (Motani et al. 2015a;
90   Jiang et al. 2016; Huang et al. 2019; Moon 2019). In this paper, non-ichthyosaurian
91   ichthyosauromorphs are referred as basal ichthyosauromorphs, and non-ichthyosaurian
92   ichthyosauriforms are referred as basal ichthyosauriforms.
93
94   In addition to the five hupehsuchian genera mentioned before, a variety of other basal
95   ichthyosauromorph genera have been also reported from the Lower Triassic (Table 1). Most of
96   these ichthyosauromorphs are from South China (Young & Dong 1972c; Chen et al. 2013;
97   Motani et al. 2015a; Jiang et al. 2016; Huang et al. 2019), Spitsbergen (Wiman 1910; Wiman
98   1929; Callaway & Massare 1989; Maisch & Matzke 2003; Maisch 2010) or Canada (Nicholls &
99   Brinkman 1995; Cuthbertson et al. 2013), although others are from Thailand (Mazin et al. 1991)
100 or Japan (Shikama et al. 1978).
101 The upper Lower Triassic Vikinghøgda Formation in Spitsbergen has yielded many
102 ichthyosauromorph specimens (Table 1). The skull and forelimbs of the small (1-1.5 m in length)
103 species *Grippia longirostris* have been well studied (Wiman 1929; Motani 1997; Motani 2000;
104 Hansen et al. 2018). *Omphalosaurus*, considered to be a durophagous animal, is represented by
105 Vikinghøgda material that is indeterminate at the species level (Ekeheien et al. 2018).
106 *Quasianosteosaurus vikinghoegdai* is an ichthyosauriform known from an unusual, relatively
107 complete skull (Maisch & Matzke 2003), whereas *Isfjordosaurus minor* (Wiman 1910; Motani
108 1999) is represented only by an isolated humerus (Maisch 2010). *Pessopteryx nisseri* is relatively
109 large (Wiman 1910), and is diagnosed by traits of the humerus (Motani 1999; Maisch 2010;
110 Engelschiøn et al. 2018). Material referable to *Cymbospondylus* sp. has also been recovered from
111 the Lower Triassic of Spitsbergen (Engelschiøn et al. 2018). Both *Cymbospondylus* and
112 *Pessopteryx* are considered to belong within the derived clade Ichthyosauria (Moon 2019).
113
114 In Canada, ichthyosauromorphs are found in the Lower to possibly Middle Triassic Sulphur
115 Mountain Formation in the Wapiti Lake area, British Columbia (Scheyer et al. 2014). The
116 Sulphur Mountain ichthyosauromorphs include *Parvinatator wapitiensis* (Nicholls & Brinkman
117 1995), *Gulosaurus helmi* (Cuthbertson et al. 2013), and specifically indeterminate specimens of
118 *Grippia* and *Utatsusaurus* (Brinkman et al. 1992; Nicholls & Brinkman 1993a).

119

120 Early Triassic ichthyosauromorphs are abundant in South China. Setting aside the five
121 hupehsuchian taxa, they mainly represent four species belonging to the genus *Chaohusaurus*.
122 Among them, *Chaohusaurus geishanensis* (Young & Dong 1972c), *C. chaoxianensis* (Chen
123 1985; Mazin & Sander 1993; Motani & You 1998; Motani et al. 2015b) and *C. brevifemoralis*
124 (Huang et al. 2019) are from the Nanlinghu Formation of Anhui Province, whereas the large
125 fourth species, *C. zhangjiawanensis*, is known from well-preserved material from the Jialingjiang
126 Formation of Hubei Province (Chen et al. 2013). Two additional Early Triassic
127 ichthyosauriforms from South China, *Sclerocormus breviceps* (Jiang et al. 2016) and
128 *Cartorhynchus lenticarpus* (Motani et al. 2015a), both have a short skull and a robust forelimb.
129 They have been recovered in phylogenetic analyses as sister taxa forming the basalmost
130 ichthyosauriform clade Nasorostra (Jiang et al. 2016; Huang et al. 2019). In addition, recent
131 research has identified some similarities in dental morphology between *Cartorhynchus* and
132 *Omphalosaurus* (Huang et al. 2020), which may imply a close relationship between Nasorostra
133 and Omphalosauridae (Qiao et al. 2021).

134

135 The ichthyopterygian *Utatsusaurus hataii* from Japan (Shikama et al. 1978) differs from
136 *Chaohusaurus* in being a larger animal with a more robust forefin skeleton. In a recent
137 phylogenetic analyses (Jiang et al. 2016; Moon 2019), *Utatsusaurus* was found to be among the
138 basalmost ichthyopterygians. *Thaisaurus chonglakmanii* (Mazin et al. 1991) might be even more
139 primitive within Ichthyopterygia than *Utatsusaurus*, but is too incompletely known for its
140 phylogenetic position to be certain (Liu et al. 2018).

141

142 Early Triassic ichthyosauriforms can generally be divided into two morphological categories
143 (Zou et al. 2020). Type A includes *Chaohusaurus geishanensis*, *C. zhangjiawanensis*,
144 *Utatsusaurus hataii*, *Parvinatator wapitiensis*, *Grippia longirostris* and *Gulosaurus helmi*. These
145 taxa are relatively large (some exceeding 1 m in length), have elongate zeugopodial elements and
146 a comparatively compact forelimb bone arrangement, and are considered to have been strong
147 swimmers capable of long-distance migration, allowing them to disperse and diversify on a
148 worldwide scale. Type B includes *C. chaoxianensis* (and possibly also *C. brevifemoralis*),
149 *Cartorhynchus lenticarpus* and *Sclerocormus breviceps*, smaller forms (body length less than 70
150 cm) that share a short, anteroposteriorly broad, and relatively flexible forelimb. They are
151 considered to have been weaker swimmers that had little capacity for migration, explaining why
152 taxa of this type occur only in Anhui Province, China (Zou et al. 2020).

153

154 In 2017, a Guizhou Geological Survey field crew collected a partial skeleton of a new marine
155 reptile, which is recognizable as an ichthyosauromorph, from the Lower Triassic Luolou
156 Formation of the northwest margin of the Nanpanjiang Basin in Zhebao Township, Longlin
157 County, Baise City, Guangxi Province, China (Fig. 1).

158

159 The Luolou Formation in the Nanpanjiang Basin consists of limestone rich in ammonoids and

160 conodonts, deposited on a shallow marine carbonate shelf. In the Zhebao section, the formation
161 is 98 meters thick and can be divided into 22 beds from bottom to top. The specimen described
162 here was found in bed 14, which comprises a light gray medium-to-thinly-bedded limestone
163 intercalated with calcareous mudstone, and contains a large number of ammonites and bivalves.
164 Conodonts present in bed 14 include: *Triassospathodus homeri, Tr. symmetricus, Neospathodus*
165 *triangularis, Ns. brochus, Ns. curtatus, Gladigondolella tethydis, Cypridodella müelleri,* and
166 *Neohindeodella triassica*. The newly recovered ichthyosauromorph specimen, which we refer to
167 the new genus and species *Baisesaurus robustus*, accordingly occurs within the
168 *Triassospathodus symmetricus-Tr. homeri* assemblage zone of the Luolou Formation (Xiang et
169 al. 2020), which is of late Spathian age. Here, we give a detailed description of this specimen,
170 which is an important, morphologically novel addition to the previously known early record of
171 ichthyosauromorphs.

172

Materials & Methods

174 The specimen described here was collected by Kunpeng Xiang, Yongzhong He and Housong
175 Zhang from Guizhou Geological Survey in the course of surveying the regional geology and
176 paleontology of Guangxi Province. Guizhou Geological Survey is allowed to carry out a regional
177 geological survey in Guangxi Province, including collect fossils, based on the entrusted work
178 assignment WT- [2016]-177 from Chengdu Geological Survey Center. The specimen is housed
179 in the School of Earth Sciences, China University of Geosciences (Wuhan), under the collection
180 number CUGW VH107.

181

182 CUGW VH107 consists of a single limb element and a disarticulated trunk skeleton including
183 some dorsal vertebrae (twelve centra and seven neural arches, most of the neural arches being
184 separated from the corresponding centra), gastralia and ribs. Most of these bones display surface
185 striations where intact, and spongy internal structure where broken (Fig. 2). The disarticulated
186 nature of the skeleton, combined with the good preservation of individual elements, suggests that
187 CUGW VH107 was buried essentially in situ, but that water currents may have disturbed the
188 skeleton after the associated muscle tissue had decayed. A large isolated object at the upper left
189 corner of the fossil-bearing slab (Fig. 2) has a curved triangular outline and a rough surface. It is
190 unlikely to be a bone, given the lack of any surface striations or spongy internal structure.

191

192 For comparison to CUGW VH107, we calculated ratios of centrum height to centrum length for
193 the dorsal vertebrae of 26 other marine reptile specimens, based on data and images from the
194 literature (see Table S1 in Supplementary Information). Measurements for nine specimens were
195 taken directly from publications, while those for the other 17 taxa were estimated from photos of
196 known scale. The data were graphed as a scatter plot using Excel.

