

An aberrant amphicyonid mammal from the latest Eocene of the Bose Basin, Guangxi, China

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A new genus and species of an amphicyonid from the Bose Basin of Guangxi, south China, is short-jawed with relatively bunodont cheek teeth that are characterized by reduction in cusp number. This taxon is the oldest record of an amphicyonid from south Asia and possibly for all of Asia. Despite its antiquity, it is derived in the development of brachygnathy and differs from other early amphicyonids that have shortened faces. Evidently brachygnathy was established in this species without loss of p1–2 or m2–3, which became single-rooted from a primitive double-rooted condition.

Key words: Carnivora, Amphicyonidae, Eocene, Bose Basin, Nadu Formation.

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Donald E. Savage passed away on April 5, 1999.

Introduction

In the spring of 1983, under the sponsorship of the Chinese Academy of Sciences and the U.S. National Science Foundation, a paleontological reconnaissance was made of the Bose Basin, one of the northwestern ring of a series of chain-like basins developed along the Youjiang River in Guangxi Province, southern China (Fig. 1). Located about 175 kilometers NW of the city of Nanning, the basin is interpreted as being late Eocene to early Oligocene in age. Mammalian fossils have been found at scattered localities in the strata exposed in this basin (e.g., Chow 1957; Qiu 1977; Xu 1977; Tang 1978; Russell and Zhai 1987; Tong 1989; Liu 2001). The age of Bose Basin strata is problematic because biostratigraphic correlation to other areas is hampered by the largely endemic nature of the fauna (Holroyd and Ciochon 1994). Two formations, the Nadu (previously spelled Naduo) and overlying Gongkang, are exposed here (Fig. 1). As discussed by Russell and Zhai (1987), the faunas of the two formations have been somewhat confused in the existing literature, and a ?Late Eocene age for the Nadu Formation and Late Eocene to Early Oligocene age for the overlying Gongkang Formation

is consistent with the possible biostratigraphic correlations. Long thought to be comparable in age to the Pondaung fauna of Burma (Myanmar) based on correlation of anthracotheriid taxa (e.g., Chow 1957; Qiu 1977), it has since been recognized as possessing its own unique fauna. Recently, Liu (2001) has favorably compared the suids from the Nadu Formation with those from the Late Eocene Krabi fauna of Thailand. Liu and Yang (1999) have described Nadu Formation palynofloras that are similar to those from other Late Eocene sites in China and Gilder et al. (1993) have reported that Nadu Formation sediments occur within a reversed paleomagnetic chron, as do the Krabi faunas (Benammi et al. 2001). All of these findings are consistent with a Late Eocene age for Nadu Formation sediments.

While the original goal of the joint China-America field project was to recover fossil mammals in southern China comparable to the Pondaung fauna, unexpected new mammals were found during the process of collecting. The dentary of the unusual carnivoran described below was discovered on an outcropping of gray mudstone on the afternoon of June 14, 1983 by Donald Savage. The dentary was left in place overnight, and the following day the humerus and tibia were

exposed in place while preparing the jaw for a plaster jacket (Fig. 2). All three bones were then removed as a single block. A return to the site the following day and additional excavation failed to uncover any other bone.

The existence of this amphicyonid in south China has been previously noted by Hunt (1998a) and Kordikova et al. (2000) and as a *nomen nudum*, *Guangxicynodon sino-californiae*, in faunal lists by Russell and Zhai (1987) and Tsubamoto et al. (2000). Although the age cannot be determined with certainty, the new genus is the oldest known record of the family in South Asia, and probably all of Asia. Asian amphicyonids were previously only known from Oligocene and younger localities (see Kordikova et al., 2000 for a summary). The family is known in North America from the Middle Eocene (represented by *Daphoenus*) and from Europe by the questionably related *Simamphicyon* from the late Middle Eocene. The appearance of amphicyonids in North America and Europe corresponds with the arrival from Asia of a number of immigrant mammalian taxa near the end of the Eocene (Janis et al., 1998). This suggests that Asia may have been the geographic source area for amphicyonids, even though no earlier Eocene amphicyonids or their apparent ancestors are known from this continent as yet.

The specimens described in this paper are housed at the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, abbreviated as IVPP.

Systematics

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Infraorder Arctoidea Flower, 1869

Family Amphicyonidae Haeckel, 1866

Guangxicynodon gen. nov.

[*Guangxicynodon* nomen nudum Russell and Zhai, 1987]

Type species: Guangxicynodon sinoamericanus sp. nov.

Known range: Late Eocene, Bose Basin, Guangxi Province, China.

