

A new amynodontid from the Eocene of South China and phylogeny of Amynodontidae (Perissodactyla: Rhinoceroidea)

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(Received 5 April 2016; accepted 21 September 2016; published online 1 December 2016)

Cadurcodon maomingensis sp. nov. is described based on a partial skull and associated vertebrae from the middle–upper Eocene Youganwo Formation in the Maoming Basin, Guangdong Province, China. The taxonomy of *Cadurcodon* Kretzoi, 1942 (= *Sianodon* Xu, 1965, syn. nov.; = *Paracadurcodon* Xu, 1966, syn. nov.) is revised, and a new diagnosis of the genus is provided. It includes six species: *C. ardynensis* (Osborn, 1923), *C. kazakademius* Biryukov, 1961, *C. bahoensis* (Xu, 1965) comb. nov., *C. suhaituensis* (Xu, 1966) comb. nov., *C. houldjinensis* B.-Y. Wang, Qiu, Zhang, Wu, & Ning, 2009 and *C. maomingensis* sp. nov. A new phylogenetic hypothesis of Amynodontidae is based on the cladistic analysis of the distribution of 48 characters in 16 amynodontid taxa. The family is divided into two sister taxa, Metamynodontini (*Paramynodon*, *Megalamynodon* and *Metamynodon*) and Cadurcodontini (*Procadurcodon*, *Zaisanamynodon*, *Cadurcodon* and *Cadurcotherium*). The remaining amynodontid genera are considered *incertae sedis*. The evolution of amynodontids was confined mainly to Central and East Asia, with four dispersal events to North America (*Amynodon*, *Amynodontopsis*, *Metamynodontini* and *Procadurcodon*), and one to Europe and South Asia (*Cadurcotherium*). The holotype of *C. maomingensis* sp. nov. is an adult male with body mass estimated as 1.4 tons. Amynodontids show considerable increase in size during evolution, with the largest species weighing over two tons (*C. kazakademius*, *Zaisanamynodon borisovi* and *Procadurcodon orientalis*).

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Keywords: Mammalia; Perissodactyla; Amynodontidae; phylogeny; Eocene; China

Introduction

Amynodontidae are an extinct group of Rhinoceroidea which were among the dominant herbivorous mammals during the Eocene and early Oligocene (Gromova 1954; Belyaeva 1971; Wilson & Schiebout 1981; Wall 1989, 1998; Lucas & Emry 1996). They had different locomotor adaptations and lifestyles (Wall 1989; Wall & Heinbaugh 1999). The most unusual specialization of amynodontids is enlarged tusk-like canines, with the lower canines shearing anterior to the uppers, as in hippopotami. In other rhinocerotoids the canines are either very small or absent, and the tusks, when present, were formed by incisors (Prothero *et al.* 1989). Amynodontids were present on all northern continents (Asia, North America and Europe), but were most abundant and diverse in Asia. The majority of amynodontid records come from Central Asia and a few amynodontid remains were found in South China, mostly in Yunnan Province (Xu 1961; Xu & Chiu 1962; Chow *et al.* 1964; Qi 1992). Here we report on a

new amynodontid species from the middle–upper Eocene of the Maoming Basin in Guangdong Province, South China. It is based on a partial skull and associated vertebrae preserved in a single concretion that was found by local farmers and subsequently obtained by Sun Yat-sen University in Guangzhou.

Material and methods

Stratigraphy and geological age

The Maoming Basin is an asymmetrical, north-west–south-east elongated upper Mesozoic–Cainozoic sedimentary basin nearly 40 km long and 16 km wide, located in south-west Guangdong Province, South China (Figure 1). The Upper Cretaceous–Neogene sedimentary sequence of the Maoming Basin is subdivided into the Sanyajiang, Tongguling, Shangdong, Youganwo, Huangniuling, Shangcun, Laohuling and Gaopengling formations (Nan & Zhou 1996). All known vertebrate remains from the

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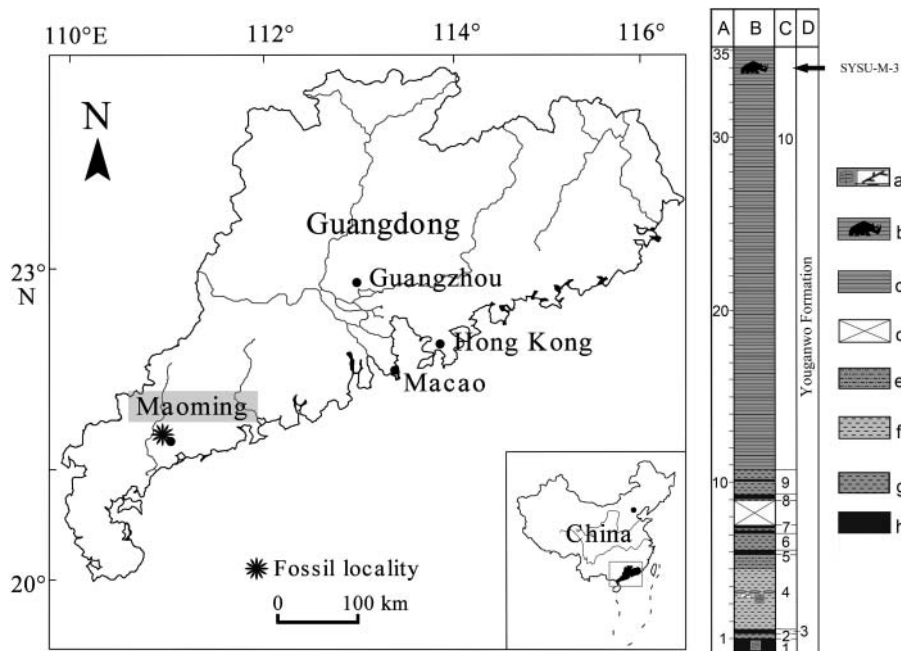


