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

Jin-Young Park [a, b], Susan E. Evans [c], Min Huh [b, *]

[a] Paleontological Consultants for the Public (PCP) Headquarters, 808 Ho, 203 Dong, Hyundai Apt., Hongeun 2-dong, Seodaemun-gu, Seoul 120-772, Republic of Korea
[b] Faculty of Earth Systems and Environmental Sciences & Korea Dinosaur Research Center, Chonnam National University, Gwangju 500-757, Republic of Korea
[c] Research Department of Cell and Developmental Biology, Anatomy Building, UCL, University College London, Gower Street, London WC1E 6BT, UK

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ABSTRACT

Upper Cretaceous deposits in Mongolia, Chinese Inner Mongolia, and, more recently, southern China, have yielded individually rich and taxonomically diverser lizard assemblages. Here we describe the remains of a new terrestrial lizard, *Asprosaurus bibongriensis* gen. et sp. nov., from the Upper Cretaceous of South Korea. It represents the first record of a Mesozoic lizard from the Korean Peninsula and, although incomplete, is exceptional in its very large size. Characters of the mandible support attribution to crown-group Anguimorpha, with the closest similarities being to monstersaurs, the group represented today by the venomous North American Beaded lizard and Gila monster, genus *Heloderma*. This group is well-represented in the Upper Cretaceous fossil record in of eastern Asia, and the remains of large monstersaurs have been recovered from several dinosaur egg localities, suggesting dietary preferences similar to those of the living genus. The new Korean lizard, recovered from the Boseong Bibong-ri Dinosaur Egg Site, fits the same pattern.

1. Introduction

Cretaceous nonmarine deposits are well exposed along the southern coast of South Korea, and many fossil sites have been reported from these deposits (e.g., Dong et al., 2001; Lee et al., 2001; Lim et al., 2001; Yun and Yang, 2001; Hwang et al., 2002; Huh et al., 2003; Yun et al., 2004; Kim et al., 2005; Lee and Lee, 2007; Huh et al., 2011). Boseong Bibong-ri Dinosaur Egg Site, located in Bibong-ri, Deungnyang-myeon, Boseong-gun, Jeollanam-do, is one of the richest localities for dinosaur eggs in South Korea (Huh et al., 1999a,b; Huh and Zelenitsky, 2002; Paik et al., 2004; Huh et al., 2006; Paik et al., 2012; Huh et al., 2013) (Fig. 1). It was first excavated in 1999 and has yielded various specimens including dinosaur eggs (more than 200 individuals), a possible testudine egg (Huh and Zelenitsky, 2002), and the skeleton of a small ornithopod dinosaur, *Koreanosaurus boseongensis* (Huh et al., 2011) (Fig. 2). Five separate fossiliferous sites have been reported from the area (Huh et al., 2006) (Fig. 1C), and the dinosaur egg clutches appear in at least four separate layers at all five sites (Fig. 2). Although egg fossils are abundant, vertebrate body fossils are rare in this area.

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

2. Geological setting and materials

The rock units that form the Boseong Bibong-ri Dinosaur Egg Site are epiclastic, pyroclastic, and intermediate to acidic volcanic rocks. They can be divided into the Seonso Conglomerate, Seonso Formation, Pilbong Rhyolite, Mudeungsan Flow, Obongsan Brecciated Tuff, and Docheonri Rhyolite, in stratigraphic order (Hwang and Cheong, 1968; Huh et al., 1999a; Paik et al., 2004; Huh et al., 2006). The dinosaur egg-bearing layers, the Seonso Conglomerate and the overlying Seonso Formation, are primarily clastic, and are composed of conglomerates, sandstones, and mudstones (Huh

* Corresponding author.
E-mail address: minhuh@chonnam.ac.kr (M. Huh).

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et al., 1999a; Paik et al., 2004; Huh et al., 2006) (Fig. 2). Isotope analysis of the overlying Pilbong Rhyolite (^{40}Ar-^{39}Ar age of 81.0 ± 2.4 Ma) and the lapilli tuff below (^{40}Ar-^{39}Ar age of 81.1 ± 1.4 Ma), suggests that the fossil-bearing deposits are Campanian in age (81 Ma) (e.g., Huh et al., 2006; Kim, 2008; Kim et al., 2008).

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

The associated skeleton (Fig. 3), described in this paper, was collected during the first excavation period in 2000, from site 1 (Fig. 2), which is located in the southernmost part of the Boseong Bibong-ri Dinosaur Egg Site (Fig. 1C). The specimen was in situ, preserved in a thick purple sandy mudstone layer between a lower cross-laminated coarse grained sandstone horizon and an upper horizon consisting channel lag gravels (Fig. 2). No other fossils were collected from the same horizon, but dinosaur egg clutches were excavated from above and below the lizard specimen (Fig. 2). Preliminary preparation work was done during 2000, with additional preparation from 2005 to 2010. The final preparation work (2012–2013) was done by the first author.

The specimen is deposited at the Korea Dinosaur Research Center, Chonnam National University, Republic of Korea, under the collection number KDRC-BB4 (Korea Dinosaur Research Center - Boseong Bone fossil Catalogue Number).