Diagnosis.—Short-faced amphicyonid with very large c1, small and single-rooted p1–2 and m2–3. No rotation of teeth or crowding of premolars; p3–m1 relatively bunodont and without accessory cusps. Blade of m1 short and set in an oblique direction; metaconid strong and lower than protoconid, equivalent in height to paraconid; large, centrally placed, knob-like hypoconid; entoconid lacking.

Differential diagnosis.—*Guangxicynodon* differs from ursid arctoids (*sensu* Hunt 1998b) generally in lacking a pre-masseteric fossa, talonid basin of m1 not labially closed by a prehypocristid (hypoconid crest of Hunt, 1998b), and in the apparent absence of entoconid and entoconulid on m1. *Guangxicynodon* differs from Oligocene ursids in lacking a posterior accessory cusp in p4. *Guangxicynodon* differs from the Early Oligocene and the earliest ursid (*sensu* Hunt 1998b) *Amphicyonodon* (see Cirot and de Bonis 1992), in being larger

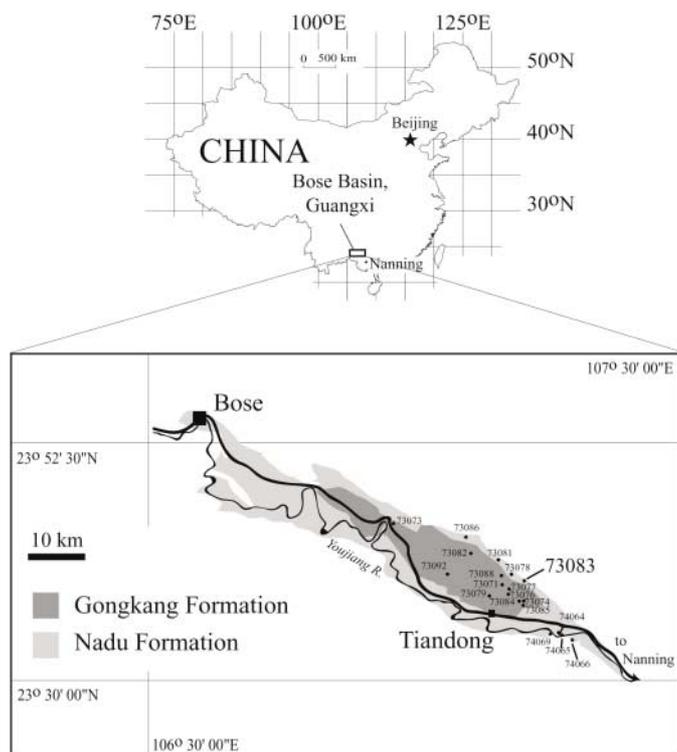


Fig. 1. Map showing position of Bose Basin, Guangxi Province, southern China, and simplified outcrop map of Bose Basin, illustrating position of type locality IVPP 73083 (after Tang et al. 1974).

and having m1 much more blunt. *Guangxicynodon* differs from the Late Oligocene and Early Miocene earliest hemicyonine ursid *Cephalogale* (see de Beaumont 1965) in being larger, having the paracone of m1 longer relative to the length of the protoconid, and the metaconid placed less posteriorly. Besides its unique tooth morphology with single-rooted p1, p2, m2, and m3, *Guangxicynodon* differs from the late Middle Eocene supposed amphicyonid *Simamphicyon* (see e.g., Crochet 1988) in being much larger, having the m1 trigonid much more stout, and the m1 talonid relatively longer. *Guangxicynodon* differs from other short-faced Paleogene amphicyonids (e.g., *Brachycyon*, *Haplocyon*) in the shorter, blunter, and less compressed p3–m1 and the centrally placed hypoconid of m1 talonid. *Guangxicynodon* differs from all Oligocene amphicyonids in lacking the posterior accessory cusp in p4. *Guangxicynodon* shares the structure of m1 trigonid with the Oligocene amphicyonids *Brachycyon* and *Haplocyon*. Moreover, it shares its peculiar talonid morphology with the amphicyonid *Pseudocyonopsis* (see e.g., Kuss 1965; Ginsburg 1966).

Etymology.—*Guangxicynodon*, dog-like mammal from Guangxi; *sinoamericanus*, a commemorative name referring to the cooperative research project between vertebrate paleontologists from China and America.

Guangxicynodon sinoamericanus sp. nov.

Figs. 2–7.