197

198 The bone histology of CUGW VH107 was examined using a sample from the distal part of a rib.

199 The sample was embedded in Araldite-2020 one-component resin, cut with an STX-202A
200 diamond wire automatic microtome, and ground to a thickness of about 100 μm with P400,
201 P800, P1000 and P2000 abrasive paper. The polished thin section was then observed under
202 transmitted and polarized light, and photographed using a ZEISS Primotech optical microscope.
203
204 **Nomenclatural acts.** The electronic version of this article in Portable Document Format (PDF)
205 will represent a published work according to the International Commission on Zoological
206 Nomenclature (ICZN), and hence the new names contained in the electronic version are
207 effectively published under that Code from the electronic edition alone. This published work and
208 the nomenclatural acts it contains have been registered in ZooBank, the online registration
209 system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the
210 associated information viewed through any standard web browser by appending the LSID to the
211 prefix http://zoobank.org/. The LSID for this publication is:
212 urn:lsid:zoobank.org:pub:CE9FCC42-4F06-42A4-B724-AD2AD3E8589A . The online version
213 of this work is archived and available from the following digital repositories: PeerJ, PubMed
214 Central SCIE and CLOCKSS.

215

216 **Results**

217 **Systematic Paleontology**

218

219 Reptilia Linnaeus, 1758
220 Diapsida Osborn, 1903
221 Ichthyosauromorpha Motani et al. 2015

222
223 *Baisesaurus* gen. nov.
224 **Etymology.** "Baise" indicates the provenance of the only known specimen of the genus, which
225 was discovered in Zhebao Township in Baise City; -*saurus* is a common suffix for genus names
226 of fossil reptiles.
227 **Type Species**. *Baisesaurus robustus* sp. nov.
228 **Diagnosis.** As for the type and only known species.

229
230 *Baisesaurus robustus* sp. nov.
231 **Etymology.** The Latin word *robustus* means "robust".
232 **Holotype.** CUGW VH107, a partial associated postcranial skeleton.
233 **Locality and horizon**. Northwest margin of the Nanpanjiang Basin, Zhebao Township, Longlin
234 County, Baise City, Guangxi Province, China; upper part of the Luolou Formation, Lower
235 Triassic (upper Spathian).

236 **Diagnosis.** A large basal ichthyosauromorph with a unique combination of postcranial characters
237 (* denotes an autapomorphy): anterior dorsal centra deeply amphicoelous, with an average
238 height to length ratio of about 1.2; neural spine long and inclined posteriorly, with the
239 postzygapophyses much more dorsally positioned than the prezygapophyses; parapophyses
240 subrectangular with their anteroventral corners extended to form ventrally directed apices, and
241 situated adjacent to the anterior margins of the centra; diapophyses well developed and
242 semicircular in outline; deep fossae present posterior to the diapophyses*; and radius strong,
243 elongate, and bearing two distal facets, the posterior facet being 80% as wide as the anterior
244 one*.

245

246 **Description**

247 **Vertebrae.** Twelve isolated centra and seven recognizable neural arches are preserved (Fig. 3A).
248 The centra are from the anterior dorsal region. The first preserved centrum is exposed in
249 approximate midsagittal section due to breakage, and is strongly amphicoelous (Fig. 3B, C).
250 Similarly amphicoelous centra are present in a wide range of other Triassic marine reptiles,
251 including ichthyosauromorphs and sauropterygians (Rieppel 1998c; Cheng et al. 2012;
252 Takahashi et al. 2014; Roaldset 2017; Ekeheien et al. 2018). The lateral and anterior surfaces of
253 the second centrum are partly missing. However, the lateral surface is exposed in the 3rd, 4th,
254 6th, 7th, 8th, 9th and 10th centra, the anterior surface in the 11th and 12th centra, and the
255 posterior surface in the 5th centrum. The 10th, 11th and 12th centra are almost completely
256 preserved. The 1st, 4th, 5th, 6th and 7th neural arches are exposed in lateral view, whereas the
257 2nd and 3rd neural arches are anteroposteriorly compressed and exposed in posterior view. The
258 neural arches are well preserved, but most are separated from their corresponding centra,
259 suggesting a lack of neurocentral fusion (Sander & Faber 2003).

260

261 The lateral surfaces of the centra are subrectangular in outline. The ventral surfaces are smooth,
262 and display a concavity centered on the anteroposterior midpoint (Fig. 3A, centra 6 and 10). The
263 anterior surfaces of the centra have a hexagonal outline, whereas the posterior surfaces are
264 circular (Fig. 3A, centra 5 and 11). Large parapophyses are present on the lateral surfaces of the
265 centra (Fig. 3B). They are subrectangular with their anteroventral corners extended to form
266 ventrally directed apices, extend anteroposteriorly from the anterior margins of the centra to their
267 mid-regions. The parapophyses of *Baisesaurus* are similarly shaped to those of *Grippia*, but
268 unlike those of *Chaohusaurus*, which have a triangular outline (personal observation, specimen
269 number AGM AGB6256 and AGM AGB7401, AGM is the abbreviation of Anhui Geological
270 Museum) (Roaldset 2017; Ekeheien et al. 2018). In hupehsuchians, the parapophyses are always
271 more posteriorly and ventrally positioned (Chen et al. 2014b; Chen et al. 2014a; Chen et al.
272 2015). In ichthyosaurs such as *Cymbospondylus*, the centra are shortened, and the parapophyses
273 are much more dorsoventrally elongated than in *Baisesaurus* (Ekeheien et al. 2018; Engelschiøn
274 et al. 2018). Among some early sauropterygians, the neural arches bear well-developed
275 transverse processes, but parapophyses are weak or absent (Rieppel 1998a; Rieppel 1998b; Li &
276 Liu 2020). The articular facets for the neural arches of *Baisesaurus* are prominent and rugose,

277   and the floor of the neural canal on each centrum is narrow (Fig. 3C).

278

279   Most of the neural arches are separated from the centra, but the arches would generally have
280   articulated with the anterior-middle portions of the centra in life. The neural arches have well-
281   developed prezygapophyses and postzygapophyses extending, respectively, anteriorly and
282   posteriorly (Fig. 3B). The diapophyses of the neural arches are well developed and robust, and
283   extend laterally. The anterior and posterior margins of the diapophyses are straight or slightly
284   concave, whereas the dorsal margins are convex (Fig. 3D). The posterodorsal corners of the
285   diapophyses are prominent and sharply pointed. There are no discernible boundaries between the
286   diapophyses and parapophyses (Fig. 3B), suggesting that these articular facets are combined to
287   form large synapophyses or apophyses for single-headed ribs. The neural arches contribute
288   significantly to the articular facets as in *Chaohusaurus* (Huang et al. 2019), but unlike the
289   condition in *Omphalosaurus* (Sander & Faber 2003). In hupehsuchians, the diapophyses of the
290   neural arches also contribute to synapophyseal facets, but the facets are positioned more
291   posteriorly than *Baisesaurus* (Chen et al. 2014b; Chen et al. 2015; Wu et al. 2016). The
292   prezygapophysis is well preserved in the 7th neural arch, and separated from the corresponding
293   diapophysis by a smooth, concave surface (Fig. 3B). A deep fossa is present posterior to the
294   diapophysis (Fig. 3B and D). This fossa is not seen in other ichthyosauromorphs or in early
295   sauropterygians, and may represent an autapomorphy. The postzygapophyses are small, paired
296   triangular processes situated on the posterior margins of the neural spines. Their articular
297   surfaces are concave and directed posteroventrally (Fig. 3D). They are much more dorsally
298   positioned than the prezygapophyses, suggesting that the neural spines were inclined posteriorly
299   in order to bring each pair of postzygapophyses into articulation with the prezygapophyses of the
300   following neural arch, as in *Chaohusaurus* (personal observation, specimen number AGM
301   AGB6256 and AGM AGB7401) and *Utatsusaurus* (Shikama et al. 1978). In many early
302   sauropterygians the postzygapophyses are also more dorsally positioned than the
303   prezygapophyses, but the neural spines are more elongate and closely spaced, and are not
304   inclined posteriorly (Rieppel 1998a; Cheng et al. 2012; Cheng et al. 2016; Li & Liu 2020). The
305   neural spines have relatively thin anterior and posterior margins, and are thickest in the central
306   part (Fig. 3D). The anterior margin is slightly concave, whereas the posterior margin has a
307   straight dorsal portion and a concave ventral portion. The facet for articulation with the neural
308   arch extends onto the lateral sides of the centrum, rather than being limited to the dorsal surface
309   (Fig. 3B). The anteroposterior mid-regions of the neural arches protrude ventrally, creating a V-
310   shaped profile in lateral view, and the lateral edges of the dorsal surfaces of the centra have a
311   matching indentation for articulation with the neural arches. The neural arches lack transverse
312   processes.