3. Systematic paleontology

Squamata Oppel, 1811
Anguimorpha Fürbringer, 1900
cf **Monstersauria** Norell and Gao, 1997
Asprosaurus bibongriensis **gen. et sp. nov.**

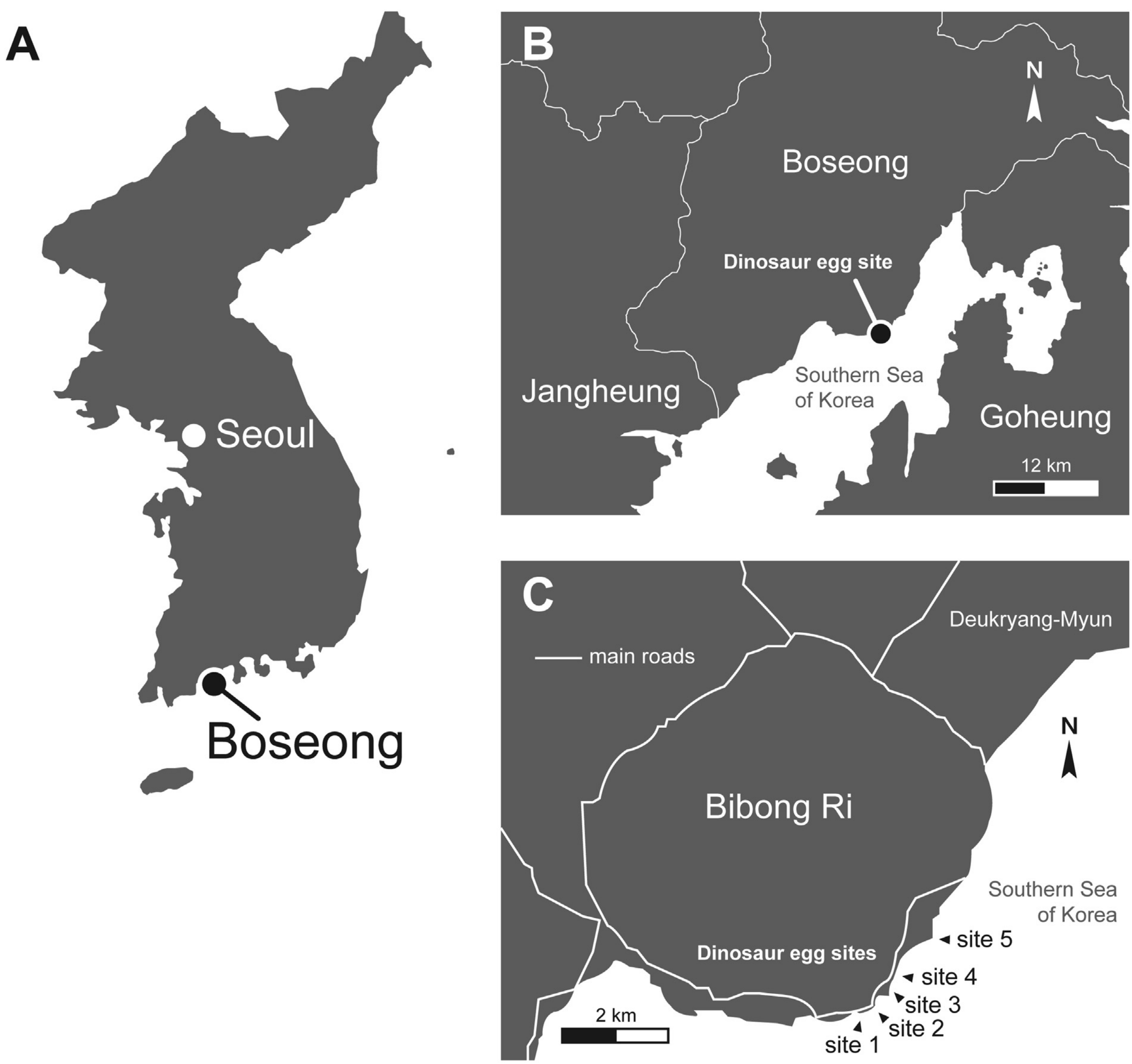

Fig. 1. Location of the Boseong Bibong-ri Dinosaur Egg Site. A, map of the Korean Peninsula; B, enlarged map of Boseong area; C, enlarged map of Bibong Ri area showing the five main dinosaur egg sites. Modified from Paik et al., 2004.

