

DOI: 10.19615/j.cnki.1000-3118.170803

Taxonomic reassessment and phylogenetic test of *Asiatosuchus nanlingensis* Young, 1964 and *Eoalligator chunyii* Young, 1964

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Abstract The present paper revalidated *Asiatosuchus nanlingensis* Young, 1964 and *Eoalligator chunyii* Young, 1964 in taxonomy based on a detailed comparative study on those relevant specimens. New information derived from this study revealed that *A. nanlingensis* and *E. chunyii* were truly distinguishable from each other and therefore, diagnosis was further revised for each of them. *A. nanlingensis* is large, with a moderately long or a very elongate snout, and characterised mainly by the combination of the following characters such as: the quadrate with a lateral condyle much larger than the medial one, the surangular pinched off before reaching the end of the retroarticular process, the dental margins (at least the posterior portion) of the jaws nearly straight, and the presence of a fossa/sulcus on the lateral surface of the surangular lateral to the mandibular fossa. *E. chunyii* is a median-sized, short-snouted animal and characterised mainly by the combination of the following characters such as: the condyles of the quadrate similar in size, the dental margins of the jaws strongly concavo-convex, the dentary symphyses very short, the splenial not entering the mandibular symphysis, and the presence of a fossa/sulcus on the lateral surface of the surangular lateral to the mandibular fossa. With new information derived from this study, the phylogenetic relationships of *A. nanlingensis* and *E. chunyii* were tested, which did not support the view that the two species formed a monophyletic clade and opposed that *E. chunyii* could be considered as the synonym of *A. nanlingensis*.

Key words China, Cretaceous-Paleocene, Crocodylia, taxonomy, anatomy

Citation Wu X C, Li C, Wang Y Y, 2018. Taxonomic reassessment and phylogenetic test of *Asiatosuchus nanlingensis* Young, 1964 and *Eoalligator chunyii* Young, 1964. *Vertebrata Palasiatica*, 56(2): 137–146

1 Introduction

Eoalligator chunyii Young, 1964 and *Asiatosuchus nanlingensis* Young, 1964 were established based on materials possibly from the Paleocene of Nanxiong Basin, Guangdong

加拿大自然博物馆基金(编号: RS09)和现代古生物学和地层学国家重点实验室(中国科学院南京地质古生物研究所)基金(编号: 153105)资助。

收稿日期: 2017-06-15

Province. Both of these two species are poorly preserved although the former is represented by a number of fragmentary specimens. Recently, Wang et al. (2016) re-evaluated the osteology, taxonomy and phylogenetic affinities of the holotype and referred material of *A. nanlingensis* and of the material assigned to *E. chunyii* and synonymized *E. chunyii* to *A. nanlingensis* within the Crocodylidae.

During the course of study on a new crocodylian from the Upper Cretaceous of Jiangxi Province, we examined the materials referred to *E. chunyii* and *A. nanlingensis* for a comparative purpose in the January of 2017. After a detailed examination, we disagreed with the conclusion of Wang et al. (2016) on the phylogeny and taxonomic status of *E. chunyii* and *A. nanlingensis*, i.e., the two formed a monophyletic clade and the former was considered to be the junior synonym of the latter. On the contrary, we support the view of Young (1964) that *E. chunyii* is truly different from *A. nanlingensis* with the exclusion of the referred specimens. Here, we focused on those specimens which are evident in difference between the two species. With new information, we clarified the taxonomic status and tested the phylogeny of the two species.

2 Material and methods

The crocodylian specimens were further prepared with mechanical tools (needles) and photographed from various perspectives with a Nikon D610 digital camera. The figures were prepared on Adobe Photoshop CS6 and Illustrator CS6 software, and some of photos used in figures (Fig. 1A, F, G) were reflected along the X-axis for comparative purpose on Adobe Illustrator CS6 software. Line marks on the specimens were made on the basis of these photos and checked against the original material.

Institutional abbreviations CMN, Canadian Museum of Nature, Ottawa, Canada; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; ROM, Royal Ontario Museum, Toronto, Canada.