313

314   The preserved anterior dorsal centra have height to length ratios ranging from 1.0 to 1.3, with an
315   average of about 1.2 (Table 2). Such values are comparable to those seen in many basal
316   ichthyosauromorphs, including *Utatsusaurus* (average ratio of about 1.2, based on 13 anterior
317   dorsal centra) (Shikama et al. 1978) and *Grippia* (average ratio of about 1.0-1.1, based on 273

318   dorsal centra) (Roaldset 2017), but are slightly larger than the value for *Chaohusaurus* (about
319   0.9) (Motani et al. 1996) and smaller than the values for *Omphalosaurus* (ratio of 1.6 for a single
320   anterior dorsal centrum) (Sander & Faber 2003) and all species from the Middle-Late Triassic,
321   Jurassic and Cretaceous (Fig. 4). The ratio of centrum height to centrum length seen in
322   *Baisesaurus* is also similar to the values for some early sauropterygians, including *Chinchenia*
323   *sungi* (Rieppel 1998b), *Sanchiaosaurus dengi* (Rieppel 1998b), *Corosaurus alcovensis* (Rieppel
324   1998a), *Augustasaurus hagdorni* (Sander et al. 1997) and *Yunguisaurus liae* (Wang et al. 2019).
325
326   **Ribs.** About 30 recognizable dorsal ribs are preserved in *Baisesaurus*. Some are almost
327   complete, while others are broken. The ribs are generally long, with lengths ranging from 100
328   mm to 200 mm, and have relatively thin distal shafts. The ribs are not pachyostotic, even in their
329   proximal portions, and the rib heads are not distinctly expanded and appear trapezoidal in
330   proximal view (Fig. 5A and B). The ribs are curved in their proximal and middle parts, but their
331   distal parts are straight. All the ribs are single-headed, and each rib head would have articulated
332   with the synapophysis formed by the centrum and neural arch of the corresponding vertebra,
333   similar to many other early ichthyosauromorphs and to early sauropterygians (Jiang et al. 2014;
334   Cheng et al. 2016; Jiang et al. 2016; Wu et al. 2016; Huang et al. 2019; Li & Liu 2020). In
335   *Utatsusaurus*, by contrast, some of the ribs are double-headed (Shikama et al. 1978). The heads
336   of the ribs are slightly thickened dorsoventrally, but not widened anteroposteriorly. Grooves are
337   present on the anterior and posterior surfaces of the dorsal ribs, giving the rib shafts a figure-
338   eight cross section, but the grooves do not extend distally beyond the middle portions of the rib
339   shafts. Similar grooves are present on the ribs of ichthyopterygians (Sander 2000). The distal
340   ends of the ribs are small, and round in outline.
341
342   **Gastralia.** The gastralia of *Baisesaurus* have been disarticulated, and their original arrangement
343   is unclear. The gastralia include Y-shaped median elements and long, slightly curved lateral
344   elements, and comparisons to other early ichthyosauromorphs suggest that each median gastral
345   element would have been flanked in life by two lateral elements (Fig. 6). Each median gastral
346   element consists of two long lateral splints and a long, sharp anterior process, with the lateral
347   splints set at an angle of about 150° to one another and an angle of about 100° to the middle
348   process. The gastralia of *Baisesaurus* differ from those of sauropterygians, but resemble those of
349   *Chaohusaurus* (Fig. 6), in having sharp anterior processes. The distance between the distal ends
350   of the paired lateral splints is about 68.5 mm. Each lateral gastral element is a single bar, which
351   is thick in the central part of the shaft and becomes thinner towards the proximal and distal ends
352   (Fig. 5C). About seven complete median gastral elements and more than seven pairs of lateral
353   gastral elements are definitely present. The gastralia are all small, elongate bones with
354   subcircular cross-sections, and are less than a quarter as thick as the ribs.
355
356   **Radius.** A single limb bone is present, and is well preserved with a maximum length of 69.8 mm
357   and maximum width of 32.1 mm (maximum length/width ratio of 2.33). The outline of the limb
358   bone is highly symmetrical in both dimensions, and the proximal and distal ends are both

359   expanded. The exposed surface of the element may be either dorsal or ventral, but in any case is
360   flattened and bears numerous, radially arranged striations (Fig. 5D). One margin of the shaft is
361   straight, whereas the other is concave (Fig. 5D). The proximal end is slightly convex, and the
362   distal end bears two articular facets (Fig. 5D). The smaller one is 80% as wide as the bigger one,
363   and the angle between the facets is about 120°.

364

365   The limb element is difficult to identify with certainty given that the rest of the appendicular
366   skeleton is missing, but bears a greater general resemblance to the radii and ulnae of other early
367   ichthyosauromorphs than to their humeri, femora, tibiae or fibulae. In most early
368   ichthyosauromorphs, such as *Chaohusaurus*, *Grippia*, *Sclerocormus* and *Cartorhynchus*, the
369   humeri and femora are shorter and much more robust than the preserved limb element in
370   *Baisesaurus*, whereas the tibiae and fibulae are slenderer and more anteroposteriorly
371   asymmetrical (Motani et al. 2015a; Motani et al. 2015b; Jiang et al. 2016; Roaldset 2017; Huang
372   et al. 2019; Zou et al. 2020). The fact that the other elements preserved in the fossil slab are
373   generally from the anterior part of the trunk also suggests that this element is most likely to be
374   from the forelimb. The limb element is somewhat comparable to the radii and ulnae of
375   hupehsuchians (Fig. 7 B-E), which are long and robust (Carroll & Dong 1991; Chen et al. 2014b;
376   Chen et al. 2015). However, the radius of *Utatsusaurus* (Fig. 7I) resembles the limb element of
377   *Baisesaurus* even more closely, being long, relatively symmetrical in both dimensions, enlarged
378   at both ends, and equipped with a single proximal articular surface and two adjacent distal
379   articular surfaces (Mazin 1986).

380

381   The limb element differs from the forearm bones of other basal ichthyosauriforms, such as
382   *Chaohusaurus* and *Grippia*. In these taxa the radius and ulna are relatively short, expanded at
383   only one end, and/or strongly anteroposteriorly asymmetric (Fig. 7F-H). The elongate forelimb
384   elements of sauropterygians (Fig. 7J-L) and thalattosaurs (Fig. 7M) could be considered similar
385   to the *Baisesaurus* limb element to some degree, but are significantly less robust in the shaft
386   region, and have only a single distal facet. In general, we consider the *Baisesaurus* limb element
387   to most closely resemble the radius of *Utatsusaurus*, given that both have a long, robust shaft and
388   a double distal facet, and therefore to be tentatively identifiable as a radius. However, we cannot
389   completely rule out the possibility that the limb element is an ulna, as the radius and ulna are
390   generally similar in morphology in early ichthyosauromorphs.

391

392   **Bone histology.** The distal rib cross-section displays a large medullary cavity (Fig. 8). The
393   cortex is very thin and contains only a few longitudinal vascular canals, as in previously
394   sectioned ribs of *Omphalosaurus* (Sander & Faber 2003) and *Utatsusuaurus* (Nakajima et al.
395   2014). Large erosional cavities are apparent in the inner region of the cortex. Parallel-fibered
396   bone is present near the periphery, and a growth line can be seen in the outer cortex (Fig. 8D),
397   suggesting that the only known individual of *Baisesaurus* was growing slowly near the end of its
398   life (Kolb et al. 2011; Houssaye et al. 2014; Nakajima et al. 2014).

399

400 **Discussion**

401 *Baisesaurus* is represented only by a partial postcranial skeleton. The centra of *Baisesaurus* are
402 similar in height-to-length ratio to those of both early ichthyosauromorphs and sauropterygians
403 (Fig 4). However, this specimen preserves typical ichthyosauromorph characters that preclude
404 referral to other marine reptile groups present in the Early Triassic, including not only
405 Sauropterygia but also Thalattosauria. Vertebral transverse processes are absent in *Baisesaurus*,
406 as in other ichthyosauromorphs (Motani et al. 2015a), but are well developed in all known Early
407 Triassic sauropterygians (Rieppel 1998a; Rieppel 1998b; Rieppel 1998c; Jiang et al. 2014; Li &
408 Liu 2020). The dorsal ribs of *Baisesaurus* are generally thin and are not pachyostotic even
409 proximally, as in ichthyosauromorphs outside Hupehsuchia and Nasorostra (Fig. 6A-B) (Young
410 & Dong 1972b; Shikama et al. 1978; Sander 2000; Chen et al. 2013; Takahashi et al. 2014;
411 Huang et al. 2019). By contrast, pachyostotic dorsal ribs occur in most sauropterygians (Fig. 6C-
412 D), such as *Majiashanosaurus* (Jiang et al. 2014), *Lariosaurus* (Li & Liu 2020), *Hanosaurus*
413 (Rieppel 1998c), *Serpianosaurus* and *Neusticosaurus* (Rieppel 1998a). In addition, the gastralia
414 of *Baisesaurus* include slender median gastral elements with sharp, relatively long anterior
415 processes, a condition seen in other ichthyosauromorphs (Fig. 6F-H) (Shikama et al. 1978;
416 Maisch 2001; Huang et al. 2019). The median gastral elements of sauropterygians are more
417 robust (Rieppel 1998b; Jiang et al. 2014; Cheng et al. 2016; Li & Liu 2020), and either bear
418 short, blunt anterior processes (Rieppel 1998c; Li & Liu 2020) or lack anterior processes entirely
419 (Fig. 6I-J) (Rieppel 1998b). Thalattosaurs usually have vertebral transverse processes (Nicholls
420 & Brinkman 1993b; Müller 2005; Müller 2007), unlike *Baisesaurus*, and the distal ends of their
421 dorsal ribs are always expanded (Fig. 6E) (Müller 2005; Rieppel et al. 2006; Müller 2007).
422
423 Recent studies have defined the clade Ichthyosauromorpha as comprising the last common
424 ancestor of *Hupehsuchus nanchangensis* and *Ichthyosaurus communis*, and all of its descendants
425 (Motani et al. 2015a; Moon 2019). The diagnostic characters of this clade pertain mainly to the
426 limb elements and neural arches (Motani et al. 2015a). *Baisesaurus* possess three features that
427 are only seen in Ichthyosauromorpha and may represent synapomorphies of the group: neural
428 arches lacking transverse processes, ribs that are not pachyostotic proximally, and median gastral
429 elements with sharp anterior processes. Among Early Triassic ichthyosauromorphs, *Baisesaurus*
430 can be excluded from the clades Hupehsuchia and Nasorostra. Although the limb element of
431 *Baisesaurus* is similar to the forearm bones of hupehsuchians to some degree, the axial skeleton
432 displays clear differences from the hupehsuchian condition. The neural arches of hupehsuchians
433 are tall, with bipartite neural spines that each comprise two vertically stacked segments, and their
434 dorsal ribs are always expanded, having anterior and/or posterior flanges (Carroll & Dong 1991;
435 Chen et al. 2014b; Chen et al. 2015). Similarly, *Baisesaurus* differs from Nasorostra (i.e.,
436 *Sclerocormus* and *Cartorhynchus*), in which the trunk is heavily built with thickened ribs,
437 symmetrical median gastral elements are absent, and the zeugopodial bones are short and robust
438 (Motani et al. 2015a; Jiang et al. 2016). *Baisesaurus* may be a member of the clade
439 Ichthyopterygia (Jiang et al. 2016; Moon 2019), but clear ichthyopterygian or even