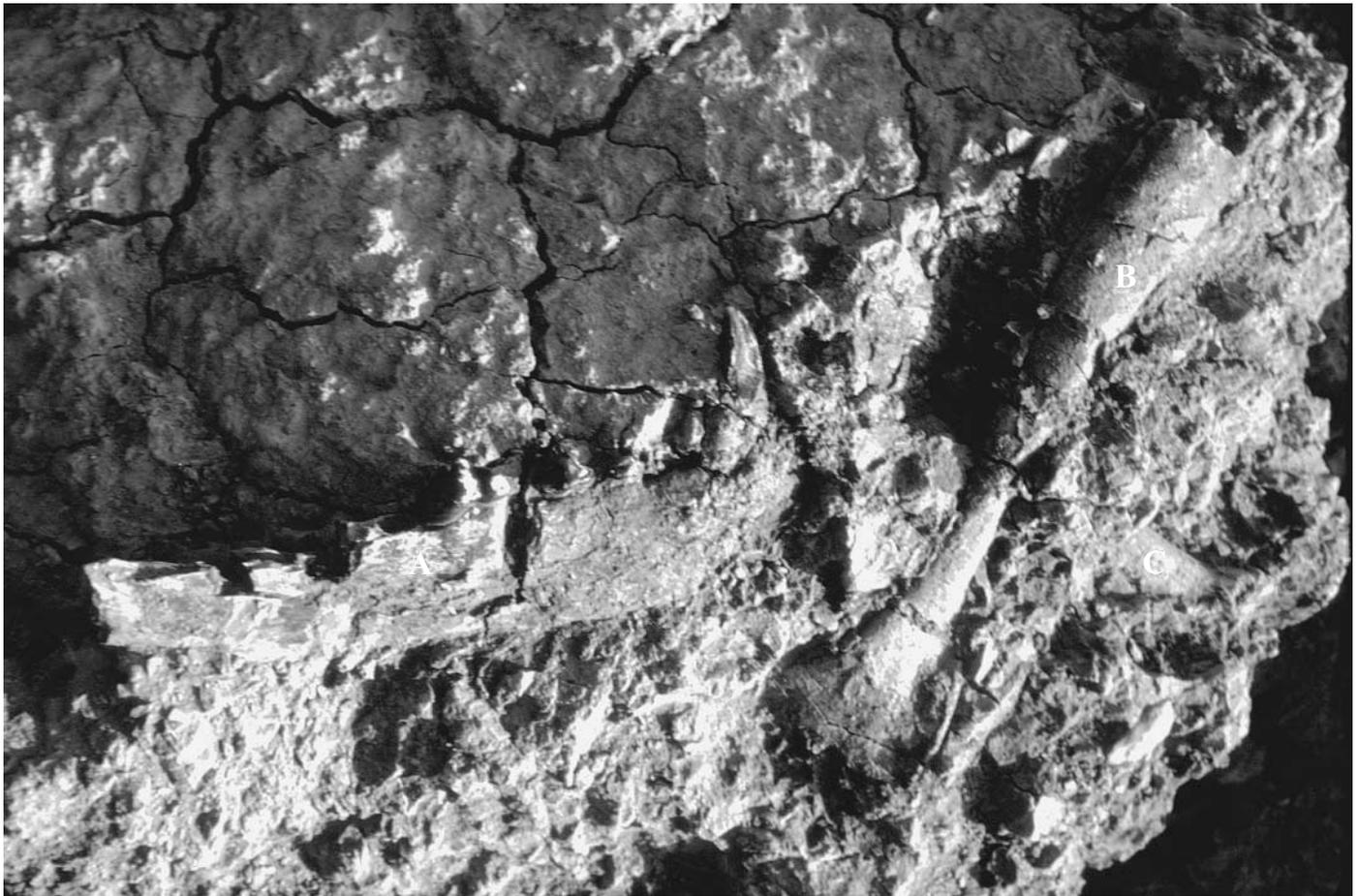


Fig. 2. *Guangxicyon sinoamericanus* gen. et sp. nov., IVPP V11818, in situ, immediately prior to jacketing and removal, mandible (A), humerus (B), tibia (C).

Table 1. Dental dimensions (mm) of *Guangxicyon sinoamericanus* gen. et sp. nov. (holotype) compared with two European amphicyonids, *Brachycyon palaeolycos* and *Pseudocyonopsis quercensis* (measurements taken from Ginsburg, 1966).