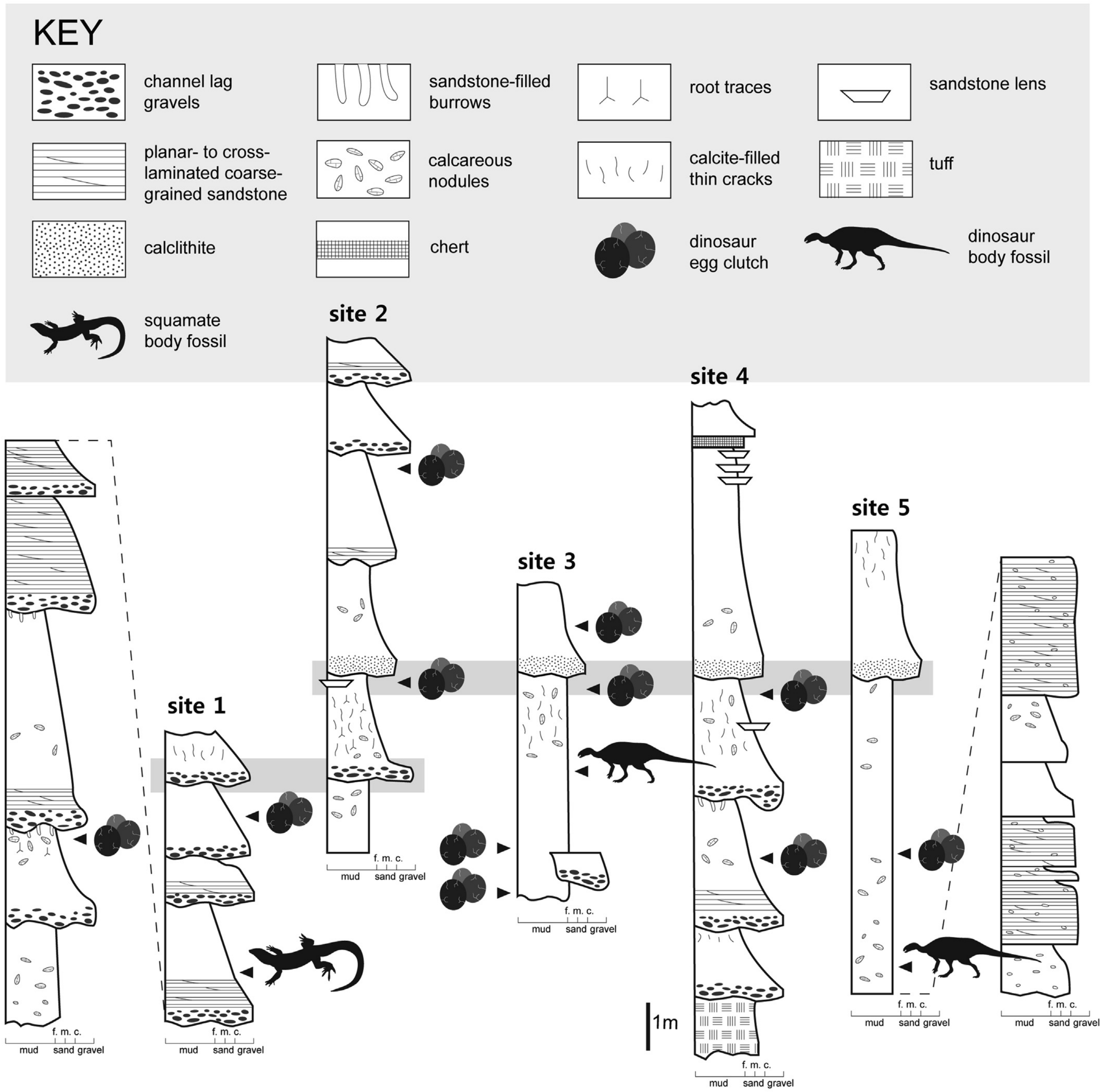

Fig. 2. Stratigraphic sections of five sites of Boseong Dinosaur Egg Site, modified from Huh et al., 1999a; 1999b; Paik et al., 2004; Huh et al., 2006, 2011; Paik et al., 2012.

3.1. Derivation of name

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

3.2. Holotype

KDRC-BB4, an associated specimen, originally on a single block (Fig. 3) but with each element now prepared out and comprising a right jugal, partial squamosal, partial left quadrate, left pterygoid, partial left mandible, left scapulocoracoid, left humerus, a metacarpal, part of a rib or clavicle, and several unidentified bone fragments.

3.3. Type locality

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

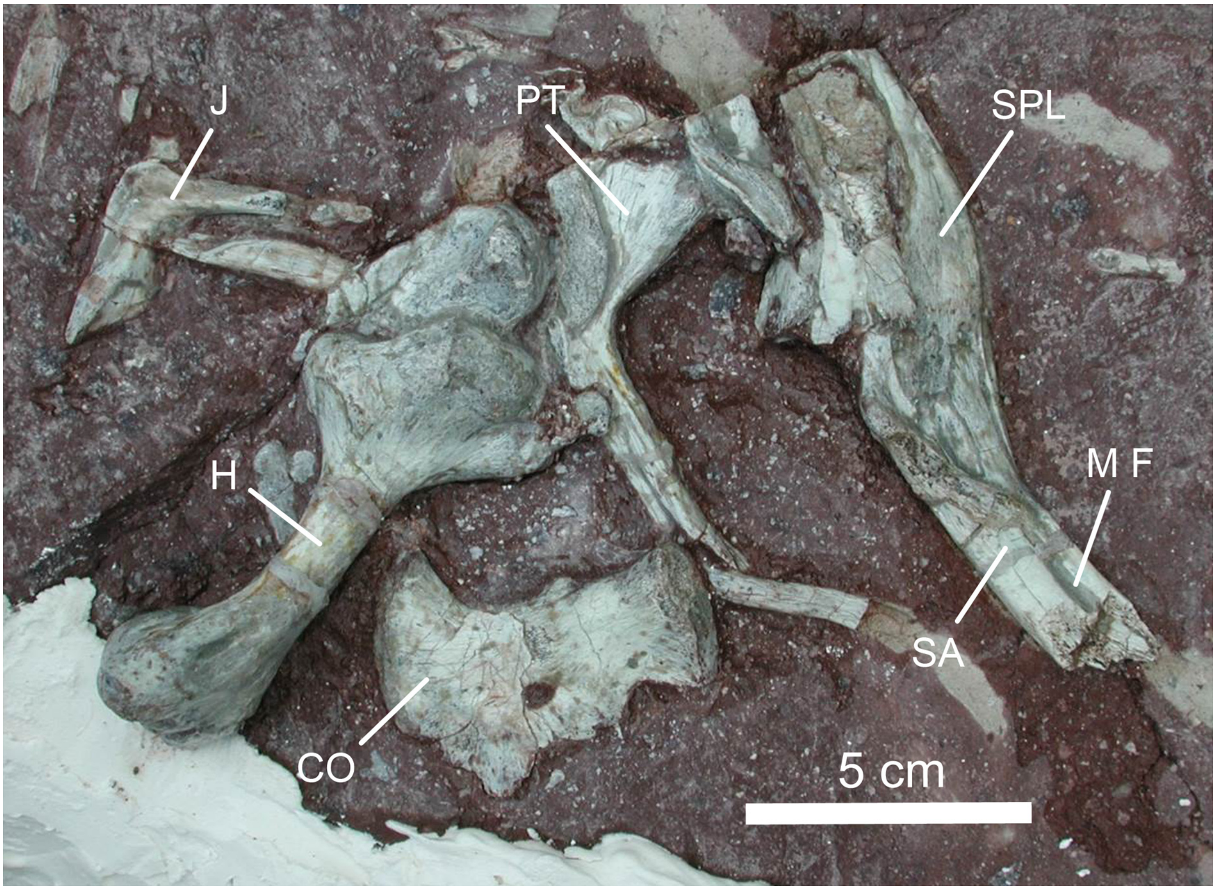

Fig. 3. Photo of associated specimen of *Asprosaurus bibongriensis* gen. et sp. nov. (holotype; KDRC-BB4) in original single block. Abbreviations CO, scapulocoracoid; H, humerus; J, jugal; M F, mandibular fossa; PT, pterygoid; SA, surangular; SPL, splenial.

