

1 The first lizard fossil (Reptilia: Squamata) from the Mesozoic of South Korea

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10 Abstract

11 Late Cretaceous deposits in Mongolia, Chinese Inner Mongolia, and, more recently, southern China,
12 have yielded a rich and diverse lizard assemblage. Here we describe the remains of a new terrestrial
13 lizard, *Asprosaurus bibongria* gen. et sp. nov., from the Late Cretaceous of South Korea. It represents
14 the first record of a Mesozoic lizard from the Korean Peninsula and, although incomplete, is
15 exceptional in its very large size. Characters of the mandible place support attribution to Anguimorpha,
16 with the closest similarities being to monstersaurs, the group represented today by the venomous
17 North American Beaded lizards and Gila Monsters, genus *Heloderma*. This group is well-represented
18 in the Late Cretaceous of eastern Asia, and the remains of large monstersaurs have been recovered
19 from several dinosaur egg localities, suggesting dietary preferences similar to those of the living
20 genus. The new Korean lizard, recovered from the Boseong Bibong-ri Dinosaur Egg Site, fits the
21 same pattern.

22 **Key words:** Squamata - lizard - Late Cretaceous - Anguimorpha - Monstersauria - Dinosaur eggs

23 1. Introduction

24 Cretaceous nonmarine deposits are well exposed along the southern coast of South Korea, and many
25 fossil sites have been reported from these deposits (e.g., Dong et al., 2001; Lee et al., 2001; Lim et al.,
26 2001; Yun and Yang, 2001; Hwang et al., 2002; Huh et al., 2003; Yun et al., 2004; Kim et al., 2005;
27 Lee and Lee, 2007; Huh et al., 2011). Boseong Bibong-ri Dinosaur Egg Site, located in Bibong-ri,
28 Deungnyang-myeon, Boseong-gun, Jeollanam-do, is one of the richest localities for dinosaur eggs in
29 South Korea (Huh et al., 1999a; 1999b; Huh and Zelenitsky, 2002; Paik et al., 2004; Huh et al., 2006;
30 Paik et al., 2012; Huh et al., 2013) (Fig. 1). It was first excavated in 1999 and has yielded various

31 specimens including dinosaur eggs (more than 200 individuals), a possible testudine egg (Huh and
32 Zelenitsky, 2002), and body fossils of a small ornithomimid dinosaur, *Koreanosaurus boseongensis* (Huh
33 et al., 2011) (Fig. 2). Five separate fossiliferous sites have been reported from the area (Huh et al.,
34 2006) (Fig. 1, C), and the dinosaur egg clutches appear in at least four separate layers at all five sites
35 (Fig. 2). Although egg fossils are abundant, vertebrate body fossils are rare in this area.

36 In 2000, an associated vertebrate body fossil (Fig. 3) was collected from site 1 (Fig. 2), and was
37 temporally classified as testudine (Huh et al., 2006). However, preparation and re-examination has
38 shown this specimen to be a large lizard (Squamata). It is named, described and discussed herein,
39 and represents the first Mesozoic lizard fossil recorded from the Korean Peninsula.

40 **2. Geological setting and materials**

41 The rock units that form the Boseong Bibong-ri Dinosaur Egg Site are epiclastic, pyroclastic, and
42 intermediate to acidic volcanic rocks. They can be divided into the Seonso Conglomerate, Seonso
43 Formation, Pilbong Rhyolite, Mudeungsan Flow, Obongsan Brecciated Tuff, and Docheonri Rhyolite,
44 in stratigraphic order (Hwang and Cheong, 1968; Huh et al., 1999a; Paik et al., 2004; Huh et al.,
45 2006). The dinosaur egg-bearing layers, the Seonso Conglomerate and the overlying Seonso
46 Formation, are primarily clastic, and are composed of conglomerates, sandstones, and mudstones
47 (Huh et al., 1999a; Paik et al., 2004; Huh et al., 2006) (Fig. 2). Isotope analysis of the overlying
48 Seonso Ashflow Tuff and the underlying Pilbong Rhyolite, suggests that the fossil-bearing deposits
49 are Santonian to Campanian in age (e.g., Huh et al., 2006; Kim, 2008; Kim et al., 2008).

50 Palynological records and the common development of palaeosols within the layers (Fig. 2),
51 indicates that the paleoenvironment of this area was warm and dry (Choi, 1985; Paik and Kim, 1995;
52 Paik et al., 1997; Paik and Lee, 1998; Paik et al., 2004). The abundance of channel deposits with
53 erosive bases suggests that a fluvial system was involved during the formation of this area (Paik et al.,
54 2004) (Fig. 2).

55 The associated body fossil (Fig. 3), described in this paper, was collected during the first
56 excavation period in 2000, from site 1 (Fig. 2), which is located in the most southern part of the
57 Boseong Bibong-ri Dinosaur Egg Site (Fig. 1, C). The specimen was in situ, preserved in a thick
58 purple sandy mudstone layer between a lower cross-laminated coarse grained sandstone horizon and
59 an upper horizon consisting channel lag gravels (Fig. 2). No other fossils were collected from the
60 same horizon, but dinosaur egg clutches were excavated from above and below the specimen (Fig. 2).

61 Preliminary preparation work was done during 2000, with minor additional preparation from 2005 to
62 2010. The final preparation work (2012-2013) was done by the first author.

63 **3. Systematic paleontology**

64 **Squamata** Oppel, 1811

65 **Anguimorpha** Fürbringer, 1900

66 cf **Monstersauria** Norell and Gao, 1997

67 ***Asprosaurus bibongria* gen. et sp. nov.**

68 **3.1 Derivation of name**

69 'aspros', meaning 'white' in Greek (since the specimen is white in color), 'saurus', meaning 'lizard' in
70 Latin, and 'bibongri', from the type locality where the holotype was found.

71 **3.2 Holotype**

72 KDRC-BB4 (Korea Dinosaur Research Center - Boseong Bone fossil Catalogue Number), an
73 associated specimen, originally on a single block (Fig. 3) but with each element now prepared out and
74 comprising a right jugal, partial squamosal, partial left quadrate, left pterygoid, partial left mandible,
75 left scapulocoracoid, left humerus, a metacarpal, part of a rib or clavicle, and several unidentified
76 bone fragments.

77 **3.3 Type Locality**

78 From Site 1, southern coast of Seonso Village, Bibong-ri, Boseong County, Chollanam-do Province,
79 South Korea (north latitude : 34° 40' ~ 34° 50', east longitude : 127° 00' ~ 127° 15').

80 **3.4 Stratigraphic horizon**

81 From the Upper Cretaceous (?Santonian - Campanian) Seonso Conglomerate.

82 **3.5 Diagnosis**

83 A very large, robust-limbed, terrestrial lizard (skull length ~180-200mm) resembling monstersaurian
84 and varaniform anguimorphs (sensu Conrad et al., 2011a) in having a deep, almost vertical dentary
85 alveolar margin with no subdental shelf; a Meckelian fossa that is anteroventrally positioned; a small
86 adductor fossa; no posterodorsal coronoid process on the dentary; a reduced splenial-dentary contact;
87 and a splenial that does not extend posterior to the apex of the coronoid process. Differs from
88 previously described Asian Late Cretaceous anguimorph lizards including *Cherminotus*, *Chianghsia*,
89 *Estesia*, *Gobiderma*, *Ovöo*, *Paravaranus*, *Parviderma*, *Proplatynotia*, *Saniwides*, and *Telmasaurus* in
90 the combination of a strongly angulated jugal in which the postorbital process is wider than the

91 suborbital process; a complete postorbital bar; a concave medial margin to the pterygoid palatal plate;
92 a straight dentary-postdentary contact but no intramandibular joint; a posteriorly shallow, rather than
93 triangular, splenial; no cranial osteoderms; and a convexo-concave ventral jaw margin.

