Taxonomic Revision of *Eoalligator* (Crocodylia, Alligatorinae) and the Paleogeographic Origins of the Chinese Alligatoroids

Yanyin Wang, Corwin Sullivan, Jun Liu

Backgroud. The Neotropical distribution of living alligatorids raises questions as to when and how the ancestors of *Alligator sinensis* migrated to China. As phylogeny provides a necessary framework for evaluating historical biogeographic issues, determining the phylogenetic positions of the Chinese alligatoroids is a crucial step towards understanding global alligatoroid paleobiogeography. Besides the unnamed “Maoming specimen” from the Eocene of Guangdong Province, three Chinese fossil taxa have been referred to Alligatoroidea, but never included in a cladistic analysis: *Alligator luicus*, *Eoalligator chunyii*, and *Eoalligator huiningensis*. The genus *Eoalligator* was established to accommodate *E. chunyii* from Guangdong Province. *E. huiningensis* from Anhui Province was later erected as a second species despite sharing no distinctive characters with *E. chunyii*. By contrast, the putative crocodyline *Asiatosuchus nanlingensis* was established based on material from Guangdong Province, which is close to *E. chunyii* geographically and stratigraphically. Furthermore, specimens of *A. nanlingensis* and *E. chunyii* share four distinctive characters, but display no evident differences. As a result, the taxonomic relationships of these three species require restudy.

Method. In this paper all specimens of *E. chunyii* and *E. huiningensis* are reassessed in detail, and compared to specimens of *A. nanlingensis*. Detailed re-descriptions and revised diagnoses are provided for *E. chunyii* and *E. huiningensis*, and two cladistic analyses are carried out to assess the phylogenetic positions of *E. chunyii*, *E. huiningensis* and *A. nanlingensis*.

Result. The analyses recover *E. chunyii* and *A. nanlingensis* as sister taxa among basal Crocodylidae, while *E. huiningensis* is posited as an alligatoroid. Two key characters strongly support the monophyletic group *E. chunyii* + *A. nanlingensis*: sulcus within surangular, and anteroposteriorly oriented surangular-articular suture. The former character is unique to *E. chunyii* and *A. nanlingensis* among crocodylians. Detailed comparisons show *E. chunyii* to be the junior synonym of *A. nanlingensis* based on page priority. *E. huiningensis* is a putative alligatoroid with uncertain position. In particular, *E. huiningensis* retains primitive characters such as a lacrimal that extends further anteriorly than the prefrontal, and a notch at the premaxilla-maxilla suture. However, *E. huiningensis*

also shares one important derived character, a complete nasal bar, with alligators. As *E. chunyii* is invalid, *E. huiningensis* is designated as the new type species of *Eoalligator*. As a result, four alligatoroids are currently known from China, and these species must have dispersed from North America to Asia in more than one event.

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Abstract

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Key words: *Eoalligator*, Alligatoroidea, Crocodylinae, phylogeny, taxonomy, paleobiogeography.

Introduction

Crocodylia is a group of reptiles containing twenty three extant species and divided into the three major clades Gavialoidea, Crocodyloidea and Alligatoroidea. Alligatoroidea contains two extant clades, Alligatorinae and Caimaninae. The latter includes six species, whereas the former includes only one genus and two species: *Alligator sinensis* from China and *Alligator*

mississippiensis from the southeastern United States. To clarify the historical biogeography of Alligatoroidea, it is necessary to first evaluate the phylogenetic relationships among fossil and extant members of this clade.

Alligatoroidea is low in extant diversity compared to many other reptile groups, but the alligatoroid fossil record contains much greater taxonomic richness. Around the world, fossil alligatoroids are known from China, North and South America, and Europe. The oldest known member of the clade, *Leidyosuchus canadensis*, is from the Upper Cretaceous of North America (Lambe, 1907). The crown group of Alligatoroidea, Alligatoridae, is defined as the last common ancestor of *Alligator mississippiensis* and *Caiman crocodilus* plus all of its descendants. All known alligatorids come from China and the Americas, apart from two extinct basal European species: *Hassiacosuchus haupti* and *Arambourgia gaudryi*. More broadly, most fossil alligatoroids are from North America, which may represent an evolutionary center from which alligatoroids have repeatedly dispersed to other continents. However, the specific pattern of these dispersals, and therefore the basis for the presence of *A. sinensis* and various fossil alligatoroids in Asia, remain unresolved. This problem is especially intriguing considering that all extant members of Alligatoroidea other than *Alligator sinensis* lack a salt gland (Brochu, 1999), an osmoregulatory organ in the tongue that excretes excess salt and therefore confers tolerance of high salinity. Extant alligatorids without salt glands are restricted to freshwater environments. This was presumably also true of at least a subset of extant alligatoroids, and would have limited their potential dispersal routes to ones that did not require crossing sea barriers.

Besides *Alligator sinensis*, the following nominal Chinese fossil crocodylian species have been referred to Alligatoroidea: *Alligator luicus*, *Eoalligator chunyii* and *E. huiningensis* (Li and Wang, 1987; Young, 1964, 1982). *A. luicus* was established based on a single skeleton from the Miocene of Shandong Province (Li and Wang, 1987), *E. chunyii* based on materials from the Paleocene of Nanxiong County, Guangdong Province (Young, 1964), and *E. huiningensis* based on a partial skull from the Paleocene of Huaining County, Anhui Province (Young, 1982). Of the putative Chinese alligatoroids, only *A. sinensis* has been included in previous cladistic analyses (Brochu, 1997, 1999, 2004; Salisbury et al., 2006), leaving the phylogenetic positions of the other three species uncertain. The two *Eoalligator* species also pose problems at an alpha taxonomic level. Young (1964) assigned a number of undescribed and/or not even fully prepared bones to *E. chunyii* without comparing them explicitly to the holotype material, and the diagnosis of *E. huiningensis* (Young, 1982) does not include any comparisons with specimens of *E. chunyii*. Furthermore, Young (1964) erected not only *E. chunyii* but also a putative crocodyline, *Asiatosuchus nanlingensis*. The specimens Young (1964) assigned to *A. nanlingensis* were similar in geographic and stratigraphic provenance to those he assigned to *E. chunyii*, but he did not compare the two species morphologically or identify any characters that distinguished them from one another. Surprisingly, *A. nanlingensis* shares strong morphological similarities with some of the specimens referred to *E. chunyii*, suggesting that the two species are synonymous even though they purportedly belong to different crocodylian lineages. Therefore, *A. nanlingensis* must be considered in any comprehensive revision of *Eoalligator*.

This paper re-evaluates the osteology, taxonomy and phylogenetic affinities of the single specimen of *E. huiningensis* and the more extensive material assigned to *E. chunyii*. The holotype and referred material of the crocodylid *A. nanlingensis* are also re-examined, and *E. chunyii* is

shown to be a junior synonym of this species within Crocodylidae. The results of this revision have important implications for future studies of alligatoroid evolution and paleobiogeography.

Materials

The numerous bones and bone fragments assigned by Young (1964) to *Eoalligator chunyii* were recovered from three localities that are all within 8 km of each other in Nanxiong County (Fig. 1): one southwest of Xiongzhou Town, and close to highway G 323 (locality 1, L1); one near Fengmenao Village, though its exact position is uncertain (L2); and one situated 1 km east of Xiuren Village (L3). L1 belongs to the lower Paleocene Shanghu Formation; L2 may be situated on the K-T boundary; and L3 belongs to the Upper Cretaceous Zhenshui Formation (Zhang et al., 2013). The specimens assigned to *Asiatosuchus nanlingensis* were recovered from L3 and two additional localities in the same county (Fig. 1): one 2 km northwest of Hukou village (L4), and one 4 km west of Xiongzhou Town (locality 5, L5). The specimens from L4 and L5 date to the Paleocene (Zhang et al., 2013). The material assigned by Young (1964) to *E. chunyii* includes six indeterminate specimens that cannot even be identified conclusively as crocodylian (and in some cases are clearly of chelonian origin), which are not considered further in this paper. Comprehensive information on the localities and stratigraphic positions of individual specimens is provided in Table 1 below.

The nominal holotype of *E. chunyii* (IVPP V 2716) is a collection of bones from L1, some of which remained unprepared at the time of Young's (1964) original description. The numbers IVPP V 2716-1 to IVPP V 2716-14 were assigned at some point to different parts of the holotype, although they were not used by Young, and recently additional numbers have been assigned to individual bones within IVPP V 2716-1 and V2716-2. Young (1964) considered all the material included in IVPP V 2716 to "apparently" belong to one individual, but his description focused almost exclusively on a partial skull with the atlas-axis complex still attached (IVPP V 2716-1.1) and a fragment of a right mandible (IVPP V 2716-1.2). It is uncertain whether even these two specimens belong to a single individual. The additional material from L1 (see Table 1) is fragmentary, and includes a partial skull (IVPP V 2716-11) that clearly represents a different individual from IVPP V 2716-1.1. It is difficult to determine whether the other fragments from L1 belong to the individual represented by IVPP V 2716-1.2, the second individual represented by IVPP V 2716-11, or neither. The only other specimens ever referred to *E. chunyii* were additional ones listed in the original description (Young, 1964), including a single incomplete, poorly preserved left mandible (IVPP V 2771) from L2 and a few fragments from L3 (Table 1). The referred specimens, and even the components of the holotype other than IVPP V 2716-1, have never been fully described. In some cases (particularly that of IVPP V 2771), little evidence is available to support their conspecificity with IVPP V 2716-1.1, the most morphologically informative part of the holotype.

Young (1964) designated a collection of bones and coprolites from L4 (IVPP V 2773) as the holotype of *A. nanlingensis*, and referred additional mandibular and postcranial fragments from L3, L5 and L6 to the same species (Table 1). The most informative component of the holotype is a pair of large, incomplete mandibles (V2773.1) that agree closely in size and morphology and probably come from the same individual. However, the holotype collection includes vertebrae of different sizes, so more than one individual is clearly represented in the material. Among the

referred material is a collection from L5 that includes specimens probably referable to two separate taxa distinct from *A. nanlingensis*, as well as other fragments likely attributable to this species.

The only known specimen of *Eoalligator huiningensis* (IVPP V4058), an incomplete skull with the lower jaw in place, was recovered from Huaidinghuawu in the southwest part of Huaining County, Anhui Province. The deposits that yielded this holotype specimen belong to the upper part of Wanghudun Formation, and are middle Paleocene in age.

Table 1. Material assigned by Young (1964, 1982) to *Eoalligator chunyii*, *Asiatosuchus nanlingensis* and *Eoalligator huiningensis*, with information on the provenance, ontogenetic stage and taxonomic status of each specimen.

Eoalligator chunyii Locality: Three localities in Nanxiong County, Guangdong Province (see also text and Figure 1). Locality 1(L1), southeast of Xiongzhou Town; Locality 2 (L2), exact location uncertain, but near Fengmenao Village; Locality 3 (L3), 1 km east of Xiuren Village. Horizon: Zhenshui and Shanghu Formations, Cretaceous (?)—Paleocene.					
Specimen number	**Identification**	**L**	**H**	**DS**	**ST**
V2716-1.1	**Posterior part of skull**	**L1**	**P**	**late**	**HT**
V2716-1.2	**Incomplete right mandible**	**L1**	**P**	**late**	**HT**
V2716-2.1	**Incomplete left premaxilla**	**L1**	**P**	**late**	**HT**
V2716-2.2	**Incomplete left maxilla**	**L1**	**P**	**Early**	**HT**
V2716-2.3	**Anterior part of left mandible**	**L1**	**P**	**Late**	**HT**
V2716-3	**Left lower jaw in articulation with skull bones**	**L1**	**P**	**Late**	**HT**
V2716-4	**Unidentifiable bones**	**L1**	**P**	**UN**	**HT**
V2716-5	**Proximal end of left femur**	**L1**	**P**	**Early**	**HT**
V2716-6	**Incomplete humerus**[a]	**L1**	**P**	**UN**	**HT**
V2716-7	**Six disarticulated osteoderms**	**L1**	**P**	**Late**	**HT**
V2716-8	**Unidentifiable bones**	**L1**	**P**	**UN**	**HT**
V2716-9	**Unidentifiable bones**	**L1**	**P**	**UN**	**HT**
V2716-10	**Unidentifiable bones**	**L1**	**P**	**UN**	**HT**
V2716-11	**Incomplete skull**	**L1**	**P**	**Early**	**HT**
V2716-12	**Incomplete right jugal with right ectopterygoid**	**L1**	**P**	**Late**	**HT**
V2716-13	**Posterior part of the skull**	**L1**	**P**	**Early**	**HT**
V2716-14	**Incomplete right jugal and dorsal part of postorbital**	**L1**	**P**	**Early**	**HT**
V2721.1	**Left jaw**	**L3**	**K**	**Early**	**RS**
V2721.2	**Left foot**[a]	**L3**	**K**	**Early**	**RS**
V2721.3	**Unidentifiable bone**	**L3**	**K**	**UN**	**RS**
V2721.4	**A caudal vertebra**	**L3**	**K**	**Early**	**RS**
V2721.5	**Incomplete right dentary**	**L3**	**K**	**Early**	**RS**
V2771	**Incomplete left mandible**[b]	**L2**	**P (?)**	**Early**	**RS**

Eoalligator huiningensis Locality: Huaidinghuawu Huaining, Anhui. Horizon: Wanghudun Formation, Paleocene.					
V4058	**Anterior part of skull with lower jaw**	**HD**	**P**	**Early**	**HT**
Asiatosuchus nanlingensis Locality: Three localities in Nanxiong County, Guangdong Province (see also text and Figure 1). Locality 3 (L3), 1 km east of Xiuren Village; Locality 4 (L4), 2 km northwest of Hukou Village; Locality 5 (L5), 4 km west of Xiongzhou Town; Locality 6 (L6). Horizon: Zhenshui and Shanghu Formations, Cretaceous (?)—Paleocene.					
V2721a	**Fragment of mandible**	**L3**	**K**	**UN**	**RS**
V2772.1	**Incomplete dentary**	**L5**	**P**	**UN**	**RS**
V2772.2	**Incomplete dentary symphysis**[c]	**L5**	**P**	**UN**	**RS**
V2772.3	**11 isolated teeth**[c]	**L5**	**P**	**UN**	**RS**
V2772.4	**Five isolated vertebrae**	**L5**	**P**	**UN**	**RS**
V2772.5	**Incomplete left dentary**	**L5**	**P**	**UN**	**RS**
V2772.6	**Three craniomandibular fragments**	**L5**	**P**	**UN**	**RS**
V2772.7	**Incomplete right scapula**	**L5**	**P**	**UN**	**RS**
V2772.8	**Incomplete left humerus**	**L5**	**P**	**UN**	**RS**
V2772.9	**23 possible coprolites**	**L5**	**P**	**UN**	**RS**
V2773.1	**Pair of incomplete mandibles**	**L4**	**P**	**Late**	**HT**
V2773.2	**Four isolated vertebrae**	**L4**	**P**	**Late**	**HT**
V2773.3	**Left coracoid**	**L4**	**P**	**Late**	**HT**
V2773.4	**Distal end of right femur**	**L4**	**P**	**Late**	**HT**
V2775	**Posterior end of right mandible**[d]	**L6**	**P**	**Late**	**RS**

[a] non-crocodylian fossil; [b] may not be conspecific with other material assigned by Young (1964) to *E. chunyii*; [c] not conspecific with other material assigned by Young (1964) to *A. nanlingensis*; [d] likely conspecific either with *A. nanlingensis*, or with unknown crocodilian represented by V2772.2. Abbreviations: DS: Developmental Stage; H: Horizon; HD: Huaidinghuawu; HT: Holotype; L: Locality; RS: Referred Specimen; ST: Specimen Type. UN: Uncertain.

Institutional Abbreviation—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

SYSTEMATIC PALEONTOLOGY

Crocodylia Gmelin, 1789, sensu Benton and Clark, 1988

Crocodyloidea Fitzinger, 1826

Crocodylidae Laurenti, 1768

Genus *Asiatosuchus* Mook, 1940

Asiatosuchus nanlingensis Young, 1964

Synonymy—*Eoalligator chunyii* Young, 1964

Revised diagnosis—Very large crocodylid with the following unique combination of characters (autapomorphic character indicated by an asterisk): Well-developed sulcus present between

supratemporal fenestrae (STF); medial hemicondyle of quadrate enlarged; mandibular symphysis extends to level of fourth dentary tooth; distinct sulcus present on surangular next to glenoid fossa*; outline of proatlas in shape of isosceles triangle; the surangular-articular suture is oriented anteroposteriorly within the glenoid fossa. Distinguished from the rest of crocodylis by the anteroposteriorly oriented surangular-articular suture; from mekosuchines by enlarged medial hemicondyle of quadrate; and from tomistomines and *Asiatosuchus grangeri*_by mandibular symphysis extending only to fourth dentary tooth.