	<i>Brachycyon palaeolycos</i>	<i>Pseudocyonopsis quercensis</i>	<i>Guangxicyon sinoamericanus</i>
Length of lower premolar series	41.1	43.4	35.2
Length of lower cheek tooth series	85.7	75.9	71.6
Length of p3–m1	48.8	47.0	45.4
p3 Length	11.9	12.2	9.2
p3 Width	6.9	5.0	5.4
p4 Length	13.6	14.0	13.5
p4 Width	8.1	7.3	8.0
m1 Length	21.7	20.8	20.6
m1 Width	9.9	10.0	9.2

Guanxicyonodon sinocaliforniae nomen nudum; Russell and Zhai, 1987: 200.

Guanxicyonodon sinocaliforniae nomen nudum; Tsubamoto et al., 2000: 63.

Holotype: IVPP V11818-1, a left mandible with c1 and p3–m1 and with alveoli for p1–2 and m2–3; V11818-2, left humerus; and V11818-3, a right tibia.

Type locality and stratigraphic position: Holotype specimens were found in a mudstone with associated pebble lens in the Nadu Formation, IVPP locality 73083, latest Eocene, 1 km east of Quelin Village, Tiendong, Guangxi (Fig. 1; see also Russell and Zhai, 1987: figs. 41 and 42).

Diagnosis.—As for genus.

Measurements — See Table 1 for measurements of holotype and comparative taxa.

Description.—The outstanding feature of the mandible is the short and relatively deep horizontal ramus (Figs. 3B, C, 4B). It is similar to *Brachycyon* Filhol from the Oligocene of Europe, but the ramus is deeper than in *B. reyi* (Ginsburg 1966). The mandible is slightly deeper than the dentary of *B. palaeolycos*, especially in the anterior part, maintaining an