94 **3.6 Description**

95 The specimen was recovered as a close association of disarticulated elements (Fig. 3). Given the
96 rarity of body fossils in the deposit, we can be confident that the bones belong to a single individual.
97 Some bones, like the left pterygoid, left scapulocoracoid, left humerus, and a metacarpal are well-
98 preserved. Other bones are more fragmentary and there was further damage during preparation,
99 before the specimen was identified as a lizard. The individual was clearly adult, as evidenced by:
100 closed mandibular sutures; humeral epiphyses fused to the shaft; strong humeral rugosities and
101 muscle attachment sites; and closed scapulocoracoid suture.

102 **3.6.1 Cranial**

103 The skull is represented by a jugal, squamosal, partial quadrate, pterygoid, and mandible, all but the
104 jugal are apparently from the left side of the individual.

105 The jugal (Fig. 4) is a laterally flattened, biradiate bone, the two rami of which are set at almost
106 90° to one another. One ramus is broad and mediolaterally flattened. It bears a deep medial facet at
107 its distal end (Fig. 4, B), although this was damaged during preparation. The other ramus is narrower
108 and rounded to triangular in cross-section. It bears a narrow facet along the external (non-orbital)
109 surface. As originally preserved, it was obviously longer. Photographs of the original block (Fig. 3)
110 show there was a short distal section separated from the remainder by a small space. By comparison
111 with other Asian anguimorphs like *Gobiderma* and *Estesia*, this bone, in external view, has the
112 appearance of a left jugal, with a deep suborbital ramus and a long, tapering postorbital one. However,
113 the positions of the facets are not consistent with that interpretation, particularly the large deep facet
114 on the internal surface of the broader ramus. The facet for the maxilla and/or for the ectopterygoid
115 would be ventral not dorsal. We therefore interpret the bone as a right jugal, such that the narrow
116 ramus is suborbital with a long narrow ventral facet for the maxilla. If this is correct, then the jugal may
117 have excluded the maxilla from the suborbital margin, but is likely to have been confined to its dorsal
118 rim. The broader, mediolaterally compressed ramus formed the postorbital margin, with the
119 dorsomedial facet receiving a flange from the postorbital or postorbitofrontal. There is no additional
120 posterior facet and it is unlikely that the jugal and squamosal were in contact. The postorbital ramus

121 bears a dorsolateral concavity, but this does not appear to represent an articulation surface.
122 Posteroventrally, the bone terminates in a rounded angle. This is relatively smooth laterally, but bears
123 a posteromedial rugosity that may have been associated with the lateral head of the ectopterygoid or
124 a thickening of the temporal fascia.

125 A slender, curved and mediolaterally compressed rod-like element is interpreted as the posterior
126 part of a squamosal (Fig. 5, A), probably the left. The bone has the classic 'hockey-stick' shape found
127 in many lizards with the downcurved tip meeting the dorsal head of the quadrate.

128 The quadrate may be represented by the ventral part of a robust shaft and narrower articular
129 surface (Fig. 5, B, C). The dorsal tympanic crest has been lost, but from traces of the lateral conch,
130 this appears also to be a left bone. A large concavity is present on the medial side, presumably for
131 muscle attachment.

132 The left pterygoid (Fig. 5, D, E) is relatively well-preserved. It has a wide, flat, palatine plate that
133 appears triangular but is broken anteriorly. The medial border of the palatal plate bears a conspicuous
134 emargination, adding to the posterior breadth of the interpterygoid vacuity. Laterally, the palatal plate
135 tapers into a faceted process that articulated with the ectopterygoid. As preserved, the palatal surface
136 appears smooth, but unfortunately the anterior edge is eroded, so it is impossible to know whether
137 pterygoid teeth were present. Posteriorly, the plate narrows, meeting the quadrate ramus at a fairly
138 sharp angle. The articular surface for the basipterygoid process of the basisphenoid lies at the medial
139 point of the angulation. Dorsal to it, the bone bears a narrow, elongated pit for the epipterygoid (fossa
140 columellae). The quadrate process itself is straight and narrow, with a triangular cross-section. A
141 longitudinal ventral groove accommodated part of the pterygoideus muscle. The strong angulation of
142 the palatal plate in relation to the quadrate process suggests the interpterygoid vacuity may have
143 been quite wide.

144 As preserved, the left mandible (Fig. 6) is relatively long and slender. It has a somewhat sigmoid
145 shape, due to the pronounced posteroventral concavity and an apparent reduction in posterior height.
146 The individual elements are in articulation but the bones have separated slightly at the sutures,
147 suggesting these were not fully closed at death. The dentary tapers slightly from posterior to anterior.
148 The anterior part is lost and it is difficult to judge the original length. The alveolar margin is
149 represented by a deep, almost vertical surface with no subdental shelf or ridge (Fig. 6, C). However,
150 no teeth are preserved nor are tooth positions evident. Either this region was originally edentulous or

151 the tooth sockets were shallow and their edges have been eroded. Laterally, there are no
152 neurovascular foramina on this portion of the bone. Medially, the posterior part of the Meckelian fossa
153 is filled by a splenial, which tapers postero-anteriorly and has a small exposure on the anterolateral
154 surface (Fig. 6, C), indicating that the Meckelian fossa was more ventral than medial in its anterior
155 part. Towards its anterior end, the dorsal margin of the splenial is emarginated by a long low notch,
156 interpreted here as the margin of an anterior inferior alveolar foramen lying between the splenial and
157 dentary. If this is correct, it is likely that there was originally a significant length of dentary anterior to
158 this point. Ventral, and slightly posterior to this emargination the splenial bears an ovoid depression
159 which may represent the anterior mylohyoid foramen. There is a relatively wide gap between the
160 dorsal margin of the splenial and the dentary, suggesting connective tissue attachment in life,
161 Posteriorly, the splenial overlaps the angular, surangular, and coronoid, but does not extend to the
162 level of the coronoid apex and it lacks the strongly triangular shape seen in some monstersaurs (e.g.
163 *Heloderma*, *Gobiderma*) (Fig. 6, C). This could be due to damage, but it is not obviously so. The
164 dentary-postdentary overlap is not extensive, and the lateral suture between the dentary and
165 surangular is almost vertical, but slightly imbricated (Fig. 6, A). However, there was not an
166 intramandibular joint. Where the dentary and surangular have pulled apart slightly, it is clear that a
167 flange from the surangular passed medial to the dentary, but it is not possible to judge how far this
168 reached anteriorly. There is no posterodorsal dentary coronoid process. The coronoid itself is
169 preserved in its antero- and posteroventral parts, although the coronoid process is broken through its
170 base. The anterior and posterior rami are roughly equal in length. The coronoid lies entirely medial to
171 the surangular, but its articulation with the dentary is a little more complex. The surangular and
172 dentary meet lateral to the coronoid but the posterodorsal margin of the dentary turns through an
173 angle of almost 90 degrees to the long axis of the surangular, forming a distinct 'corner' into which the
174 anterolateral edge of the coronoid fits (Fig. 6, B). At this point, therefore, the coronoid abuts the
175 dentary. However, an anterior flange of the coronoid overlaps the medial surface of the dentary just
176 behind the alveolar margin. Thus the coronoid both abuts and clasps the posterodorsal end of the
177 dentary. Seen in medial view, however (Fig. 6, C), only the overlap is apparent. The coronoid
178 posteroventral process extends from the dorsal margin of the surangular to the edge of the small
179 mandibular fossa. The angular is long and thin, with a relatively narrow exposure on both the medial
180 and lateral surfaces of the mandible. Medially, it lies below the prearticular, which forms the ventral

181 margin of the mandibular fossa. The surface of the angular is damaged but seems to be pierced
182 laterally at the level of the dentary-surangular suture. This may be a posterior mylohyoid foramen.

183 The original photographs show no evidence of associated osteoderms, but without the skull roof
184 bones (frontal, parietal) we cannot be certain whether they were originally completely absent.

185 **3.6.2 Postcranial skeleton**

186 The postcranial skeleton is represented by a left scapulocoracoid and humerus, as well as a single
187 metapodial element and a curved element that may have been a rib or clavicle.