3 Comparative study

Both Young (1964) considered IVPP V 2772.1 (an incomplete right dentary from locality 3 of Wang et al., 2016) to be equivalent to the anterior portion of the holotypic right jaw (IVPP V 2773) of *Asiatosuchus nanlingensis* and Wang et al. (2016) thought that this referral of the former to the later was likely valid. Our examination of the relevant specimens did not agree with the conclusion. The holotypic left ramus of the mandible of *A. nanlingensis* (V 2773) is more complete than the right and preserved the posterior portion of the dentition, bearing seven or eight teeth as indicated by the preserved tooth roots and alveoli (see Fig. 1A–C). We compared this dentary portion of seven or eight teeth with that of V 2772.1 and found that the two specimens were clearly different from each other in the morphology of this portion. The dental margin of this portion in V 2773 is nearly straight and did not evidently raise up

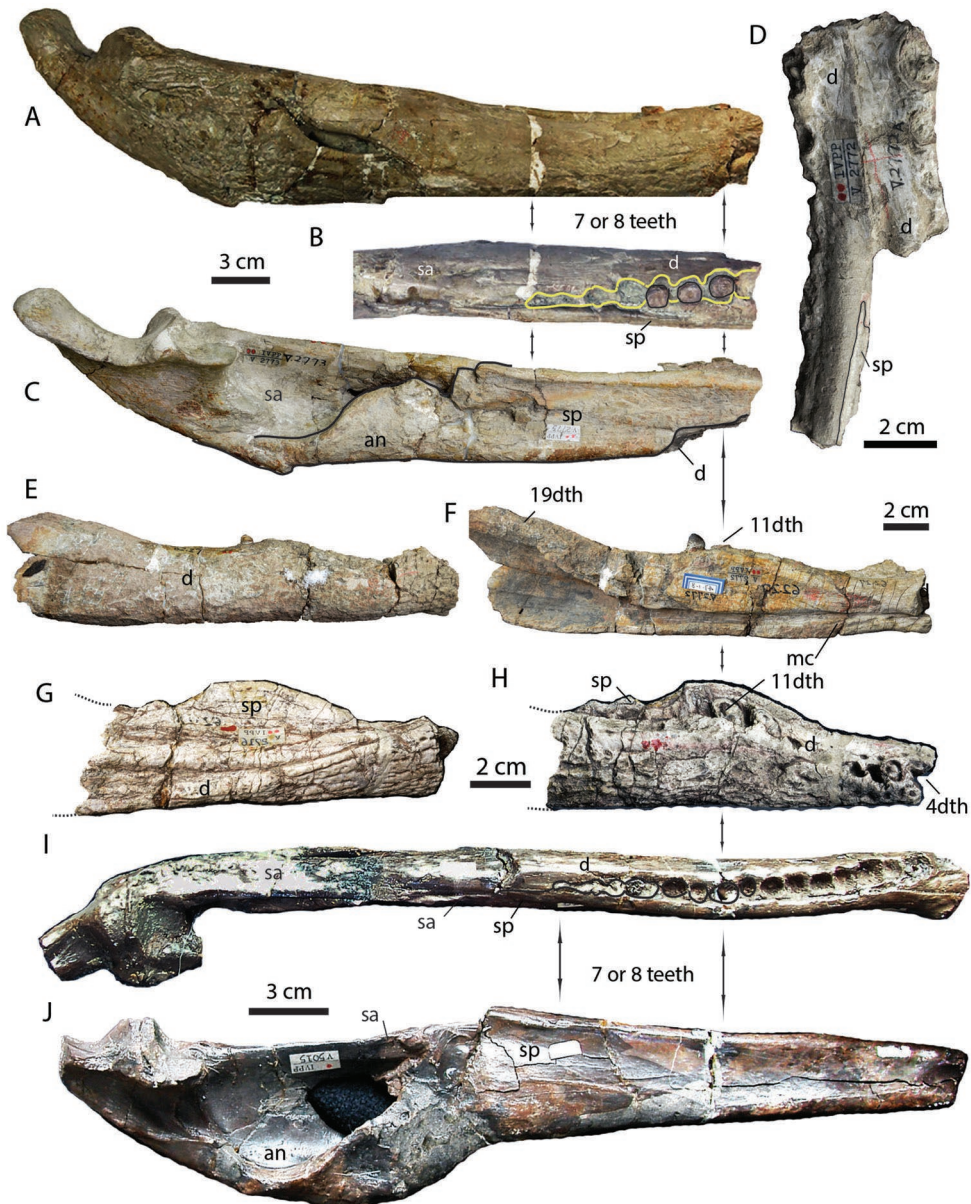


Fig. 1 Incomplete mandibles or dentaries of some of crocodylians

A–C. posterior portion of the holotypic left ramus of mandible (IVPP V 2773) of *Asiatosuchus nanlingensis* in lateral (a reflection of the specimen along the X-axis for comparative purpose), dorsal, and medial views;