Description of material originally assigned to *Eoalligator chunyii*

Seven of the fragments that were originally assigned by Young (1964) to *Eoalligator chunyii* can be identified as adult based on size and fusion of neurocentral sutures (Brochu, 1996): IVPP V 2716-1.1, IVPP V 2716-1.2, IVPP V 2716-2.1, IVPP V 2716-2.2, IVPP V 2716-2.3, IVPP V 2716-3, IVPP V 2716-6, IVPP V 2716-12, and IVPP V 2721.4. Only informative specimens are described below.

Skull

Premaxilla—IVPP V 2716-2.1 (Fig. 2 A, B) comprises the lateral portion of a left premaxilla, with a small fragment of the maxilla still attached. In lateral view, the ventral margin curves posterodorsally as in *Crocodylus porosus*. In *Alligator sinensis* the margin is less strongly curved. Four alveoli are preserved, and damage to the anterior end of the bone has probably removed one additional alveolus. Given that crocodylian premaxillae consistently contain either four or five teeth, the preserved alveoli are probably the second through fifth. Broken tooth crowns are preserved within the second, third and fifth alveoli. The third alveolus is the largest in diameter, the second and fourth considerably smaller and subequal in size, and the fifth alveolus is the smallest. Posterior to the fifth alveolus, the premaxilla-maxilla suture runs laterally across a dorsal recess located immediately posterior to the fifth alveolus. This recess likely accommodated the fourth dentary tooth, which thus would have been partly concealed when the jaw was closed. The first maxillary alveolus is situated just posterior to the recess, and is equal in diameter to the fifth premaxillary alveolus.

Maxilla—IVPP V 2716-2.2 is a partial left maxilla with a piece of the lacrimal attached, whereas the partial skull IVPP V 2716-11 includes large portions of both maxillae. In IVPP V 2716-2.2 (Fig. 2 C, D, E), only the posterior part of the left maxilla is preserved. This bone contains four alveoli with damaged teeth, rather than the five described by Young (1964). The second and fourth preserved teeth have relatively intact crowns, which are blunt with smooth (unserrated) carinae. The teeth are clearly somewhat laterally compressed, demonstrating that *E. chunyii* lacks the extremely bulbous, almost ball-shaped tooth crowns seen in globidontan alligatoroids.

In IVPP V 2716-11 (Fig. 2 F, G, H, I), the dorsomedial portions of the two maxillae are preserved over a long interval representing the antorbital region of the skull. Each maxilla contacts the nasal medially and the lacrimal posteriorly. There is no maxillary process either intruding into the area occupied by the lacrimal or projecting between the lacrimal and nasal. Such a maxillary process is also absent in some basal gavialoids, some basal crocodyloids, *Mecistops cataphractus*, most *Crocodylus*, *Osteolaemus*, *L. canadensis*, diplocynodontines, a few

caimanines and *Paleosuchus*. Poorly preserved sculpturing is visible on the dorsal surfaces of both maxillae. In ventral view, the nasal channel (NAC) is exposed anteriorly due to postmortem damage.

Lacrimal—Lacrimals are preserved in IVPP V 2716-2.2 and IVPP V 2716-11. In IVPP V 2716-2.2 (Fig. 2 C, D, E), the anterior part of the left lacrimal is present and contacts the maxilla anteriorly. In medial view, the nasolacrimal duct is apparent as a groove extending anteriorly towards the external naris (EN). The duct is "V"-shaped in cross section, with the apex pointing laterally.

In IVPP V 2716-11 (Fig. 2 F, G), the anterior part of the left lacrimal is intact and contacts the maxilla anteriorly and the nasal medially. The posteromedial contact with the prefrontal may also be preserved, but the suture is not clearly apparent. Similarly, the right side of the skull retains part of the lacrimal and possibly a small part of the prefrontal, but sutural boundaries in this region are uncertain. However, the lacrimal certainly extends further anteriorly than the prefrontal, and contacts the nasal. The lacrimal also extends anteriorly beyond the prefrontal in gavialoids, crocodyloids, *L. canadensis*, diplocynodontine, *Caiman*, *Melanosuchus niger* and *Paleosuchus*.

Nasal—Both nasals are preserved in IVPP V 2716-11 (Fig. 2 F, G, H, I), although they are damaged anteriorly. Each nasal contacts its counterpart medially, the maxilla laterally, and the lacrimal posterolaterally, but the posterolateral contact with the prefrontal is not clearly preserved on either side of the skull. The lateral border of the nasal is straight, rather than concave as in *A. sinensis*.

Jugal—IVPP V 2716-12 comprises a fragment of a right jugal preserved with the ectopterygoid, and IVPP V 2716-14 includes a small piece of a right jugal. The portion of the bone preserved in IVPP V 2716-12 (Fig. 2 J, K) appears to be a posterior fragment of the jugal, probably situated below the infratemporal fenestra (ITF). It is slightly disarticulated from the ectopterygoid. A recess with a sharp, shelf-like ventral margin is present on the lateral surface of the preserved part of the jugal. A recess in the equivalent position, approximately below the ITF, is absent in extant alligators and at least some *Crocodylus* species (*C. porosus* and *C. niloticus*). The lateral surface of the jugal is sculptured, and the contact with the quadratojugal is not preserved.

The jugal fragment in IVPP V 2716-14 (Fig. 2 L, M) consists only of the base of the ascending process, which contributes to the postorbital bar, and the adjacent part of the jugal body. The preserved part of the postorbital bar is formed entirely by the jugal, implying that the descending process of the postorbital does not reach the base of the postorbital bar. There is no groove on the dorsal surface of the jugal between the base of the ascending process and the lateral margin of the bone.

Postorbital—IVPP V 2716-14 (Fig. 2 N) includes a small postorbital that was originally attached by matrix to the partial right jugal. The two bones were separated during preparation, but the postorbital fragment reveals no important morphological information.

Ectopterygoid—A right ectopterygoid is preserved in IVPP V 2716-12, and both ectopterygoids are preserved in IVPP V 2716-11. In IVPP V 2716-12 (Fig. 2 J, K), the body of the ectopterygoid is preserved but the maxillary and pterygoid processes are broken away. The anterior edge of the ectopterygoid, which forms the posterolateral margin of the suborbital

fenestra (SOF), is strongly concave.

In IVPP V 2716-14 (Fig. 2 F, G, H, I), the medial part of the left ectopterygoid and a compressed portion of the right ectopterygoid are preserved. Each ectopterygoid contacts the maxilla laterally and the pterygoid medially. The narrow and deeply concave posterior apex of the left suborbital fenestra is enclosed by the pterygoid, but the ectopterygoid's contribution to the margin of the fenestra begins only a short distance anterolateral to the apex.

Palatine—Both palatines are preserved in IVPP V 2716-11 (Fig. 2 F, G, H, I), but are damaged anteriorly. Each palatine contacts the pterygoid posteriorly. The posterior part of the lateral margin of the palatine trends posterolaterally. The palatine does not contribute to the concave posterior apex of the left SOF. The palatine-pterygoid suture extends transversely between the SOFs. Based on the position of the palatine-pterygoid suture, the choana must be surrounded entirely by the pterygoid, but the pterygoid is too poorly preserved for this to be confirmed by direct observation.

Pterygoid—The pterygoid is preserved in IVPP V 2716-1.1 and IVPP V 2716-11. The pterygoid of IVPP V 2716-1.1 (Fig. 3 E, F, G, H) is represented only by a small fragment that remains in articulation with the braincase but has been deflected towards the right side of the skull. The fragment comprises the median part of the bone, and includes the small, damaged left and right posterior processes. The pterygoid is preserved in contact with the basioccipital dorsally and the quadrates dorsolaterally. The basisphenoid and laterosphenoid presumably also contact the preserved part of the pterygoid, but the boundaries of these bones are not clearly visible. Unfortunately, the orientation of the posterior process is uncertain due to distortion.

In IVPP 2716-11 (Fig. 2 H, I), the anteromedial part of the pterygoid is preserved but the posterior part is severely damaged. The pterygoid contacts the palatine anteriorly and the ectopterygoid anterolaterally.

Quadratojugal—The posterolateral part of the right quadratojugal is preserved in IVPP V 2716-1.1 (Fig. 3 A, B, C, D, G), as a small piece of bone attached to the lateral margin of the quadrate.

IVPP V 2716-3 comprises the posterior end of a left mandible preserved in contact with the quadrate region of the skull. The posterior part of the quadratojugal is preserved, and contacts the quadrate medially (Fig. 4 A, B). The quadratojugal extends to the posterior tip of the lateral hemicondyle of the quadrate, obscuring the hemicondyle in lateral view. Anteriorly, the root of the quadratojugal spine (QJS) remains intact. The position of this structure suggests the spine would have protruded out into the infratemporal fenestra rather than following the superior margin of this opening, a character shared with *Gavialis gangeticus*, *Crocodylus* and *Osteolaemus*. Sculpturing is preserved on the lateral surface.

Quadrate—One or both quadrates are preserved in IVPP V 2716-1.1, IVPP V 2716-3 and IVPP V 2716-13. In IVPP V 2716-1.1 (Fig. 3 A, B, C, D, G), the right quadrate is relatively complete apart from damage to the margins and the absence of the condyles, but the left quadrate is less well-preserved. The quadrate contacts the squamosal dorsally, the parietal and the exoccipital medially, the pterygoid ventrally, the quadratojugal laterally and the laterosphenoid anteriorly. Anteriorly, the quadrate and laterosphenoid surround the dorsal part of the foramen ovale (FO), meeting at a nearly vertical suture that intersects the dorsal border of the FO. In the midline of the skull, a remnant of the basisphenoid contributes to the floor of the braincase and is

visible in anterior view because the front part of the skull is missing. Below the posterior rim of the supratemporal fenestra (STF), the quadrate appears to contribute to the floor of the posttemporal canal (PTC) (Fig. 3 A, B), intruding between the parietal and squamosal. This character is shared with *L. canadensis* and other non-alligatoroid crocodylians. In posteroventral view, there is a crest on the ventral side of quadrate for attachment of the adductor mandibulae posterior (AMP). An equivalent, but less well-developed, crest is present in *A. sinensis*.

In IVPP V 2716-3 (Fig. 4 A, B) the body of the left quadrate is preserved, and contacts the exoccipital dorsomedially and the quadratojugal laterally. The lateral hemicondyle of the quadrate is covered by the quadratojugal laterally. As in other crocodylians, there is no thin crest on the dorsal surface of the quadrate. The medial hemicondyle of the quadrate is larger than the lateral hemicondyle, as in extant *Crocodylus*. No foramen aerum (FA) is evident on the dorsal surface. The dorsal surface above the medial hemicondyle is damaged, as is the nearby part of the medial side of the quadrate. Furthermore, the ventromedial corner of the quadrate has broken away from the rest of the bone along a vertical crack and has been displaced a short distance posteriorly. The FA may have originally been located either on the line of the crack or on the medial surface of the quadrate. The latter possibility seems more likely, given that the FA on the articular is located close to the medial edge of the dorsal surface (see below). A fragment of the paroccipital process is preserved in articulation with the quadrate. Ventromedial to this fragment, the cranioquadrate canal (CQC) is exposed by post mortem damage.

Fragments of the ventral process of the left quadrate are preserved in the damaged partial skull IVPP V 2716-13, and the crest for the AMP is visible as in IVPP V 2716-1.1. However, no other important morphological details are discernable.

Laterosphenoid—A remnant of the laterosphenoid is preserved in IVPP V 2716-1.1, near the foramen ovale (FO). It contacts the quadrate posteriorly, the parietal dorsally and the pterygoid ventrally, although the suture with the pterygoid is unclear.

Parietal—The parietal is preserved in IVPP V 2716-1.1 and IVPP V 2716-13. In IVPP V 2716-1.1 (Fig. 3 A, B, C, D), the parietal is nearly complete, except that the anterior part of the bone is damaged. The parietal contacts the squamosals laterally, the exoccipitals posterolaterally, and the supraoccipital posteriorly, and exhibits an inverted "Y" shape in dorsal view. The intertemporal bar bears a deep longitudinal sulcus that is absent in extant alligators, and less distinct in adult *Crocodylus niloticus* than in IVPP V 2716-1.1. The rims of the STFs are elevated above the skull table. The sculpturing on the surface of the parietal is better-developed near the squamosal than elsewhere.

In IVPP V 2716-13 (Fig. 2 O) the middle of the posterior portion of the parietal is preserved, but the surface is badly damaged. The parietal has also been displaced to the left relative to the occipital condyle and the rest of the braincase. The sulcus between the STFs is less well-developed than in IVPP 2716-1.1, and the intertemporal bar is substantially broader. Both differences might reflect ontogenetic variation.

Squamosal—The medial part of the left squamosal, and most of the right squamosal apart from the anterior process, are preserved in IVPP V 2716-1.1 (Fig. 3 A, B, C, D, G). The squamosal contacts the parietal medially, the quadrate ventrally, the supraoccipital posteromedially, and the exoccipital ventrally. The posterior process extends posterolaterally, rather than posteriorly as in extant alligators, and reaches the posterior tip of the exoccipital

process. In occipital view, the squamosal-exoccipital suture extends horizontally, but its lateral portion has an irregular ventral concavity. In lateral view, the squamosal-quadrate suture runs alongside the posterior margin of the otic recess for a short distance before curving anteriorly to intersect the edge of the recess. The posterior margin of the otic recess forms a small posterior notch (Fig. 3 G).

Supraoccipital—The supraoccipital is completely preserved in IVPP V 2716-1.1 and IVPP V 2716-13. The supraoccipital contacts the parietal anteriorly, the squamosal laterally and the exoccipital ventrolaterally. In IVPP V 2716-1.1 (Fig. 3 A, B, C, D, E, F), the portion of the supraoccipital that is exposed on the skull table is semicircular. The supraoccipital is excluded from the foramen magnum (FM) by both exoccipitals, as in extant crocodylians.

In IVPP V 2716-13 (Fig. 2 O, P), the supraoccipital is less well-preserved and well-exposed. The supraoccipital appears morphologically similar to its counterpart in IVPP V 2716-1.1, but makes a smaller contribution to the skull table.

Exoccipital—One or both exoccipitals are preserved in IVPP V 2716-1.1, IVPP V 2716-3 and IVPP V 2716-13. In IVPP V 2716-1.1 (Fig. 3 A, B, C, D, E, F) the entire right exoccipital and the medial part of the left exoccipital are present. Each exoccipital contacts the supraoccipital dorsomedially, the squamosal dorsally, the quadrate ventrolaterally and the basioccipital ventromedially. The exoccipital forms the lateral margin of the foramen magnum (FM). Further laterally, the exoccipital bears a tapering ventral flange that extends to the same level as the ventral margin of occipital condyle. Two foramina are preserved lateral to the occipital condyle and medial to the suture with the quadrate: the dorsolaterally positioned jugular foramen transmitting the glossopharyngeal (IX), vagus (X), and accessory (XI) nerves, and the medioventrally positioned carotid foramen. Situated further dorsally, and lateral to the FM, is the hypoglossal canal for branches of the hypoglossal nerve (XII).

Only a small fragment of the exoccipital, preserved in contact with the quadrate, is present in IVPP V 2716-3. Similarly, only fragments of the right exoccipital are preserved in IVPP V 2716-13 (Fig. 2 O, P). The sutural boundaries of the bone are unclear due to postmortem damage. However, the exoccipital has a ventral flange of about the same extent seen in IVPP V 2716-1.1.

Basioccipital—The basioccipital is complete in IVPP V 2716-1.1 and IVPP V 2716-13. In IVPP V 2716-1.1 (Fig. 3 A, B, C, D, E, F) the basioccipital contacts the exoccipitals dorsolaterally and the pterygoid ventrally, and contributes to the ventral part of the FM. The occipital condyle is wide and suboval in occipital view, being somewhat dorsoventrally compressed, and projects posteriorly. A small basioccipital tuber appears to be present on the left side of the basioccipital, but there is no evidence of the midline crest below the occipital condyle that combines with the tubera to define a "W" shape in ventroccipital view (Fig. 3 E) in extant alligators and *C. niloticus*.