188 The left scapulocoracoid (Fig. 8, A, B) is broad and relatively flat with a large posterolateral
189 glenoid fossa. The two components are completely fused, although a trace of the suture is visible
190 medially (note that there is also a deep crack across the bone ventral to the real suture line). The
191 coracoid plate is perforated by a large coracoid foramen. Ventromedially, it is moderately expanded
192 and bears a curved posterior extension (metacoracoid process). This margin is thickened and, in life,
193 would have supported the epicoracoid cartilage. Further anteriorly, the bone is thinner and partially
194 damaged (but see below). The scapula component is relatively short with a wide, rugose dorsal
195 margin that would have been continued in life by the cartilage suprascapula. Overall, as is typical, the
196 scapulocoracoid is thickest along the posterior margin and thins anteriorly. The anterior margin is
197 damaged in part, but there is certainly a scapulocoracoid emargination. A thickening at the level of the
198 scapulocoracoid suture (base of the procoracoid process) separates the scapulocoracoid
199 emargination from a second emargination at the level of the coracoid foramen (anterior coracoid
200 emargination). This, in turn, is limited anteroventrally by a second thickening, below which the bone
201 appears to thin again. However, it is not clear whether there is an accessory coracoid emargination at
202 this position.

203 On the original block (Fig. 3), a curved bone lies close to the dorsal border of the scapula. Only
204 one half of the bone is preserved, but the impression on the matrix appears to become wider. This
205 could be a rib, but the difference in the width of the two ends suggests it may be a clavicle.

206 The left humerus (Fig. 7) is generally well-preserved, although parts of the distal condylar
207 surfaces are missing. The epiphyses are fully fused. Overall, the bone is robust with strong muscle
208 attachment crests and rugosities. The broad proximal and distal ends are set at almost 90° to one
209 another and are separated by a relatively short, narrow shaft. The shaft is straight and sub-cylindrical
210 in cranial view, and is slightly curved anteriorly in lateral view. The proximal and distal ends are both

211 about 40 mm in width. At the proximal end, there is a screw-shaped surface for articulation with the
212 glenoid cavity. Close to it, and pointing slightly laterally, is a strong area of attachment for the
213 subcoracoscapularis muscle. On the opposite side, a prominent deltopectoral crest curves slightly
214 anteriorly, forming a deep proximal concavity. At the distal end of the bone, a deep concavity, widest
215 distally, separates the ectepicondyle and entepicondyle. An ectepicondylar foramen is visible in
216 superior view (Fig. 7, C).

217 One metapodial element is preserved. From its size and length, it is probably a metacarpal (Fig.
218 8, C). The bone is slender, with proximal and distal expansions.

219 **3.7 Remarks**

220 Few of the described Late Cretaceous Asian taxa preserve forelimb elements to compare with the
221 very robust humerus of *Asprosaurus*. However, the scapulocoracoid resembles that of *Gobiderma*
222 and differs from *Heloderma* in having both scapulocoracoid and anterior coracoid emarginations, but
223 differs from *Gobiderma* in that the scapula component is shorter and of similar width throughout
224 (dorsally expanded in *Gobiderma*). *Asprosaurus* is also substantially larger than any Late Cretaceous
225 terrestrial lizard described to date, although size should be used with caution in diagnosis, particularly
226 with monotypic specimens. Based on jaw, pterygoid and jugal proportions, the skull of *Asprosaurus* is
227 estimated to have been ~180-200 mm in length. This compares to those of the largest Asian
228 Cretaceous anguimorphs currently known, *Gobiderma* (~60mm, Conrad et al., 2011b), *Telmasaurus*
229 (~55-70mm, Conrad et al., 2011b), *Estesia* (~125mm, Conrad et al., 2011b) and *Chianghsia* (175-
230 180mm, Mo et al., 2012).

231 **4. Phylogenetic position**

232 KDRC-BB4 represents parts of a single, mature reptile skeleton (fused scapulocoracoid components,
233 humeral epiphyses fused to shaft) that was large and terrestrial (robust humerus with powerful muscle
234 crests). The morphology of the scapulocoracoid (fused components, emarginated anterior margin)
235 and the slender curved squamosal identify this as a squamate, not a testudine as originally proposed.
236 Within squamates, the deep dentary alveolar margin with no subdental shelf is suggestive, even
237 without the teeth, of the kind of modified pleurodonty (Zaher and Rieppel, 1999) found in anguimorphs
238 (Conrad, 2008; Conrad et al., 2011a; 2011b; Gauthier et al., 2012). Other features of the mandible,
239 including the reduced mandibular fossa, anteroventral Meckelian canal, and shortened splenial are
240 consistent with this attribution.

241 In order to explore the phylogenetic position of *Asprosaurus*, we coded it into two recent
242 morphological data matrices - that of Conrad et al. (2011b) and of Gauthier et al. (2012).

243 Gauthier et al. (2012) represents the largest morphological character matrix to date (610
244 characters; 192 taxa). As they ran their analysis using PAUP, we used the same programme, with
245 their ordering of characters. A heuristic search yielded 179 equally parsimonious trees (L=5196;
246 CI=0.187; RC=0.148), of which a strict consensus placed *Asprosaurus* in an unresolved polytomy with
247 *Lanthanotus*, *Saniwa*, *Varanus* (3 species), *Heloderma* (2 species), and *Aiolosaurus*, *Estesia* and then
248 *Gobiderma* were placed as consecutive outgroups to this clade. We then ran a Branch and Bound
249 analysis with 15 taxa (the 11 listed above + *Shinisaurus*, *Xenosaurus*, *Elgaria* and *Anniella*, the latter
250 three as a monophyletic outgroup). This second analysis resulted in six trees (L=520; CI=0.621;
251 RC=0.38), in which *Asprosaurus* moved between a helodermatid clade (2 trees) and a varanid clade
252 (4 trees). Its position in both the strict consensus and an Adam's consensus was therefore unresolved
253 with respect to these two positions, although a Bootstrap analysis gave weak (56%) support to a
254 relationship with varanids.

255 However, extensive though the Gauthier et al. (2012) matrix is, it included few of the
256 fragmentary Late Cretaceous anguimorph taxa that cluster around *Heloderma* and *Varanus* in other
257 analyses (e.g., Conrad, 2008). We therefore coded *Asprosaurus* into the anguimorph matrix of
258 Conrad et al. (2011a), adding the genus *Chianghsia* (Mo et al., 2012) from southern China and using
259 *Gephyrosaurus*, rather than *Sphenodon* (which was omitted) as outgroup, but otherwise using their
260 characters and ordering. This analysis was run with the programme TNT, using the New Technology
261 search with Ratchet (20 iterations, 1000 random addition sequences), followed by a Traditional search
262 using the trees from the Ratchet search as starting trees. The Ratchet analysis yielded two trees
263 (L=1315) which were then used as starting trees for a Traditional Search. This second analysis
264 produced 72000 trees for which we generated Strict Consensus, Combinable Component Consensus,
265 and 70% Majority Rule Consensus trees. In the Strict and Combinable component trees, *Asprosaurus*
266 was placed in an unresolved position within a clade comprising monstersaurs and varaniforms. In the
267 70% MRT (Fig. 9), it lay within Monstersauria (sensu Conrad et al., 2011a; 2011b), one node
268 crownward of *Gobiderma*. However, a bootstrap analysis did not recover this topology.

269 **5. Discussion**

270 **5.1 Phylogenetic position**

271 The phylogenetic analyses described above confirm the squamate affinities of *Asprosaurus* and its
272 placement within Anguimorpha (Gauthier et al., 2012 matrix analysis). There is no support for a
273 relationship with anguids or their fossil relatives (Anguioidea), but the position of *Asprosaurus* in
274 relation to the clades centred on *Heloderma* and *Varanus* remains ambiguous. This is partly due to
275 the fragmentary nature of the material, but it also mirrors a wider controversy as to the relationships of
276 *Heloderma* within Anguimorpha.