D. dentary symphysis of V 2772.2 in dorsal view (an unknown species); E, F. a right dentary (V 2772.1) in lateral and medial (a reflection of the specimen along the X-axis for comparative purpose) views; G, H. a right dentary (part of *Eoalligator chunyii*, V 2716-1.2) in medial (a reflection of the specimen along the X-axis for comparative purpose) and lateral views; I, J. mandible (V 5015) of *Maomingosuchus petrolica* (= "*Tomistoma*" *petrolica* Yeh, 1958) in dorsal and medial views

Abbreviations: an. angular; d. dentary; mc. Meckelian canal; sa. surangular; sp. splenial; 4dth, 11dth, 19dth. the 4th, 11th, and 19th teeth

posterior to the last tooth, which resembles a condition seen in many longirostral taxa such as the tomistomines *Maomingosuchus petrolica* (Fig. 1I, J; Shan et al., 2017: figs. 2B, 3B), *Dollosuchoides densmorei* (Brochu, 2007a: fig. 4) and *Maroccosuchus zennaroi* (see Jouve et al., 2015: fig. 2) or the gavialoid *Eosuchus minor* (Brochu, 2006: fig. 12). Therefore, it is most probable that *A. nanlingensis* (V 2773) represented a taxon with a moderately to eventually very elongated snout. In contrast, V 2772.1 shows a strongly concavo-convex dental margin (waves), which is similar in general appearance to the dentary of any short-snouted crocodylians such as *Alligator sinensis* (see Cong et al., 1998: fig. 58), i.e., the dental margin of the section of posterior seven to nine teeth is very concave (the second wave) and furthermore, the dorsal margin of the dentary posterior to the last alveolus keeps raising upward (Fig. 1E, F). With these differences, V 2772.1 and V 2773 cannot be considered to belong to a single taxon, this is against the views of both Young (1964) and Wang et al. (2016).

Wang et al. (2016) realised that IVPP V 2772.1 was similar to IVPP V 2716-1.2 (an incomplete dentary as the part of the holotype of *E. chunyii*), which was supported by us. We also thought that the posterior-most portion of V 2716-1.2 did not belong to the dentary and was not included here (see Fig. 1G, H). The most striking of the similarities shared by these two dentaries include the followings: the preserved portions of both specimens show a strongly concavo-convex dental margin (with two dental waves); the 11th tooth is the largest after the fourth dentary tooth and locates at the peak of the second dental wave (Fig. 1E-H); no diastema is present among the fourth to the 11th teeth; the mandibular symphysis ends posteriorly just posterior to the fourth dentary tooth; and the splenial does not join the formation of the mandibular symphysis. Therefore, V 2772.1 can be referred to *E. chunyii* although it came from a different locality.

IVPP V 2772.2 is represented by an incomplete symphysis (Fig. 1D), which is relatively long and was referred by Young (1964) to *A. nanlingensis*. However, Wang et al. (2016) did not support Young's reference of V 2772.2 and appeared to believe that the specimen belonged to an unknown longirostral crocodylian distinct from *A. nanlingensis*. We argued earlier that the holotypic jaw of *A. nanlingensis* most probably represented a moderately long- or a very long-snouted taxon. Therefore, it cannot be excluded that V 2772.2 came from a small individual of *A. nanlingensis*. However, we agreed with Wang et al. (2016) in the consideration of V 2772.2 as an unknown taxon at the present owing to its fragmentary nature.