Figure 1. Geographical map of the Maoming Basin, Guangdong Province, China (left; fossil site is indicated by star) and stratigraphical column of the Youganwo Formation (right; position of SYSU-M-3, the holotype of *Cadurcodon maomingensis* sp. nov., is indicated by arrow). Legend: A, thickness (m); B, lithology; C, layer; D, formation; a, fossil plant layer; b, fossil mammal layer; c, oil shale; d, absent; e, silty mudstone; f, clay shale; g, mudstone; h, coal bed.

Maoming Basin were found in dark brown oil shales in the upper part of the Youganwo Formation, which were deposited in lacustrine conditions. The Youganwo Formation has been dated based on magnetostratigraphy and palynomorph assemblages as late Eocene (J. Wang *et al.* 1994; Jin 2008), or middle–late Eocene (Aleksandrova *et al.* 2015). The vertebrate assemblage of the Youganwo Formation includes cyprinid fishes; carettochelyid, adocid, trionychid and geoemydid turtles; tomistomine and alligatorid crocodiles; a nimravid carnivore; and chalicotheroid and amynodontid perissodactyls (Chow & Liu 1955; Liu 1957; H.-K. Ye 1958, 1963, 1994; Chow & Ye 1962; Y.-Y. Wang *et al.* 2007; Tong *et al.* 2010; Claude *et al.* 2012; Danilov *et al.* 2013; Skutschas *et al.* 2014; Averianov *et al.* 2016).

Taxon sampling for phylogenetic analysis

Hyrachyus eximius is a basal rhinocerotoid from the lower–middle Eocene of USA, a possible sister taxon of the remaining Rhinoceroidea (Prothero *et al.* 1986; Emry 1989; Holbrook 1999). The species is scored from Osborn & Wortman (1895) and Wood (1934).

Wall (1982b, 1989, 1998) provided the most recent revision of North American amynodont alpha taxonomy. Four genera have been recognized: *Amyndodon* (two species), *Amyndontopsis* (one species), *Megalamyndodon* (one species) and *Metamyndodon* (three species). From these taxa we included in the analysis *Amyndodon advenus*,

Amyndontopsis bodei, *Megalamyndodon regalis* and *Metamyndodon planifrons*, which were scored based on published illustrations and descriptions (Scott & Osborn 1883; Osborn 1890, 1898; Troxell 1921; Stock 1933, 1939; Scott & Jepsen 1941; Scott 1945; Bjork 1967; Wilson & Schiebout 1981; Wall 1982b). *Amyndodon reedi*, *Metamyndodon chadronensis* and *M. mckinneyorum* were not included because they are based on fragmentary specimens and do not vary greatly from the included related taxa (Wood 1937; Stock 1939; Wilson & Schiebout 1981).

Paramyndodon birmanicus (including *P. cotteri*) from the middle–upper Eocene of Myanmar was scored from the literature (Matthew 1929; Colbert 1938).

'*Amyndodon*' *watanabei* from the middle–upper Eocene of Japan is known from a few imperfect specimens (Tokunaga 1926; Takai 1950, 1962), and was not included in the analysis.

A gigantic amynodontid '*Metamyndodon*' *bugtiensis*, from the Oligocene of Pakistan (Forster Cooper 1922), known from a single juvenile specimen with dP2–4 in place (Gromova 1954, p. 87) and erupting M3, is not included because of its incompleteness and uncertain taxonomic attribution. Kretzoi (1942) referred this species to *Paraceratherium*, but Colbert (1938) and Gromova (1954) retained it within Amyndontidae. Unfortunately, there is another rhinocerotoid species from the same stratigraphical unit named *Paraceratherium bugtiensis* (Pilgrim 1910; Antoine *et al.* 2004).

The genus *Cadurcotherium* includes four species, *C. cayluxi*, *C. minimus* and *C. nouleti* from the Oligocene of France and Switzerland, and *C. indicum* from the Oligocene of Pakistan. The two better known species, *C. cayluxi* and *C. minimus*, are included and scored from the literature (Gervais 1873; Roman & Joleaud 1909; Bonis 1995; Becker 2009).

Currently there are 31 named amynodontid species from the Eocene and Oligocene of Central Asia (Mongolia, China, Kazakhstan and Kyrgyzstan), placed in 12 genera (listed in chronological order): *Amynodon*, *Cadurcodon*, *Sharamynodon*, *Gigantamynodon*, *Hypsamynodon*, *Procadurcodon*, *Sianodon*, *Lushiamynodon*, *Paracadurcodon*, *Zaisanamynodon*, *Rostriamynodon* and *Andarakodon*.

The genus *Andarakodon* was proposed for *Lushiamynodon? kirghisensis* from the lower Eocene of Kyrgyzstan (Belyaeva 1971; Averianov & Potapova 1996; Averianov & Godinot 2005). Lucas & Emry (2001) referred this species to *Sharamynodon*. This is the oldest Asiatic amynodontid, known from maxillary fragments and isolated cheek teeth. It cannot be scored for the majority of the characters and is not included in the analysis.

Rostriamynodon grangeri, known from the single skull with mandible from the middle Eocene of Mongolia, is the most primitive amynodontid. The scorings are based on the original description (Wall & Manning 1986).