Lower jaw

Dentary—In the partial mandible IVPP V 2716-1.2 (Fig. 4 C, D), the middle part of the right dentary is in contact with the medially positioned splenial, and the entire preserved section of the mandible has been laterally compressed. A second mandibular fragment has been attached with plaster to the posterior end of the main fragment, and was tentatively described by Young (1964) as though this represented its natural position. However, the second fragment appears to represent

a small portion of the opposite (left) mandible of either the same individual or another of similar size.

Anteriorly, the main fragment of IVPP V 2716-1.2 is preserved almost to the level of the symphysis. The upper margin of the dentary as seen in lateral view has a slight undulating curvature in most crocodylians, although this margin is straight in some taxa such as *Gavialis gangeticus*. In some alligatoroids the upper margin of the dentary is more strongly curved, and in these cases the lower margin tends to become convex. In IVPP V 2716-1.2 the lower margin of the preserved part of the dentary is straight, whereas the dorsal margin is relatively straight posteriorly, rises to a low eminence containing sockets for two relatively large teeth, and slopes gently anteroventrally towards the anterior end of the bone. The curvature of the mandible thus appears to match the gently curved condition of typical crocodylians.

The variation in the size of the alveoli helps to distinguish IVPP V 2716-1.2 from *G. gangeticus*, in which no alveoli are distinctly enlarged. The preserved series of alveoli extends along the entire preserved part of the main fragment and may represent the fourth to seventeenth dentary teeth, but the anteriormost and posteriormost alveoli are incomplete. Young's (1964) estimate that twenty-three teeth would have been present in life included the alveoli present on the posterior fragment. The incomplete anteriormost alveolus on the main fragment, which we identify as the fourth, appears to be the largest in the series. The fifth through ninth alveoli are relatively small, whereas the tenth and particularly the eleventh are somewhat enlarged. The twelfth alveolus is considerably smaller than the eleventh. The more posterior alveoli are also relatively small, and appear to have suffered from lateral compression.

The posterior fragment included in IVPP V 2716-1.2 contains five alveoli that probably represent teeth 10-14 of a left mandible, based on their size and the presence of an anteriorly widening shelf medial to the tooth row. This fragment corresponds closely in morphology to the equivalent part of the main fragment. The medial surface of the posterior fragment bears a subdued area, bounded dorsally by the prominent medial edge of the shelf, which may represent part of the articular surface for the splenial. Below this is a longitudinal furrow that presumably corresponds in part to the Meckelian groove, but seems to have been enlarged by damage to the mandible.

IVPP V 2716-2.3 is the anterior part of a left dentary (Fig. 4 E, F), whereas IVPP V 2721.5 is the anterior part of a right dentary (Fig. 4 G, H). IVPP V 2771 is a poorly preserved left dentary that may not pertain to the same species as the other material (Fig. 4 I, J, K), since it shows no diagnostic characters of *A. nanlingensis* and is the only crocodylian specimen recovered from L2. An anteriorly tapering depression on the medial surface of IVPP V 2716-2.3 represents the anterior end of the Meckelian groove. The mandibular symphysis consistently extends posteriorly to the level of the fourth dentary tooth, but without reaching the tooth's posterior margin. Five alveoli (for teeth 4-8) are preserved in IVPP 2716-2.3, whereas four alveoli (for teeth 4-7) are preserved in IVPP 2721.5 and eight indeterminate alveoli are preserved in IVPP V 2771. The part of IVPP V 2771 immediately posterior to the symphysis is relatively intact, and may include the splenial, but more posteriorly the mandible is damaged, distorted and laterally compressed. The fourth tooth is large, although the apex is missing. About 2 cm posterior to the fourth tooth is preserved a small tooth with an acute, laterally compressed crown and smooth carinae (Fig. 4 J). A tortoise pleural bone (TPB) is attached to the medial surface of the mandible, near the posterior

end of the preserved portion.

Splenial—The main fragment of IVPP V 2716-1.2 (Fig. 4 C, D) includes a preserved partial splenial, whose anterior tip is slightly broken but clearly would have closely approached the symphysis in the intact mandible (Fig. 4 E, F). The splenial contacts the dentary laterally, and the medial surface of the former bone lacks any evident perforation. In IVPP V 2771 a fragment of the splenial may be present immediately caudal to the symphysis (Fig. 4 I, J, K). In IVPP V 2716-2.3, the Meckelian groove ends a short distance posterior to the mandibular symphysis, implying the splenial would not quite have entered the symphysis even if it covered the groove completely.

Surangular—The left surangular is preserved in both IVPP V 2716-3 and IVPP V 2721.1. In IVPP V 2716-3 (Fig. 4 A, B) the surangular is nearly complete, although the ventral part of the bone is distorted. The surangular contacts the articular medially and the angular posteroventrally. The dorsal margin of the surangular is flush with the transverse ridge at the posterior edge of the glenoid fossa, so that the surangular fully conceals the glenoid fossa in lateral view. Immediately lateral to the glenoid fossa, there is a sulcus within the narrow dorsal margin of the surangular. This sulcus is a unique feature among crocodylians, seen only in specimens originally assigned to *Eoalligator chunyii* and *Asiatosuchus nanlingensis*. The surangular extends posterodorsally, covering the anterior part of the lateral surface of the retroarticular process. However, it is uncertain whether the surangular reaches the distal end of the retroarticular process, which is damaged.

In IVPP V 2721.1 (Fig. 4 L, M) the sulcus next to the glenoid fossa is better developed than in the considerably larger IVPP V 2716-3, which indicates that the sulcus becomes less distinct during ontogeny. The surangular-articular suture runs anteroposteriorly near the lateral edge of the glenoid fossa. Participation of the surangular in the glenoid fossa is feature shared with *Gavialis gangeticus*, *Crocodylus niloticus* and extant *Alligator*.

Angular—The left angular is preserved in IVPP 2716-3 and IVPP V 2721.1 (Fig. 4 A, B, M). The angular contacts the surangular anterodorsally and the articular medially, extending up the retroarticular process.

Articular—The left articular is preserved in IVPP V 2716-3 and IVPP V 2721.1. In IVPP V 2716-3 (Fig. 4 B) the articular is nearly complete, although the posterodorsal tip of the retroarticular process is missing. This bone is covered laterally by the angular and surangular. In medial view, no lingual foramen is evident either on or near the articular-surangular suture. In contrast to the condition in many crocodylians, the articular does not form a lamina that projects forward to form an overlapping contact with the medial face of the surangular. In dorsal view, the foramen aerum (FA) is visible on the medial part of the articular. The presence of an FA on the articular is typical among crocodylians, but in allligatoroids, the position of the FA in alligatoroids is displaced dorsolaterally, rather than remaining medially positioned as in IVPP V 2716-3.

In IVPP V 2721.1 (Fig. 4 L, M), the left articular is nearly intact, although the posterodorsal tip is damaged. The articular is smaller than that of IVPP V 2716-1. The glenoid fossa contains a small longitudinal ridge separating the recesses that accommodate the two hemicondyles of the quadrate. The medial recess is much narrower than the lateral one.

460 **Postcrania**

461 **Proatlas**—A proatlas is preserved in IVPP V 2716-1.1 (Fig. 3 A, B, C, D, H), and is
462 complete but displaced from its original position. The proatlas approximates the shape of an
463 isosceles triangle in dorsal view. Anteriorly, it forms an obtuse point, similar to the apex of the
464 proatlas in *Alligator sinensis* (Cong et al., 1998) but quite different from the prominent anterior
465 process characterizing Diplocynodontinae (Brochu, 1999). The sagittal crest is damaged, but
466 appears to extend anteroposteriorly. A small ventral tuberosity (Fig. 3 H), representing the point
467 of attachment of the atlantoccipital ligament (Cong et al., 1998), is situated halfway along the
468 exposed left anterolateral surface of the proatlas. The posterior margin of the proatlas is linear
469 instead of smoothly concave as in *Crocodylus acutus*.

470 **Atlas**—The left half of the neural arch of the atlas is preserved, surrounded by matrix, in
471 IVPP V 2716-1.1 (Fig. 3 A, B, C, D, H). An embayment is present in the anterior margin of the
472 neural arch, and the proatlas likely articulated with a tapering anterior prominence that is situated
473 dorsal to the embayment. The atlas intercentrum is preserved separately, positioned to the right of
474 the occipital condyle and close to the axis. The intercentrum is similar to the proatlas in size, and
475 has a transversely broad ventral surface that would be tilted to face somewhat anteriorly if the
476 skull and cervical vertebrae were in natural articulation (anterior surface of Brochu, 1999, fig.
477 39). In contrast to the condition in extant *Alligator* (Brochu, 1999), the posterior margin of the
478 ventral surface does not form a recess between the two posterolaterally facing facets for the
479 atlantal ribs, and the intercentrum as a whole is not anteroposteriorly compressed.

480 **Axis**—The axis is almost completely preserved in IVPP V 2716-1.1 with the odontoid
481 process (atlantal centrum) in place (Fig. 3 A, B, C, D), although only the base of the neural spine
482 is present. The odontoid process (Fig. 3 H) is not fused to the axis centrum, and remains in
483 contact with the atlantal intercentrum although this joint has undergone slight disarticulation. On
484 the anterior part of the lateral surface of the centrum is a small longitudinal crest, dorsal and
485 ventral to which are two shallow recesses. The hypapophysis on the ventral surface of the
486 centrum is long and well-developed, occupying the anterior half of the centrum's length. What
487 appear to be the first two right cervical ribs are preserved in contact with the right side of the
488 axis, although not in their natural positions (Fig. 3 H). Further anteriorly, a rib from one of the
489 postaxial cervicals is preserved adjacent to the atlantal intercentrum and the left quadrate.

490 **Caudal Vertebra**—IVPP V 2721.4 is a disarticulated, procoelous caudal vertebra (Fig. 5
491 A, B, C). The prezygapophysis extends further laterally than the postzygapophysis. Remnants of
492 the transverse processes indicate that these structures were originally wide and well-developed,
493 extending for half the length of the centrum. A ventral groove (VG) is present on the ventral
494 surface of the centrum near the posterior condyle. The presence of the VG suggests that this
495 vertebra is from the anterior part of the tail. There is no visible neurocentral suture, indicating
496 that this specimen probably represents a mature individual. However, it could still be a sub-adult,
497 as the sutures close first in the caudal vertebrae during ontogeny (Brochu, 1997).

498 **Femur**—IVPP V 2716-5 is a left femoral head (Fig. 5 D, E), resembling in gross
499 morphology the equivalent structure in extant crocodylians. Judging from its size, the femur
500 belongs to an immature individual.

501 **Osteoderms**—IVPP V 2716-7 is a cluster of six disarticulated osteoderms with dorsal
502 keels (Fig. 5 F, G). Two of the osteoderms are distinctly narrower in the direction perpendicular

to the keel, whereas three are approximately square. The sixth osteoderm is incomplete and concealed by the others. The narrow osteoderms have keels that extend for almost their entire lengths, whereas the keel of the only well-preserved and well-exposed square osteoderm is separated from the embayed anterior margin by a small subdued area. The pits along the anterior margin of this osteoderm are small and transversely narrow in the vicinity of the keel, whereas the other visible pits are larger and more round. The sculpturing of the narrow osteoderms appears to consist entirely of round pits.

Description of material originally assigned to *Asiatosuchus nanlingensis*

The most informative component of the holotype of *Asiatosuchus nanlingensis* (IVPP V 2773) is a pair of very large incomplete mandibles (IVPP V 2773.1), each representing the articular region and a part of the ramus (Fig. 6 A, B, C, D, E). A small section of dentary containing four alveoli, with the corresponding piece of the splenial still in place medially, may represent an anterior fragment of the right mandible of IVPP V 2773.1 as suggested by Young (1964). The size and proportions of the fragment seem compatible with those of the large mandibles, under the assumption that the fragment originally occupied an anterior position within the right mandible, and the alveoli in the isolated fragment are similar in diameter to those preserved in the left mandible. The dorsal margin of the fragment slopes gradually anteroventrally, a feature consistent with anterior placement within the lower jaw. The ventral part of the external surface of the fragment is heavily sculptured, but the fragment provides little morphological information.

The left mandible of IVPP V 2773.1 preserves three incomplete teeth, lacking the crowns. There are two empty alveoli immediately posterior to the teeth, and a third immediately anterior to them. A single displaced tooth, bearing smooth carinae, is preserved in contact with the medial surface of the right mandible. Young (1964) considered the small size of the external mandibular fenestra (EMF) in both mandibles to be a diagnostic character, but this condition appears exaggerated by dorsoventral compression. The curvature of the dorsal and ventral margins of the EMF suggests, in both jaws, that this structure was originally larger. In particular, the ventral margin is distinctly concave, implying that the EMF was both larger and rounder than the slit-shaped opening seen in *Planocrania hengdongensis* (Li, 1984). However, it is difficult to be sure whether the intact EMF would have been very large, as in *Alligator*, or only moderately large as in *Crocodylus niloticus*. Most sutures on both mandibles are fused, presumably as a result of aging. There is no foramen aerum (FA) preserved on either articular. It is conceivable that the FA closed as the individual continued to develop ontogenetically, but there is no evidence to support closure of the FA with advancing age in any crocodylian.

As originally designated by Young (1964), the holotype also includes four cervical and dorsal vertebrae (IVPP V 2773.2), an incomplete left coracoid (IVPP V 2773.3), and the distal end of a right femur (IVPP V 2773.4). Two of the vertebrae are much smaller than the others, and clearly do not belong to the same individual represented by either of the large vertebrae or by the large mandibles. All four vertebrae are procoelous, as expected in any eusuchian.

Two mandibular fragments (IVPP V 2772.1 and IVPP V 2772.2) from a site (L5) several km from the locality that produced the holotype (L4) were both referred to *A. nanlingensis* by Young (1964), but differ from one another in some important morphological features. The

articular region is absent in both cases, limiting the potential for comparisons with the holotype mandibles. In IVPP V 2772.1 (Fig. 6 F, G), the mandibular symphysis extends to what is almost certainly the fourth dentary tooth, based on its large diameter. This corresponds to the condition in specimens assigned to *Eoalligator chunyii* (IVPP V 2716-1.2), but distinguishes IVPP V 2772.1 from *Asiatosuchus grangeri* from the Eocene of Inner Mongolia, in which the symphysis extends back to the sixth dentary tooth (Mook, 1940). In IVPP V 2772.2, however, the symphysis extends to an alveolus that can be identified as the seventh. Also, IVPP V 2772.2 (Fig. 6 H, I) has a dorsoventrally compressed symphysis, unlike IVPP V 2772.1 and specimens assigned to *Eoalligator chunyii* but as in longirostral taxa such as *Gavialis gangeticus*. In IVPP V 2772.2, the fourth dentary alveolus is smaller than all three posterior alveoli seen in IVPP V 2773, indicating that IVPP V 2772.2 must represent a smaller individual. Based on the length and dorsoventral compression of the mandibular symphysis, IVPP V 2772.2 likely represents a different species from the holotype, in which the middle part of the left mandibular ramus is sufficiently deep to indicate that the skull is not particularly longirostral. IVPP V 2772.1 is similar to IVPP V 2716-1.2 in that the dentary symphysis extends back to the fourth dentary alveolus, and in that the tenth to twelfth dentary alveoli are enlarged. These morphological similarities and the provenance of IVPP V 2772.1 suggest that referral of this specimen to *A. nanlingensis* is likely valid, although some uncertainty remains given that IVPP V 2772.1 shares no highly distinctive synapomorphies with either the holotype of *A. nanlingensis* or specimens referred to *E. chunyii*. IVPP V 2772.2, by contrast, seems to represent an unidentified longirostral crocodylian different from *A. nanlingensis*.

IVPP V 2772 also includes 11 isolated teeth (V2772.3), a number of coprolites and possible coprolites (V2772.9), and several additional non-diagnostic cranial and postcranial fragments (Table 1). All of the material, except possibly some of the coprolites, does appear to be of crocodyliform origin, but the isolated teeth have serrated carinae and therefore represent a taxon distinct from *A. nanlingensis*. They are also unlikely to be conspecific with the longirostral form represented by IVPP V 2772.2, because no Paleocene longirostral crocodyliforms is known to have a ziphodont dentition. The teeth are not necessarily from a crocodylian, but it is notable that five vertebrae included in the holotype collection (IVPP V 2772.4) are procoelous, implying that they are at least of eusuchian origin. These vertebrae, along with the other indeterminate cranial and postcranial fragments in the sample, could belong to any of the three species (the longirostral form, the ziphodont form and tentatively identified *A. nanlingensis*) present at L5.