4 Phylogeny

We practiced the phylogenetic analysis using a data matrix derived from that of Wang et al. (2016). The modifications we made for the data matrix were focused on the following four characters. Character 49 related to the mandibular symphysis was coded by us as “?” for *A. nanlingensis* because no such a part preserved in the taxon when V 2772.1 was re-assigned by us to *E. chunyii*; character 72 related to the posterior extension of the surangular was coded by us as “1” for *A. nanlingensis*. Our further examination revealed that the surangular did

not extend posteriorly to the end but pinched off far anterior to the end of the retroarticular process (see Fig. 2A); character 190 related to the position of the largest premaxillary tooth was coded by us as “2” for *Leidyosuchus canadensis*. This character is uncertain but it is clear that the fourth premaxillary tooth is the largest in this species (see Wu et al., 2001: fig. 12). Wang et al. (2016) claimed that the presence of a sulcus (fossa—character 191) just lateral to the mandibular fossa of the mandible was a unique character state for *A. nanlingensis* (plus *E. chunyii*). In our knowledge, it is not true. *Voay robustus*, a crocodyline from the Upper Quaternary of Madagascar (Brochu, 2007b: fig. 4), and a basal alligatoroid, *Leidyosuchus*

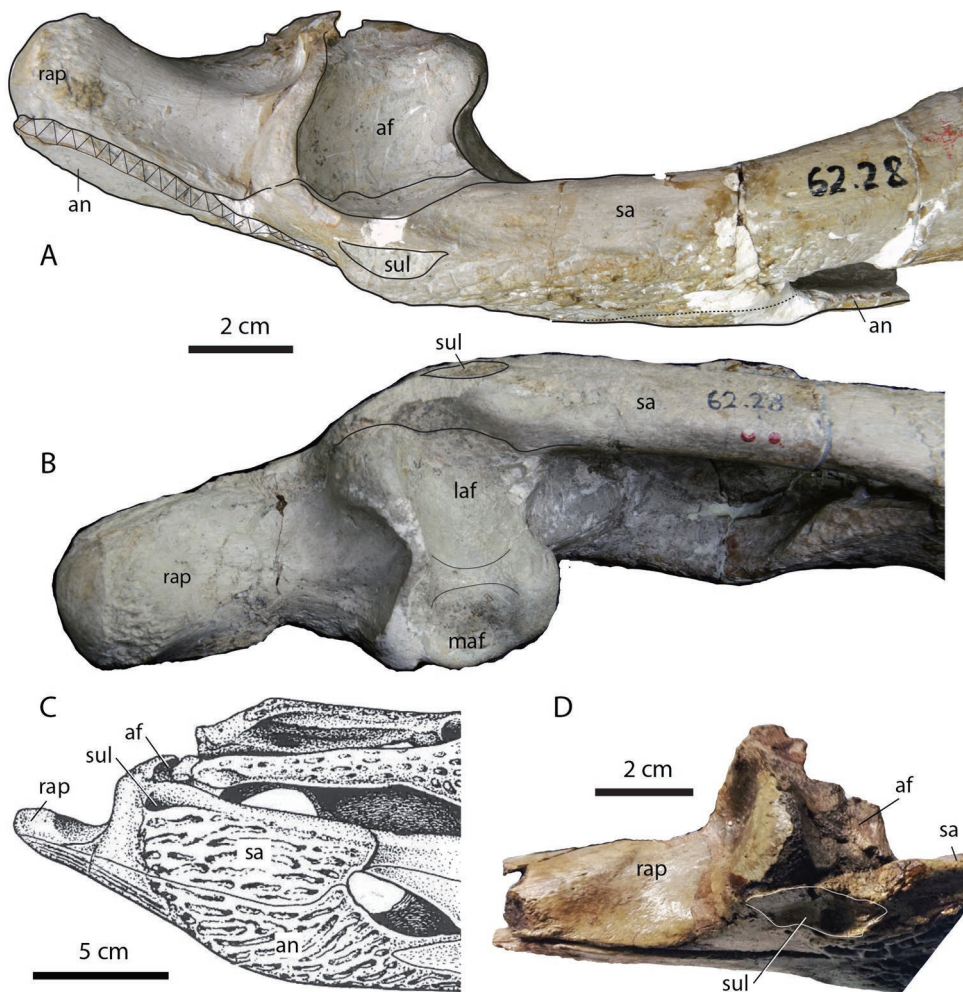


Fig. 2 Posterior portions of the mandibular rami of some of crocodylians
 A, B. holotypic right and left rami of the mandible of *Asiatosuchus nanlingensis* (IVPP V 2773)
 in dorsal and slightly lateral and dorsal views, respectively;
 C, D. posterior portion of the skull and mandible (ROM 1903) and the posterior portion of the right ramus
 of a mandible (CMN 8543) of *Leidyosuchus canadensis* in lateral and dorsal views, respectively
 Abbreviations: af. articular fossa; an. angular; laf. lateral articular fossa; maf. medial articular fossa;
 rap. retroarticular process; sa. surangular; sul. sulcus