440   ichthyosauriform synapomorphies are absent in the available partial skeleton. Accordingly, we
441   regard *Baisesaurus* at present as a basal ichthyosauromorph of uncertain phylogenetic position,
442   although definitely not a member of Hupehsuchia or Nasorostra.

443

444   Early Triassic ichthyosauriforms can be divided into two morphological categories, as mentioned
445   in the Introduction (Zou et al. 2020). Assuming the bone we tentatively identify as the radius of
446   *Baisesaurus* really is from the forearm, then *Baisesaurus* is comparable to Zou et al.'s Type A
447   ichthyosauriforms in having elongate zeugopodial elements, and differs from *Chaohusaurus*
448   *chaoxianensis* (and perhaps also *C. brevifemoralis*) in having more robust forearm bones.
449   *Baisesaurus* is also distinguished from most basal ichthyosauriforms (including *Chaohusaurus*,
450   *Parvinatator*, *Grippia* and *Gulosaurus*) by larger body size and some morphological details of
451   the centra. For example, the parapophyses of *Baisesaurus* are subrectangular with ventrally
452   directed apices, whereas those of *Chaohusaurus* are triangular (personal observation, specimen
453   number AGM AGB6256 and AGM AGB7401). The parapophyses are less well developed in
454   *Grippia* (Roaldset 2017; Ekeheien et al. 2018) than in *Baisesaurus*. Ichthyosaurs are represented
455   in the Lower Triassic by some large *Cymbospondylus* and *Pessopteryx* specimens from
456   Spitsbergen (Engelschiøn et al. 2018), but like other members of the highly derived clade
457   Ichthyosauria (Moon 2019), these taxa differ from *Baisesaurus* in many respects. For example,
458   they possess significantly shortened centra, and shortened forearm bones.

459

460   *Baisesaurus* shares more similarities with *Utatsusaurus hataii* from Japan than with any other
461   previously reported ichthyosauromorph. Both *Baisesaurus* and *Utasusaurus* are relatively large,
462   some specimens of the latter being close to 300 cm in length (Shikama et al. 1978; Sander 2000).
463   The limb element of *Baisesaurus* is also very similar to the radius of *Utatsusaurus* (Fig. 7), as
464   both are long, robust, highly symmetrical, and endowed with two distal articular facets (Shikama
465   et al. 1978; Mazin 1986). There are also some differences between the two taxa. The ribs of
466   *Utatsusaurus* are gently broadened distally, and some of them are double-headed (Shikama et al.
467   1978), whereas the preserved ribs of *Baisesaurus* are all single-headed and have unexpanded
468   distal ends. In *Utatsusaurus* the proximal end of the radius is flat and the more posterior of the
469   two distal facets is much smaller than the anterior one (Mazin 1986), whereas in *Baisesaurus* the
470   proximal end of the possible radius is convex and the two distal facets are similar in size, the
471   posterior facet being 80% as wide as the anterior one.

472

473   The specimen CUGW VH107 comprises only some remains from the anterior part of the trunk,
474   but represents the first Early Triassic ichthyosauromorph to be discovered in Guangxi Province.
475   The specimen differs in important respects from all previously known Early Triassic
476   ichthyosauromorphs, displaying the following autapomorphies: deep fossae present posterior to
477   the diapophyses; and robust radius bearing two distal facets, the posterior facet being 80% as
478   wide as the anterior one. CUGW VH107 is also the largest Early Triassic ichthyosauromorph so
479   far discovered in China, with an estimated body length about two times greater than that of
480   *Sclerocormus*, which was previously considered to be the largest ichthyosauromorph known

481   from the Early Triassic of China (Jiang et al. 2016). For these reasons, and despite the
482   incompleteness of the specimen, we consider CUGW VH107 to clearly represent a new, large
483   basal ichthyosauromorph, *Baisesaurus robustus*, from the Lower Triassic of South China. Based
484   on the single preserved limb element, *Baisesaurus* can be tentatively inferred to have had
485   elongate, compactly arranged forelimb bones, and to have been a strong swimmer capable of
486   dispersing over long distances (Zou et al. 2020). In this respect, *Baisesaurus* was likely similar to
487   *Utatsusaurus*, which occurs in both Japan (Shikama et al. 1978) and Canada (Nicholls &
488   Brinkman 1993a).

489

490   *Baisesaurus* is much larger than *Chaohusaurus*, and comparable in body size to *Utatsusaurus*.
491   The 10 dorsal centra of *Baisesaurus* whose lengths can be measured have an average length of
492   27.8 mm, whereas in *Chaohusaurus* the length of any single centrum is less than 10 mm (Young
493   & Dong 1972c; Huang et al. 2019). Nevertheless, *Chaohusaurus* and *Utatsusaurus* are two well-
494   studied basal ichthyosauromorph taxa, so their body proportions can provide a reliable basis for
495   estimating the total length of an intact *Baisesaurus*. In the holotype (AGB7401) of *C.
496   brevifemoralis* (Huang et al. 2019), the average length of the anterior dorsal vertebrae is about 7
497   mm, and the total body length is about 80 cm. Assuming similar skeletal proportions, the total
498   length of *Baisesaurus* would be about 318 cm. Similarly, the length of a single anterior dorsal
499   vertebra in the holotype (specimen No. K1, collection number IGPS 95941) of *U. hataii*
500   (Shikama et al. 1978) is about 13.8 mm, and the total body length is estimated as 140 cm. Based
501   on the proportions of *U. hataii*, the estimated length of *Baisesaurus* would be about 300 cm.
502   With a total body length of about 3 m in life, *Baisesaurus* was relatively large among basal
503   ichthyosauromorphs (e.g., *Chaohusaurus*, 60-100 cm; *Sclerocormus*, 160 cm; *Utatsusaurus*,
504   140-300 cm; *Gulosaurus* and *Grippia*, estimated at less than 120 cm) (Wiman 1910; Young &
505   Dong 1972c; Shikama et al. 1978; Sander 2000; Cuthbertson et al. 2013; Jiang et al. 2016;
506   Huang et al. 2019).

507

508   **Conclusions**

509   *Baisesaurus* represents a newly reported large basal ichthyosauromorph from the Lower Triassic
510   of South China. Among previously described taxa, *Baisesaurus* is most similar to *Utatsusaurus*,
511   and differs from other, smaller Chinese early ichthyosauromorphs. *Baisesaurus* is the first Early
512   Triassic ichthyosauromorph to be reported from Guangxi Province. Together with
513   *Cartorhynchus* (Motani et al. 2015a), *Sclerocormus* (Jiang et al. 2016) and two recently
514   discovered species of *Chaohusaurus* (Chen et al. 2013; Huang et al. 2019), *Baisesaurus* expands
515   the known geographical distribution of early ichthyosauromorphs in China. Alongside other
516   recent finds, *Baisesaurus* implies a need for further studies of the paleoecology and
517   paleogeography of Early Triassic ichthyosauromorphs in order to understand their role in the
518   ecosystem at the eastern margin of the Paleo-Tethys. The discovery of *Baisesaurus* has
519   considerable paleogeographic significance, as well as adding to the documented taxonomic

520   diversity of South China's ichthyosaur fauna in the Spathian interval of the Early Triassic.

521

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528

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Figure 1

Fossil location.