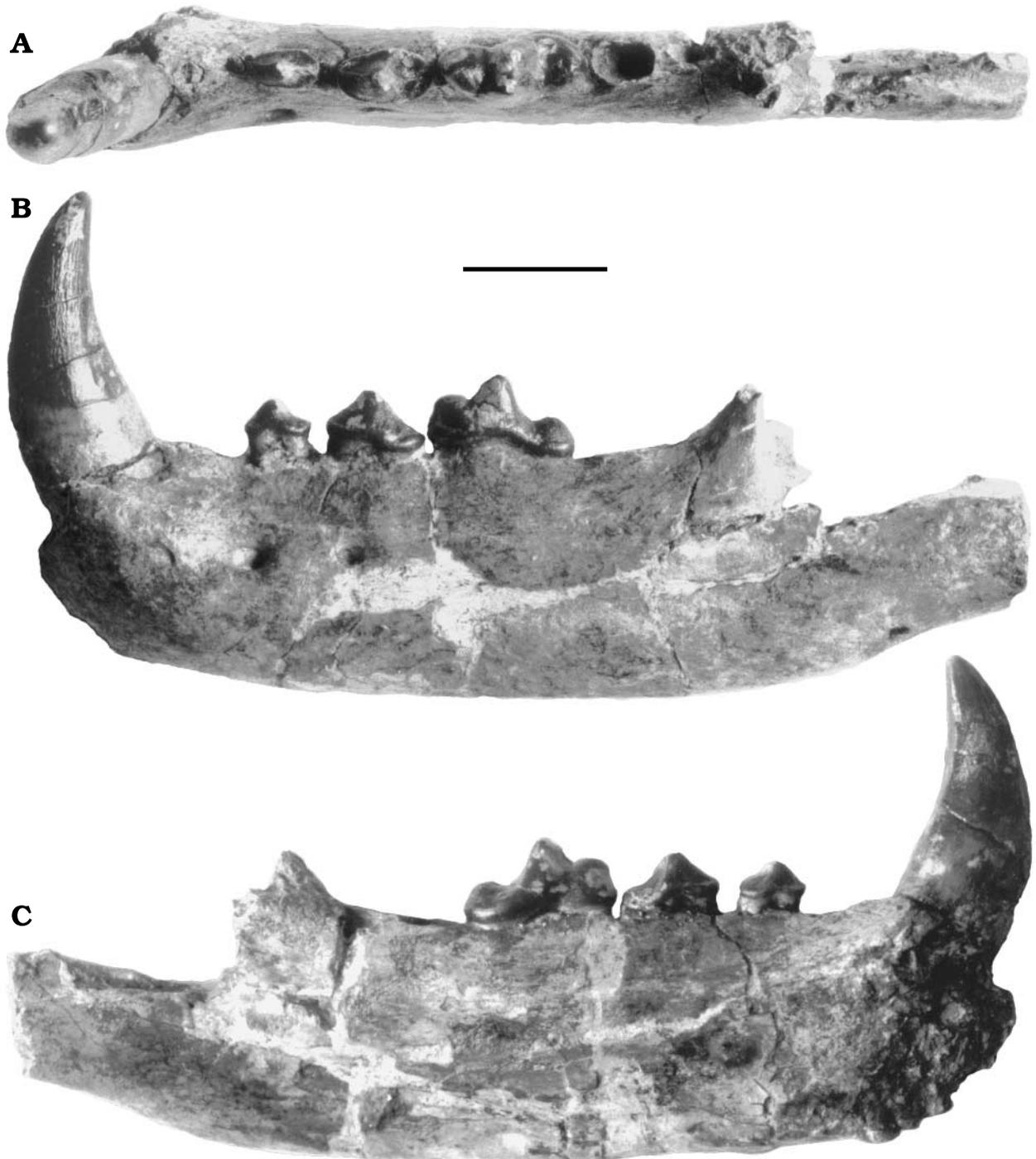


Fig. 3. *Guangxicyon sinoamericanus* gen. et sp. nov., IVPP V11818-1, photographs of the left lower jaw with p3–m1 and alveoli for p1–2 and m2–3; in occlusal (A), lateral (B), and medial (C) views. Scale bar 2 cm.

almost constant depth along the ramus from the symphysis to the area below m3. The lower border of the ramus is straight and there is no premasseteric fossa on the lateral face as in some ursids. The area of the horizontal ramus beneath the masseteric fossa is considerably deeper than in true canids such as *Enhydrocyon*, and is comparable in depth to *Cynelos*. The symphysis is not fused. There are three mental foramina present, a large one beneath the anterior root of p3, another

large one beneath the anterior root of p4, and a very small one beneath the root of p1.

The incisor region in this specimen is broken away, so no information on these anterior teeth is available. The canine is large and robust as is usual in amphicyonids. It is oval in cross-section and had no cutting blade.

Unfortunately, p1–2 and m2–3 are missing in this specimen. However, the alveoli of these lost cheek teeth provide a