3.4. Stratigraphic horizon

Upper Cretaceous (Campanian) Seonso Conglomerate.

3.5. Diagnosis

A very large, robust-limbed, terrestrial lizard (skull length ~180–200 mm) resembling monstersaurian and varaniform anguimorphs (sensu Conrad et al., 2011a) in having a deep, almost vertical dentary alveolar margin with no subdental shelf; a Meckelian fossa that is anteroventrally positioned; a small adductor fossa; no posterodorsal coronoid process on the dentary; a reduced splenial-dentary contact; and a splenial that does not extend posterior to the apex of the coronoid process. Differs from previously described Asian Late Cretaceous anguimorph lizards including *Cherminotus*, *Chianghsia*, *Estesia*, *Gobiderma*, *Ovöo*, *Paravaranus*, *Parviderma*, *Proplatynotia*, *Saniwides*, and *Telmasaurus* in the combination of a strongly angulated jugal in which the postorbital process is wider than the suborbital process; a complete postorbital bar; a concave medial margin to the pterygoid palatal plate; a straight dentary-postdentary contact but no intramandibular joint; a posteriorly shallow, rather than triangular, splenial; no cranial osteoderms; and a convexo-concave ventral jaw margin.

3.6. Description

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

3.6.1. Cranial

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

The jugal (Fig. 4) is a laterally flattened, biradiate more or less a L-shaped bone, the two rami of which are set at almost 90° to one another. One ramus is broad and mediolaterally flattened. Medial and lateral surfaces are clearly identified from the pattern of facets, medial ridge (sensu Čerňanský et al., 2014) and rugosities. The bone bears a deep medial facet at its distal end (Fig. 4B), although this was damaged during preparation. The other ramus is

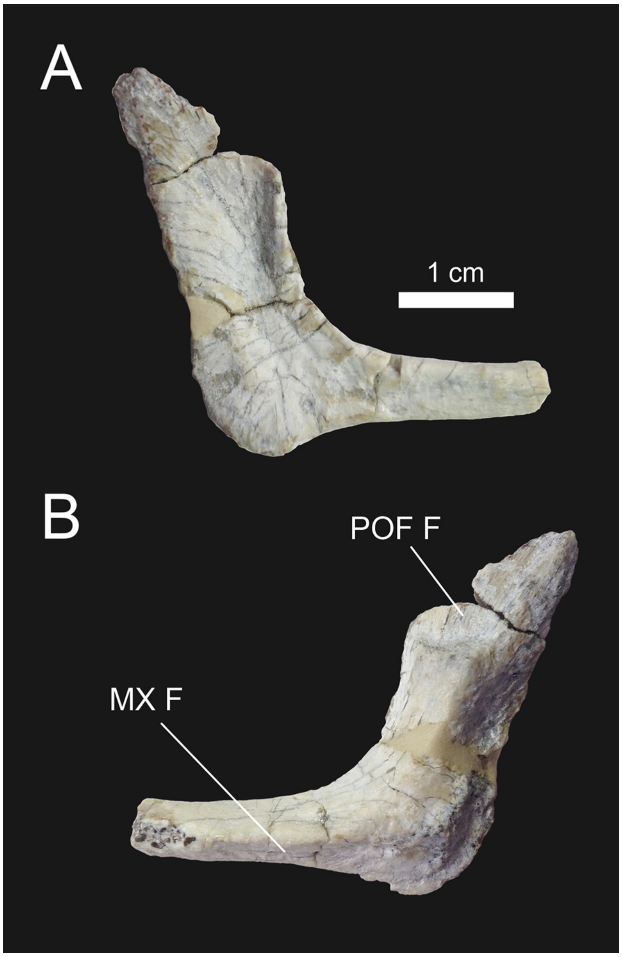

Fig. 4. Right jugal of *Asprosaurus bibongriensis* gen. et sp. nov. (KDRC-BB4). A, lateral; B, medial view. Abbreviations MX F, maxillary facet; POF F, Postorbitofrontal facet.

narrower and rounded to triangular in cross-section. It bears a narrow facet along the external (non-orbital) surface. As originally preserved, it was obviously longer. Photographs of the original block (Fig. 3) show there was a short distal section separated from the remainder by a small space. By comparison with other Asian anguimorphs like *Gobiderma* and *Estesia*, this bone, in external view, has the appearance of a left jugal, with a deep suborbital ramus and a long, tapering postorbital one. However, the positions of the facets are not consistent with that interpretation, particularly the large deep facet on the internal surface of the broader ramus. The facet for the maxilla and/or for the ectopterygoid would be ventral not dorsal. We therefore interpret the bone as a right jugal, such that the narrow ramus is suborbital with a long narrow ventral facet for the maxilla. If this is correct, then the jugal may have excluded the maxilla from the suborbital margin, but is likely to have had only its dorsal rim exposed. The broader, mediolaterally compressed ramus formed the postorbital margin, with the dorsomedial facet receiving a flange from the postorbital or postorbitofrontal. There is no additional posterior facet and it is unlikely that the jugal and squamosal were in contact. The postorbital ramus bears a dorsolateral concavity, but this does not appear to represent an articulation surface. Posteroventrally, the bone terminates in a rounded angle. This is relatively smooth laterally, but bears a posteromedial rugosity that may have been associated with the lateral head of the ectopterygoid or a thickening of the temporal fascia.