canadensis from the Upper Cretaceous of Canada, also show such a fossa or sulcus (Fig. 2B, C). Therefore, character 191 was coded as “1” by us for *V. robustus* and *L. canadensis*.

To test the phylogenetic relationships obtained by Wang et al. (2016) for *A. nanlingensis* and *E. chunyii*, a cladistic analysis was conducted using TNT 1.1 (Goloboff et al., 2003). With the same setting as in Wang et al. (2016), a new technology search on the basis of a modified version of the data matrix produced 235 most parsimonious trees (MPTs), with a tree length of 704, a CI of 0.344 and a RI of 0.813. Phylogenetic patterns derived from our analysis for *A. nanlingensis* and *E. chunyii* as well as other included taxa were very different from those of Wang et al. (2016), which were discussed below.

5 Discussion

Among the diagnoses revised by Wang et al. (2016) for *A. nanlingensis* based on the specimens of both *A. nanlingensis* and *E. chunyii*, there is one relevant to the quadrate, i.e., two hemicondyles of the quadrate subequal in size (probably based on the specimen referred to *E. chunyii*). Our further examination did not support this. Although there is no quadrate preserved in the original material of *A. nanlingensis*, the articular fossa of the mandible can reflect the condition of the quadrate condyles. It is very evident that the lateral portion of the articular fossa of the holotypic left ramus of the mandible is much larger than the medial one (see Fig. 2B; Wang et al., 2016: fig. 8A), which clearly indicates that the lateral condyle of the quadrate should have been much bigger than the medial one in *A. nanlingensis*.

For the phylogenetic relationships of the included taxa, the most striking of the differences between us and Wang et al. (2016) were relevant to the phylogenetic positions of *A. nanlingensis* and *E. chunyii*. As shown in the strict consensus tree (Fig. 3), *A. nanlingensis* and *E. chunyii* no longer formed a monophyletic clade; *A. nanlingensis* had a phylogenetic position much basal within the Crocodylia than in the study of Wang et al. (2016) although its exact position was not resolved, whereas *E. chunyii* was more crown in position than in Wang et al. (2016) and grouped into a monophyletic group including Maoming specimen (Skutschas et al., 2014) and extant species within the Crocodylinae. In contrast, fragmentary Maoming specimen was considered by Wang et al. (2016) as an alligator. This analysis supported our view that *A. nanlingensis* and *E. chunyii* could not be classified into a single species. Those features shared by the two species should have obtained independently by convergence. We know that both *A. nanlingensis* and *E. chunyii*, especially the former, are fragmentary. Therefore, it should not be surprised when their phylogenetic relationships changes on the basis of new and better materials available in future. On the other hand, it is also too early to predict the paleogeographic origin of the Chinese groups of the Crocodylia before a stable pattern of phylogenetic relationships can be made for those forms which are poorly represented, such as *Protoalligator huiningensis* (sensu Wang et al., 2016), the Maoming specimen, *A. nanlingensis*, *E. chunyii*, etc. (see Li et al., 2008).