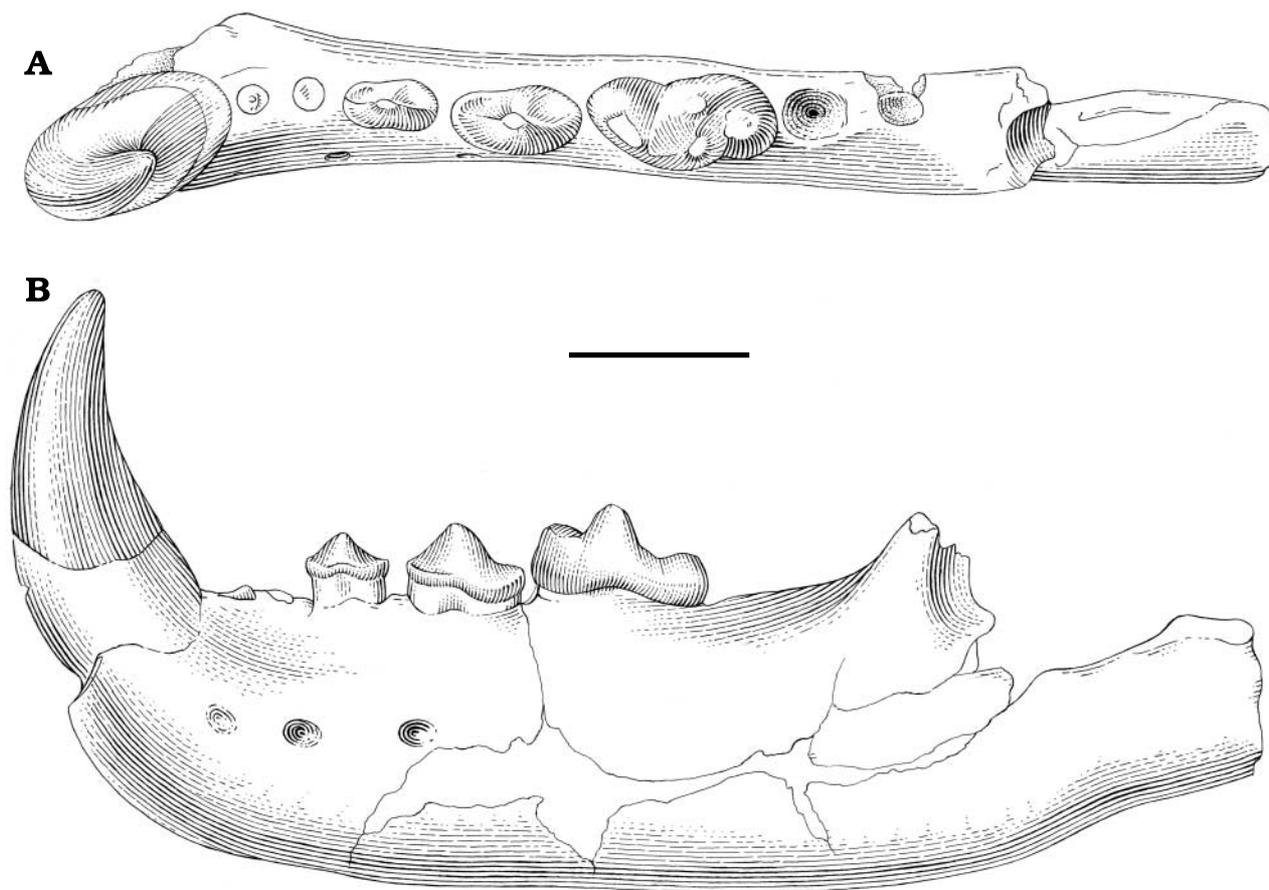


Fig. 4. *Guangxicyon sinoamericanus* gen. et sp. nov., IVPP V11818-1, line drawings of the left lower jaw with p3–m1 and alveoli for p1–2 and m2–3; in occlusal (A) and lateral (B) views. Scale bar 2 cm.

limited knowledge of their size and morphology. Anterior to the preserved p3 two small, well-separated alveoli are present. These two alveoli could be interpreted as having held a double rooted p2 (with p1 lost) or as having held two single rooted premolars. We interpret these alveoli as representing two small single rooted premolars (p1 and p2), because the length from the anterior edge of the first alveolus to the posterior edge of the second alveolus (8.7 mm) is greater than that for the preserved p3 (8.1 mm) and the lack of a bony elevation between the alveoli that is typical if two alveoli belong to the same tooth. If these alveoli were those of a single tooth, it would have possessed a crown length in excess of 9 mm and would have been greater in length than p3. Since no amphicyonid is known to have p2 longer than p3, the presence of two reduced premolars is more likely.

The three preserved cheek teeth of *Guangxicyon* also show reduction and simplification, being shorter, blunter, and less compressed than in other short-faced forms such as *Daphoenocyon* (= *Brachyrhynchocyon*, see Hunt 1998a), *Brachycyon* and *Enhydrocyon*. The p3 is small, simple and lacks an accessory cuspule posterior to the protoconid. The labial cingulid is weakly developed and discontinuous over the face of the protoconid, but continuous anteriorly and antero-lingually. The p4 is also simplified, lacking the poste-

rior accessory cusp usually seen in amphicyonids, but it does have a short posterior heel and exhibits slight internal expansion. On both p3 and p4 pre- and postprotocristids are weak, but distinct. In both teeth the roots are close together, and are even fused in their dorsal part. This configuration is consistent with the interpretation of the existence of both single rooted p1 and p2, rather than only a double-rooted p2 with widely separated roots. On p4, two additional short crests extend posterolabially and posterolingually from the protoconid, ending slightly above and disjunct from the cingulid, providing the posterior face of the p4 a triangular outline. The trigonid of m1 is similar to that seen in *Brachycyon* and *Haplocyon* with the paraconid-protoconid blade obliquely oriented and the metaconid strong though lower than the protoconid. The talonid is long relative to *Brachycyon* and is comprised of a large and centrally placed hypoconid, and a relatively high and rounded cristid obliqua. The entoconid is lacking and the posterior rim of the tooth is rounded. This condition contrasts with most amphicyonids where the hypoconid is more laterally positioned and the posterior rim is rectangular (see, e.g., Kuss 1965; Ginsburg 1966; Viranta 1996); the only exception is *Pseudocyonopsis*, which shows a morphology similar to that observed in *Guangxicyon*. The former genus, however, possesses much higher talonid cusps



Fig. 5. *Guangxicyon sinoamericanus* gen et sp. nov., IVPP V11818-2, left humerus in anterior (A) and posterior (B) views. Scale bar 2 cm.

(see, e.g., Kuss 1965: fig. 86). Based on a regression of $\ln m1$ area using the all carnivore equation of Legendre and Roth (1988), the estimated body mass of *Guangxicyon* would have been approximately 10.6 kg.