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

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

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

As preserved, the left mandible (Fig. 6) is relatively long and slender. It has a somewhat sigmoid shape, due to the pronounced posteroventral concavity and an apparent reduction in posterior height. The individual elements are in articulation but the bones have separated slightly at the sutures, suggesting these were not fully closed at death. The dentary tapers slightly from posterior to anterior. The anterior part is lost and it is difficult to judge the original length. The alveolar margin is represented by a deep, almost vertical surface with no subdental shelf or ridge (Fig. 6C). However, no teeth are preserved nor are tooth positions evident. Either this region was originally edentulous or the tooth sockets were shallow and their edges have been eroded. Laterally, there are no neurovascular foramina on this portion of the bone. Medially, the posterior part of the Meckelian fossa is filled by a splenial, which tapers postero-anteriorly and has a small exposure on the anterolateral surface (Fig. 6C), indicating that the Meckelian fossa was more ventral than medial in its anterior part. Towards its anterior end, the dorsal margin of the splenial is emarginated by a long low notch, interpreted here as the margin of an anterior inferior alveolar foramen lying between the splenial and dentary. If this is correct, it is likely that there was originally a significant length of dentary anterior to this point. Ventral, and slightly posterior to this emargination the splenial bears an ovoid depression, which may represent the anterior mylohyoid foramen. There is a relatively wide gap between the dorsal margin of the splenial and the dentary, suggesting connective tissue attachment in life. Posteriorly, the splenial overlaps the angular, surangular, and coronoid, but does not extend to the level of the coronoid apex and it lacks the strongly triangular shape seen in some monstersaurs (e.g. *Heloderma*, *Gobiderma*) (Fig. 6C). This could be due to damage, but it is not obviously so. The dentary-postdentary overlap is not extensive, and the lateral suture between the dentary and surangular is almost vertical, but

Fig. 5. Skull material of *Asprosaurus bibongria* gen. et sp. nov. (KDRC-BB4). A, squamosal in lateral view; B, lateral, and C, medial views of left quadrate; D, dorsal, and E, palatal views of left pterygoid.

slightly imbricated (Fig. 6A). However, there was not an intramandibular joint. Where the dentary and surangular have pulled apart slightly, it is clear that a flange from the surangular passed medial to the dentary, but it is not possible to judge how far this reached anteriorly. The dentary does not bear a posterodorsal coronoid process. The coronoid itself is preserved in its antero- and postero-ventral parts, although the dorsal process is broken at its base. The anterior and posterior rami are roughly equal in length. The coronoid lies entirely medial to the surangular, but its articulation with the dentary is a little more complex. The surangular and dentary meet lateral to the coronoid but the posterodorsal margin of the dentary turns through an angle of almost 90° to the long axis of the surangular, forming a distinct 'corner' into which the anterolateral edge of the coronoid fits (Fig. 6B). At this point, therefore, the coronoid abuts the dentary. However, an anterior flange of the coronoid overlaps the medial surface of the dentary just behind the alveolar margin. Thus, the coronoid both abuts and clasps the posterodorsal end of the dentary. In medial view, however (Fig. 6C), only the overlap is apparent. The posteroventral process of the coronoid extends from the dorsal margin of the surangular to the edge of the small mandibular fossa. The angular is long and thin, with a relatively narrow exposure on both the medial and lateral aspects of the mandible. Medially, it lies below the prearticular, which forms the ventral margin of the mandibular fossa. The surface of the angular is damaged but seems to be pierced laterally at the level of the dentary-surangular suture. This may be a posterior mylohyoid foramen.

No osteoderms are preserved on the specimen, and photographs of the specimen before preparation show no evidence of them (Fig. 3). However, without the skull roof bones (frontal, parietal) we cannot be certain whether they may originally have been present on some parts of the skull.

3.6.2. Postcranial skeleton

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

The left scapulocoracoid (Fig. 7A, B) is broad and relatively flat with a large posterolateral glenoid fossa. The scapula and coracoid are completely fused, although a trace of the suture is visible medially (note that there is also a deep crack across the bone ventral to the real suture line). The coracoid plate is perforated by a large coracoid foramen. Ventromedially, it is moderately expanded and bears a curved posterior extension (metacoracoid process). This margin is thickened and, in life, would have supported the epicoracoid cartilage. Further anteriorly, the bone is thinner and partially damaged (but see below). The scapular portion is relatively short with a wide, rugose dorsal margin that would have been continued in life with the cartilaginous suprascapula. Overall, as is typical, the scapulocoracoid is thickest along the posterior margin and thins anteriorly. The anterior margin is damaged in part, but there is certainly a scapulocoracoid emargination, which is associated with the scapulo-coracoid suture. A thickening at the level of the scapulocoracoid suture (base of the procoracoid process) separates the scapulocoracoid emargination from a second emargination at the level of the coracoid foramen (anterior coracoid emargination). This, in turn, is limited anteroventrally by a second thickening, below which the bone appears to thin again.