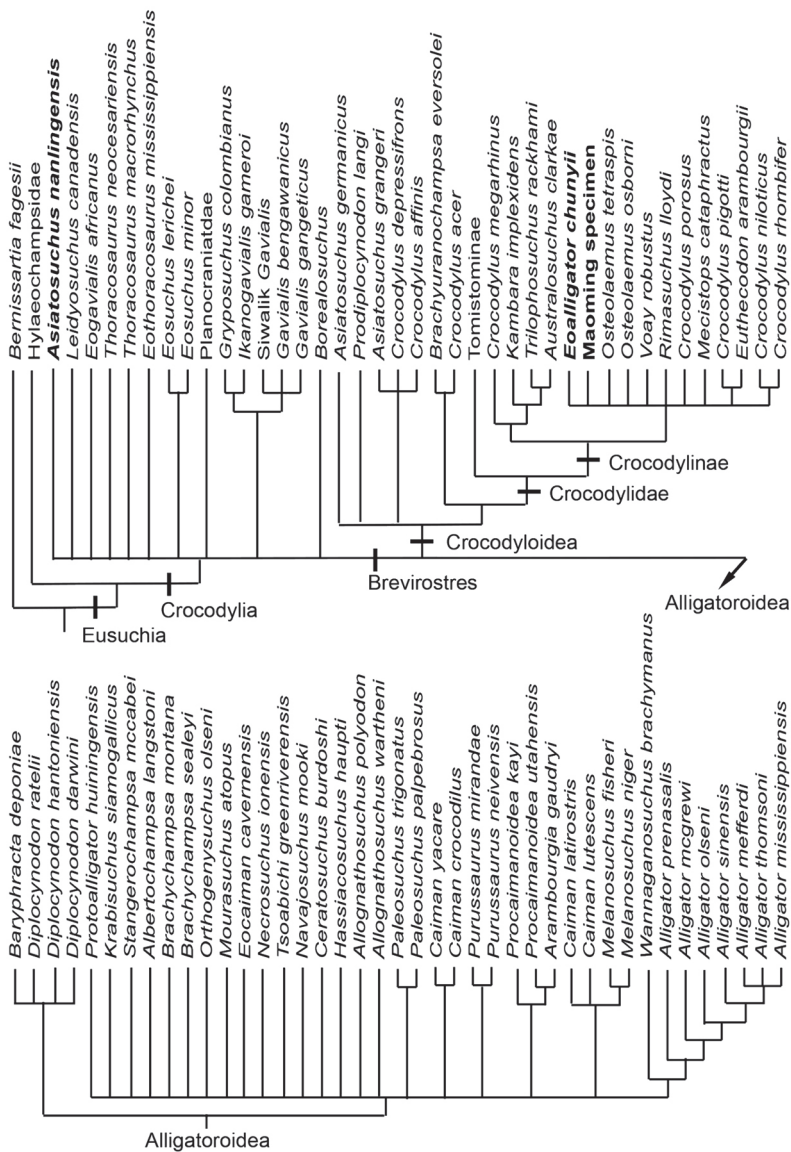


Fig. 3 Strict consensus of 235 equally most parsimonious trees found in the phylogenetic analysis based on data matrix with 105 ingroup taxa, one outgroup taxon and 191 morphologically unordered and unweighted characters

6 Systematic paleontology

Eusuchia Huxley, 1875

Crocodylia Gmelin, 1789, sensu Benton & Clark, 1988

Genus *Asiatosuchus* Mook, 1940

Asiatosuchus nanlingensis Young, 1964

Holotype IVPP V 2773 (field # 6228): the posterior portion of a left ramus of a

mandible, with posterior eight and half teeth and alveoli; the posterior portion of the right ramus of a mandible; and some fragments.

Revised diagnosis A large species with a moderate to long snout, differing from other crocodylians in the following combination of characters: a distinct sulcus/fossa lateral and slightly ventral to mandibular fossa (shared with *Voay robustus*, *Eoalligator chunyii*), surangular-articular suture anteroposteriorly oriented and situated within glenoid fossa (shared with *E. chunyii*, *Krabisuchus siamogallicus*), articular fossae corresponding to two hemicondyles of quadrate evidently uneven (shared with some others), and surangular pinching off far anterior to the end of the retroarticular process (shared with some others).

Brevirostres Zittel, 1890

Crocodyloidea Fitzinger, 1826

Crocodylidae Laurenti, 1768

Crocodylinae Cuvier, 1807

Genus *Eoalligator* Young, 1964

***Eoalligator chunyii* Young, 1964**

Holotype IVPP V 2716 (field # 6218): the posterior portion of a skull, two incomplete left mandibular rami, and some skull fragments (= V 2716-1.1, V 2716-1.2, V 2716-2.1, V 2716-2.2, V 2716-2.3, 2716-3, V 2716-6, V 2716-12 of Wang et al., 2016).