Molars posterior to $m1$ are missing, but two alveoli are preserved. The anterior of the two is comparatively large (7.3 mm length \times 5.1 mm width) and has a conical root with the deepest point just in the middle of the alveolus (Fig. 4A). The posterior one is very small (4.1 mm length \times 4.2 mm est. width). Together, the two alveoli measure 15.7 mm in length. As in the case of the anterior premolar alveoli, two interpretations are possible. These two molar alveoli could have held reduced, single-rooted $m2$ and $m3$, or a relatively large, double-rooted $m2$ with $m3$ lost. Retention of all three molars and maintaining $m1 > m2 > m3$ is the plesiomorphic condition for amphicyonids (Hunt, 1998a), and a trend toward reducing the size of the posterior molars is seen in several amphicyonid lineages. For example, *Brachycyon* has fused roots in $m2$. Loss of $m3$ without concomitant reduction of $m2$, only occurs in the most derived amphicyonids. If $m3$ were lost in *Guangxicyon*, this would have required that this loss occurred in conjunction with the retention of a relatively large

$m2$ with a much reduced talonid and a conical anterior root typical for a single-rooted tooth. This interpretation seems the less likely, and it is more parsimonious to interpret the posterior molar alveoli to have held reduced, single-rooted $m2$ and $m3$. This produces a lower dental formula of $i?/c/p1-4/m1-3$.

Guangxicyon is distinct among the Amphicyonidae in having both size and root number of anterior premolars and posterior molars reduced, accompanied by a shortening of the face. By contrast, facial shortening in *Enhydrocyon* is accompanied by loss of $p1$ and in some specimens $m3$ and oblique reorientation of the premolars. In the short-faced *Brachycyon*, the shortening of the jaw is accomplished by having all cheek teeth crowded with regard to the roots of $p2$ and $m2$. Reduction of the first premolar in the upper dentition is known from *B. gaudryi*. In Aktaucyonini, a third amphicyonid group exhibiting facial shortening, $P1$ is strongly reduced (Kordikova et al. 2000).

Found in direct association with the dentary, and undoubtedly belonging to the same individual, was a left humerus and a right tibia (Figs. 2, 5–7). The humerus lacks the proximal portion, and the distal articular surface is detached from the shaft. The total length of the humerus can be estimated at approximately 205 mm. There is a pronounced deltopectoral crest which extends along about two-thirds the length of the bone (Fig. 5A). The shaft does not exhibit much torsion. There is a strong brachioradialis (supinator) crest on the distal portion of the shaft. The grooves and depressions on the medial side of the distal humerus suggest the possible presence of an entepicondylar foramen (Fig. 5A). The distal articular surface is relatively wide without a strongly project-

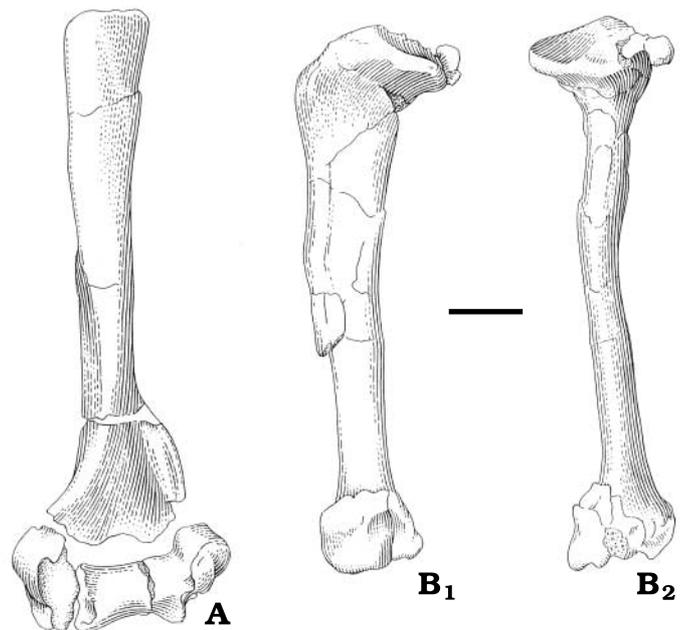


Fig. 6. *Guangxicyon sinoamericanus* gen. et sp. nov., IVPP V11818-2, left humerus and right tibia, IVPP V11818-3, line drawings. A. Left humerus, posterior view. B. Right tibia in lateral (B₁) and posterior (B₂) views. Scale bar 2 cm.