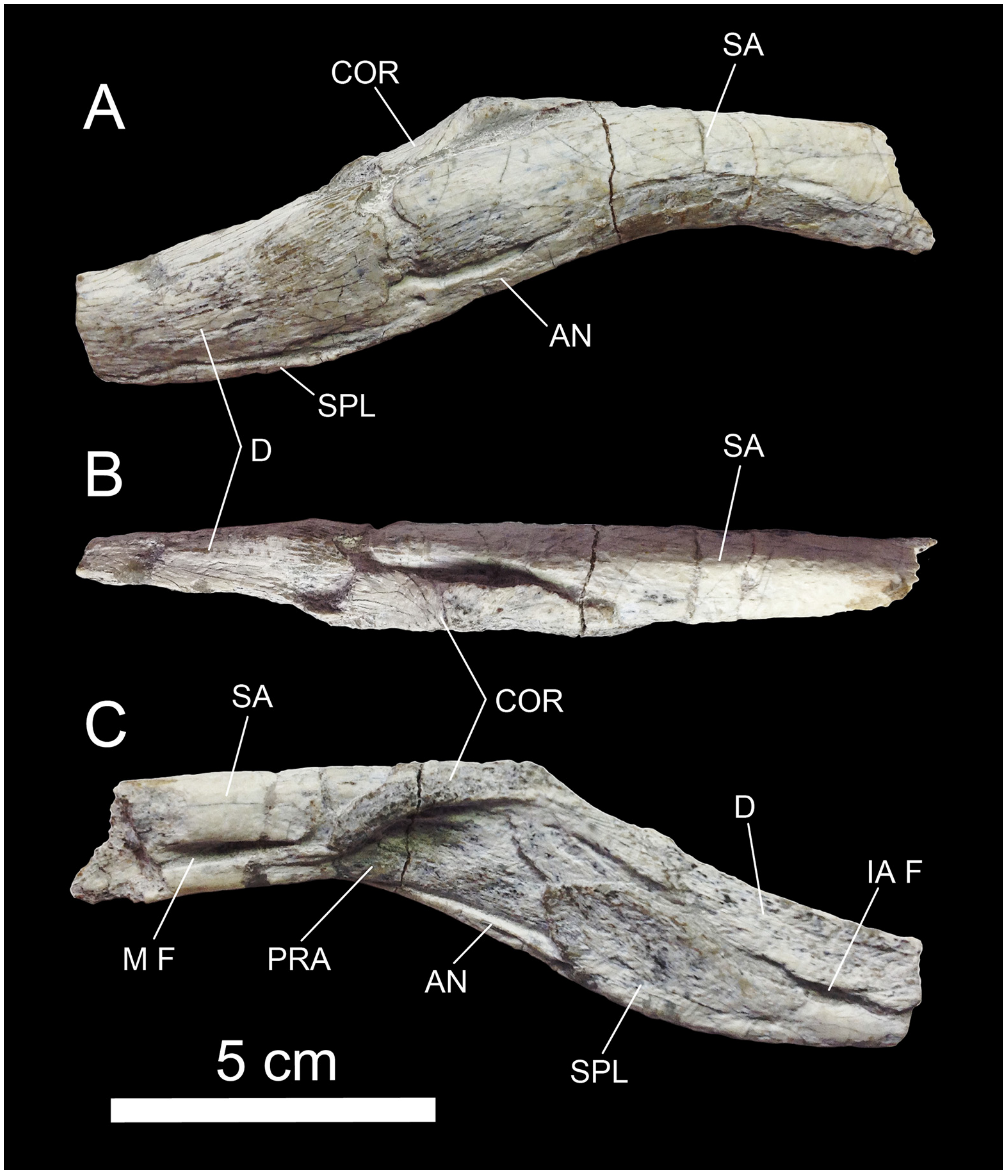

Fig. 6. Left mandible of *Asprosaurus bibongriensis* gen. et sp. nov. (KDRC-BB4). A, lateral; B, dorsal; C, medial views. Abbreviations AN, angular; COR, coronoid; D, dentary; IA F, inferior alveolar foramen; M F, mandibular fossa; PRA, prearticular; SA, surangular; SPL, splenial.

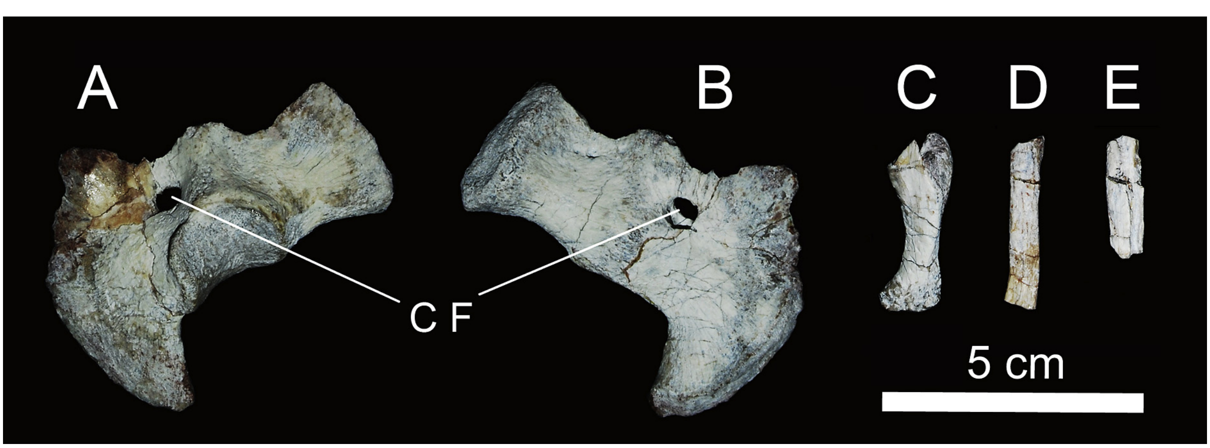

Fig. 7. Postcranial materials of *Asprosaurus bibongriensis* gen. et sp. nov. (KDRC-BB4). A, lateral, and B, medial views of scapulocoracoid; C, metacarpal; D, E, possible rib or clavicle. Abbreviations C F, coracoid foramen.

However, it is not clear whether there is an accessory coracoid emargination at this position.

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

The left humerus (Fig. 8) is generally well-preserved, although parts of the distal condylar surfaces are missing. The epiphyses are fully fused. Overall, the bone is robust with strong crests and rugosities for muscle attachment. The broad proximal and distal ends are set at almost 90° to one another and are separated by a relatively short, narrow shaft. The shaft is straight and sub-cylindrical in cranial view, and is slightly curved anteriorly in lateral view. The proximal and distal ends are both about 40 mm in width. At the proximal end, there is a screw-shaped surface for articulation with the glenoid cavity. Close to it, and pointing slightly laterally, is a strong area of attachment for the subcoracoscapularis muscle. On the opposite side, a prominent deltopectoral crest curves slightly interiorly, forming a deep proximal concavity. At the distal end of the bone, a deep sulcus, widest distally, separates the ectepicondyle and entepicondyle. An ectepicondylar foramen is visible in superior view (Fig. 8C).

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

3.7. Remarks

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

4. Phylogenetic position

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

In order to explore the phylogenetic position of *Asprosaurus*, we incorporated the new lizard taxon into two recent morphological data matrices – that of Conrad et al. (2011b) and of Gauthier et al. (2012).