'*Amynodon*' *sinensis* from the upper Eocene of Henan Province, China, is one of the most primitive Central Asiatic amynodontids, and is similar to the Eocene *Amynodon advenus* from North America. Although it is known from fragmentary materials, it is included in the analysis because of its apparent phylogenetic significance. The scoring is based on original descriptions (Zdansky 1930; Young 1937). Chow & Xu (1965) included this species in *Sianodon*, which is considered here to be a synonym of *Cadurcodon* (see Systematic palaeontology section).

The genus *Sharamynodon* was proposed for *Amynodon mongoliensis* from the upper Eocene of Mongolia (Osborn 1936; Kretzoi 1942). This was not accepted by Gromova (1954) and subsequent Chinese authors, who described a number of similar species within the genus *Amynodon* (Xu & Chiu 1962; Chow *et al.* 1964; Qi 1975). The generic distinction of Mongolian species was confirmed by Wall (1989). *Sharamynodon mongoliensis* is included in the analysis and scored from the original descriptions (Osborn 1936; Young 1937).

The genus *Lushiamynodon*, based on *L. menchiapuen-sis* from the upper Eocene of Henan Province, China (Chow & Xu 1965), is likely the synonym of *Sharamynodon* (Wall 1989). The validity of two other species of *Lushiamynodon*, known from fragmentary specimens (Chow & Xu 1965; Xu 1966), is problematic.

Cadurcodon ardynensis from the upper Eocene of Mongolia is the best known Asiatic amynodontid, represented by a sample allowing study of individual, ontogenetic and sexual variation (Osborn 1924; Gromova 1954). The second species of the genus included in the analysis is *C. bahoensis* from the upper Eocene or lower Oligocene of Shaanxi Province, China (Xu 1965). This is the type species of *Sianodon*, considered here the junior synonym of *Cadurcodon* (see Systematic palaeontology section). *Cadurcodon kazakademius* is known from a single mandible from the middle Oligocene of Kazakhstan (Biryukov 1961; Lucas & Emry 1996). Although incomplete, it is included in the analysis to resolve the phylogenetic position of *C. maomingensis* sp. nov. *Cadurcodon houldjiniensis*, known from isolated teeth and dentary fragments from the upper Eocene of Nei Mongol (B.-Y. Wang *et al.* 2009), is likely a valid species. It is not included in the analysis because of its incompleteness. *Paracadurcodon suhaituensis* from the lower Oligocene of Nei Mongol, China (Xu 1966) is referred here to *Cadurcodon* (see Systematic palaeontology section). It is known from fragmentary specimens and not included in the analysis.

Hypsamynodon progressus is known from a few isolated teeth with hypsodont crowns from the upper Eocene of Mongolia (Gromova 1954). Wall (1982a, p. 566) believed that *H. progressus* belonged to the European genus *Cadurcotherium* and that the Asiatic species was ancestral to the European taxon, but later he chose not to synonymize the two genera (Wall 1989, p. 351). This problematic taxon is not included in the analysis.

Gigantamynodon cessator is another problematic taxon from the upper Eocene of Mongolia. It is based on a dentary fragment with m3 and referred isolated incisors and upper premolars (Gromova 1954). Wall (1989) considered this taxon a *nomen dubium*. The validity of three Chinese species referred to *Gigantamynodon* (Xu 1961, 1966; Qi 1992) is not certain, and they are not included in the analysis.

Procadurcodon orientalis is known from fragmentary specimens from the Upper Eocene of Primorskii Territory, Russia (Gromova 1960). Wall (1989) considered this taxon invalid, but he largely misread Gromova's diagnosis. This taxon is included in the analysis and scored from the original description. Lucas (2006) described '*Zaisanamynodon*' *protheroi* from upper Eocene of Oregon, USA. Previously these materials were referred to *Procadurcodon* (Hanson 1996). Lucas (2006) considered *Procadurcodon orientalis nomen dubium* and referred the type series from Russia to '*Zaisanamynodon*' *protheroi*. We consider *Procadurcodon orientalis* a valid species and the American species is either its junior synonym or a species of *Procadurcodon*.

Zaisanamynodon borisovi is based on a reasonably complete skull and partial skeleton from the upper Eocene of Kazakhstan (Belyaeva 1971). Lucas *et al.* (1996) referred to this species additional specimens from the

upper Eocene of Nei Mongol, China. The species is scored from the published descriptions and illustrations.

Character sampling for phylogenetic analysis

We selected 48 characters from the original descriptions and previous diagnoses of the amynodontid taxa (see Supplemental Appendix 1 for the list of characters). We used the most informative characters, for which the distribution is better known among amynodontid taxa. Of these 48 characters, nine characters are synapomorphies for the Amynodontidae and do not vary between the ingroup taxa (characters 11, 26, 31, 37, 40, 41, 43, 45 and 46). One character (13) is an autapomorphy of *Amyndontopsis bodei*. It is retained for diagnostic purposes.