IVPP V 2721a (Fig. 6 J, K) is a small dentary fragment from a locality that has also produced specimens assigned to *Eoalligator chunyii* (L3). This specimen was listed by Young (1964) as belonging to *A. nanlingensis*. The fragment clearly belongs to a large individual, and bears some sculpturing on the lateral surface, but no diagnostic morphological features are preserved. Its provenance suggests it likely belongs to *A. nanlingensis*, assuming *E. chunyii* is indeed a junior synonym of this taxon.

IVPP V 2775, the only specimen in this study recovered from L6, is the posterior end of a large right crocodylian mandible referred to *A. nanlingensis* by Young (1964). This poorly preserved fragment shows no diagnostic features, and could conceivably belong to either *A. nanlingensis* or the unidentified longirostral taxon represented by IVPP V 2772.2.

Alligatoroidea Gray, 1844, sensu Brochu, 2003
Eoalligator Young, 1964

Type Species—*Eoalligator huiningensis* Young, 1964

Horizon and Locality—Wanghudun Formation, middle Paleocene. Huaidinghuawu, Anhui Province, China.

Revised diagnosis—Very short snouted alligatoroid with the following unique combination of characters: complete nasal bar bisects external naris; fourth dentary tooth accommodated in notch between premaxilla and maxilla; eleventh and twelfth lower teeth are largest posterior teeth in dentary. Distinguished from all other alligatoroids outside *Alligator* by the complete nasal bar; from most alligatoroids by the notch between the premaxilla and maxilla that receives the fourth dentary tooth; from alligatorines by the large eleventh and twelfth posterior dentary teeth; and from the rest of alligatoroids by the proportionally very short snout.

Description of material assigned to *Eoalligator huiningensis*

Eoalligator huiningensis is the second nominal species of *Eoalligator* (Young, 1982). The holotype and only known specimen comprises a snout and the anterior parts of both mandibles (Fig. 7 A, B, C, D). The following description is intended to supplement that of Young (1982).

Skull

Premaxilla—The premaxillae form the anterolateral margins of the naris, which appears oval in dorsal view. Each premaxilla contacts its counterpart medially and the maxilla posteriorly. The premaxilla bears four slender teeth, which increase in length posteriorly. The fourth is the largest in diameter, as in extant alligators and *Crocodylus niloticus*, whereas in *Asiatosuchus nanlingensis* the third premaxillary tooth is largest. Near the contact with the maxilla, the lateral margin of the premaxilla is recessed to form the anterior part of the notch for the fourth dentary tooth. At the anterior margin of the external naris (EN), the two premaxillae combine to form a posterior process that protrudes a short distance into the EN but is clearly incomplete. In basal Alligatorinae, there is no such process, and the nasal bar is formed entirely by the nasals and fails to fully bisect the EN. In *Alligator*, which is characterized by a complete nasal bar that bisects the EN (Wermuth, 1953; Malone, 1979; Norell, 1988; Brochu, 1999), the anterior part of the bar is always formed by a process of the premaxillae. The presence of a posterior process of the premaxillae may therefore indicate that the nasal bar completely bisected the EN in the intact skull of *E. huiningensis*.

Maxilla—The maxillae are complete, and form the main part of the snout. Each maxilla contacts the premaxilla anteriorly, the nasal medially, the lacrimal posteromedially and the jugal posteriorly. The anterior part of the lateral margin is embayed by a recess that is continuous with the similar feature on the premaxilla, forming the posterior part of the notch for the fourth dentary tooth. Posterodorsal to this notch is the more anterior of the two depressions that Young (1982) described on the lateral surface of the maxilla and regarded as a distinguishing feature of *E. huiningensis*. This depression is shallow, irregular and transversely elongate, extending from just above the alveolar margin to a point on the suture with the nasal. The depression is bounded posteriorly by a low elevation aligned with the large fifth maxillary tooth. The opposite side of the skull is unfortunately damaged in this region, and the snout is distorted by leftward skew.

There is at least a slight anterior depression corresponding in position to the one on the right side, but it may not be equally large and well-developed. Even if the anterior depression is a genuine morphological feature rather than an artifact of distortion, it represents little more than an irregularity in the surface of the snout, and its taxonomic value is questionable.

A partial lacrimal is preserved on the right side of the skull. There is no discernable maxillary process either intruding into the lacrimal or projecting between the lacrimal and the nasal. The medial part of the maxilla-lacrimal suture is transverse, but the lateral part of the suture extends posterolaterally and is situated just within a second depression on the maxilla. This posterior depression has the shape of an irregular oval, and is separated from the alveolar margin by a prominent area of bone. The left side of the skull is again damaged in the corresponding region, in that the surface of the maxilla is worn away and the body of the maxilla is interrupted by a slit-like hole that is clearly artifactual. Young (1982) considered the posterior depression to represent a degenerate antorbital fenestra, but this interpretation seems untenable. As with the anterior depression, it is difficult to rule out the possibility that the posterior depression is simply a product of damage and/or deformation, particularly given that the sculpturing inside the depression appears eroded. Furthermore, the region of the crocodylian snout believed to correspond to the formerly open antorbital fenestra is situated mainly on the maxilla, with a small degree of lacrimal participation, but does not extend onto the jugal (Witmer, 1995). However, the right jugal of *E. huiningensis* does contribute to the posterior depression on the snout. Young compared *E. huiningensis* with a notosuchian, *Uruguaysuchus aznarezi*, but the antorbital fenestra in *U. aznarezi* has no jugal component (Soto et al., 2011). Moreover, members of Crocodylia consistently lack an antorbital fenestra, so the presence of even a degenerate version of this feature in the specimen would be extremely surprising. For these reasons, the posterior depression is clearly not a homologue of the antorbital fenestra. Like the anterior depression, it may represent either an artifact or a genuine topological feature, but seems unpersuasive as a taxonomic character.

The left maxilla bears nine teeth, while the right bears twelve, rather than the eleven reported by Young (1982). Combining information from the two sides of the skull shows that the first two maxillary teeth share the small and slender morphology of the first three premaxillary teeth, while the third is slightly larger. The fourth tooth is larger still, and the fifth and sixth teeth are the largest in the maxilla. The seventh to ninth maxillary teeth are shorter and blunter than the fourth, but also more robust, and are probably adapted for durophagy (Aoki, 1989). The tenth to twelfth teeth are slightly larger than the fourth, but smaller than the fifth and sixth.

Lacrimal—Only an anterior remnant of the right lacrimal is preserved. A small portion of the left lacrimal may be present as well, but no suture is visible to separate this bone from the maxilla. The right lacrimal contacts the maxilla anteriorly, the nasal medially and the jugal ventrally. The fact that there is a preserved remnant of the lacrimal, but no preserved remnant of the prefrontal, indicates that the former bone extended further anteriorly in the intact snout.

Nasal—Both nasals are preserved, but are damaged in the region of the external naris (EN). Each nasal contacts its counterpart medially, the premaxilla anteriorly and the maxilla laterally, and presumably reached the frontal posteriorly. The nasals clearly extended into the EN, forming a long nasal bar, but most of this structure has been obliterated by a transverse gouge across the dorsal surface of the snout. The tips of the two nasal processes remain in place anterior

to the gouge, isolated within the narial opening. The nasal-maxilla suture is linear in dorsal view. A very thin, meandering transverse line near the posterior margin of the preserved part of the snout may represent the nasofrontal suture. If this is the case, the contact between the nasal and frontal is broad, and a small remnant of the frontal remains in place.

Jugal—As preserved, the right jugal extends posteriorly somewhat beyond the level of the postorbital bar. A small anterior part of the left jugal may be preserved in the vicinity of the orbit, but this is uncertain. The right jugal contacts the maxilla anteriorly, and the lacrimal dorsally. The base of the slightly inset postorbital bar is not separated by a depression from the lateral margin of the jugal, and bears a small longitudinal crest on its anterior surface.

Lower jaw

Dentary—The left dentary is broken at the level of the tenth maxillary tooth, with only the portion anterior to the break remaining in place. The right dentary is also broken away posteriorly, but remains intact to the level of the anterior part of the external mandibular fenestra (EMF). The dentary contacts the splenial medially and the surangular posterodorsally. The tooth-bearing portion of the dorsal margin of the dentary is similar to its equivalent in *Asiatosuchus nanlingensis* in in undulating gently along its length, whereas the posterior part of the dorsal margin slopes posterodorsally. The ventral margin of the dentary is slightly convex. The dentary symphysis extends posteriorly as far as the level of the fifth dentary tooth. The dentary-surangular suture intersects the anterodorsal margin of the EMF.

The preserved part of the left dentary bears eleven teeth, rather than the seventeen described by Young (1982), while the right bears fourteen teeth. The posteriormost dentary tooth is displaced and rotated, resting in the space between the dentary and maxilla. However, it appears to belong to the dentary because of its lack of the consistently bulbous morphology seen in the posterior maxillary teeth. The anterior two dentary teeth point dorsally, rather than anterodorsally as in some other crocodylians (e.g. *Osteolaemus tetraspis*). The fourth dentary tooth is the largest, and the third is the second-largest. The eleventh dentary tooth is also enlarged, having twice the diameter of the tenth.

Splenial—A large portion of the right splenial is preserved, although the anterior tip is missing. Posteriorly, the splenial forms the anterior margin of a low, elongate opening in the medial surface of the mandible that may represent the foramen intermandibularis medialis. The splenial appears to contact anterior processes of the angular both ventral and dorsal to this opening, but the sutural contacts are difficult to follow with certainty, and the angular cannot be traced onto the lateral surface of the mandible. Another putative suture line dorsal to the opening may represent the contact between the splenial and a small exposed strip of the coronoid. There is no evident foramen intermandibularis oralis near the symphysis or on the medial surface of splenial body. A small anteroventral portion of the left spenial is exposed, but the anteriormost part of the bone is missing or damaged.

Surangular—Only the anterior part of the right surangular is preserved, contacting the dentary anteriorly. The preserved portion of the surangular represents the tapering ventral process, which extends anteriorly near the dorsal margin of the lateral surface of the mandible. As in other alligatoroids, the ventral process is long, almost reaching the posteriormost preserved dentary teeth.

Phylogenetic Analysis

To test the proposed status of *Eoalligator chunyii* as a junior synonym of *Asiatosuchus nanlingensis*, and to explore the phylogenetic positions of the latter species and *Eoallligator huiningensis*, two cladistic analyses were conducted using TNT 1.0 (Goloboff et al., 2003) on a modified version of the matrix of Brochu (2012). "*E. chunyii*", *E. huiningensis* and *A. nanlingensis* were all coded into this matrix separately, and two more taxa from Asia were added to the analyses. One new character was added, and one new character state was added to character 74. In total, the modified character matrix consisted of 105 ingroup taxa and 190 morphological characters. *Bernissartia fagesii* was treated an outgroup taxon in both analyses (see Supplemental Information 1).

In the first analysis, the complete modified matrix was used. A new technology search based on 100 random addition sequence replicates and 1000 random seeds was implemented using TNT (version 1.1; Goloboff et al., 2008). The advanced search settings were changed to ensure enough iterations: 100 sectorial search drifting cycles, 100 ratchet iterations, 100 drift cycles and 100 rounds of tree fusion for every replicate. Multistate characters were left unordered. All characters were equally weighted.

In order to further test the topology generated by the first analysis, while excluding phylogenetic "noise" from Gavialoidea and Crocodyloidea, a second analysis was conducted with a reduced matrix (45 ingroup taxa, 190 morphological characters). This version of the modified matrix included only *Bernissartia fagesii*, "*Eoalligator chunyii"*, *Eoalligator huiningensis, Asiatosuchus nanlingensis*, *Krabisuchus siamogallicus*, all members of Alligatoroidea and the unnamed alligatorinae from the Eocene of the Maoming Basin in Guangdong Province (Skutschas et al., 2014).

The first analysis recovered 191 equally parsimonious trees, each 727 steps in length with a consistency index (CI) of 0.338 and a retention index (RI) of 0.806. The strict consensus tree is displayed in Fig. 8 with Bremer support indicated for each node. The general topology was consistent with the results of previous studies (Brochu, 1999, 2013; Martin and Lauprasert, 2010), but resolution was relatively poor within Crocodyloidea and Alligatoroidea.

Within Crocodyloidea, four monophyletic groups were recovered: Tomistominae, *Osteolaemus*, *Crocodylus pigotti* + *Euthecodon arambourgii* and *Eoalligator chunyii* + *Asiatosuchus nanlingensis*. Within Alligatoroidea, Globidonta did not emerge as monophyletic, but several monophyletic groups were recovered: a clade consisting of *Procaimanoidea kayi*, *Arambourgia gaudryi* and *Procaimanoidea utahensis*; advanced Alligatorinae (*Alligator* + *Wannaganosuchus brachymanus*); *Paleosuchus*; *Melanosuchus* + *Caiman latirostris* + *Caiman lutescens*; and *Caiman crocodilus* + *Caiman yacare*.

The second analysis recovered 178 equally parsimonious trees, each 310 steps in length with CI=0.794 and RI=0.974. The strict consensus tree included five clusters of taxa within Alligatoroidea: a polytomous clade consisting of members of Diplocynodontinae; Alligatorinae; *Paleosuchus*; *Melanosuchus niger* + *Melanosuchus fisheri* + *Caiman latirostris* + *Caiman lutescens*; and *Caiman crocodilus* + *Caiman yacare*). The topology of the majority rule tree (Fig. 9) was consistent with the strict consensus tree obtained in the first analysis. *Eoalligator chunyii* and *Asiatosuchus nanlingensis* formed a monophyletic group outside Alligatoroidea.

The two putative species of *Eoalligator* did not form a monophyletic group in either analysis: *Eoalligator chunyii* lies within Crocodylidae as the sister-taxon of *Asiatosuchus nanlingensis*, a placement consistent with the absence in specimens assigned to *E. chunyii* of one important derived feature normally seen in alligatoroids (character 70: medially positioned foramen aerum). On the other hand, *Eoalligator huiningensis* is placed in a polytomous Globidonta in the first analysis and a polytomous Alligatoroidea in the second one. In the first analysis, recovering a monophyletic *Eoalligator* required an additional three steps, and recovering a monophyletic *Eoalligator* within Alligatorinae as suggested by Young (1964, 1982) required an additional eleven steps. Furthermore, *Asiatosuchus* was not obtained as monophyletic group in the first analysis, the only one to include multiple species assigned to this genus. Although all three *Asiatosuchus* species fell within Crocodyloidea, the Mongolian species *A. grangeri* and the European species *A. germanicus* were positioned well basal to *A. nanlingensis* and were not recovered as sister-taxa. *E. huiningensis* was isolated within an alligatoroid polytomy in the first analysis, but grouped with many caimanines in the second. These inconsistent results might arise partly from the incompleteness of the only known specimen of *E. huiningensis*, and the more conservative interpretation suggested by the first analysis–that *E. huiningensis* is an alligatoroid of uncertain affinities– is preferable.

Discussion

Asiatosuchus nanlingensis and *Eoalligator chunyii* were named in the same paper based on material discovered in the Nanxiong Basin, and one locality (L3) even yielded putative specimens of both taxa. Despite a distinct size difference between specimens assigned to *A. nanlingensis* and those assigned to *E. chunyii*, mandibles of the two putative taxa share four significant morphological characters: (1) dorsally positioned sulcus within the surangular, which is unique to these two nominal species; (2) surangular-articular suture that extends anteroposteriorly within the lateral hemi-fossa of the glenoid (shared by various crocodyloids); (3) posterodorsally pointing retroarticular process; and (4) gently curved mandible. The two cladistic analyses carried out for this study recovered "*E. chunyii"* and *A. nanlingensis* as sister taxa (Fig. 8, Fig. 9), although only the first tested their monophyly with respect to a range of crocodyloids. In the first analysis, they were positioned within Crocodylidae and their sister-group relationship was supported by two of the morphological characters listed above: a sulcus within the surangular (character 73), and an anteroposteriorly oriented surangular-articular suture (character 74). The posterodoally pointed retroarticular process is shared with most crocodylians, and the gently curved mandible is shared with many members of Brevirostres. Furthermore, there are no clear morphological differences between *A. nanlingensis* and *E. chunyii*. Because the two species are essentially indistinguishable in distribution and morphology, *E. chunyii* is regarded as a junior synonym of *A. nanlingensis* based on page priority (Young, 1964). As the type species of *Eoalligator*, *E. chunyii,* is now invalid, we designate *E huiningensis* as the new type species.