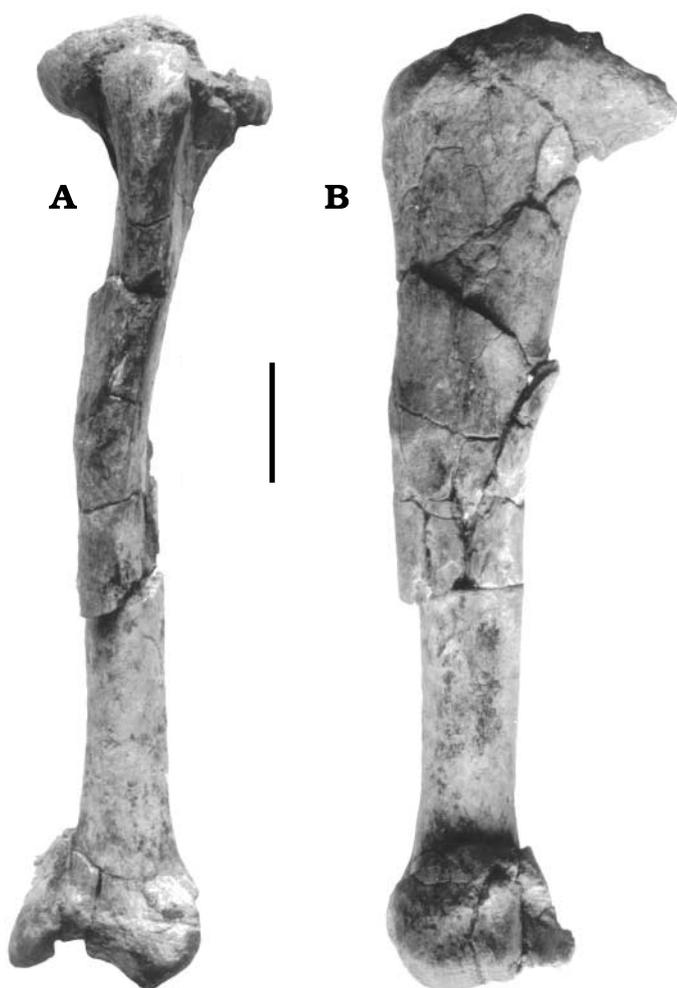


Fig. 7. *Guangxicyon sinoamericanus* gen et sp. nov, IVPP V11818-3, right tibia, photographs in anterior (A) and lateral (B) views. Scale bar 2 cm.

ing medial trochlear ridge or capitulum. The medio-lateral distal articular width is 46 mm.

The tibia (Figs. 6B, 7A, B) is complete, but is cracked and somewhat distorted in the central portion of the shaft. At its proximal end the medial condylar surface is broken away, and the intercondylar eminence is damaged. There is a pronounced tibial tuberosity which is knob-like. The tibial shaft appears flattened medio-laterally, but part of this could be due to its damaged condition. On the distal articular surface the grooves for articulation with the astragalus can be seen. The medial malleolus is cracked and slightly displaced in a proximal direction. The total length of the tibia is estimated to be 165 mm.

Comparison of the humerus and tibia of *Guangxicyon* with those of other amphicyonid taxa shows relatively strong similarities to *Amphicyon*. However, these elements of *Guangxicyon* are more robust and relatively shorter than those of *Amphicyon*. Postcranially, *Guangxicyon* appears quite divergent from more specialized *Temnocyon* and *Enhydrocyon*. It differs from *Cynelos* (Springhorn, 1977), as

well as *Brachycyon* (Filhol, 1873), in having broader distal condyles on the humerus and tibia, suggesting a less cursorial gait. Therefore, *Guangxicyon* probably retained the primitive, ancestral condition for the Amphicyonidae.

Hunt (1972) discussed in detail the humerus of a Miocene amphicyonid, *?Ysengrinia*. He concluded that, in nearly all details of morphology, the *?Ysengrinia* humerus is very similar to living ursids, especially the Giant Panda, *Ailuropoda*. The humerus of *Guangxicyon* exhibits some of the features discussed by Hunt (1972) such as a large deltopectoral crest, a strong brachioradialis crest, a broad distal trochlea, and an elaborate lateral epicondyle. These features suggest an animal capable of extensive lateral rotation of its forearm with a plantigrade posture (Ginsburg 1961). *Guangxicyon* was a less cursorially adapted animal than *Daphoenodon* or *Cynelos*, both of which had more elongate limbs although not as relatively elongate as in extant canids.

Conclusion

In summary, *Guangxicyon*, from the latest Eocene of southern China, is placed in Amphicyonidae as an aberrant taxon that differs significantly from other members of the family. However, its exact relationship to other amphicyonids is not well understood at the present time. Superficially, the dentary is similar to other short-faced amphicyonids, yet it became short-faced without reduction in the number of teeth. It had also evolved a specialized, simplified, more bunodont dentition. Thus, *Guangxicyon* appears to be convergently similar to the other short-faced amphicyonids, although it has achieved this similarity through a unique combination of characters.

Acknowledgments

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