Phylogenetic analysis

We compiled a data matrix containing 16 better known amynodontid taxa plus one outgroup taxon (*Hyrachyus eximius*), and 48 characters (see Supplemental Appendix 2 for the data matrix). The characters are taken mostly from Gromova (1954), Belyaeva (1971), Wall (1989) and published diagnoses of the amynodontid taxa. All characters were equally weighted, and six multistate characters were treated as additive (characters 6, 10, 29, 30, 35 and 47). Two analyses were performed. The branch-and-bound algorithm of PAUP* 4.0b10 (Swofford 2002) produced 12 most parsimonious trees with a length of 97 steps, a consistency index of 0.66 and a retention index of 0.75. Ten thousands of repetitions of the parsimony ratchet (island hopper) algorithm of NONA version 2.0 (Goloboff 1999) run with the Winclada version 1.00.08 interface (Nixon 1999) produced three most parsimonious trees with a length of 97 steps, a consistency index of 0.66 and a retention index of 0.75. On the strict consensus tree from 12 PAUP trees, all four species of *Cadurcodon* form a polytomy, while on the NONA consensus tree the relationships within the *Cadurcodon* species are fully resolved. Otherwise, the two consensus trees are identical. The Bremer support values were found by TNT version 1.1 (Goloboff *et al.* 2008). The bootstrap support values (10,000 replicates) were calculated using NONA and Winclada.

Palaeobiogeographical analysis

We reconstructed the ancestral area for the clades using the Statistical Divergence-Variance methodology implemented in the S-DIVA 1.9 software (Yu *et al.* 2010). For this analysis we used the 12 most parsimonious trees obtained by PAUP. The geographical distribution of taxa used in the analysis was established according to major continental landmasses where fossil remains of amynodontids have been found (Asia, North America and Europe).

Body mass estimation

The size of the molars is a proxy of body mass in mammals, allowing estimation of the body mass in extinct species (Gingerich *et al.* 1982; Conroy 1987; Legendre 1989; Damuth 1990; Fortelius 1990; Van Valkenburgh 1990; Schwartz *et al.* 1995; Bloch *et al.* 1998). The first molars are the least variable among the molar series (Gingerich 1974) and thus most suitable for the body mass estimation. We used a regression equation calculated for generalized ungulates by Legendre (1989):

$$\ln Y = 1.5133 \times \ln X + 3.6515$$

where X is length multiplied by width of m1 in mm², and Y is body mass in g. Calculated values for 47 amynodontid specimens of 18 species are given in Supplemental Table 1. The average value of Ln Y and standard error for multiple samples are presented in Supplemental Table 2. The standard error and coefficient of correlation between Ln Y and clade rank were calculated by STATISTICA 7.1 ©StatSoft, Inc. 1984–2005.

Abbreviations

Institutional abbreviations

AMNH: American Museum of Natural History, New York, USA; IVPP: Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing, China; SYSU-M: Mammal fossil collection from the Maoming Basin in the School of Life Sciences, Sun Yat-sen University, Guangzhou, China.

Measurement abbreviations

L, length; W, width.

Systematic palaeontology

Class **Mammalia** Linnaeus, 1758
 Infraclass **Eutheria** Gill, 1872
 Order **Perissodactyla** Owen, 1848
 Superfamily **Rhinoceroidea** Gray, 1825
 Family **Amyndontidae** Scott & Osborn, 1883
 Genus **Cadurcodon** Kretzoi, 1942

1942 *Cadurcodon*; Kretzoi: 146.

1965 *Sianodon*; Xu: 83, syn. nov.

1966 *Paracadurcodon*; Xu: 145, syn. nov.

Type species. *Cadurcotherium ardynense* Osborn, 1923.

Revised diagnosis. 1(2) premaxilla-nasal contact absent, maxilla forming part of the external naris border; 2(1) premaxillae fused and thickened; 3(1) nasals reduced; 4(2)

anterior margin of nasals squared; 5(1) nasals not overhang external naris; 6(1) posterior extension of nasal incision above P4; 7(0) maxilla-frontal contact on rostrum absent; 8(1) diastema between upper incisors and canine absent; 9(1) upper postcanine diastema short, distinctly shorter than upper premolar length; 10(1) preorbital skull region less than 40% of the condylobasal skull length; 12(1) preorbital fossa large and extends medial to orbit; 13(0) inner surface of anterior orbital bar not concave in continuation with the preorbital fossa; 14(3) infraorbital foramen positioned above M2; 15(0) anterior border of orbit positioned above M2–3; 16(1) orbit positioned low on the skull; 17(1) well-developed rugosities for attachment of strong snout musculature present on lacrimal; 18(1) postglenoid and posttympanic processes adjacent; 19(0) extensive supraglenoid shelf covering the external auditory meatus absent; 20(1) convex ventral margin of mandibular ramus in lateral view; 21(1) posterior end of mandibular symphysis positioned at p4; 22(1) two upper incisors; 23(2) I3 distinctly smaller than I2; 24(1+2) one or two lower incisors; 25(1) i3 much larger than i2 (when two incisors present); 27(1) cheek teeth covered with cement; 28(0) labial cingulid on lower cheek teeth well developed; 29(2) upper premolars, length ratio to upper molars 0.45 or less; 30(2) lower premolars, length ratio to lower molars 0.45 or less; 32(0) P2–4, additional loph distal to metaloph ('inner cingulum') absent; 34(1) P4, crista between metaloph and protoloph present; 35(1) P4, two external foldings along the ectoloph (between parastyle-paracone and paracone-metacone); 36(1) P4 lingual cingulum complete; 38(1) p2 absent (present as individual variation in *C. ardynensis*); 39(2) p3 distinctly shorter than p4 and premolariform, with talonid reduced or absent; 42(0) upper molars, parastyle and anterior rib not confluent; 44(0) M3 metaloph similar in length with protoloph. The numbers of characters and states correspond to the list of characters in Supplemental Appendix 1.