The specimen was found in Zhebao Township, Longlin County, northwest part of Baise City, Guangxi Province.

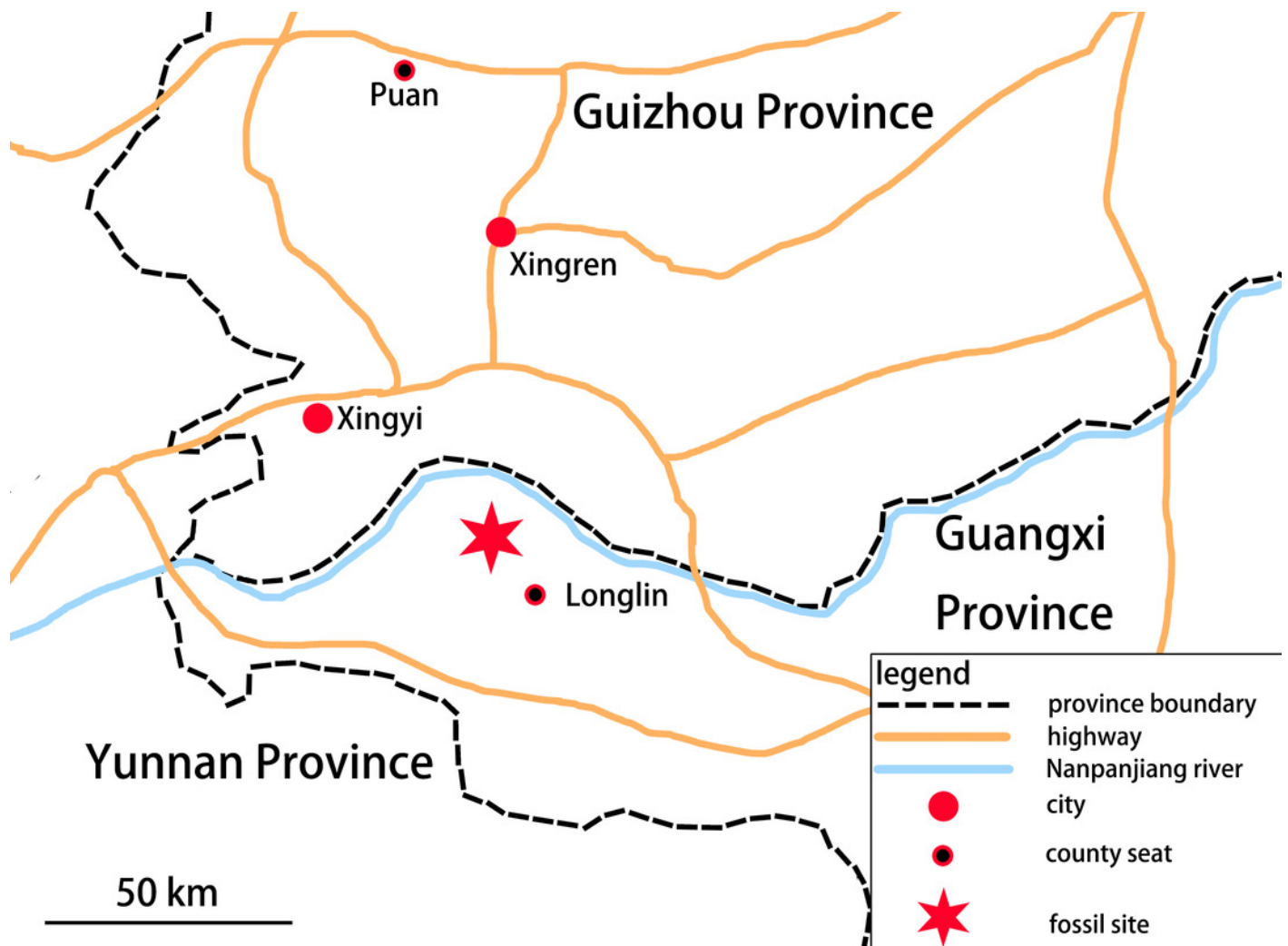



Figure 2

Photograph and outline drawing of *Baisesaurus.*

It shows semi-articulated incomplete vertebrae, limb element, ribs and gastralia. **Abbreviations**: **Dv**, dorsal vertebrae; **L**, limb element; **G**, gastralia; **R**, ribs.

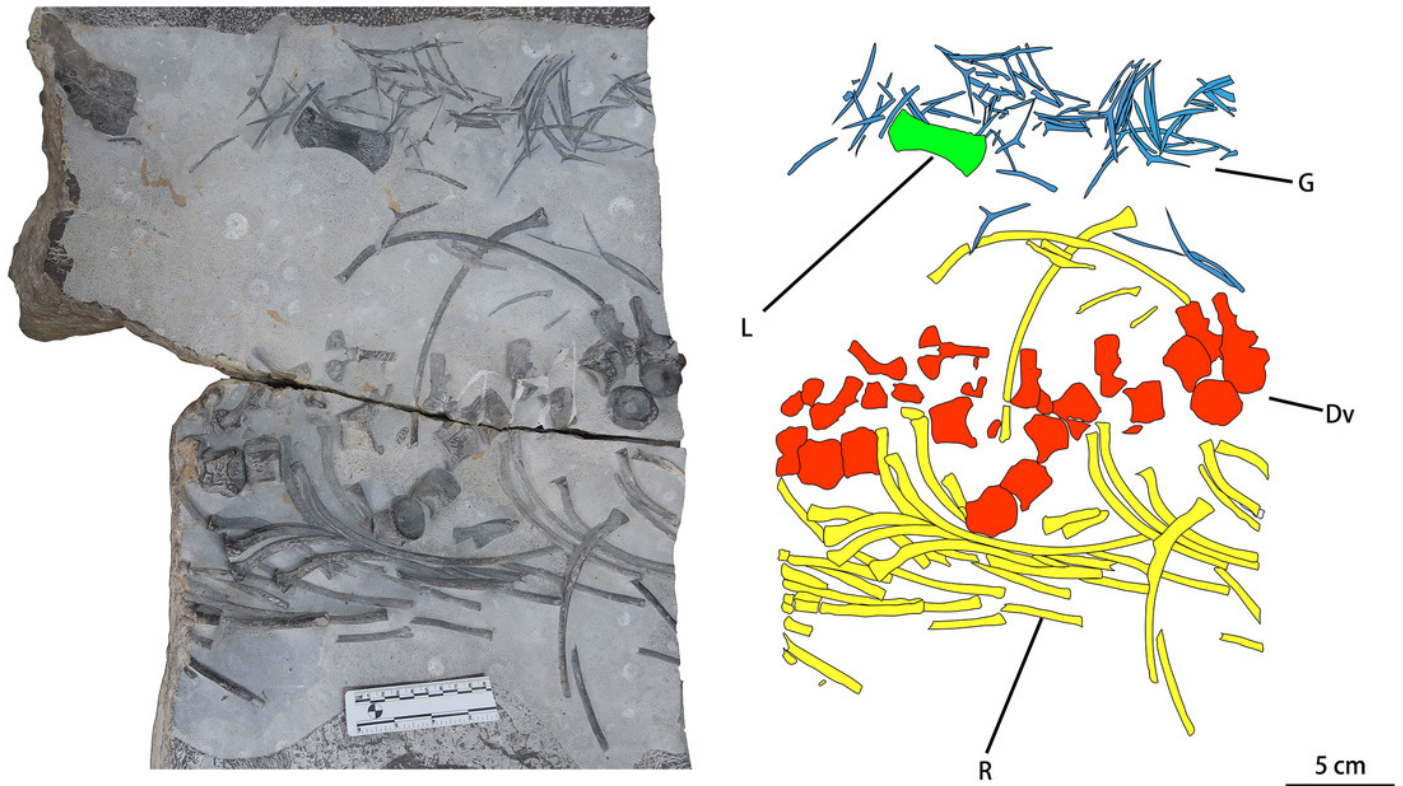



Figure 3

Photographs of the vertebrae of *Baisesaurus*.

(A) all preserved vertebrae, with centra numbered 1-12 in red and neural arches numbered 1-7 in blue, both in order of preservation on the slab; (B) three centra (Nos. 10, 11, 12) and two neural arches (Nos. 6, 7); (C) articulated centra (Nos. 1, 2, 3), showing amphicoelous morphology; (D) isolated neural arch (No. 1) in posterolateral view. **Abbreviations**: **dph**, diapophysis; **f**, fossa; **nc**, neural canal; **nf**, neural arch articular facet; **poz**, postzygapophysis; **pph**, parapophysis; **prz**, prezygapophysis.