Given that *E. huiningensis* lies well outside *Alligator*, the apparent presence of a complete nasal bar that bisects the external naris (EN) is intriguing. To move *E. huiningensis* within *Alligator*, maintaining the nasal bar as a synapomorphy exclusive to this genus among alligatoroids, requires only three additional steps. However, placing *E. huiningensis* within *Alligator* would be inconsistent with the presence of certain primitive characters in this species

(lacrimal extends further anteriorly than prefrontal, notch for fourth dentary tooth present between premaxilla and maxilla). Additional fossils that provide morphological information regarding the posterior part of the skull, and regarding taxonomically important postcranial bones such as the scapula and coracoid (Brochu, 1995) have the potential to further improve our knowledge of interrelationships within Alligatoroidea. An issue of particular concern is the relationship between *E. huiningensis* and Caimaninae, as *E. huiningensis* was positioned close to various caimanines in some of the equally parsimonious trees found by two cladistic analysis in this study as well as in the majority rule tree from the second analysis (Fig. 9). However, the individual equally parsimonious trees normally are not considered to carry much weight, nor should they be.

Based on the taxonomic revision presented in this paper, four alligatoroid species are currently known in the Chinese fossil record: *Eoalligator huiningensis* from the Paleocene of Anhui, *Alligator luicus* from the Miocene of Shandong, *Alligator sinensis*, which may date back to the upper Pleistocene (Shan et al., 2013) and The Maoming specimen from the Eocene of Guangdong (Skutschas et al., 2014). Brief comparisons among these taxa reveal some interesting similarities. In *E. huiningensis*, *A. luicus*, and the Maoming specimen, the lacrimal extends further anteriorly than the prefrontal. However, the prefrontal is the more anteriorly extensive of the two bones in most non-Caimaninae alligatorines; this is the case in *Allognathosuchus*, *Wannaganosuchus brachymanus*, *Procaimanoidea, Arambourgia gaudryi*, *Alligator*, although in some caimanines (*Purussaurus*, and *Mourasuchus atopus*) the lacrimal is more anteriorly extensive. In *E. huiningensis* and the Maoming specimen, the medial edge of the lacrimal contacts the nasal broadly, and no maxillary intrusion is present either within the lacrimal or between the lacrimal and the nasal. However, a maxillary intrusion is present within the lacrimal in *A. sinensis*. *A. luicus* lacks a maxillary intrusion, and only the anterior tip of the lacrimal contacts the nasal. The absence of a maxillary intrusion is a plesiomorphic character shared with some basal crocodylians (e.g. *Borealosuchus*), some basal alligatoroids (*Leidyosuchus canadensis* and diplocynodontines) and some caimanines (*Tsoabichi greenriverensis*, *M. atopus*, and *Paleosuchus*). In most alligatoroids that are more advanced than the diplocynodontines, except *E. huiningensis* and The Maoming specimen, the maxillary intrusion is present within the lacrimal. However, this intrusion of the maxilla is positioned between the lacrimal and the nasal in a few stem-alligatoroids: *Stangerochampsa mccabei*, *Albertochampsa langstoni*, and *Brachychampsa*. The distribution of character states suggests that the maxillary intrusion may have first appeared as a process situated between the lacrimal and nasal, and subsequently shifted in more derived forms to lie fully within the lacrimal. However, this scenario cannot be confirmed at present, because of the poorly resolved phylogeny. In *E. huiningensis*, *A. luicus* and *A. sinensis*, the external naris (EN) is bisected by a complete nasal bar, The Maoming specimen seems to lack this character, although preservation is poor near the EN (Skutschas et al., 2014). Whereas the shortness of the prefrontal relative to the lacrimal is a plesiomorphic condition shared by *E. huiningensis*, *A. luicus* and The Maoming specimen, the complete nasal bar is a highly derived feature present at least in *E. huiningensis*, as well as in *A. luicus* and other species of *Alligator* presumably as a result of convergent evolution.

Although the results of both cladistic analyses are rather poorly resolved, they have some paleobiogeographic implications. The node corresponding to Crocodyloidea in the phylogeny

generated in the first analysis (Fig. 8) is a polytomy, so this tree does not provide a clear framework for investigating crocodyloid evolution and paleobiogeography. *Prodiplocynodon langi* from the Cretaceous of North America (Mook, 1941) is the oldest known crocodyloid, but is not much older than *A. nanlingensis*, implying a rapid series of divergences within Crocodyloidea. However, more time will be available for these divergences if older crocodyloids that are more basal than *P. langi* are discovered in the future. *A. nanlingensis* was recovered as a crocodylid in the first phylogenetic analysis, and represents the oldest known member of this clade given its occurrence in the Cretaceous and Paleocene of Guangdong.

In the consensus tree recovered by the first analysis (Fig. 8), Tomistominae emerged as a monophyletic group whereas taxa usually assigned to Crocodylinae formed various lineages within a polytomy at the base of Crocodylidae. The phylogeny includes the oldest known tomistomine, namely *Kentisuchus spenceri* from Paleocene-Eocene boundary strata in the United Kingdom (Brochu, 2007). If *A. nanlingensis* is also a basal tomistomine, the split between Tomistominae and Crocodylinae must have occurred before the end of the Cretaceous. This phylogenetic placement would also make *A. nanlingensis* the first tomistomine, and would imply that Tomistominae might have originated in Asia. Although the typical tomistomine longirostral snout with a long symphysis is not present in *A. nanlingensis*, the long snouted *Mecistops cataphractus* and shorter snouted *Crocodylus* provide a good example of taxa that have very different snout shapes but nevertheless are closely related. By contrast, *A. nanlingensis* might represent a crocodyline. This alternative would place the origin of Tomistominae possibly in Europe, if not in the United Kingdom, and the Tomistominae-Crocodylinae divergence again in the Cretaceous. Furthermore, *Kambara implexidens* from the lower Eocene of Australia (Willis et al., 1993) would then be the second-oldest crocodyline included in the phylogeny, with only *A. nanlingensis* being older. Assuming the phylogenetic positions of *A. nanlingensis* and *K. implexidens* were congruent with their geological ages, the common ancestors of fossil Australian crocodylines and *A. nanlingensis* could be inferred to have likely inhabited Asia before they reached Australia. Regardless of whether *A. nanlingensis* is a tomistomine or a crocodyline, however, more data on basal crocodylids will be needed to arrive at a well-resolved phylogeny that can provide a basis for robust biogeographic interpretations.

The phylogeny generated in the first analysis (Fig. 8) also indicates that there must have been at least two historical dispersals of alligatoroids into China, the first involving ancestors of *E. huiningensis* and the second involving ancestors of *A. sinensis*. *E. huiningensis* is known only from the middle Paleocene Wanghudun Formation of Anhui (Young, 1982). The only known fossil specimen that can be securely attributed to *A. sinensis* is a skull from the Penghu Channel of Taiwan, which is probably late Pleistocene in age (Shan et al., 2013).

Accordingly, the first dispersal must have occurred no later than the middle Paleocene, whereas the second must have occurred no later than the Pleistocene. One possible route by which the ancestors of *E. huiningensis* could have migrated to China led west from North America, via the Bering Land Bridge. This land bridge facilitated many terrestrial faunal exchanges between Asia and North America during the late Paleocene and early Eocene (Beard, 2002; Smith et al., 2004; Solé & Smith, 2013), a time interval characterized by the globally elevated temperatures of the Paleocene-Eocene Thermal Maximum (PETM) event. However, *E. huiningensis* is from the Wanghudun Formation, which appears to correlate with the upper part of

the Shanghu Formation and the lower part of the Nongshan Formation in the Nanxiong Basin (Missiaen, 2011). The Shanghu Formation has produced mammalian species belonging to various groups, such as mesonychids and carnivorans, which are shared with North and South America (McKenna and Bell, 1997). However, these taxa are insufficiently well known to provide a strong basis for biogeographic interpretations (Missiaen, 2011). The Nongshan Formation contains mammals such as arctostylopids and *Ernanodon*, but the presence of these taxa is no longer considered to represent evidence for early Paleocene migrations between Asia and the Americas (Missiaen et al., 2006; Rose, 2006). As a result, the mammalian species currently known from the early Paleocene of China are now considered to belong to endemic groups (Missiaen, 2011; Ting et al., 2011). However, a recent report on a spadefoot toad from the upper Paleocene of Mongolia suggests that members of this clade migrated from North America to Asia at some point prior to the larger-scale mammalian faunal exchange of Paleocene-Eocene boundary times (Chen et al., 2016). Given that *E. huiningensis* is middle Paleocene in age, its ancestors must have come to Asia no later than the early middle Paleocene. This datum also suggests a migration from North America to Asia predating the mammalian exchange, but whether *E. huiningensis* and the Mongolian spadefoot toad dispersed in the same event remains unknown. The driving factors behind the Paleocene dispersal(s) of these taxa are equally uncertain.

In principle, the ancestors of *E. huiningensis* might have reached Asia by dispersing eastward from North America through Europe, rather than westward across the Bering Land Bridge. However, the terrestrial fauna exchanges via the European route that have so far been documented did not begin until around the Paleocene-Eocene boundary (Godinot & Lapparent de Broin, 2003; Solé & Smith, 2013), perhaps because a marine barrier such as the Turgai Straits blocked this pathway in the Paleocene. As a result, dispersal via the Bering Land Bridge currently seems more likely for the ancestors of *E. huiningensis*.

Conclusions

1) *Eoalligator chunyii* is a junior synonym of *Asiatosuchus nanlingensis*.

2) *Asiatosuchus nanlingensis* is currently the oldest crocodylid that has been included in any phylogenetic analysis.

3) *Eoalligator huiningensis* is an alligatoroid of uncertain affinities that both retains several primitive alligatoroid characters and displays an advanced character otherwise limited to *Alligator* among Alligatoroidea (a complete nasal bar).

4) In the early Paleocene, the ancestors of *Eoalligator huiningensis* are likely to have migrated from North America to Asia via the Bering Land Bridge.

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Figure captions:

Figure 1 Localities (L1-L5) in Nanxiong County, Guangdong Province that have produced specimens assigned to *Eoalligator chunyii* and/or *Asiatosuchus nanlingensis*.

Figure 2 *Asiatosuchus nanlingensis* specimens originally assigned by Young (1964) to *Eoalligator chunyii*, including: IVPP V 2716-2.1, incomplete left premaxilla, in ventral (A) and lateral (B) views; IVPP V 2716-2.2, incomplete left maxilla, in dorsal (C), ventromedial (D) and posterior (E) views; IVPP V 2716-11, incomplete skull, in dorsal (F, G) and ventral (H, I) views; IVPP V 2716-12, incomplete right jugal with ectopterygoid, in lateral (J) and ventral (K) views; IVPP V 2716-14, incomplete right jugal in lateral (L) and anterior (M) views, and dorsal part of right postorbital in dorsal view (N); IVPP V 2716-13, posterior part of skull, in dorsal (O) and occipital (P) views. Arrows point anteriorly. Abbreviations: bo: basioccipital; ect: ectopterygoid; exo: exoccipital; ITF: infratemporal fenestra; j: jugal; l: lacrimal; mx: maxilla; mxa: maxillary alveolus; mxt: maxillary tooth; n: nasal; nld: nasolacrimal duct; oc: occipital condyle; p: parietal; pal: palatine; pf: prefrontal; pm: premaxilla; pma: premaxillary alveolus; pmt: premaxillary tooth; pt: pterygoid; so: supraoccipital; SOF: suborbital fenestra; STF: supratemporal fenestra; sul: sulcus; vp: ventral process.

Figure 3 *Asiatosuchus nanlingensis* (IVPP V 2716-1.1), posterior part of skull originally designated by Young (1964) as part of the holotype of *Eoalligator chunyii*, in dorsal (A, B), posterodorsal (C, D), posteroventral (E, F), right lateral (G), and left ventrolateral (H) views. Abbreviations: AMP: attachment of adductor mandibulae posterior; at: atlas; ax: axis; bo: basioccipital; cf: carotid foramen; cv: cervical rib; exo: exoccipital; f IX-X-XI, foramen for glossopharyngeal (IX), vagus (X) and accessory (XI) nerves; f XII, foramen for hypoglossal nerve; FO: foramen ovale; FM: foramen magnum; h: hypapophysis: nc: neural canal; o: osteoderm; or: otic recess; p: parietal; pr: proatlas; pt: pterygoid; PTC: opening of posttemporal canal; q: quadrate; qj: quadratojugal; s: squamosal; so: supraoccipital; STF: supratemporal fenestra; sul: sulcus; vt: ventral tuberosity.

Figure 4 *Asiatosuchus nanlingensis* specimens originally assigned by Young (1964) to *Eoalligator chunyii*, including: IVPP V 2716-3, left jaw articulated with part of skull, in dorsal (A) and lateral (B) views; IVPP V 2716-1.2 (part of the holotype of *E. chunyii*), two incomplete right mandibles, in lateral (C) and medial (D) views; IVPP V 2716-2.1, left dentary, in dorsal (E) and medial (F) views; IVPP V 2721.5, anterior part of right dentary, in dorsal (G) and ventral (H) views; IVPP V 2771, left mandible, in dorsal (I), lateral (J) and medial (K) views; IVPP V 2721.1, left posterior mandibular fragment in dorsal (L) and lateral (M) views. Most specimens are referable to *Asiatosuchus nanlingensis*, but the taxonomic identity of IVPP V 2771 is uncertain. Arrows point anteriorly. Abbreviations: an: angular; art: articular; CQC: cranioquadrate canal; d: dentary; da: dentary alveolus; dt: dentary tooth; exo: exoccipital; FA: foramen aerum; fw: full width; mg: Meckelian groove; o: osteoderm; q: quadrate; qj: quadratojugal; qjs: quadratojugal spine; sa: surangular; sp: splenial; sul: sulcus; sy: symphysis; tpb: tortoise pleural bone.

Figure 5 *Asiatosuchus nanlingensis* specimens originally assigned by Young (1964) to *Eoalligator chunyii*, including: IVPP V 2721.4, caudal vertebra, in dorsal (A) ventral (B) and lateral (C) views; IVPP V 2716-5, proximal end of left femur, in lateral (D) and medial (E) views; IVPP V 2716-7, six disarticulated osteoderms, in dorsal (F) and ventral (G) views. Abbreviations: vg: ventral groove.

Figure 6 Specimens assigned by Young (1964) to *Asiatosuchus nanlingensis*, including: IVPP V 2773 (holotype), left mandible in dorsal (A), lateral (B) and medial (C) views, and right mandible in lateral (D) and medial (E) views; IVPP V 2772.1, right dentary in lateral (F) and medial (G) views; IVPP V 2772.2, dentary symphysis in dorsal (H) and ventral (I) views; IVPP V 2721a, dentary fragment in medial (J) and lateral (K) views. IVPP V 2772.2 appears to represent a longirostral crocodylian distinct from *A. nanlingensis*. Abbreviations: da: dentary alveolus; dt: dentary tooth; EMF: external mandibular fenestra.