Included species. *Cadurcotherium ardynense* Osborn, 1923, *C. kazakademius* Biryukov, 1961, *C. bahoensis* (Xu, 1965) comb. nov., *C. suhaituensis* (Xu, 1966) comb. nov., *C. houldjinensis* B.-Y. Wang, Qiu, Zhang, Wu, & Ning, 2009 and *C. maomingensis* sp. nov.

Remarks. Kretzoi (1942) established *Cadurcodon* for *Cadurcotherium ardynense* from the upper Eocene Ergilin Dzo Formation of Mongolia (Osborn 1923, 1924), but did not provide a formal diagnosis of the genus. The first diagnosis of *Cadurcodon* was compiled by Gromova (1954, 106–107). Nine of her characters are included in the revised diagnosis (characters 6(1), 18(1), 21(1), 22(0), 24(1+2), 27(1), 29(2), 30(2) and 39(2)).

The next diagnosis of *Cadurcodon* was provided by Wall (1989, p. 348). From this diagnosis five characters are retained here (characters 1(2), 2(1), 3(1), 12(1) and 38

(1)). Wall indicates for *Cadurcodon* one to two upper incisors and one lower incisor, which is a mistake; it has two upper and one to two lower incisors. Two characters of this diagnosis are conflicting and cannot be present at the same time: 'premaxilla ends approximately halfway up the narial canal where it contacts a descending process of the nasal' and 'maxilla borders a significant portion of the external nares'. The character 'nasal incision expanded back to a point above M2' is likely an artefact of skull orientation.

The genus *Sianodon* with type species *S. bahoensis* was first described from the lower Oligocene Bailuyuan Formation of Shaanxi, China (Xu 1965). The original description does not contain a comparison with *Cadurcodon* except that the new genus is more primitive than *Cadurcodon* (Xu 1965, p. 86). All characters mentioned in the original diagnosis are found also in *Cadurcodon*, except the labial groove separating the trigonid and talonid on lower molars, which is shallower or absent in other *Cadurcodon* species. Wall, in his revision of Amynodontidae had no strong opinion of *Sianodon*. He wrote (Wall 1989, p. 346) that "*Sianodon* and *Cadurcodon* are similar in many ways and only one genus may be valid", but two pages later (Wall 1989, p. 348) found that "the closest affinities of *Sianodon* are with *Cadurcodon*, but because of the retention of significant primitive character states, it cannot be placed in that genus." According to Wall (1989, p. 348), the primitive characters of *Sianodon* compared with *Cadurcodon* are "retention of two pairs of lower incisors, less extreme posterior expansion of the nasal incision, relatively less massive premaxillae and nasals, and more distinct postorbital constriction." However, the number of lower incisors in *Cadurcodon* is a sexual character: males with large canines have space for only one incisor and females with smaller canines have two incisors (Gromova 1954). In both genera the nasal incision has a similar expansion, at the level of P4 (Gromova 1954; Xu 1965). Massiveness of the premaxillae and nasals is difficult to formalize, and these characters are prone to ontogenetic and sexual variation. The phylogenetic significance of postorbital constriction is not clear. *Sianodon* Xu, 1965 is considered here a junior subjective synonym of *Cadurcodon* Kretzoi, 1942.

'*Sianodon*' *ulusuensis* from the upper Eocene Shara Murun Formation of Nei Mongol, China (Xu 1966), and '*Sianodon*' *gaowangouensis* from the lower Oligocene Bailuyuan Formation of Shaanxi, China (Li 2003), with three upper incisors, do not belong to *Cadurcodon*. Three other species referred to *Sianodon* and known from fragmentary specimens from the upper Eocene of Henan, China (Chow & Xu 1965), are small primitive amynodonts possibly referable to '*Amynodon*' *sinensis*.

The genus *Paracadurcodon* with type species *P. suhaituensis* was based on dentary fragments and isolated teeth

from the lower Oligocene Chaganbulage Formation of Nei Mongol, China (Xu 1966). It is diagnosed, in particular, by the presence of a single lower incisor; three lower premolars, although premolars are not preserved on the holotype dentary (Xu 1966, pl. 14, fig. 3); and very short mandibular symphysis. The presence of p2 was noted as an individual variation for *C. ardynensis* (Gromova 1954). *Paracadurcodon* Xu, 1966 is considered here a junior subjective synonym of *Cadurcodon* Kretzoi, 1942. By dental measurements, *C. suhaituensis* is distinctly smaller than *C. maomingensis* sp. nov. and similar to *C. ardynensis*.

Cadurcodon maomingensis sp. nov.
(Figs 2–8)

Holotype. SYSU-M-3, a partial skull with the mandible and associated vertebrae found in a single concretion.

Type locality and horizon. The oil shale quarry (21°42'N, 110°53'E) located near Maoming City, Maoming Basin, Guangdong Province, China; Youganwo Formation, middle–upper Eocene.

Differential diagnosis. Differs from *C. ardynensis*, *C. bahoensis* and *C. kazakademius* by character 48(1), m3 length-to-width ratio more than 2.2. Differs from *C. bahoensis* and *C. kazakademius* by character 24(2), one lower incisor (this character possibly sexually correlated).

Differs from *C. ardynensis* by character 33(2), P4 metaloph much shorter than protoloph. Differs from *C. bahoensis* by character 47(2), labial grooves on lower molars separating trigonid and talonid absent. Differs from *C. ardynensis*, *C. bahoensis* and *C. suhaituensis* by larger size, and from *C. houldjinensis* and *C. kazakademius* by smaller size. The numbers of characters and states correspond to the list of characters in Supplemental Appendix 1.