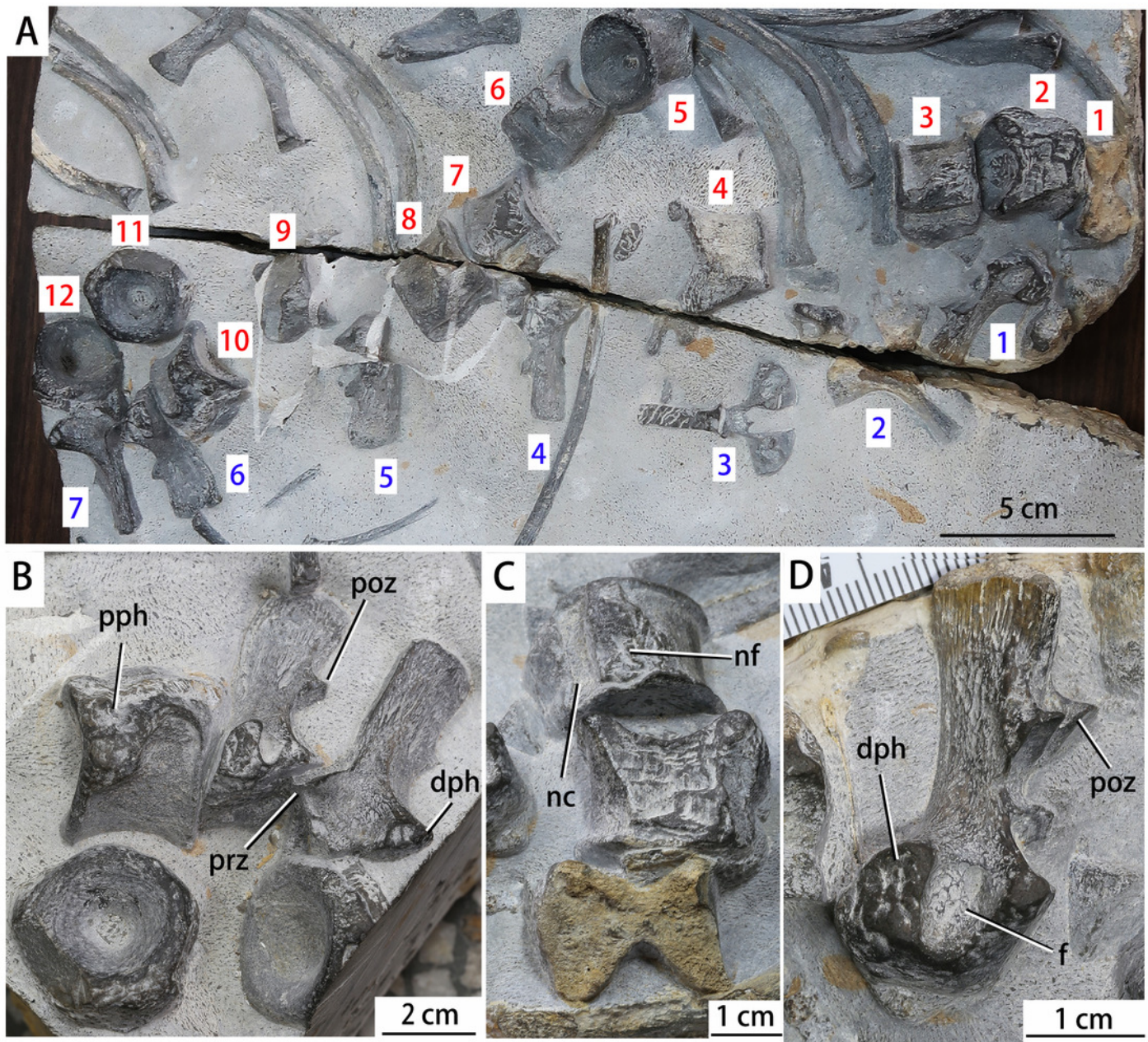



Figure 4

Comparison of centra height and length (in mm) in different marine reptiles.

Black diamond represents *Baisesaurus*; blue circles represent other Early Triassic non-ichthyosaurian ichthyosauromorphs; green triangles represent more derived ichthyosaurian members; red squares represent sauropterygians.

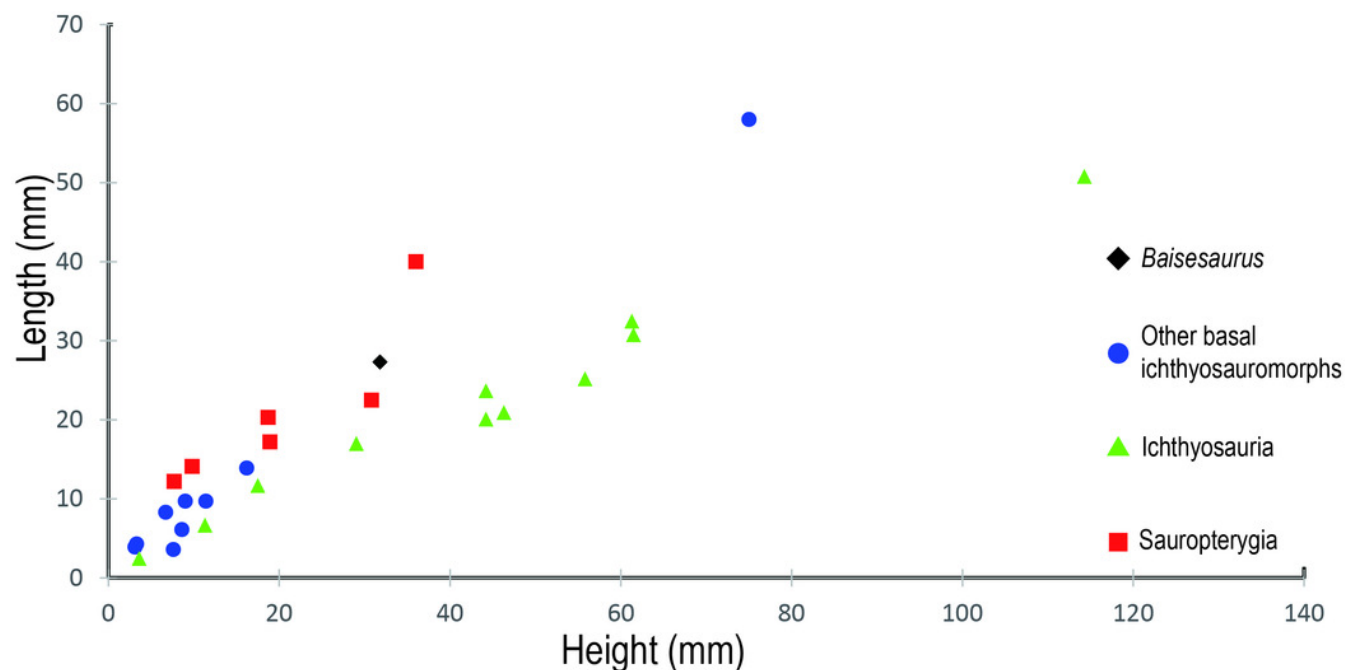



Figure 5

Photographs of the dorsal ribs, gastralia and limb element of *Baisesaurus*.

(A) dorsal ribs; (B) rib heads in proximal view (red arrow) and rib shaft in cross-section (black arrow); (C) gastralia; (D) limb element. **Abbreviations**: **l**, gastral lateral element; **m**, gastral median element.

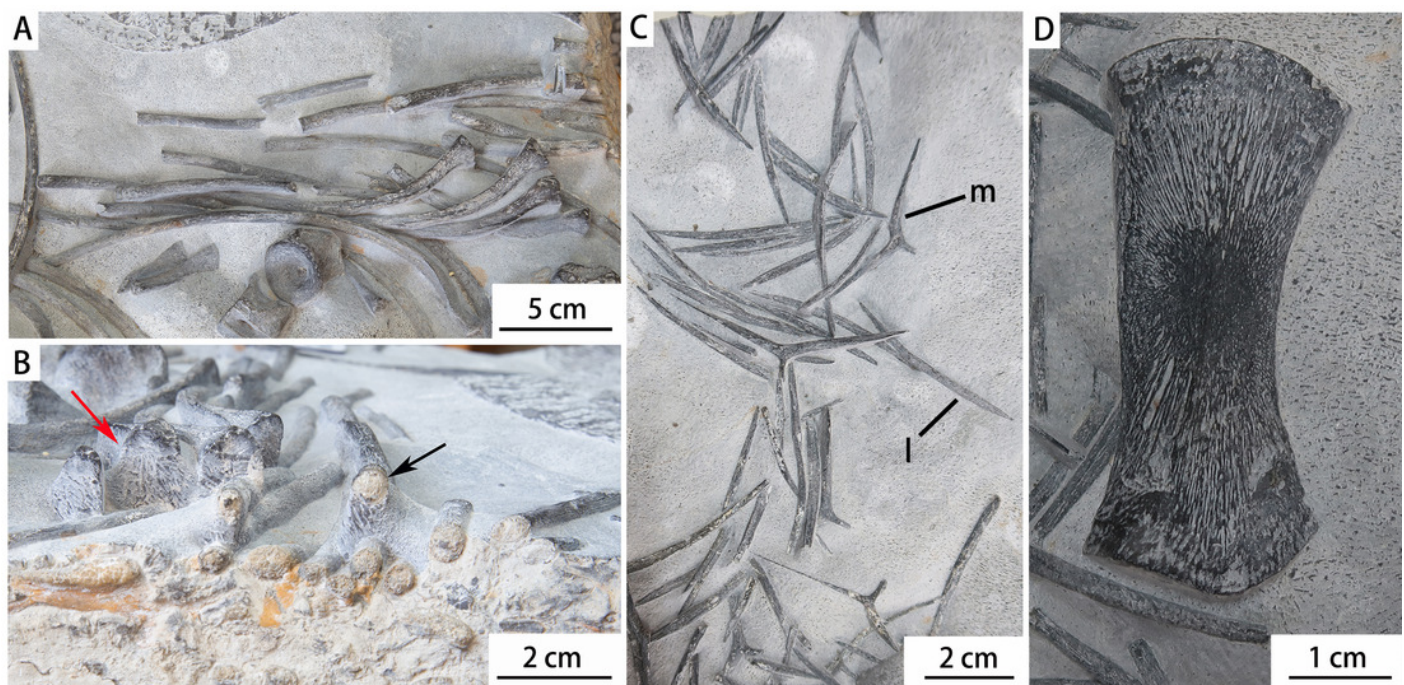



Figure 6

Drawings of dorsal ribs (A-E) and median gastral elements (F-J) of different marine reptiles.