277 Most recent cladistic analyses of squamates, whether morphology-only (e.g., Conrad, 2008;
278 Gauthier et al., 2012), molecular (e.g., Townsend et al., 2004; Vidal and Hedges, 2005, 2009; Pyron et
279 al., 2012), or combined data (e.g., Wiens et al., 2010; Conrad et al. 2011a,b), recognize five main
280 clades of living Anguimorpha: Anguidae, *Xenosaurus*, *Shinisaurus*, *Heloderma* and Varanidae
281 (*Varanus+Lanthanotus*). There is general agreement that *Xenosaurus* is more closely related to
282 Anguidae than to Varanidae (e.g., Conrad, 2008; Conrad et al., 2011a; 2011b; Pyron et al., 2012;
283 Wiens et al., 2010; 2012; Jones et al., 2014), providing a dichotomy between anguoid
284 (Anguidae+*Xenosaurus*) and varanid anguimorphs, but there are significant differences in the
285 hypothesized relationships of both *Heloderma* and *Shinisaurus*. The traditional classification, based
286 on morphological characters (e.g., Estes et al., 1988; Lee, 1997; Caldwell, 1999; Conrad, 2008;
287 Conrad et al., 2011a; Gauthier et al., 2012) places *Heloderma* as the sister group of Varanidae
288 (=Varanoidea, Gauthier et al., 2012). However, molecular analyses (e.g., Townsend et al., 2004; Vidal
289 and Hedges, 2005; 2009; Wiens et al., 2012; Pyron et al., 2012; Jones et al., 2014) have consistently
290 found *Heloderma* to be the sister taxon to Anguioidea, a position also proposed in the pioneering work
291 of Camp (1923). Combined morphology-molecular analyses have also tended to support this
292 arrangement (e.g., Wiens et al., 2010), although that of Conrad et al. (2011a) yielded the traditional
293 topology when based only on extant taxa and the 'molecular' topology when fossils were included.
294 *Shinisaurus* is similarly problematic. Estes et al. (1988) grouped *Shinisaurus* and *Xenosaurus* in the
295 Xenosauridae, a position supported by Gauthier et al. (2012). However, molecular analyses (e.g.,
296 Townsend et al., 2004; Vidal and Hedges, 2005; Pyron et al., 2012; Wiens et al., 2012; Jones et al.,
297 2014) have consistently placed *Shinisaurus* closer to Varanidae, as did the morphology-based
298 analysis of Conrad (2008), and the morphology-based, molecular, and combined evidence analyses
299 of Conrad et al. (2011a: but see Conrad et al., 2011b).

300 These differences impact on the placement of fossil taxa. Anguimorpha is well represented in the

301 Late Cretaceous, particularly in China and Mongolia (e.g., Borsuk-Bialynicka, 1984; Gao and Norell,
302 1998; Conrad et al, 2011a; 2011b). Some of these fossil taxa group consistently with Anguidae (e.g.,
303 glyptosaurus), *Xenosaurus* (= Carusioidea, sensu Conrad et al., 2011a), *Shinisaurus* (=Shinisauria,
304 sensu Conrad, 2008), *Heloderma* (=Monstersauria sensu Norell and Gao, 1997, emend. Conrad et al.,
305 2011a; 2011b, but see Gauthier et al., 2012) and Varanidae (=Varaniformes, sensu Conrad, 2008;
306 Conrad et al., 2011a). However, the placement of other taxa (e.g., *Proplatynotia*, *Parviderma*,
307 *Paraderma*, *Palaeosaniwa*, *Necrosaurus*) is less resolved and tends to vary with that of the major
308 clades (e.g., Conrad et al. 2011a; 2011b; Gauthier et al., 2012). *Heloderma* and varanids share many
309 characters (e.g., of tooth morphology and implantation, jaw morphology). Under the traditional
310 classification, these characters were regarded as synapomorphies of 'Varanoidea' and could support
311 inclusion of a fossil within that clade. However, if *Heloderma* and varanids belong to different
312 branches of Anguimorpha, then these characters have arisen convergently and are less informative.
313 This is relevant to placement of *Asprosaurus*. It possesses a suite of characters (no subdental shelf,
314 dentary with no post-coronoid process, dentary with convex ventral margin, splenial not reaching
315 posterior to coronoid apex, dentary contributing to dorsal margin of anterior inferior alveolar foramen)
316 that would support its attribution to Varanoidea (sensu Gauthier et al., 2012), as in the strict
317 consensus trees described above, but could equally support a relationship to either Monstersauria or
318 Varaniformes (sensu Conrad, 2008; Conrad et al., 2011a; 2011b).

319 For *Asprosaurus*, other characters are contradictory, and the absence of teeth further
320 complicates discussion. Like varaniforms, *Asprosaurus* lacks thick pentagonal osteoderms, but it
321 differs in having a strongly angular jugal, a coronoid lacking a long horizontal anterodorsal ramus and
322 posterior displacement of the coronoid process, and an anteriorly expanded surangular. With
323 monstersaurs like *Heloderma* and *Gobiderma*, *Asprosaurus* shares a strongly angulated jugal,
324 straight posterior dentary margin, and convex-concave ventral profile of the mandible, but it lacks their
325 short triangular splenial, enclosure of the anterior inferior alveolar foramen within the splenial (Conrad
326 et al., 2011b), and the characteristic thick osteoderms. In the latter character state, it more closely
327 resembles *Estesia* (Norell et al., 1996; Norell and Gao, 1998), another Mongolian genus usually
328 placed with monstersaurs (but see Yi and Norell, 2010).

329 On balance, *Asprosaurus* appears to be morphologically closer to monstersaurs (whatever their
330 affinity) than to varaniforms, but further material - especially of the dentition, is needed to test this.

331 **5.2 Life history**

332 More than 200 individual dinosaur egg specimens have been collected from the Boseong Bi-bong ri
333 Dinosaur egg site, including the ootaxa *Spheroolithus* (possible hadrosauroid eggs) and
334 *Faveoololithus* (possible sauropod eggs) (Huh and Zelenitsky, 2002). Both *Heloderma* and *Varanus*
335 take the eggs of birds and other reptiles. Although there are no direct evidence of nest raiding, other
336 large Cretaceous anguimorphs, such as *Palaeosaniwa* (Judith River, Montana), *Estesia* (Lizard Hill,
337 Khulsan South Gobi Aimak, Mongolia), and *Chianghsia* (Nankang, China), have been found in direct
338 proximity to dinosaur egg sites (Gilmore, 1928; Norell et al., 1992; Mo et al., 2012). As *Asprosaurus*
339 was recovered from a similar type of locality (Huh et al., 2006) (Fig. 1), it may also have been a nest
340 raider. The robust scapulocoracoid (Fig. 8, A, B) and the large proximal crests on the humerus (Fig. 7)
341 suggest that *Asprosaurus* had powerful forelimb limb muscles, possibly as an adaptation for digging
342 into nests.

343 **6. Conclusion**

344 Specimen KDRC-BB4 is reclassified from testudine to anguimorph squamate, and is named as a new
345 taxon, *Asprosaurus bibongria* gen. et sp. nov. *Asprosaurus* is the first lizard fossil recorded from South
346 Korea and the largest Mesozoic terrestrial lizard known to date. Its phylogenetic position in relation to
347 the extant *Heloderma* and *Varanus* remains uncertain, but this partially reflects a wider uncertainty
348 with respect to the ingroup relationships of Anguimorpha. *Asprosaurus* provides another example of a
349 large predatory lizard found in proximity to a dinosaur egg site.