Gauthier et al. (2012) represents the largest morphological character matrix to date (610 characters; 192 taxa). As they ran their analysis using PAUP, we used the same programme, with their ordering of characters. A heuristic search yielded 179 equally parsimonious trees (L = 5196; CI = 0.187; RC = 0.148), of which a strict consensus placed *Asprosaurus* in an unresolved polytomy with *Lanthanotus*, *Saniwa*, *Varanus* (3 species), *Heloderma* (2

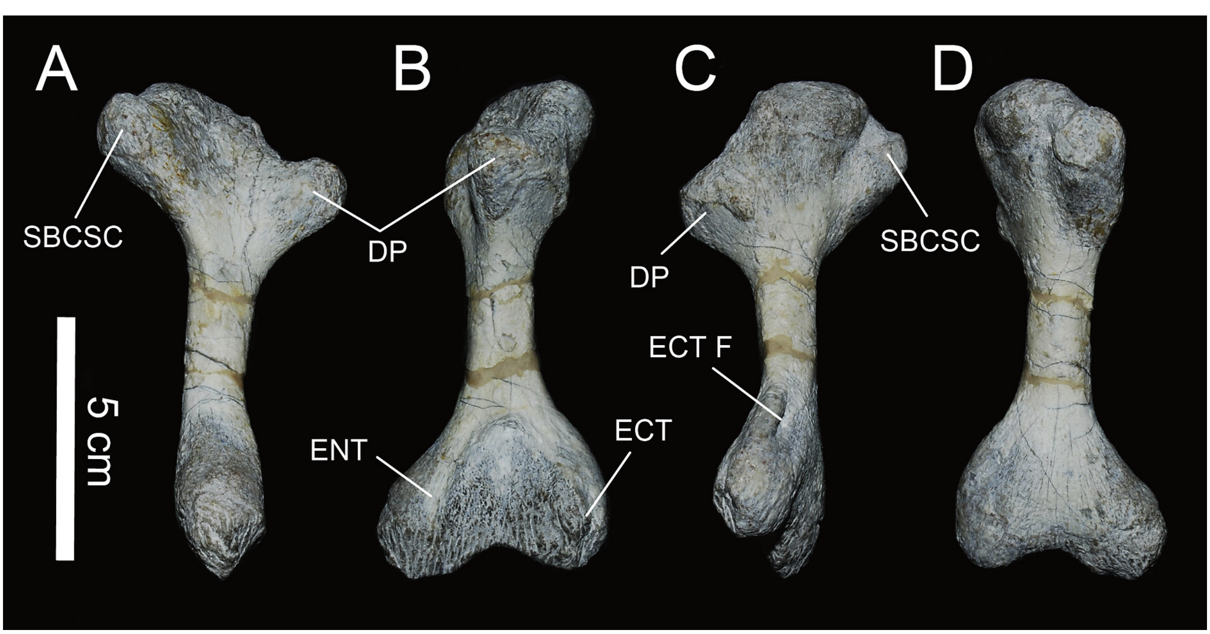

Fig. 8. Left humerus of *Asprosaurus bibongriensis* gen. et sp. nov. (KDRC-BB4). in A, ventral; B, anterior; C, dorsal; and D, posterior views. Abbreviations DP, deltopectoral crest; ECT, ectepicondyle; ECT F, entepicondylar foramen; ENT, entepicondyle; SBCSC, subcoracoscapularis.

species), and *Aiolosaurus*, *Estesia* and then *Gobiderma* were placed as consecutive outgroups to this clade. We then ran a Branch and Bound analysis with 15 taxa (the 11 listed above + *Shinisaurus*, *Xenosaurus*, *Elgaria* and *Anniella*, the latter three as a monophyletic outgroup). This second analysis resulted in six trees (L = 520; CI = 0.621; RC = 0.38), in which *Asprosaurus* moved between a helodermatid clade (2 trees) and a varanid clade (4 trees). Its position in both the strict consensus and an Adam's consensus was therefore unresolved with respect to these two positions, although a Bootstrap analysis gave weak (56%) support to a relationship with varanids.

However, extensive though the Gauthier et al. (2012) matrix is, it included few of the fragmentary Late Cretaceous anguimorph taxa that cluster around *Heloderma* and *Varanus* in other analyses (e.g., Conrad, 2008). We therefore coded *Asprosaurus* into the anguimorph matrix of Conrad et al. (2011a), adding the genus *Chianghsia* (Mo et al., 2012) from southern China and using *Gephyrosaurus*, rather than *Sphenodon* (which was omitted) as the outgroup taxon, but otherwise using their characters and ordering. This analysis was run with the programme TNT, using the New Technology search with Sectorial Searching, Ratchet (20 iterations), and Tree Fusion, and with 1000 random addition sequences). The analysis yielded 32 trees of which the Strict Consensusis shown in Fig. 9. *Asprosaurus* is within Monstersauria (sensu Conrad et al., 2011a,b), one node crownward of *Gobiderma*.

5. Discussion

5.1. Phylogenetic position

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

Most recent cladistic analyses of squamates, whether morphology-only (e.g., Conrad, 2008; Gauthier et al., 2012), molecular (e.g., Townsend et al., 2004; Vidal and Hedges, 2005, 2009; Pyron et al., 2013), or combined data (e.g., Wiens et al., 2010; Conrad et al., 2011a,b), recognize five main clades of living Anguimorpha: Anguidae, *Xenosaurus*, *Shinisaurus*, *Heloderma* and Varanidae (*Varanus*+*Lanthanotus*). There is general agreement that *Xenosaurus* is more closely related to Anguidae than to Varanidae (e.g., Conrad, 2008; Conrad et al., 2011a,b; Pyron et al., 2013; Wiens et al., 2010, 2012; Jones et al., 2013), providing a dichotomy between anguioid (Anguidae+*Xenosaurus*) and varanid anguimorphs, but there are significant differences in the hypothesized relationships of both *Heloderma* and *Shinisaurus*. The traditional classification, based on morphological characters (e.g., Estes et al., 1988; Lee, 1997; Caldwell, 1998; Conrad, 2008; Conrad et al., 2011a; Gauthier et al., 2012) places *Heloderma* as the sister group of Varanidae (=Varanoidea, Gauthier et al., 2012). However, molecular analyses (e.g., Townsend et al., 2004; Vidal and Hedges, 2005, 2009; Wiens et al., 2012; Pyron et al., 2013; Jones et al., 2013) have consistently found *Heloderma* to be the sister taxon to Anguioidea, a position also proposed in the pioneering work of Camp (1923). Combined morphology-molecular analyses have also tended to support this arrangement (e.g., Wiens et al., 2010), although that of Conrad et al. (2011a) yielded the traditional topology when based only on extant taxa and the 'molecular' topology when fossils were included. *Shinisaurus* is similarly problematic. Estes et al. (1988) grouped *Shinisaurus* and *Xenosaurus* in the Xenosauridae, a position supported by Gauthier et al. (2012). However, molecular analyses (e.g., Townsend et al., 2004; Vidal and Hedges, 2005; Pyron et al., 2013; Wiens et al., 2012; Jones et al., 2013) have consistently placed *Shinisaurus* closer to Varanidae, as did the morphology-based analysis of Conrad (2008),