(A) *Baisesaurus robustus* (CUGW VH107); (B) ichthyosauriform *Utatsusaurus hataii* (IGPS95941); (C) sauropterygian *Lariosaurus sanxiaensis* (HFUT YZS-16-01); (D) sauropterygian *Dawazisaurus brevis* (NMNS000933-F034397); (E) thalattosauriform *Askeptosaurus italicus* (PIMUZ T 4832); (F) *Baisesaurus robustus* (CUGW VH107); (G) ichthyosauriform *Chaohusaurus geishanensis* (P45-H85-23); (H) ichthyosauriform *Chaohusaurus chaoxianensis* (AGB6256); (I) sauropterygian *Kwangsisaurus orientalis* (IVPP V2338); and (J) sauropterygian *Hanosaurus hupehensis* (IVPP V3231). Yellow represents non-ichthyosaur ichthyosauriforms, and green represents non-ichthyosauromorph marine reptiles. The scale bar which equals 5 cm is for ribs, and the scale bar which equals 2 cm is for gastralia.

A

B

C D

E

5 cm

F I

G H J

2 cm

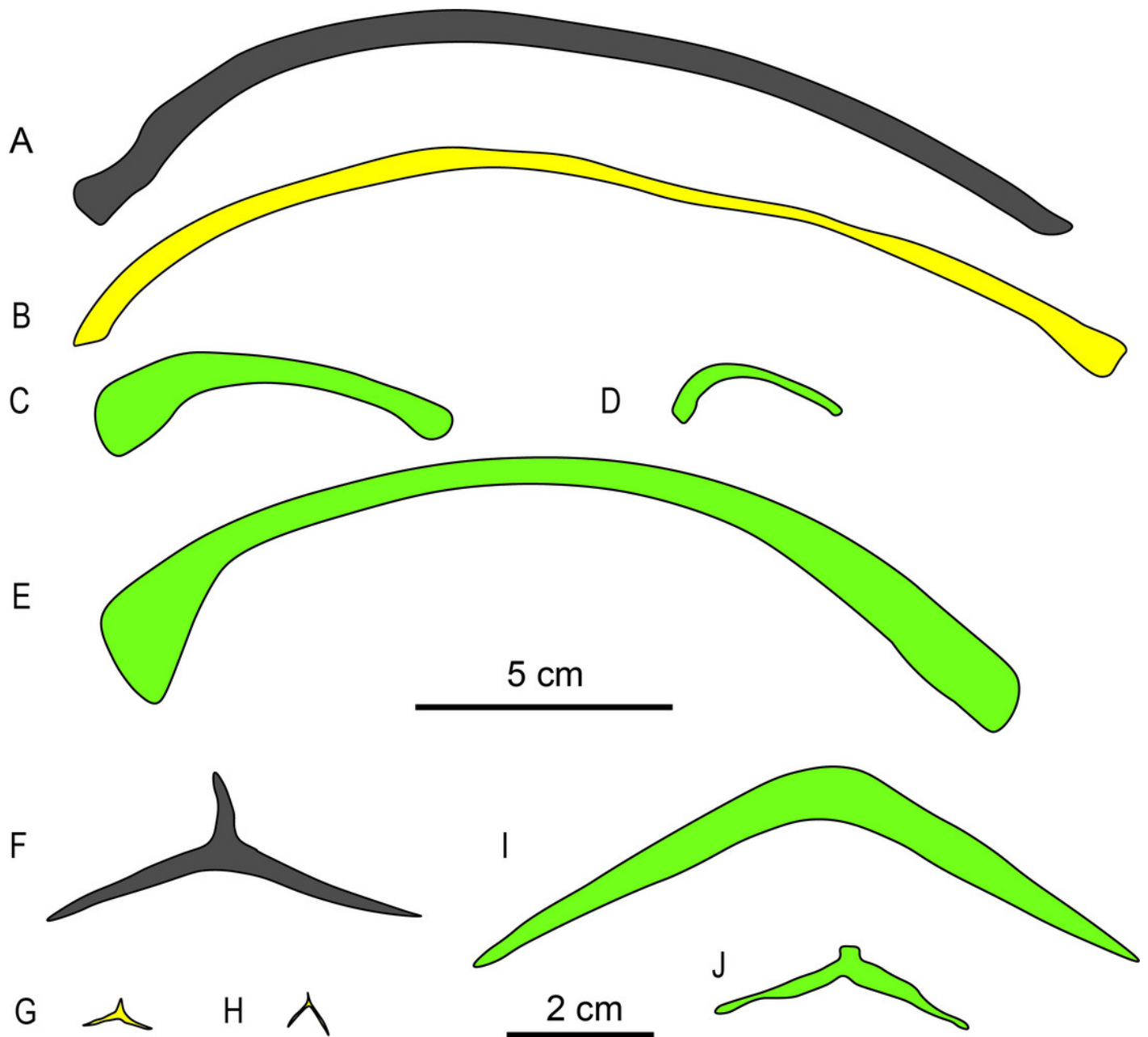



Figure 7

Drawings of forelimb bones of some selected Triassic marine reptiles.

(A) *Baisesaurus robustus* (CUGW VH107); (B) *Parahupehsuchus longus* (WGSC 26005); (C) *Hupehsuchus nanchangensis* (ZMNH M8127); (D) *Eohupehsuchus brevicollis* (WGSC V26003); (E) *Eretmorhipis carrolldongi* (WGSC V26020); (F) *Chaohusaurus brevifemoralis* (AGB7408); (G) *Chaohusaurus zhangjiawanensis* (WHGMR V26025); (H) *Grippia longirostris* (PMU R472); (I) *Utatsusaurus hataii* (IGPS95941); (J) *Majiashanosaurus discocoracoidis* (AGM-AGB5954) (Sauropterygia); (K) *Qianxisaurus chajiangensis* (NMNS-KIKO-F044630) (Sauropterygia); (L) *Dawazisaurus brevis* (NMNS000933-F034397) (Sauropterygia); and (M) *Askeptosaurus italicus* (MSNM V456) (Thalattosauria). Blue represents hupehsuchians, and other colors represent same categories as in Figure 6. (B)-(L) represent left forelimbs, whereas (M) represents a right forelimb. **Abbreviations**: **H**, humerus; **R**, radius; **U**, ulna.