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493 **Appendix**

494 Coding used in phylogenetic analyses

495 A. Coding for *Asprosaurus* in Conrad et al. (2011a)

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502 B. Coding for *Asprosaurus* in Gauthier et al. (2012)

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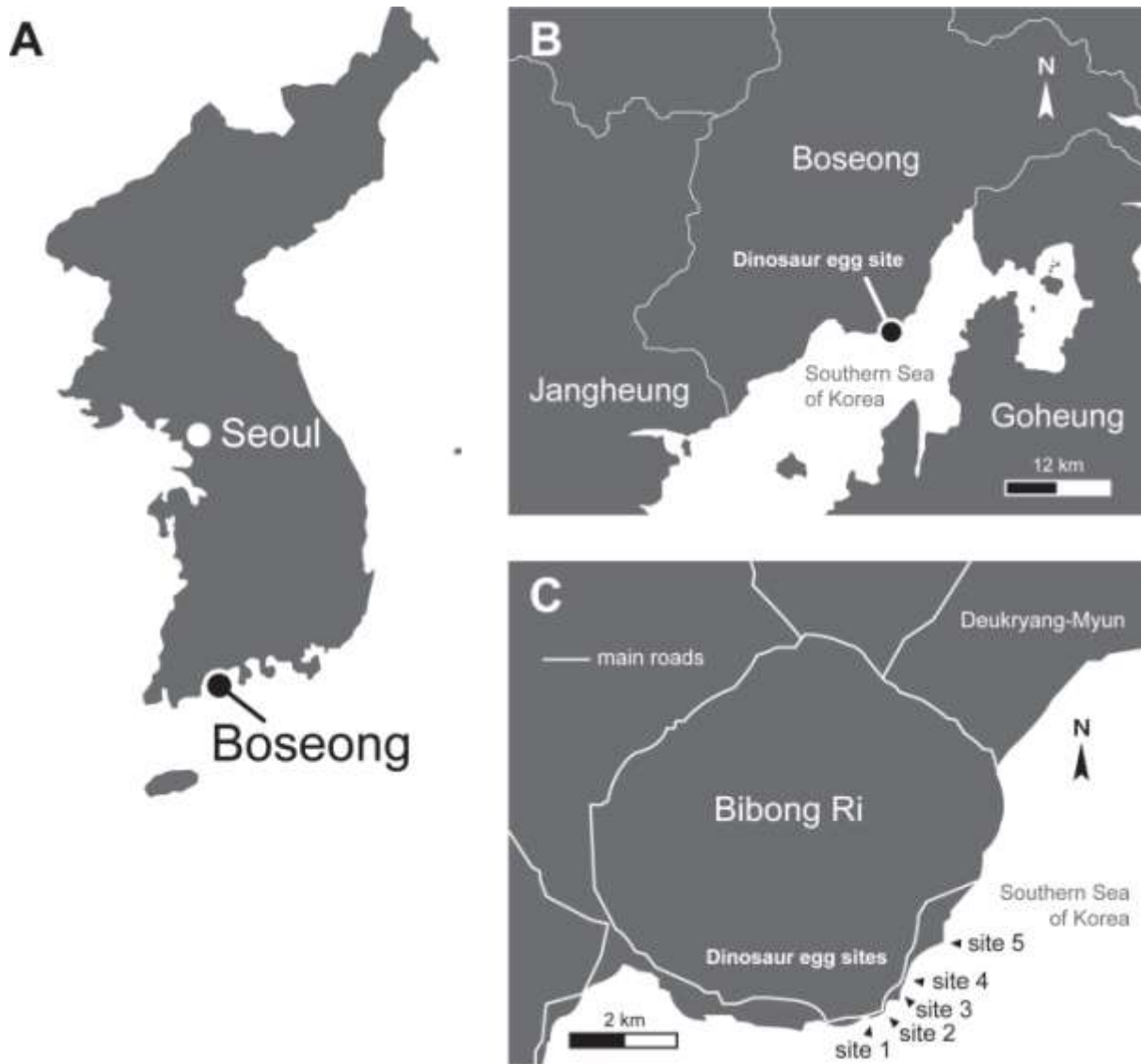
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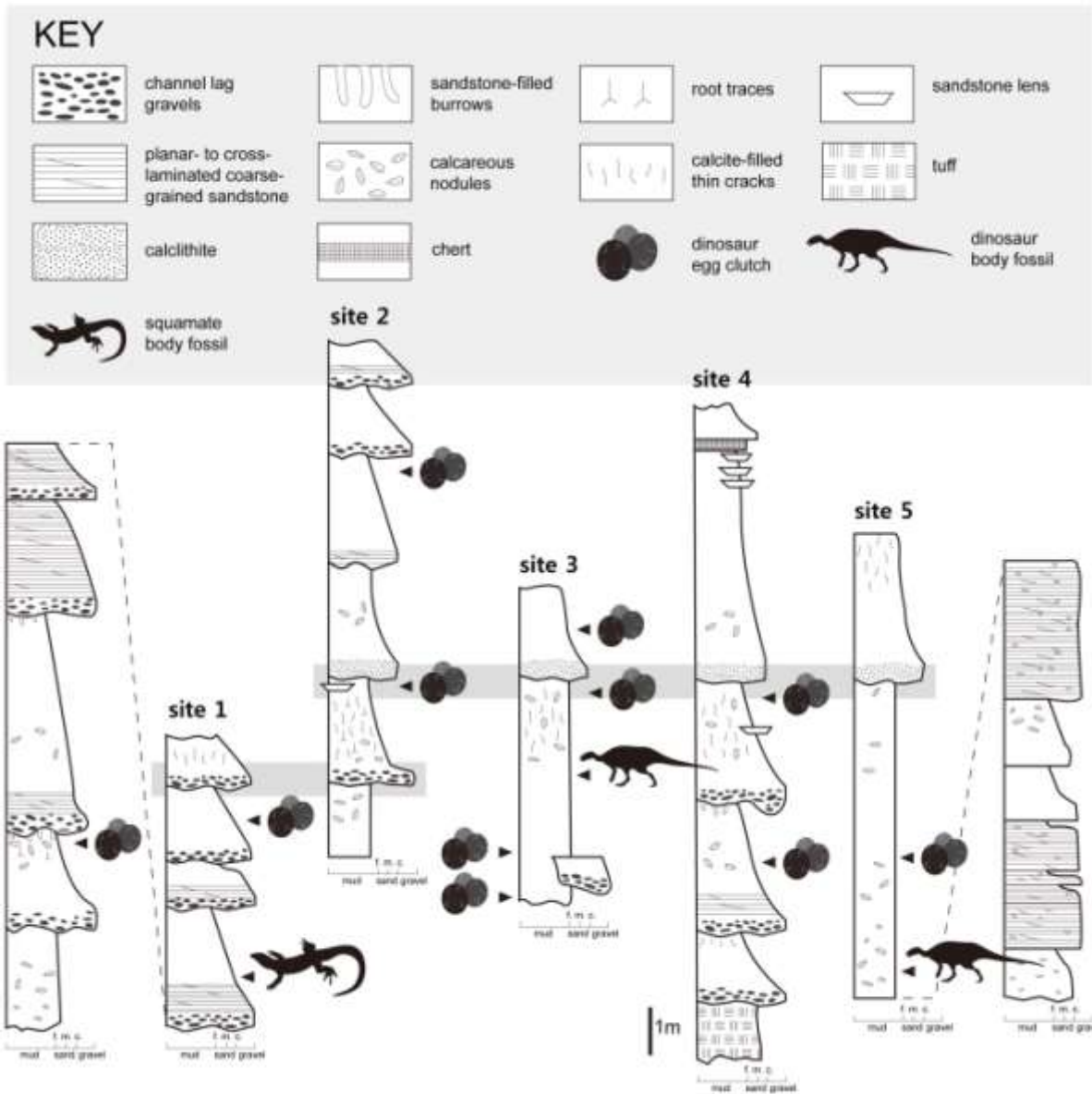
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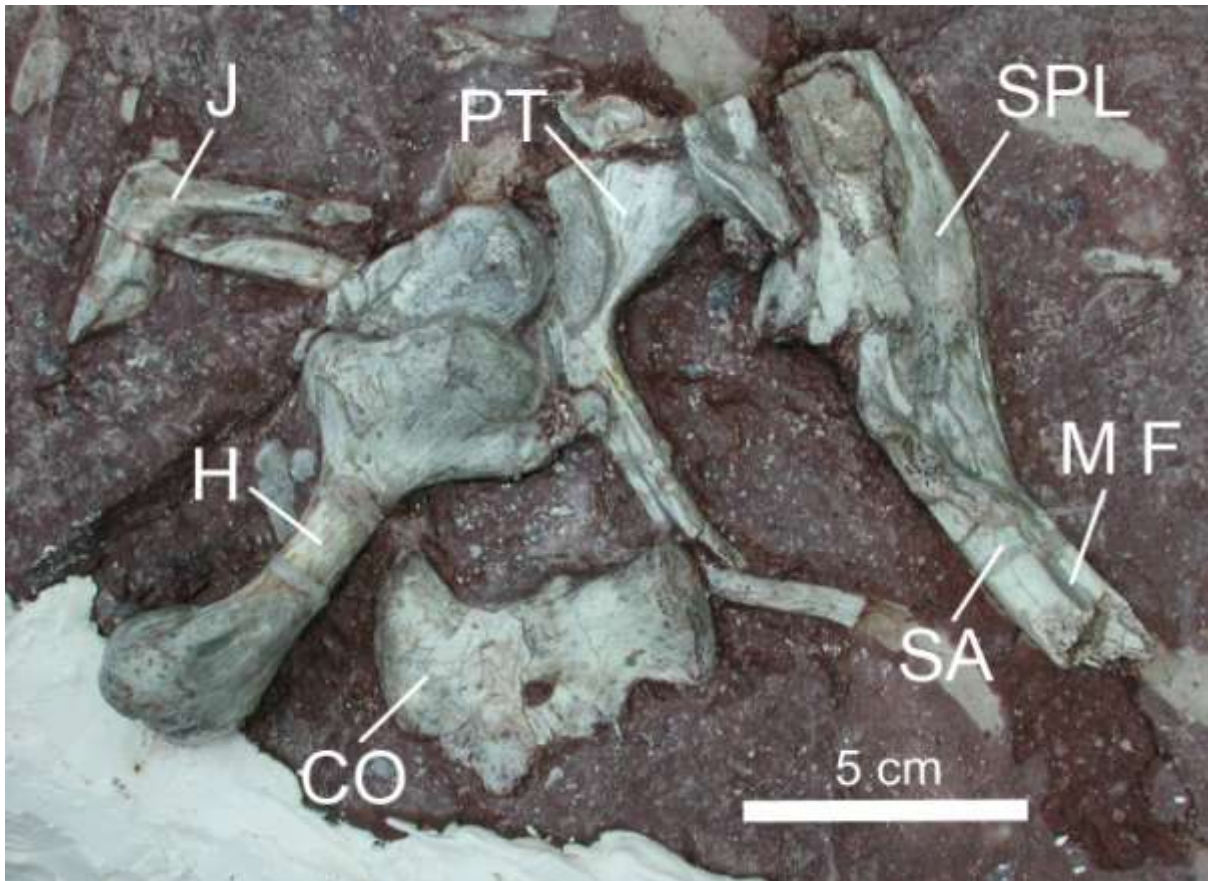
513 **Fig 1.** Location of the Boseong Bibong-ri Dinosaur Egg Site. A, map of the Korean Peninsula; B,
 514 enlarged map of Boseong area; C, enlarged map of Bibong Ri area showing the five main dinosaur
 515 egg sites. Modified from Paik et al., 2004.