Derivation of name. From Maoming City in Guangdong Province, China.

Remarks. *Cadurcodon zaisanensis* is based on a single dentary fragment with p4 and m1–2 from the lower Oligocene Buran Formation of Eastern Kazakhstan (Belyaeva 1962). The original diagnosis does not allow clear differentiation from *C. ardynensis*. Lucas & Emry (1996) considered *C. zaisanensis* a junior subjective synonym of *C. ardynensis*, but noted the unusually longer m3 of the former, 20–30% longer than in the Mongolian samples of *C. ardynensis*. The holotype of *C. zaisanensis* is about 20% smaller than the holotype of *C. maomingensis* sp. nov.

Cadurcodon houldjinensis is known from dentary fragments and isolated teeth from the upper Eocene Houldjin Formation of Nei Mongol, China (Matthew & Granger 1923; B.-Y. Wang *et al.* 2009). This is a large species,

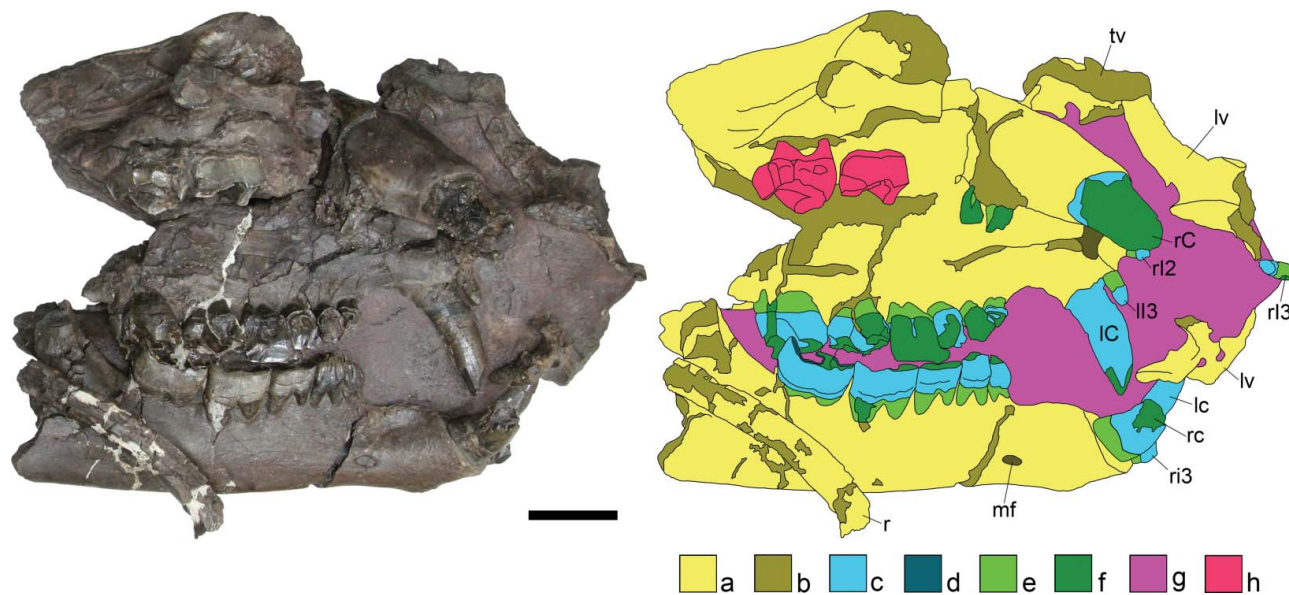


Figure 2. *Cadurcodon maomingensis* sp. nov., partial skull in left lateral view (SYSU-M-3, holotype). Maoming Basin, Guangdong Province, China; Youganwo Formation, middle–upper Eocene. Abbreviations: IC, left upper canine; lc, left lower canine; II3, left I3; lv, lumbar vertebra; mf, mental foramen; r, rib; rC, right upper canine; rc, right lower canine; r12, right I2; r13, right I3; ri3, right i3; tv, thoracic vertebra. Key to the explanatory drawing: a, bone surface; b, broken bone; c, enamel surface; d, broken or worn enamel; e, dentine surface; f, broken or exposed dentine; g, matrix; h, alien teeth glued by local collector. [See online version of paper for coloured figure.] Scale bar = 10 cm.