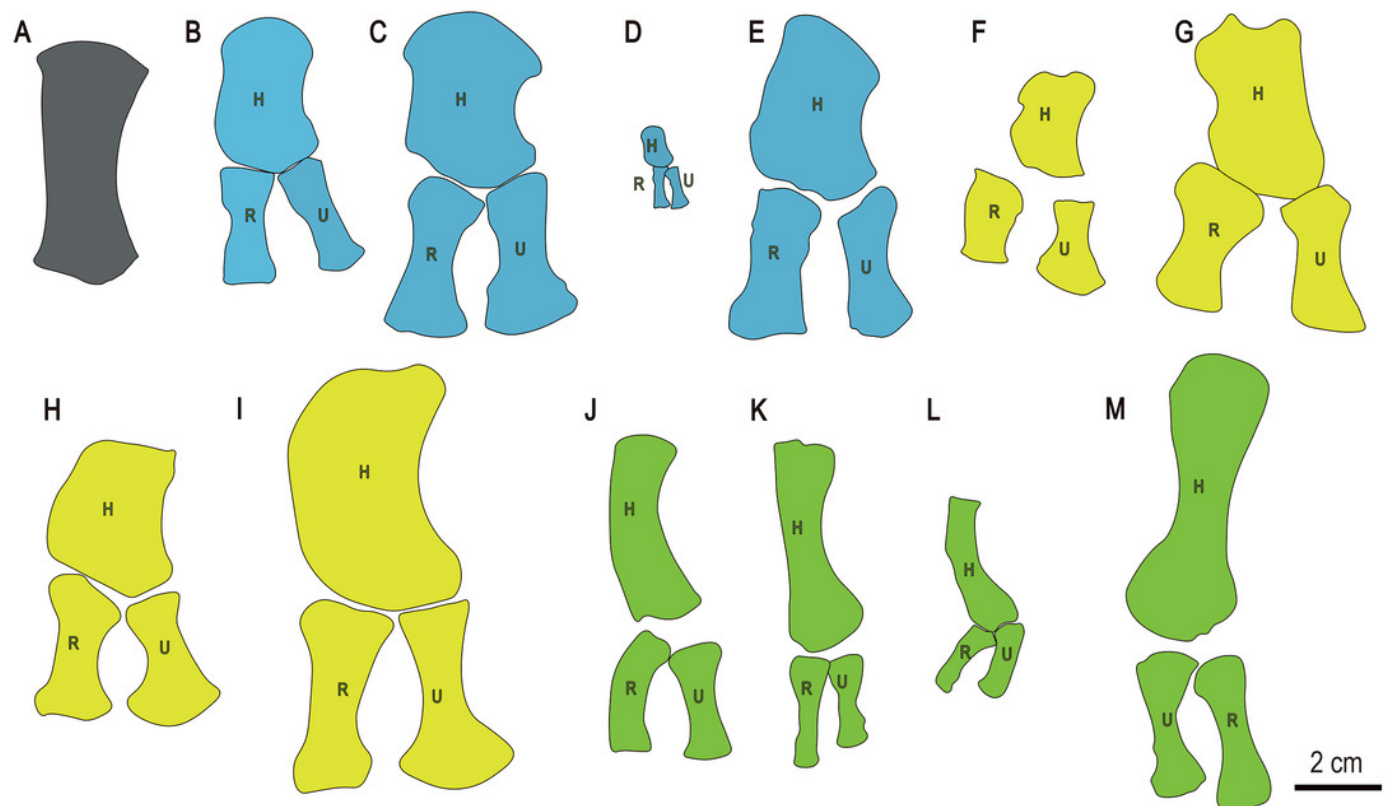
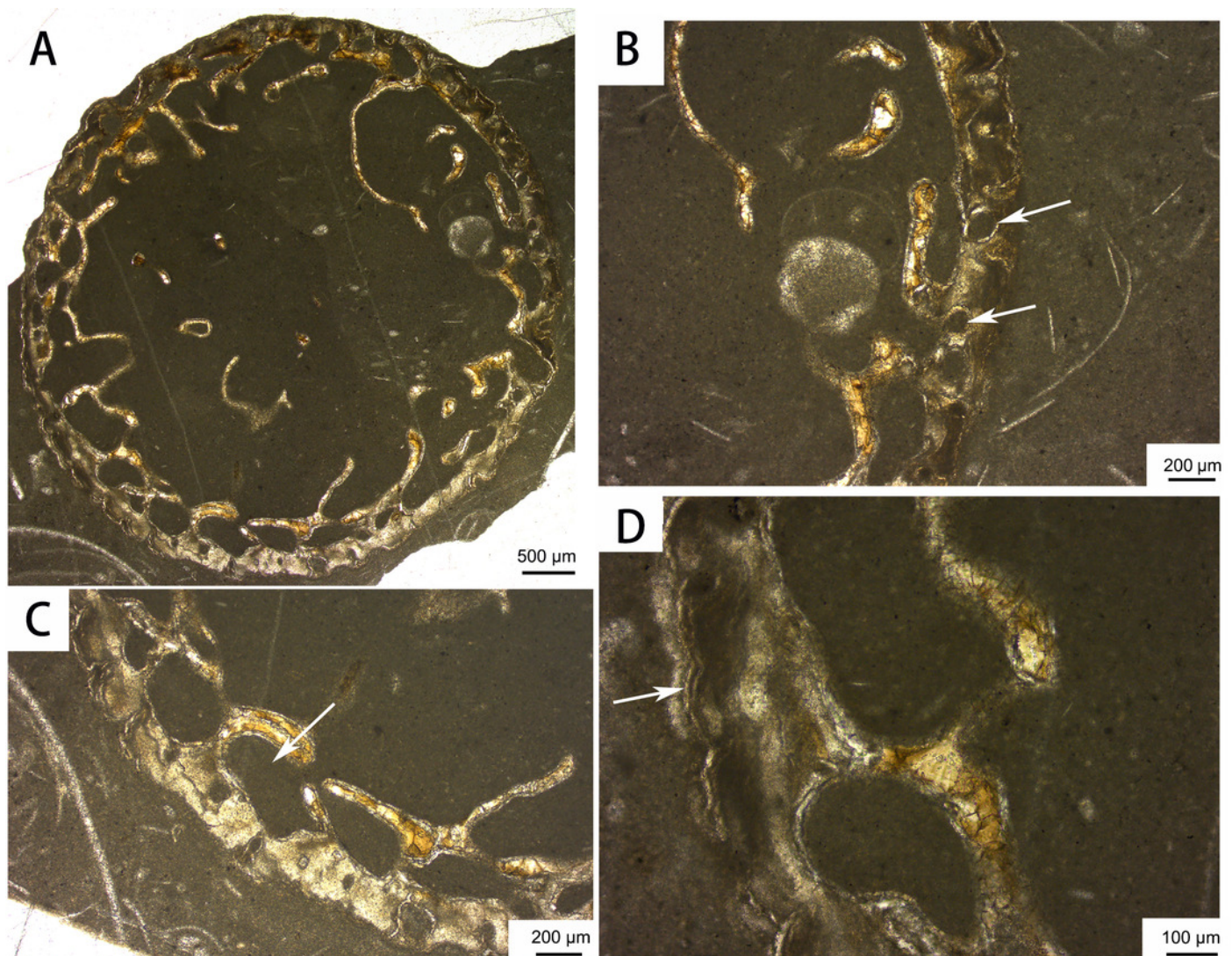



Figure 8

Bone microstructure of the distal part of a rib of *Baisesaurus*.

(A) partial cross section showing large medullary cavity and trabeculae; (B) close-up of peripheral area, with white arrows indicating vascular canals; (C) close-up of peripheral area, with white arrow indicating erosional cavity in cortex; (D) close-up of peripheral area, with white arrow indicating line of arrested growth.

List of some representative ichthyosauromorphs from the Early Triassic.

Locality	Taxon	Stratigraphic horizon	References	Remarks
Spitsbergen, Norway	*Grippia longirostris*	Vikinghøgda Formation	Wiman 1929; Motani 1997; Motani & You 1998a; Motani 2000b; Hansen et al. 2018	-
	Pessopteryx nisseri	Vikinghøgda Formation	Wiman, 1910; Maisch 2010; Engelschiøn et al. 2018	=*Merriamosaurus hulkei* (Maisch & Matzke 2002; Maisch & Matzke 2003a; Maisch, 2010)
	Quasianosteosaurus vikinghoegdai	Vikinghøgda Formation	Maisch & Matzke, 2003b	-
	Omphalosaurus merriami	Vikinghøgda Formation	Wiman, 1910; Maisch, 2010; Sander & Faber, 2003; Ekeheien et al. 2018	
	Isfjordosaurus minor	Vikinghøgda Formation	Wiman, 1910; Motani, 1999	Only a humerus
British Columbia, Canada	*Parvinatator wapitiensis*	Sulphur Mountain Formation	Nicholls & Brinkman, 1995	-
	Gulosaurus helmi	Sulphur Mountain Formation	Cuthbertson et al. 2013	-
	Grippia sp.	Sulphur Mountain Formation	Brinkman et al. 1992	-
	Utatsusaurus sp.	Sulphur Mountain Formation	Nicholls & Brinkman, 1993	-
Anhui, China	*Chaohusaurus geishanensis*	Nanlinghu Formation	Young & Dong, 1972c	-
	Chaohusaurus chaoxianensis	Nanlinghu Formation	Chen,1985; Motani et al. 2015b	=*Chensaurus chaoxianensis* (Mazin, 1991) =*Anhuisaurus chaoxianensis* (Chen, 1985)
	Chaohusaurus brevifemoralis	Nanlinghu Formation	Huang et al. 2019	-

	Cartorhynchus lenticarpus	Nanlinghu Formation	Motani et al. 2015a	-
	Sclerocormus breviceps	Nanlinghu Formation	Jiang et al. 2016	-
Hubei, China	*Chaohusaurus zhangjiawanensis*	Jialingjiang Formation	Chen et al. 2013	-
Miyagi, Japan	*Utatsusaurus hataii*	Osawa Formation	Shikama et al. 1978	-
Southern Peninsula, Thailand	*Thaisaurus chonglakmanii*	Unrecorded horizon	Mazin et al. 1991; Liu et al. 2018	Well preserved but not yet described in detail

Measurements of the preserved centra and neural arches (in mm) of CUGW VH107.

Centra			
Centrum No.	Max Length (mm)	Max Height (mm)	H/L Ratio
1	25.7	32.7	1.3
2	31.7	-	-
3	25.4	30.1	1.2
4	29.6	35.9	1.2
5	30.1	31.1	1.0
6	26.5	-	-
7	25.6	29.1	1.1
8	29.1	32.7	1.1
9	24.7	30.2	1.2
10	29.9	31.5	1.1
11	-	31.7	-
12	-	30.2	-
Neural Arches			
Neural Arch No.	Max Length (mm)	Max Height (mm)	
1	14.8	46.9	
2	-	47.9	
3	-	49.1	
4	-	47.3	
5	17.3	47.5	
6	17.5	49.6	
7	18.1	48.8	