516

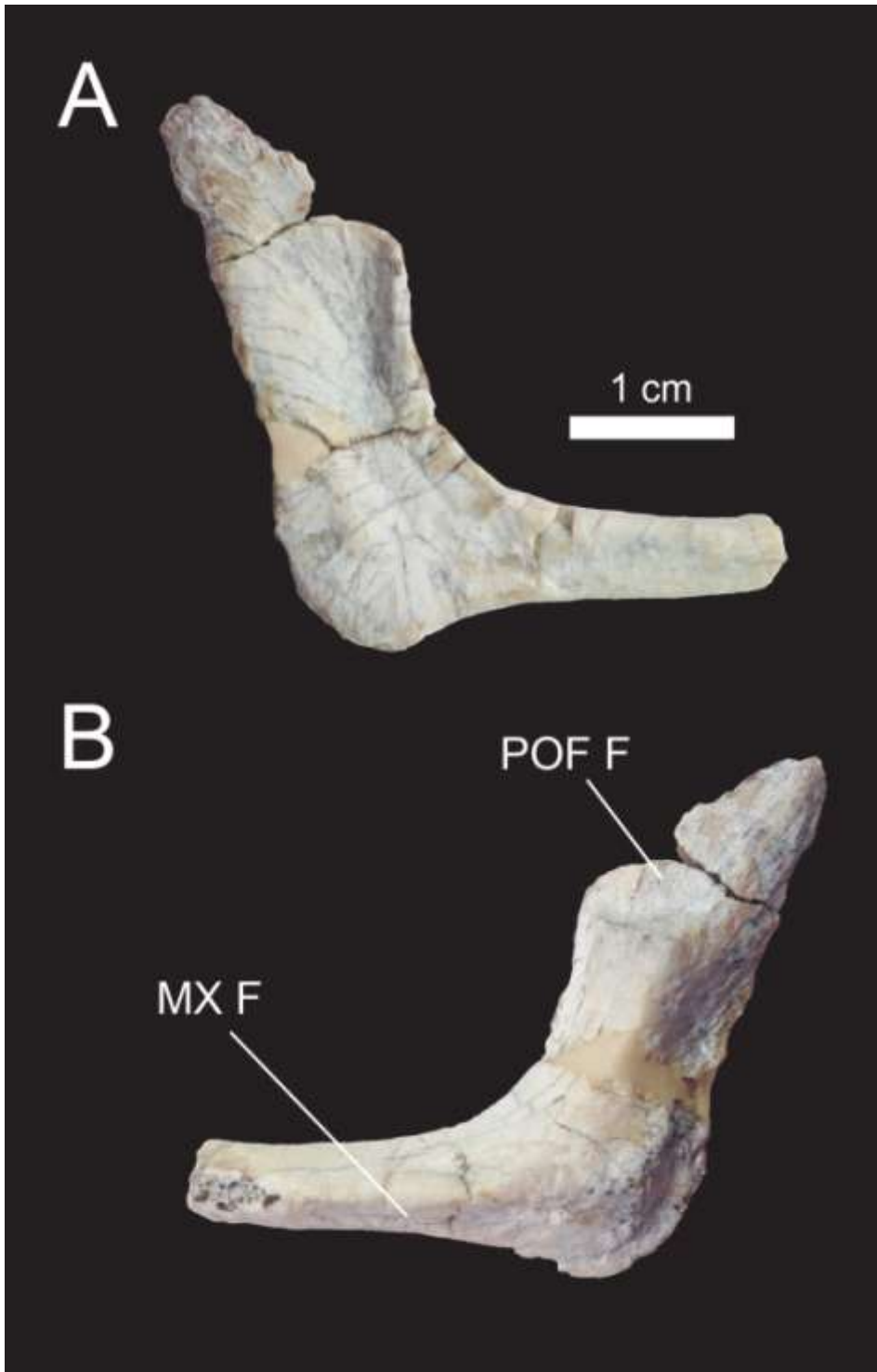
517 **Fig 2.** Stratigraphic sections of five sites of Boseong Dinosaur Egg Site, modified from Huh et al.,

518 1999a; 1999b; Paik et al., 2004; Huh et al., 2006; 2011; Paik et al., 2012.