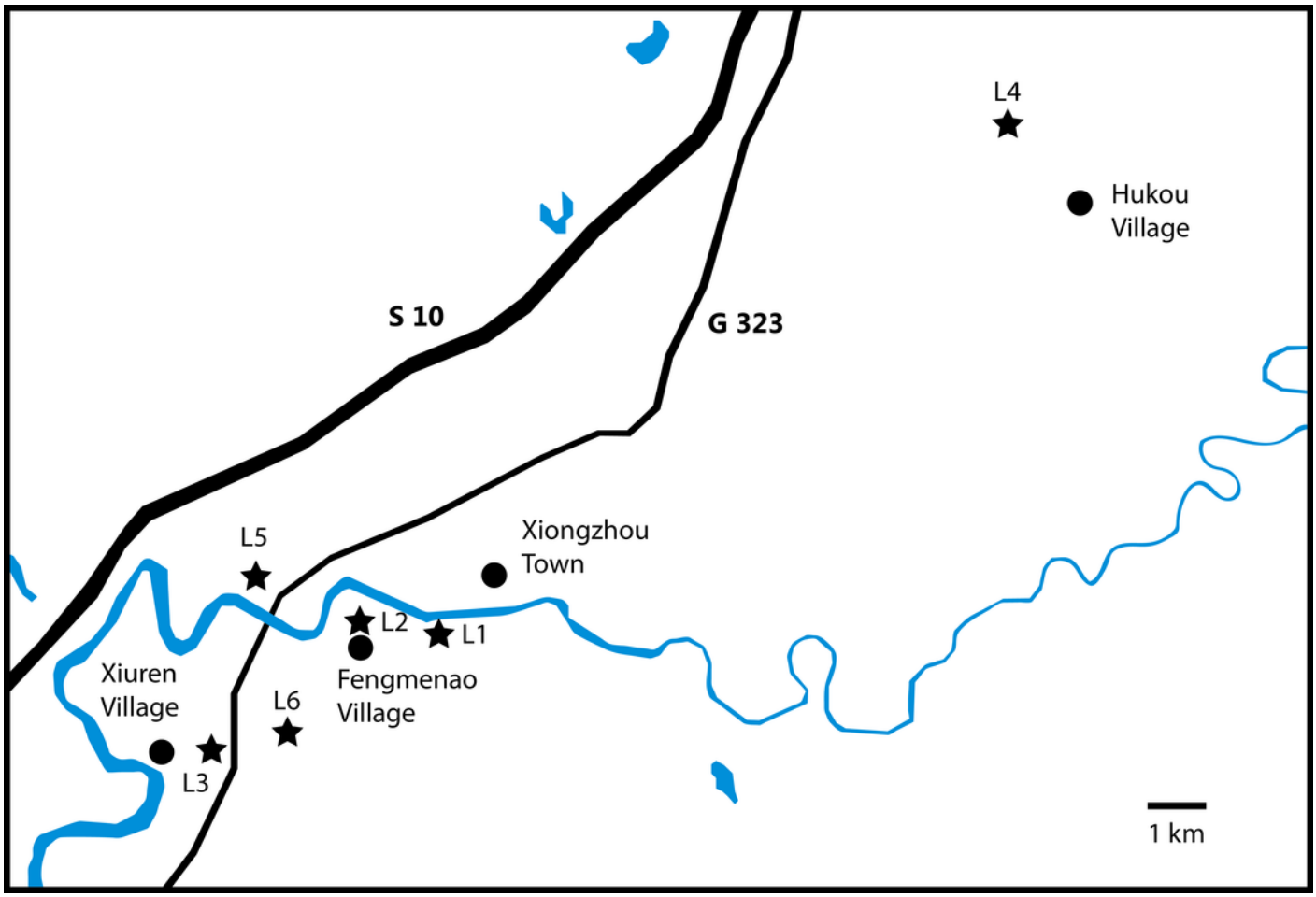
Figure 7 Holotype of *Eoalligator huiningensis* (IVPP V4058), anterior part of skull and lower jaws in dorsal (A), ventral (B), right dorsolateral (C) and left ventrolateral (D) views. Abbreviations: an: angular; c: coracoid; d: dentary; dp: depression; EN: external naris; EMF: external mandibular fenestra; j: jugal; l: lacrimal; mx: maxilla; n: nasal; pm: premaxilla; sp: splenial.

Figure 8 Strict consensus of 191 equally parsimonious trees found in the cladistics analysis of complete data matrix (105 ingroup taxa and 190 morphological characters). Length= 727 steps; Consistency Index (CI) =0.338; Retention Index (RI) =0.806. Asterisks mark two nominal species of *Eoalligator*.

Figure 9 Majority rule consensus of 178 equally parsimonious trees found in the cladistics analysis of reduced version of the complete data matrix (45 ingroup taxa and 190 morphological characters). Length=310 steps. Consistency Index (CI) = 0.794, and Retention Index (RI) = 0.974. Asterisks mark two nominal species of *Eoalligator*.

1

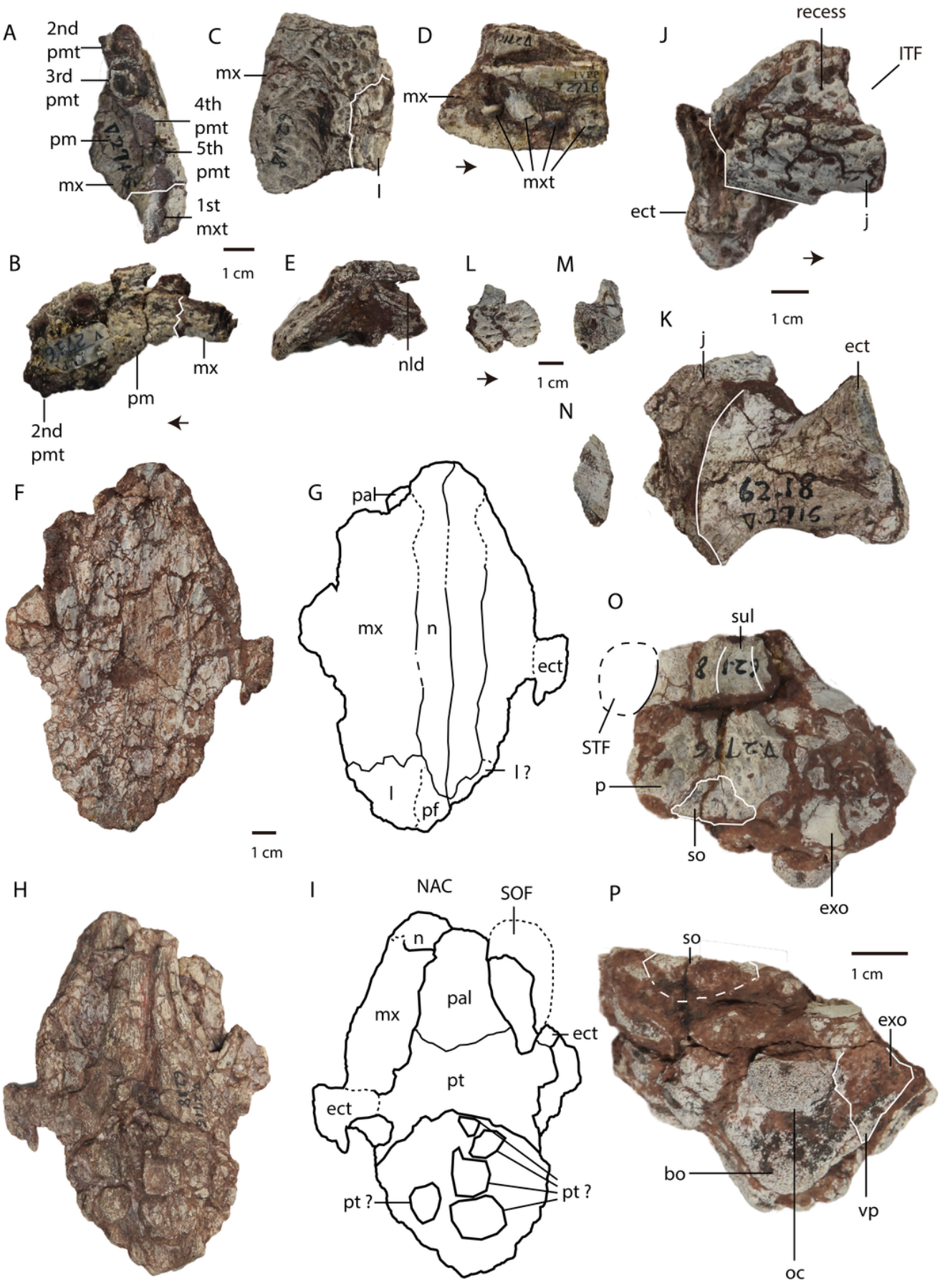
Localities (L1-L5) in Nanxiong County, Guangdong Province that have produced specimens assigned to *Eoalligator chunyii* and/or *Asiatosuchus nanlingensis*.



2

Asiatosuchus nanlingensis specimens originally assigned by Young (1964) to *Eoalligator chunyii*

Including: IVPP V 2716-2.1, incomplete left premaxilla, in ventral (A) and lateral (B) views; IVPP V 2716-2.2, incomplete left maxilla, in dorsal (C), ventromedial (D) and posterior (E) views; IVPP V 2716-11, incomplete skull, in dorsal (F, G) and ventral (H, I) views; IVPP V 2716-12, incomplete right jugal with ectopterygoid, in lateral (J) and ventral (K) views; IVPP V 2716-14, incomplete right jugal in lateral (L) and anterior (M) views, and dorsal part of right postorbital in dorsal view (N); IVPP V 2716-13, posterior part of skull, in dorsal (O) and occipital (P) views. Arrows point anteriorly. Abbreviations: bo: basioccipital; ect: ectopterygoid; exo: exoccipital; ITF: infratemporal fenestra; j: jugal; l: lacrimal; mx: maxilla; mxa: maxillary alveolus; mxt: maxillary tooth; n: nasal; nld: nasolacrimal duct; oc: occipital condyle; p: parietal; pal: palatine; pf: prefrontal; pm: premaxilla; pma: premaxillary alveolus; pmt: premaxillary tooth; pt: pterygoid; so: supraoccipital; SOF: suborbital fenestra; STF: supratemporal fenestra; sul: sulcus; vp: ventral process. p.


A
2nd pmt
3rd pmt
4th pmt
5th pmt
1st mxt
pm
mx
1 cm
B
mx
pm
2nd pmt
C
mx
l
D
mx
mxt
E
nld
L
M
1 cm
J
recess
ITF
ect
j
1 cm
K
j
ect
N
F
1 cm
G
pal
mx
n
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l ?
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I
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ect
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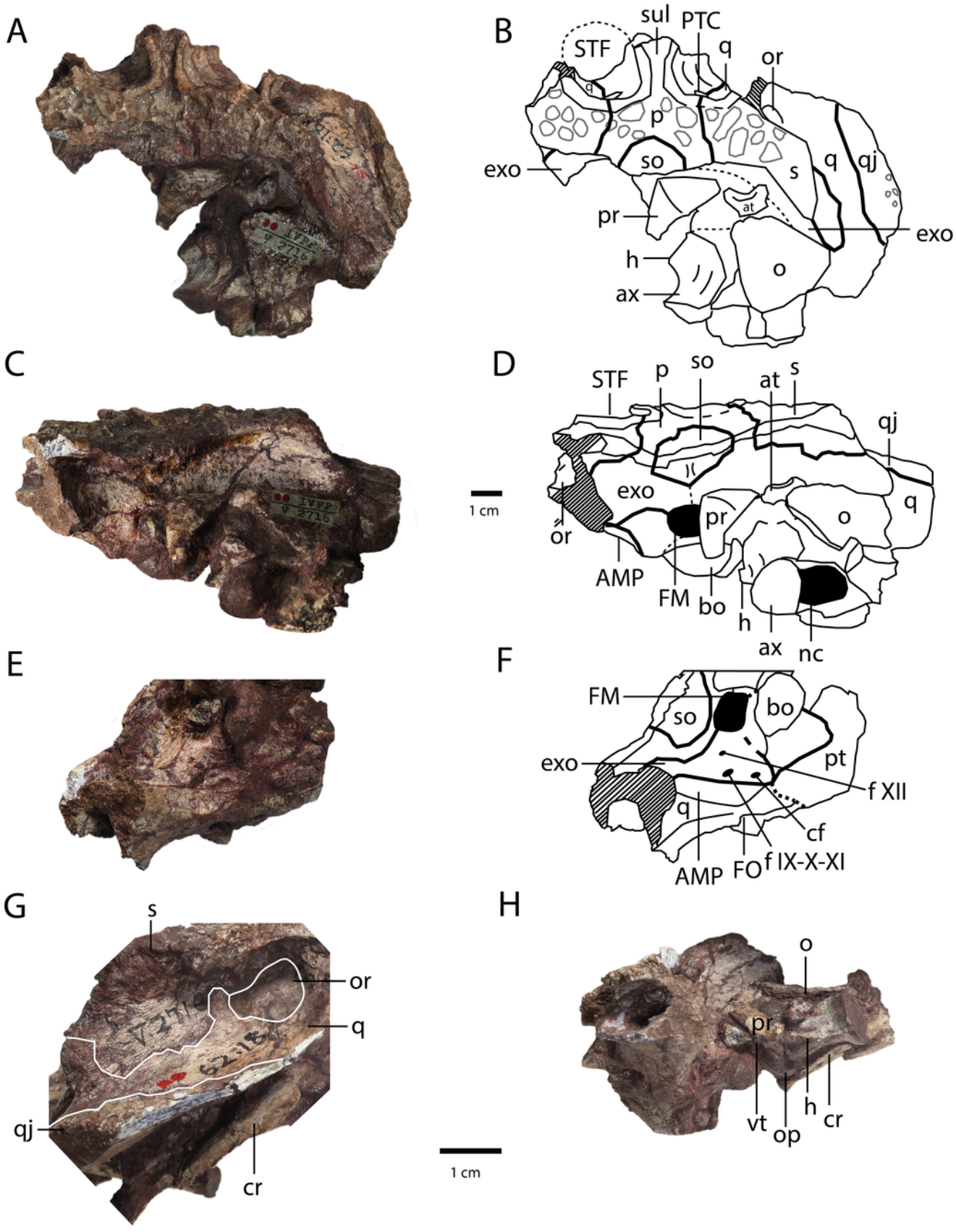
ect
pt ?
pt ?
P
so
1 cm
exo
bo
vp
oc

3

Asiatosuchus nanlingensis (IVPP V 2716-1.1), posterior part of skull originally designated by Young (1964) as part of the holotype of *Eoalligator chunyii.*

The holotype of *Eoalligator chunyii*, in dorsal (A, B), posterodorsal (C, D), posteroventral (E, F), right lateral (G), and left ventrolateral (H) views. Abbreviations: AMP: attachment of adductor mandibulae posterior; at: atlas; ax: axis; bo: basioccipital; cf: carotid foramen; cv: cervical rib; exo: exoccipital; f IX-X-XI, foramen for glossopharyngeal (IX), vagus (X) and accessory (XI) nerves; f XII, foramen for hypoglossal nerve; FO: foramen ovale; FM: foramen magnum; h: hypapophysis: nc: neural canal; o: osteoderm; or: otic recess; p: parietal; pr: proatlas; pt: pterygoid; PTC: opening of posttemporal canal; q: quadrate; qj: quadratojugal; s: squamosal; so: supraoccipital; STF: supratemporal fenestra; sul: sulcus; vt: ventral tuberosity.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FM
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f XII
q
cf
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f IX-X-XI
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qj
cr
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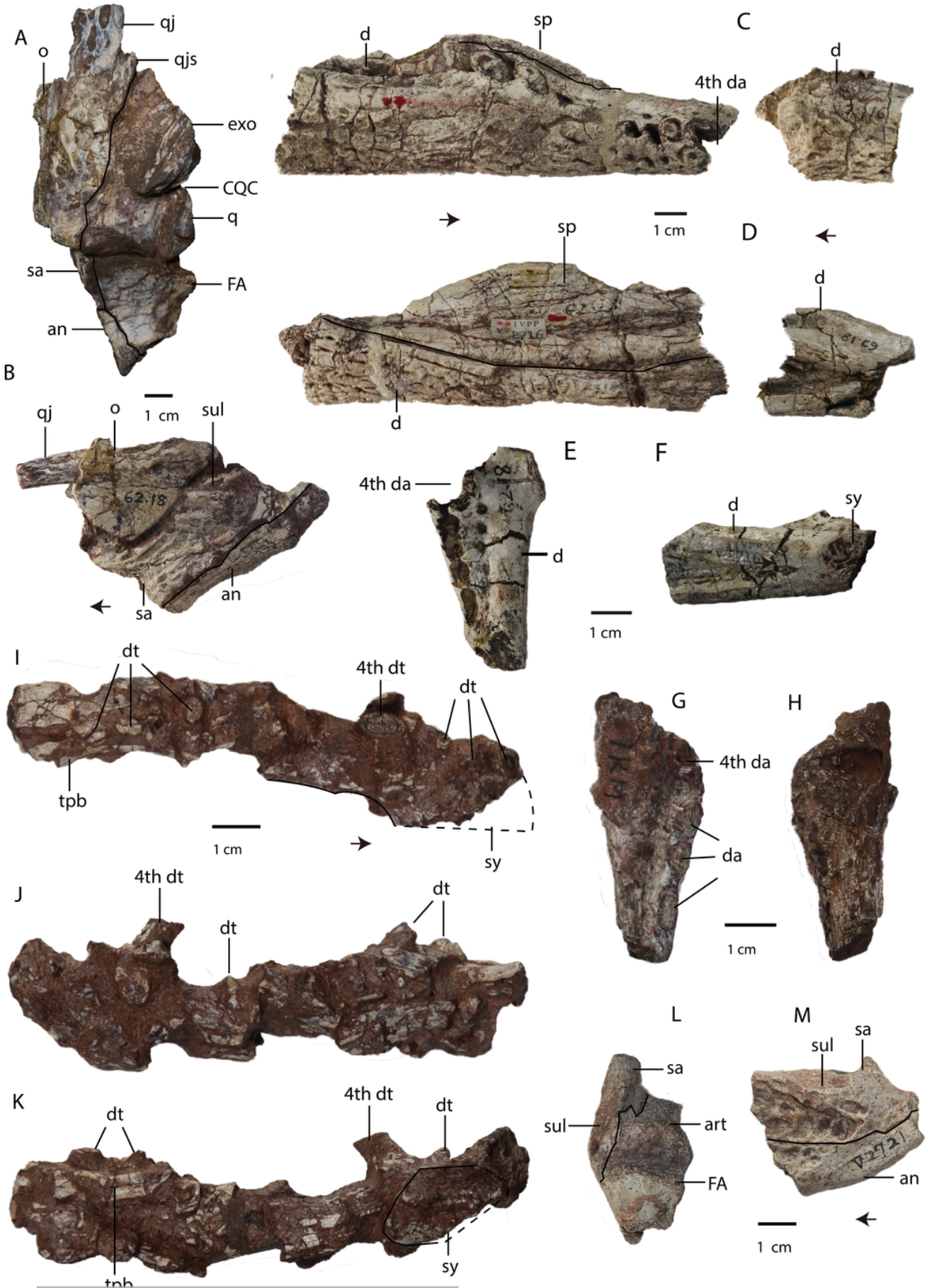
vt
op
h
cr
1 cm

4

Asiatosuchus nanlingensis specimens originally assigned by Young (1964) to *Eoalligator chunyii.*

Including: IVPP V 2716-3, left jaw articulated with part of skull, in dorsal (A) and lateral (B) views; IVPP V 2716-1.2 (part of the holotype of *E. chunyii*), two incomplete right mandibles, in lateral (C) and medial (D) views; IVPP V 2716-2.1, left dentary, in dorsal (E) and medial (F) views; IVPP V 2721.5, anterior part of right dentary, in dorsal (G) and ventral (H) views; IVPP V 2771, left mandible, in dorsal (I), lateral (J) and medial (K) views; IVPP V 2721.1, left posterior mandibular fragment in dorsal (L) and lateral (M) views. Most specimens are referable to *Asiatosuchus nanlingensis*, but the taxonomic identity of IVPP V 2771 is uncertain. Arrows point anteriorly. Abbreviations: an: angular; art: articular; CQC: cranioquadrate canal; d: dentary; da: dentary alveolus; dt: dentary tooth; exo: exoccipital; FA: foramen aerum; fw: full width; mg: Meckelian groove; o: osteoderm; q: quadrate; qj: quadratojugal; qjs: quadratojugal spine; sa: surangular; sp: splenial; sul: sulcus; sy: symphysis; tpb: tortoise pleural bone.