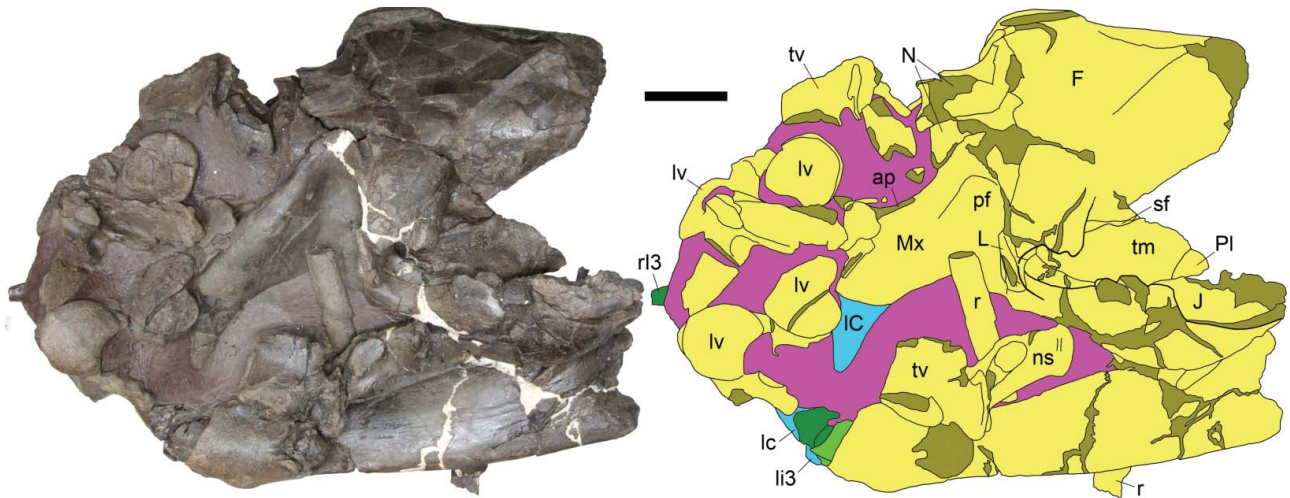


Figure 3. *Cadurcodon maomingensis* sp. nov., partial skull in right lateral view (SYSU-M-3, holotype). Maoming Basin, Guangdong Province, China; Youganwo Formation, middle–upper Eocene. Abbreviations: ap, rudimentary ascending process of premaxilla; F, frontal; L, lacrimal; IC, left upper canine; li3, left i3; lv, lumbar vertebra; Mx, maxilla; N, nasal; ns, neural spine; pf, preorbital fossa; PI, palatine; r, rib; rI3, right I3; sf, sphenoorbital fissure; tm, tuber maxillaris; tv, thoracic vertebra. For the key to the explanatory drawing see Figure 2. [See online version of paper for coloured figure.] Scale bar = 10 cm.

distinctly larger than *C. maomingensis* sp. nov. and approaching in size *C. kazakademius* (B.-Y. Wang *et al.* 2009). The P4 (Matthew & Granger 1923, fig. 4) is similar to that tooth in *C. maomingensis* in having short metaloph and strong complete lingual cingulum.

Gromova (1954) studied a large sample of *C. ardynensis* from the upper Eocene Ergilin Dzo Formation of

Mongolia. In particular, she noted two dentary morphotypes, one with large canines with open pulp cavity and a small space between the canines housing only one incisor (from each side of the mandible), and another with smaller canines with a closed pulp cavity and two pairs of incisors. She attributed the first morphotype to males and the second morphotype to females. The variation of these characters is unknown in other species of *Cadurcodon*, represented by smaller samples. If the same sexual variation was characteristic of *C. maomingensis* sp. nov., the holotype specimen with large canines and a single pair of lower incisors is an adult male.

Gigantamynodon giganteus from the lower Oligocene Caijiachong Formation of Yunnan, China (Xu 1961) is based on an isolated upper premolar (described in the text as lower p3) and dentary fragment with m1–3 (both specimens were attributed to a single collection number, IVPP V.2594). Upper molars from this locality identified as cf. *Metamynodon* sp. (Xu 1961, pl. 1, figs 3, 4) likely belong to the same species. The species is large, similar in size to *C. maomingensis* sp. nov. J. Ye *et al.* (2002) referred to *G. giganteus* some fragmentary specimens from the upper Eocene of Xinjiang, China. Because of a lack of diagnostic characters, *Gigantamynodon giganteus* Xu, 1961 is considered here a *nomen dubium*.

Gigantamynodon maguensis is based on the maxilla fragment with P3–M2 from an unknown, possibly, Oligocene locality in Yunnan, China (Qi 1992). It is a very large species, much larger than *C. maomingensis* sp. nov. *Gigantamynodon maguensis* Qi, 1992 is considered here a *nomen dubium*.

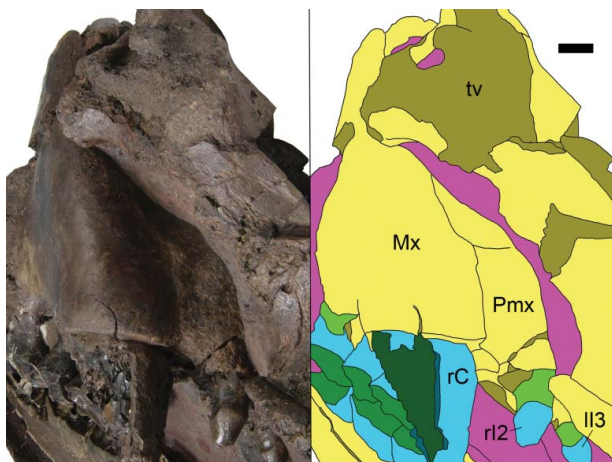


Figure 4. *Cadurcodon maomingensis* sp. nov., right rostral part in anterior view (SYSU-M-3, holotype). Maoming Basin, Guangdong Province, China; Youganwo Formation, middle–upper Eocene. Abbreviations: li3, left I3; Mx, maxilla; Pmx, premaxilla; rC, right upper canine; rI2, right I2; tv, thoracic vertebra. For the key to the explanatory drawing see Figure 2. [See online version of paper for coloured figure.] Scale bar = 2 cm.