519

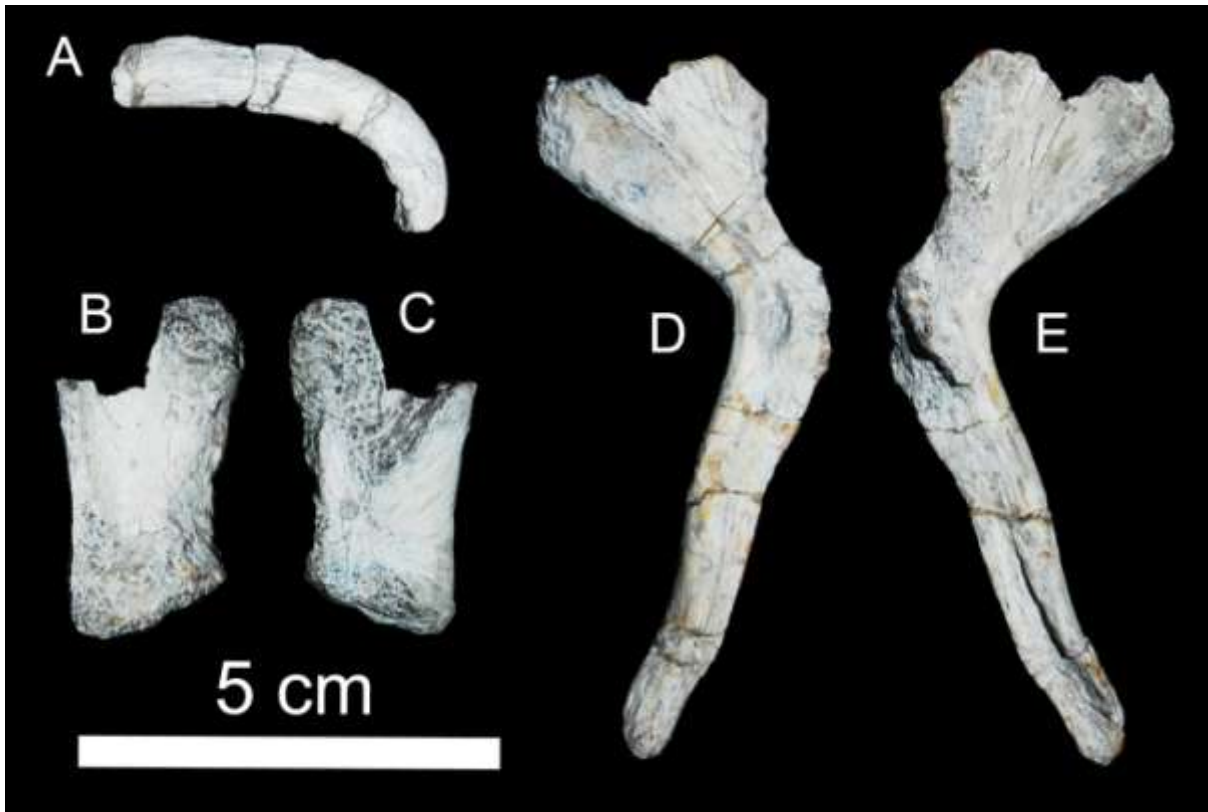
520 **Fig 3.** Photo of associated specimen of *Asprosaurus bibongria* gen. et sp. nov. (holotype; KDRC-BB4)
521 in original single block. Abbreviations CO, scapulocoracoid; H, humerus; J, jugal; M F, mandibular
522 fossa; PT, pterygoid; SA, surangular; SPL, splenial.



523

524 **Fig 4.** Right jugal of *Asprosaurus bibongria* gen. et sp. nov. A, lateral; B, medial view. Abbreviations

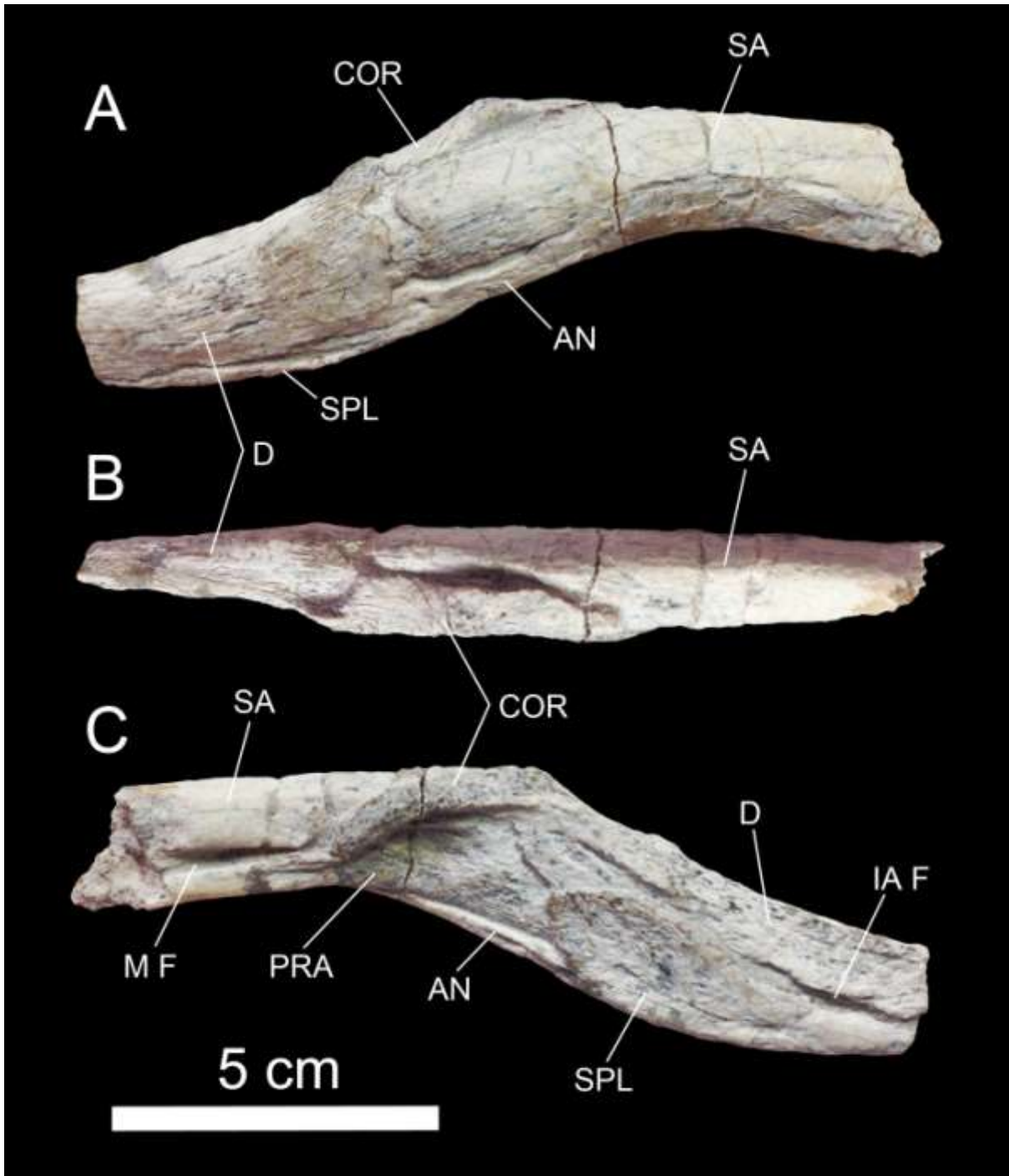
525 MX F, maxillary facet; POF F, Postorbitofrontal facet.



526

527 **Fig 5.** Skull material of *Asprosaurus bibongria* gen. et sp. nov. A, squamosal in lateral view; B, lateral,

528 and C, medial views of left quadrate; D, dorsal, and E, palatal views of left pterygoid.