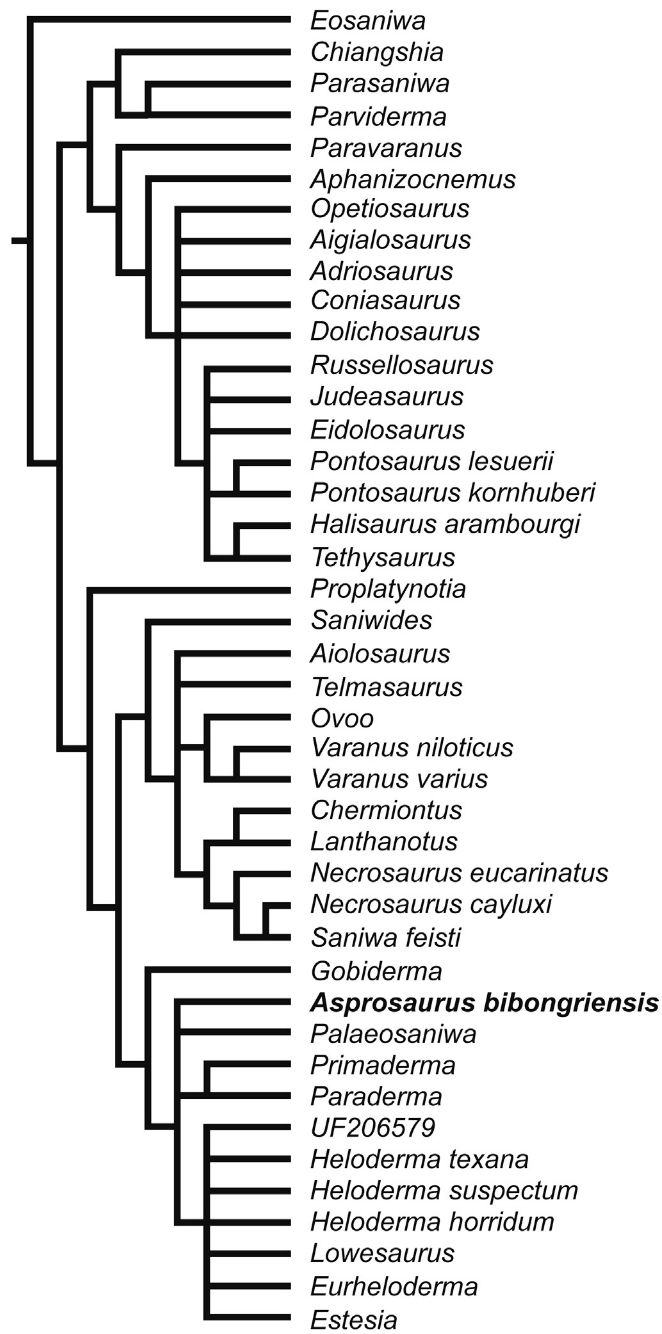

Fig. 9. Phylogenetic position of *Asprosaurus bibongriensis* gen. et sp. nov. in relevant part of 70% MRT using the data matrix of Conrad et al. (2011a). Abbreviations UF, Florida State Museum (University of Florida), United States.

and the morphology-based, molecular, and combined evidence analyses of Conrad et al. (2011a: but see Conrad et al., 2011b).

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

For *Asprosaurus*, other characters are contradictory, and the absence of teeth further complicates discussion. *Asprosaurus* differs from varaniforms by having a strongly angulated jugal, a coronoid lacking a long horizontal anterodorsal ramus and posterior displacement of the coronoid process, and an anteriorly expanded surangular. With monstersaurs like *Heloderma* and *Gobiderma*, *Asprosaurus* shares a strongly angulated jugal, straight posterior dentary margin, and convex-concave ventral profile of the mandible, but it lacks their short triangular splenial and the enclosure of the anterior inferior alveolar foramen within the splenial (Conrad et al., 2011b). As noted above, the specimen as preserved also shows no trace of the characteristic thick osteoderms of monstersaurs. If they were absent, then *Asprosaurus* would more closely resemble *Estesia* (Norell et al., 1992; Gao and Norell, 2000), another Mongolian genus usually placed with monstersaurs (but see Yi and Norell, 2010).

On balance, *Asprosaurus* appears to be morphologically closer to monstersaurs (whatever their affinity) than to varaniforms, and the results of our analysis using the Conrad et al. (2011a) matrix tend support to this, but further material - especially of the dentition, is needed to test this.

5.2. Life history

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

6. Conclusion

Specimen KDRC-BB4 is reclassified from testudine to anguimorph squamate, and is named as a new taxon, *Asprosaurus bibongriensis* gen. et sp. nov. *Asprosaurus* is the first lizard fossil recorded from South Korea and the largest Mesozoic terrestrial lizard known to date. On balance, it appears to be more closely related to monstersaurs than to varaniforms, but this is not conclusive. *Asprosaurus* provides another example of a large predatory lizard found in proximity to a dinosaur egg site.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cretres.2015.03.001.

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