A
qj
o
qjs
exo
CQC
q
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an
B
qj
o
1 cm
sul
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C
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4th da
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4th da
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1 cm
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4th dt
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1 cm
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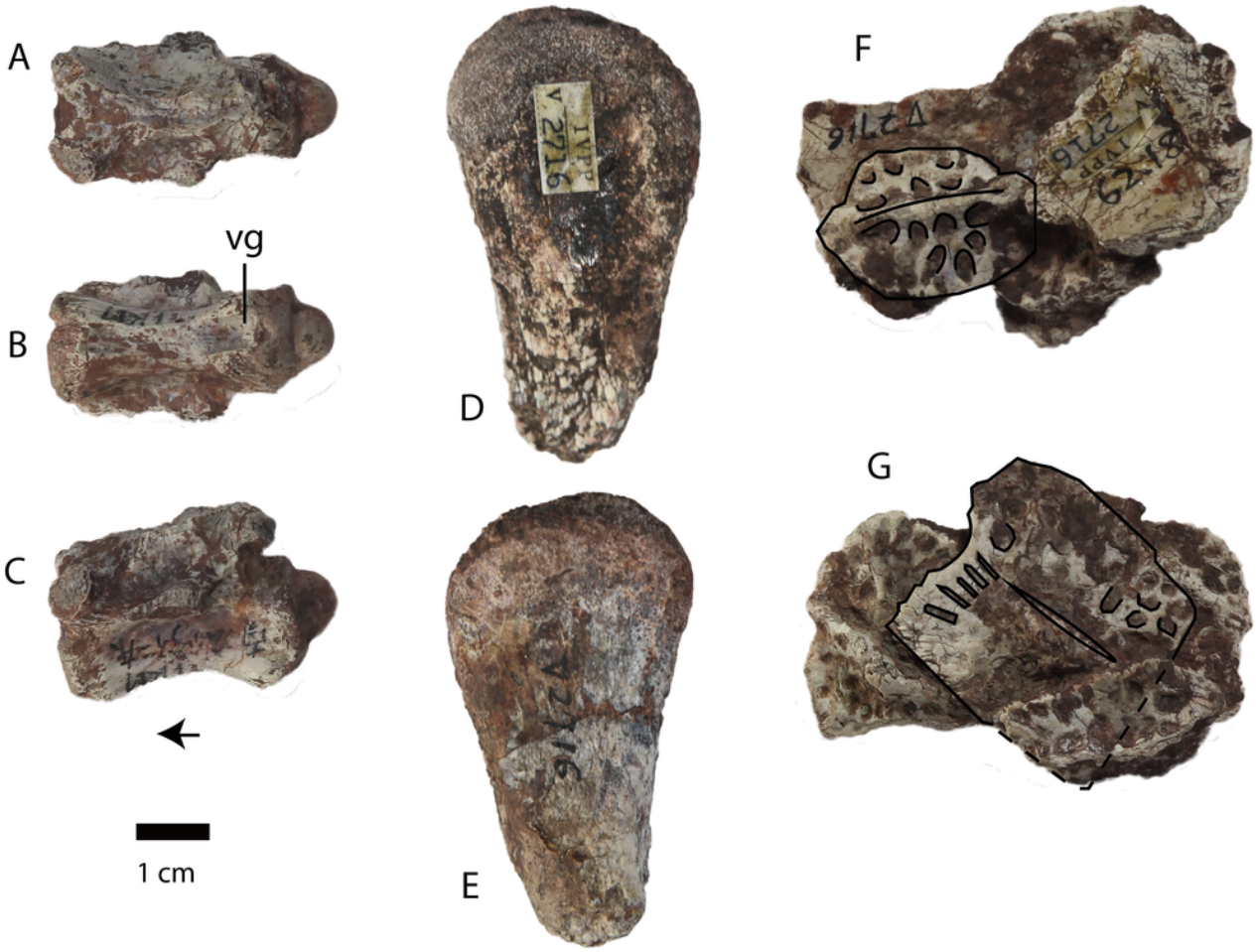
J
4th dt
dt
dt
K
dt
4th dt
dt
tpb
sy
L
sa
sul
art
FA
M
sa
sul
an
1 cm

5

Asiatosuchus nanlingensis specimens originally assigned by Young (1964) to *Eoalligator chunyii.*

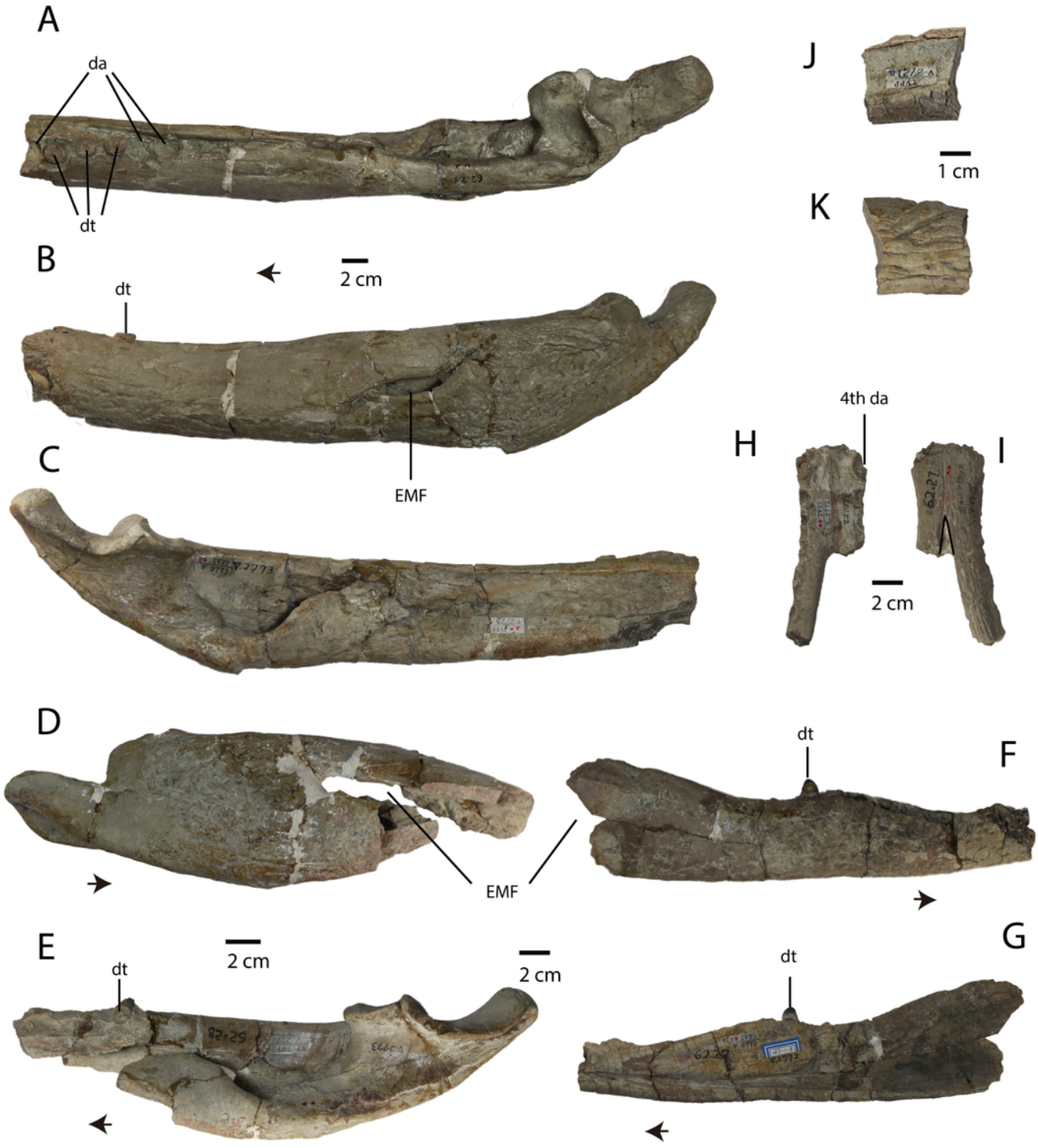
Including: IVPP V 2721.4, caudal vertebra, in dorsal (A) ventral (B) and lateral (C) views; IVPP V 2716-5, proximal end of left femur, in lateral (D) and medial (E) views; IVPP V 2716-7, six disarticulated osteoderms, in dorsal (F) and ventral (G) views. Abbreviations: vg: ventral groove.



6

Specimens assigned by Young (1964) to *Asiatosuchus nanlingensis.*

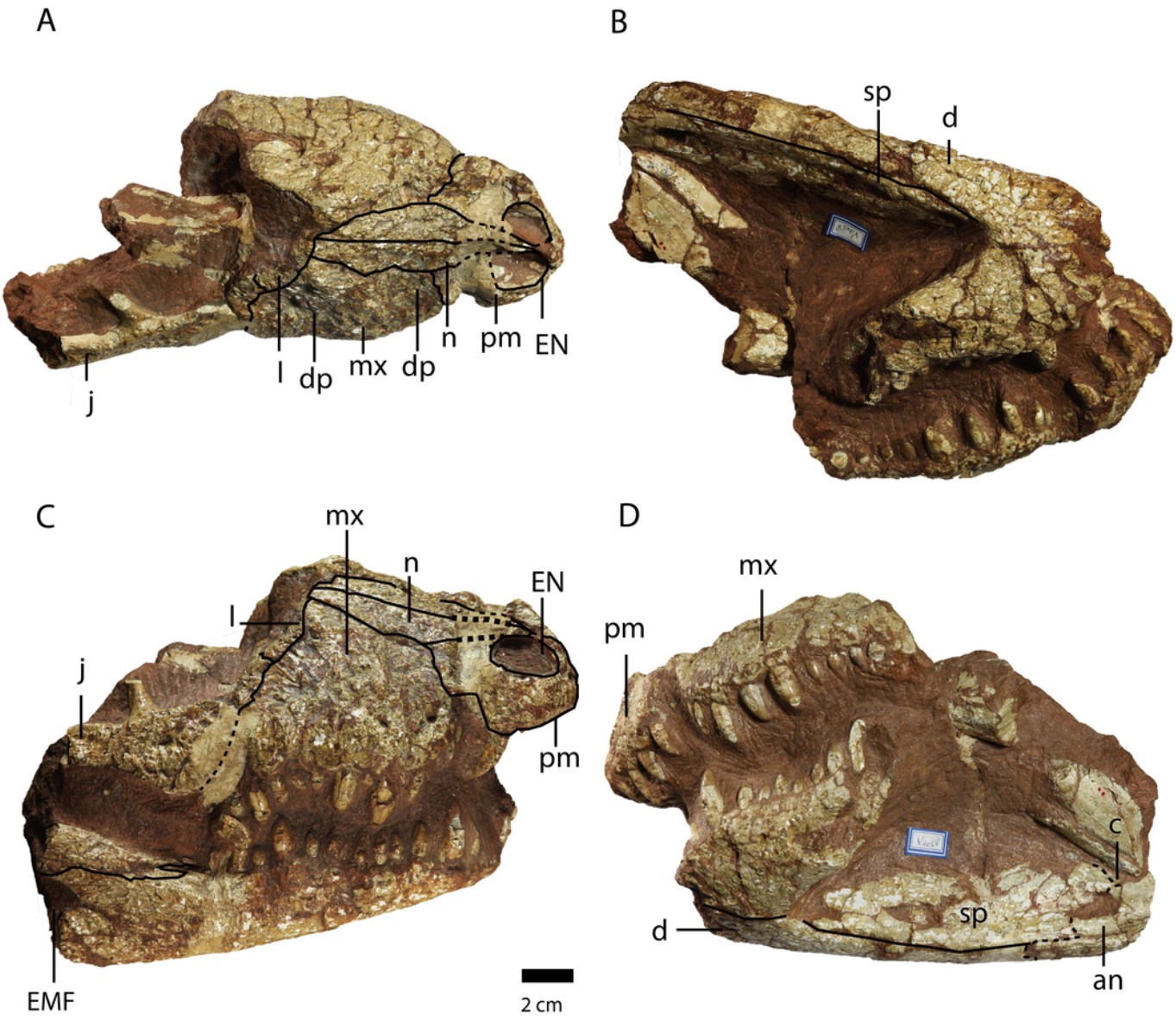
Including: IVPP V 2773 (holotype), left mandible in dorsal (A), lateral (B) and medial (C) views, and right mandible in lateral (D) and medial (E) views; IVPP V 2772.1, right dentary in lateral (F) and medial (G) views; IVPP V 2772.2, dentary symphysis in dorsal (H) and ventral (I) views; IVPP V 2721a, dentary fragment in medial (J) and lateral (K) views. IVPP V 2772.2 appears to represent a longirostral crocodylian distinct from *A. nanlingensis*. Abbreviations: da: dentary alveolus; dt: dentary tooth; EMF: external mandibular fenestra.


A
da
dt
B
2 cm
dt
EMF
C
J
1 cm
K
4th da
H
I
2 cm
D
dt
F
EMF
E
2 cm
dt
2 cm
G
dt

7

Holotype of *Eoalligator huiningensis* (IVPP V4058).