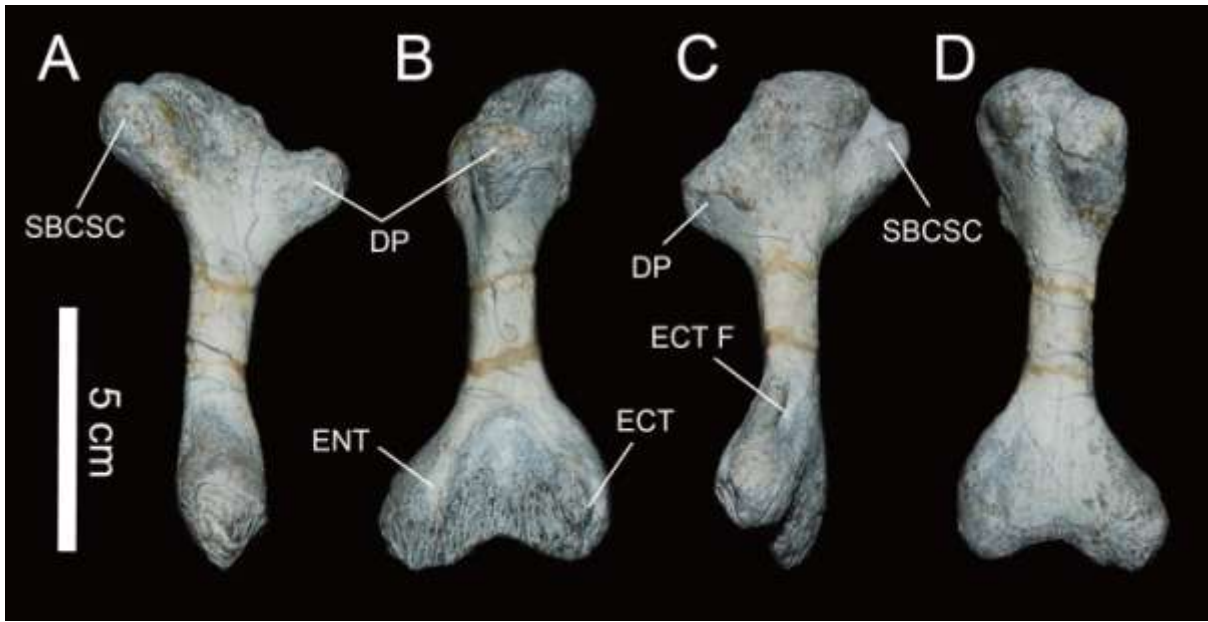


529

530 **Fig 6.** Left mandible of *Asprosaurus bibongria* gen. et sp. nov. A, lateral; B, dorsal; C, medial views.

531 Abbreviations AN, angular; COR, coronoid; D, dentary; IA F, inferior alveolar foramen; M F,

532 mandibular fossa; PRA, prearticular; SA, surangular; SPL, splenial.

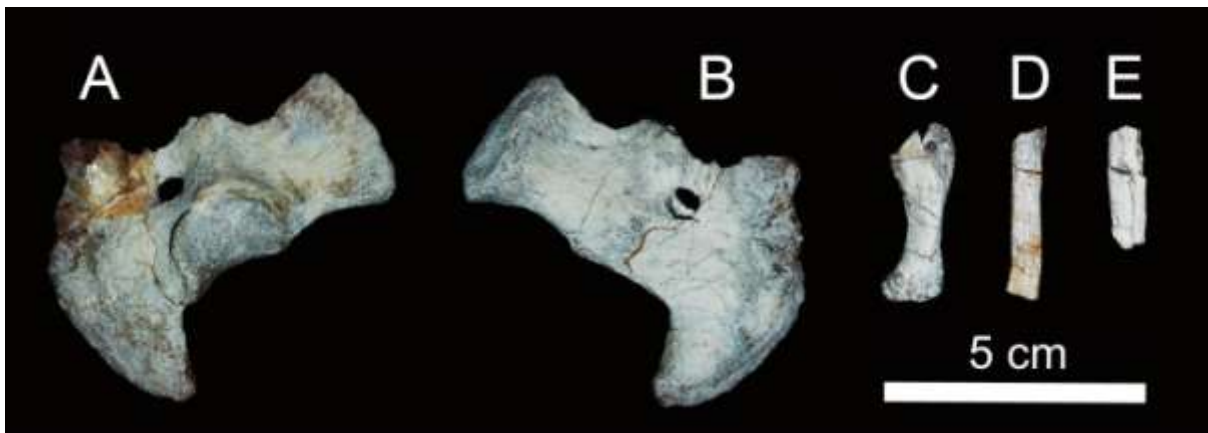


533

534 **Fig 7.** Left humerus of *Asprosaurus bibongria* gen. et sp. nov. in A, ventral; B, anterior; C, dorsal; and

535 D, posterior views. Abbreviations DP, deltopectoral crest; ECT, ectepicondyle; ECT F, entepicondylar

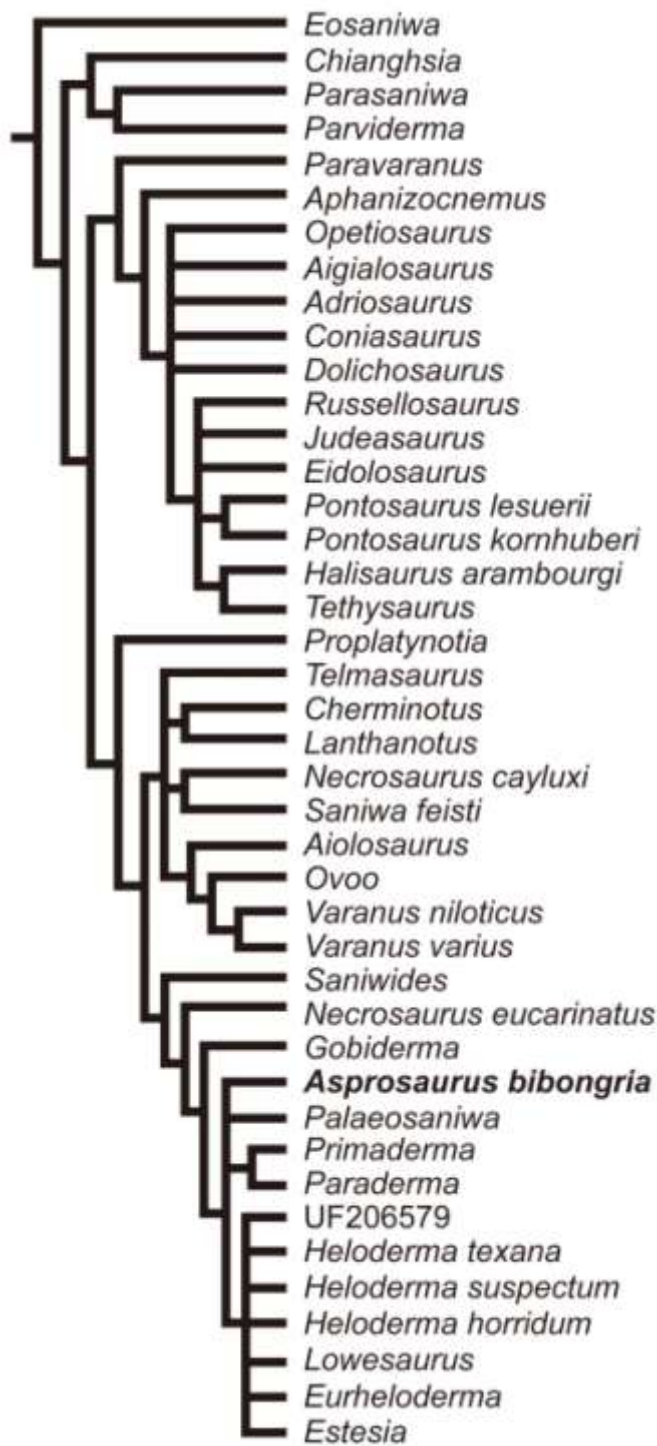
536 foramen; ENT, entepicondyle; SBCSC, subcoracoscapularis.



537

538 **Fig 8.** Postcranial materials of *Asprosaurus bibongria* gen. et sp. nov. A, lateral, and B, medial views

539 of scalpulocoracoid; C, metacarpal; D, E, possible rib or clavicle.



540

541 **Fig 9.** Phylogenetic position of *Asprosaurus bibongria* gen. et sp. nov. in relevant part of 70% MRT

542 with Gauthier et al. (2012) data matrix. Abbreviations UF, Florida State Museum (University of Florida),

543 United States.