Referred specimen IVPP V 2721 (field # 6219): the anterior portion of a right mandible, the posterior portion of the left ramus of a mandible; V 2772 (field # 6227): an incomplete dentary (= V 2772.1 of Wang et al., 2016); and V 2771 (field # 6214): an incomplete mandible.

Revised diagnosis A median-sized and short-snouted crocodyline differing from others in the following combination of characters: narrowed intersupratemporal region sulcus-like (shared with some others), presence of a sulcus lateral to mandibular fossa (shared with *A. nanlingensis*), medial condyle of quadrate expanded (shared with some tomistomines), surangular-articular suture anteroposteriorly oriented and situated within glenoid fossa (shared with *A. nanlingensis*, *Krabisuchus siamogallicus*), lateral and medial condyles of quadrate similar in size (shared with some others), short mandibular symphysis extending only to level of fourth dentary tooth (shared with some others) and third tooth largest within premaxillary dentition (shared with some others).

Remarks Wang et al. (2016) considered their *Asiatosuchus nanlingensis* (including *Eoalligator chunyii*) as a crocodylid. They correctly referred it to the Crocodyloidea but mistakenly put the latter under the Globidonta which is a subgroup of the Alligatoroidea in Systematic paleontology (see Wang et al., 2016: 7/42). In taxonomy, the Crocodyloidea and Alligatoroidea are equivalent within the Crocodylia!

Although *Asiatosuchus nanlingensis* is distinguishable from others in our restudy, it cannot be phylogenetically grouped with the type species of the genus, *Asiatosuchus grangeri*. In this case, *A. nanlingensis* should have been placed in a new genus. However,

it is not wise for us to do so in terms of its fragmentary nature. Therefore, *A. nanlingensis* retains as *Asiatosuchus germanicus* before a new specimen is collected, the latter is also not phylogenetically grouped together with *A. grangeri*.

Acknowledgments We are grateful to Ms. Zheng Fang and Mr. Geng Binghe of IVPP for their assistance during the study of the specimens housed in IVPP. Careful reviews by Prof. Li Jinling and Dr. Liu Jun of IVPP improved this paper. This work was supported by the grants from Canadian Museum of Nature (RS09 for Wu Xiao-Chun) and from State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS: No. 153105 for Li Chun).

南岭亚洲鳄和存义始猛鳄的分类重估和系统发育关系检验

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摘要: 根据对有关标本的详细对比研究, 重新评估了南岭亚洲鳄(*Asiatosuchus nanlingensis* Young, 1964)和存义始猛鳄(*Eoalligator chunyii* Young, 1964)的分类。获得的新信息表明这两种是可以彼此区分的, 因此对它们各自的鉴定特征进行了进一步修订。南岭亚洲鳄是个大型种类, 它很可能具有中等或很长的吻部(眶前段), 主要由以下一些特征组合界定: 方骨外髁比内髁大很多, 上隅骨在反关节突近端尖灭, 上、下颌齿缘(至少后段)几近平直, 以及在下颌关节窝外侧上隅骨表面具一凹或纵沟。存义始猛鳄是个中型种类, 主要可以由下列特征组合界定: 方骨内、外关节髁大小几近相当, 上、下颌齿缘强烈凹凸不平, 齿骨联合很短, 夹板骨不进入下颌联合, 以及在下颌关节窝外侧上隅骨表面具一凹或纵沟。根据新的信息对南岭亚洲鳄和存义始猛鳄原来的系统关系进行了检验, 所得结果不支持南岭亚洲鳄和存义始猛鳄可以形成一单系分支及反对后者是前者的同物异名。虽然本文研究表明南岭亚洲鳄可以和其他种类区分, 但是在系统关系上却不能和亚洲鳄典型种(葛氏亚洲鳄*Asiatosuchus grangeri*)归于同一支系, 如此应该为其建立一属。然而, 鉴于南岭亚洲鳄标本太不完整, 在没有新的、更完整的标本发现之前, 本文仍沿用其原名, 如德国亚洲鳄(*Asiatosuchus germanicus*)一样, 后者也不和亚洲鳄典型种归于同一支系。

关键词: 中国, 白垩系-古新统, 鳄目, 分类, 解剖学

中图法分类号: Q915.864 文献标识码: A 文章标号: 1000-3118(2018)02-0137-10

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