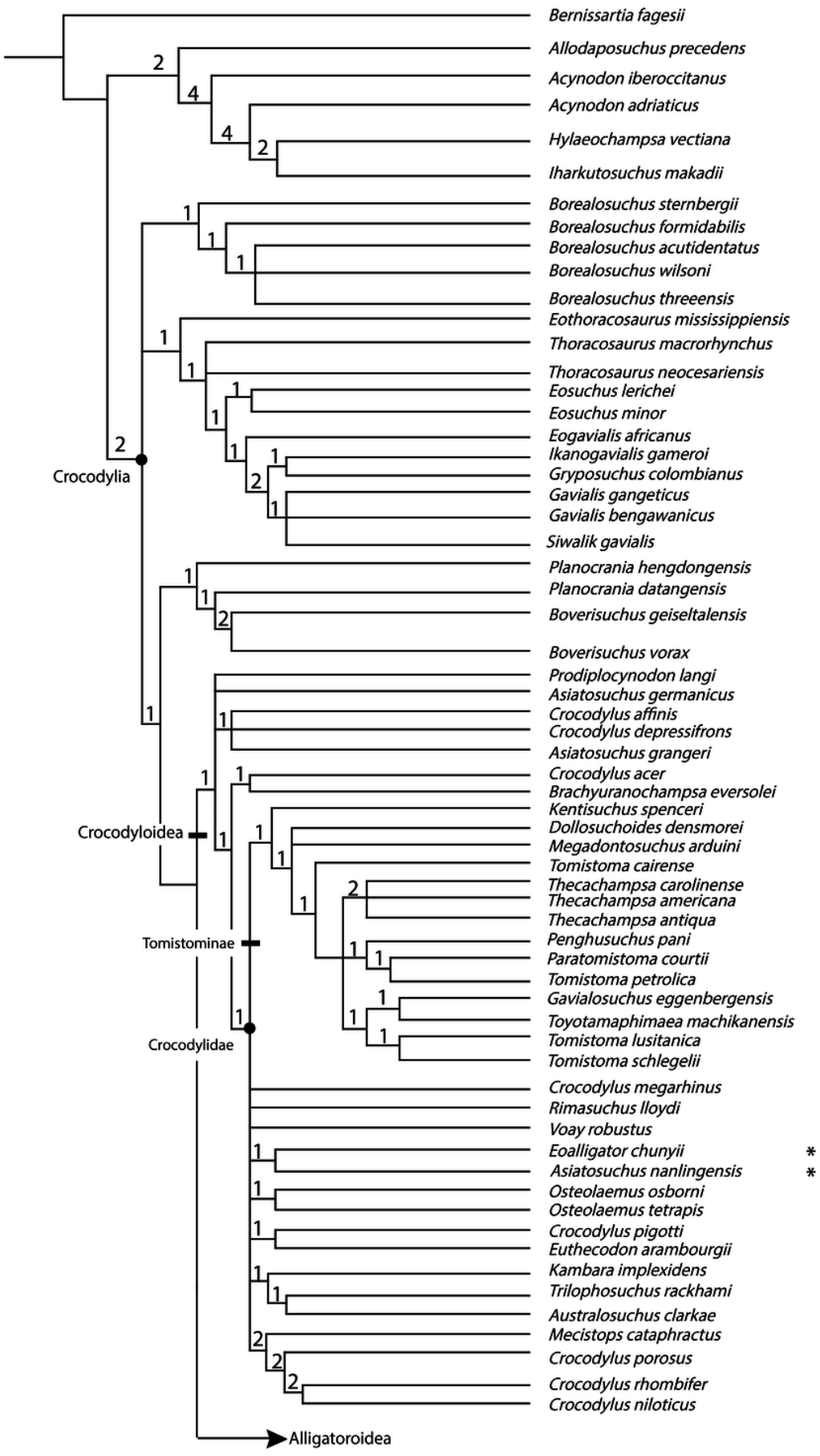
Anterior part of skull and lower jaws in dorsal (A), ventral (B), right dorsolateral (C) and left ventrolateral (D) views. Abbreviations: an: angular; c: coracoid; d: dentary; dp: depression; EN: external naris; EMF: external mandibular fenestra; j: jugal; l: lacrimal; mx: maxilla; n: nasal; pm: premaxilla; sp: splenial.



8

Strict consensus of 191 equally parsimonious trees found in the cladistics analysis of complete data matrix (105 ingroup taxa and 190 morphological characters).

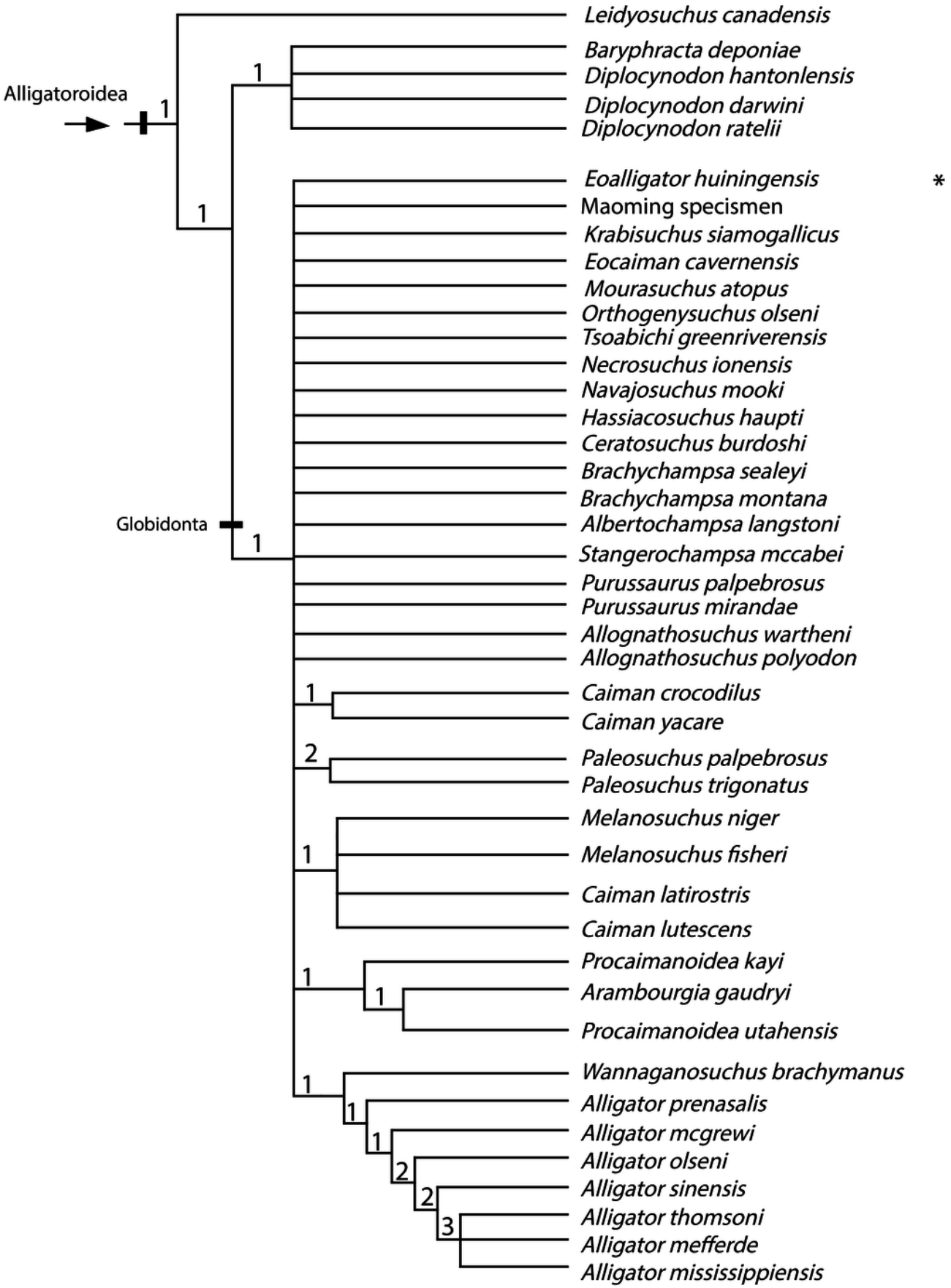
Strict consensus tree. Length= 727 steps; Consistency Index (CI) =0.338; Retention Index (RI) =0.806. Asterisks mark two nominal species of *Eoalligator* and *Asiatosuchus nanlingensis*.


Bernissartia fagesii
Allodaposuchus precedens
Acynodon iberoccitanus
Acynodon adriaticus
Hylaeochampsa vectiana
Iharkutosuchus makadii
Borealosuchus sternbergii
Borealosuchus formidabilis
Borealosuchus acutidentatus
Borealosuchus wilsoni
Borealosuchus threeensis
Eothoracosaurus mississippiensis
Thoracosaurus macrorhynchus
Thoracosaurus neocesariensis
Eosuchus lerichei
Eosuchus minor
Eogavialis africanus
Ikanogavialis gameroi
Gryposuchus colombianus
Gavialis gangeticus
Gavialis bengawanicus
Siwalik gavialis
Planocrania hengdongensis
Planocrania datangensis
Boverisuchus geiseltalensis
Boverisuchus vorax
Prodiplocynodon langi
Asiatosuchus germanicus
Crocodylus affinis
Crocodylus depressifrons
Asiatosuchus grangeri
Crocodylus acer
Brachyuranochampsa eversolei
Kentisuchus spenceri
Dollosuchoides densmorei
Megadontosuchus arduini
Tomistoma cairense
Thecachampsa carolinense
Thecachampsa americana
Thecachampsa antiqua
Penghusuchus pani
Paratomistoma courtii
Tomistoma petrolica
Gavialosuchus eggenbergensis
Toyotamaphimaea machikanensis
Tomistoma lusitanica
Tomistoma schlegelii
Crocodylus megarhinus
Rimasuchus lloydi
Voay robustus
Eoalligator chunyii *
Asiatosuchus nanlingensis *
Osteolaemus osborni
Osteolaemus tetrapis
Crocodylus pigotti
Euthecodon arambourgii
Kambara implexidens
Trilophosuchus rackhami
Australosuchus clarkae
Mecistops cataphractus
Crocodylus porosus
Crocodylus rhombifer
Crocodylus niloticus
Crocodylia
Crocodyloidea
Tomistominae
Crocodylidae
Alligatoroidea

9

Strict consensus of 191 equally parsimonious trees found in the cladistics analysis of complete data matrix (105 ingroup taxa and 190 morphological characters).

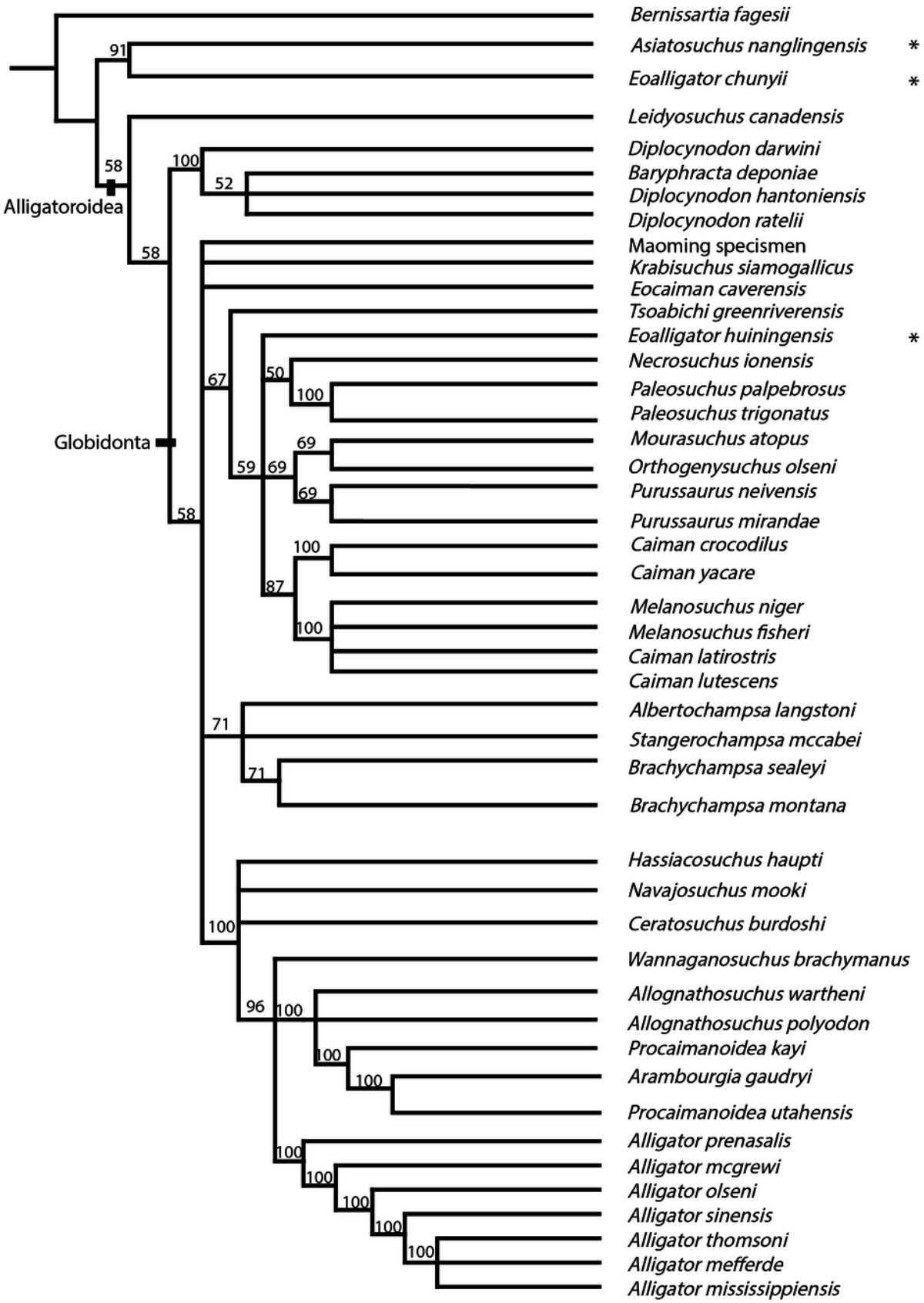
Strict consensus tree. Length= 727 steps; Consistency Index (CI) =0.338; Retention Index (RI) =0.806. Asterisks mark two nominal species of *Eoalligator and* Asiatosuchus nanlingensis .


Alligatoroidea
Globidonta
Leidyosuchus canadensis
Baryphracta deponiae
Diplocynodon hantonlensis
Diplocynodon darwini
Diplocynodon ratelii
Eoalligator huiningensis *
Maoming specismen
Krabisuchus siamogallicus
Eocaiman cavernensis
Mourasuchus atopus
Orthogenysuchus olseni
Tsoabichi greenriverensis
Necrosuchus ionensis
Navajosuchus mooki
Hassiacosuchus haupti
Ceratosuchus burdoshi
Brachychampsa sealeyi
Brachychampsa montana
Albertochampsa langstoni
Stangerochampsa mccabei
Purussaurus palpebrosus
Purussaurus mirandae
Allognathosuchus wartheni
Allognathosuchus polyodon
Caiman crocodilus
Caiman yacare
Paleosuchus palpebrosus
Paleosuchus trigonatus
Melanosuchus niger
Melanosuchus fisheri
Caiman latirostris
Caiman lutescens
Procaimanoidea kayi
Arambourgia gaudryi
Procaimanoidea utahensis
Wannaganosuchus brachymanus
Alligator prenasalis
Alligator mcgrewi
Alligator olseni
Alligator sinensis
Alligator thomsoni
Alligator mefferde
Alligator mississippiensis

10

Majority rule consensus of 178 equally parsimonious trees found in the cladistics analysis of reduced version of the complete data matrix (45 ingroup taxa and 190 morphological characters).

Majority rule tree. Length=310 steps. Consistency Index (CI) = 0.794, and Retention Index (RI) = 0.974. Asterisks mark two nominal species of *Eoalligator and* Asiatosuchus nanlingensis .


Bernissartia fagesii
Asiatosuchus nanglingensis *
Eoalligator chunyii *
Leidyosuchus canadensis
Diplocynodon darwini
Baryphracta deponiae
Diplocynodon hantoniensis
Diplocynodon ratelii
Maoming specismen
Krabisuchus siamogallicus
Eocaiman caverensis
Tsoabichi greenriverensis
Eoalligator huiningensis *
Necrosuchus ionensis
Paleosuchus palpebrosus
Paleosuchus trigonatus
Mourasuchus atopus
Orthogenysuchus olseni
Purussaurus neivensis
Purussaurus mirandae
Caiman crocodilus
Caiman yacare
Melanosuchus niger
Melanosuchus fisheri
Caiman latirostris
Caiman lutescens
Albertochampsa langstoni
Stangerochampsa mccabei
Brachychampsa sealeyi
Brachychampsa montana
Hassiacosuchus haupti
Navajosuchus mooki
Ceratosuchus burdoshi
Wannaganosuchus brachymanus
Allognathosuchus wartheni
Allognathosuchus polyodon
Procaimanoidea kayi
Arambourgia gaudryi
Procaimanoidea utahensis
Alligator prenasalis
Alligator mcgrewi
Alligator olseni
Alligator sinensis
Alligator thomsoni
Alligator mefferde
Alligator mississippiensis
Alligatoroidea
Globidonta
91
58
100
52
58
67
50
100
69
59
69
69
58
100
87
100
71
71
100
96
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