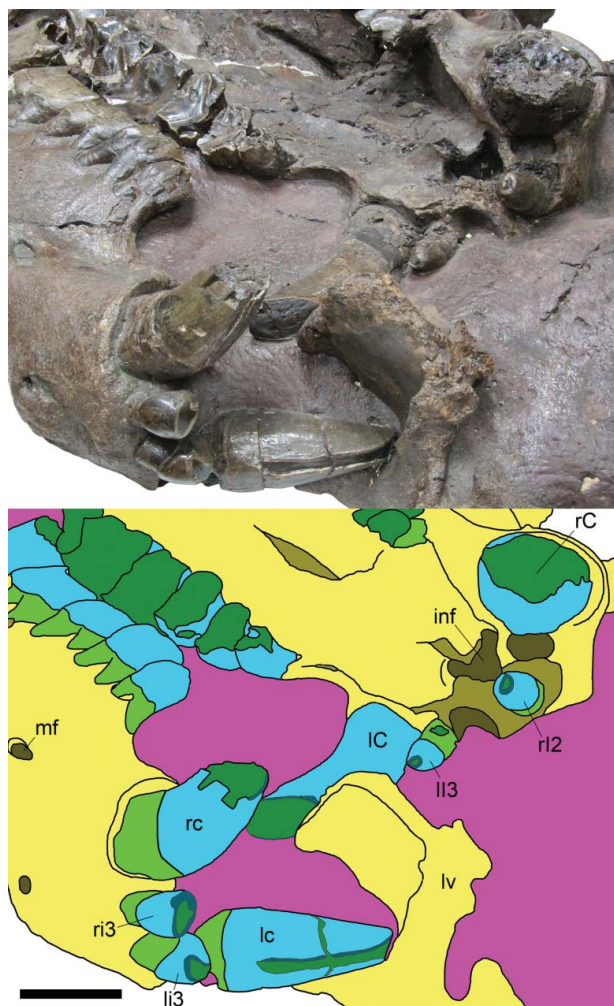


Figure 5. *Cadurcodon maomingensis* sp. nov., rostrum in ventral view and mandible in anterior view (SYSU-M-3, holotype). Maoming Basin, Guangdong Province, China; Youganwo Formation, middle–upper Eocene. Abbreviations: inf, incisive foramen; IC, left upper canine; lc, left lower canine; li3, left i3; lv, lumbar vertebra; mf, mental foramen; rC, right upper canine; rc, right lower canine; rI2, right I2; ri3, right i3. For the key to the explanatory drawing see Figure 2. [See online version of paper for coloured figure.] Scale bar = 5 cm.

Description

Skull. The skull is represented by an almost complete rostrum and orbit and partially preserved palate, zygoma and braincase. The sutures between the individual bones are obliterated in most cases.

The premaxillae are exposed in ventral, lateral and anterior views (Figs 2–4). In lateral view, the premaxilla does not contact the nasal, as some part of the lateral margin of the nasal aperture is formed by the maxilla (Fig. 3). The premaxilla–maxilla contact in lateral view is mostly obscured by the overlapping vertebrae and matrix. A small, dorsally tapering piece of bone along the narial lateral margin may represent the rudimentary ascending

process of the premaxilla (Fig. 3). Its dorsal end is approximately at the level of the mid-height of the nasal aperture. The palatal shelf of the premaxilla is almost completely occupied by two incisor alveoli (Fig. 5). The mesial alveolus is about twice as large as the lateral alveolus. The alveoli are closely packed without diastemata between them and between the distal incisor and canine. The collateral premaxillae are completely fused, as well as the palatal shelves of the premaxilla and maxilla. The posterior margin of the premaxillary palatal shelf is deeply concave and forms the anterior margin of the incisive foramen (Fig. 5). The incisor tooththrow is arcuate and convex anteriorly.

The maxilla forms a part of the narial lateral margin between the premaxilla ventrally and nasal dorsally (Fig. 3). On the lateral side of the facial process there is a deep dorsally tapering depression between the swollen canine alveolus and anterior margin of the orbit. The most deep dorsal part of this depression corresponds to the pre-orbital fossa typical of amynodontids (Fig. 3). Although the lateral margin of the nasal is not complete, it is likely that the pre-orbital fossa was roofed by the nasal. The pre-orbital fossa has a pocket-like extension medial to the orbit (Fig. 6), which is not visible in dorsal view. A large infraorbital foramen (height 34 mm, width 13 mm) is placed in the centre of this medial extension, along the maxilla–lacrimal boundary (Fig. 6). It faces anteriorly from within the pre-orbital fossa. Anterodorsal to the infraorbital foramen, there is a large bump-like projection (Fig. 6). The jugal process of the maxilla is low beneath the orbit but thickens dorsoventrally at and posterior to the maxillary postorbital process. Its tapering posterior end is completely preserved on the left side (Fig. 3). The palatal process of the maxilla is almost complete on the left side and mostly destroyed on the right side (Fig. 2). The postcanine diastema is comparable in size with the canine alveolus and about half the length of the upper premolars. The anterior side of the palatal processes forms the anteriorly convex posterior margin of the single incisive foramen (Fig. 5). The posterior end of the bony palate is at the middle of M3. The part of the maxilla containing the molars (‘tuber maxillae’) is exposed within the orbital and temporal cavities, between the lacrimal, frontal and palatine (Fig. 3).

In palatal view, there is a small part of the palatine attached to the posterior end of the maxilla near M3. This piece of the palatine is also exposed within the temporal cavity adjacent to the maxilla (Fig. 3). There is a part of the maxillo–palatine suture opposite to M2, but more anteriorly the suture is obscured.

The lacrimal is almost completely preserved on the left side (Figs 3, 6). It is a small bone forming the anterior margin of the orbit. There is a small lacrimal foramen on the lateral side near the lacrimo–maxillary suture. On the anterior side there are two strong vertical ridges (Fig. 6).

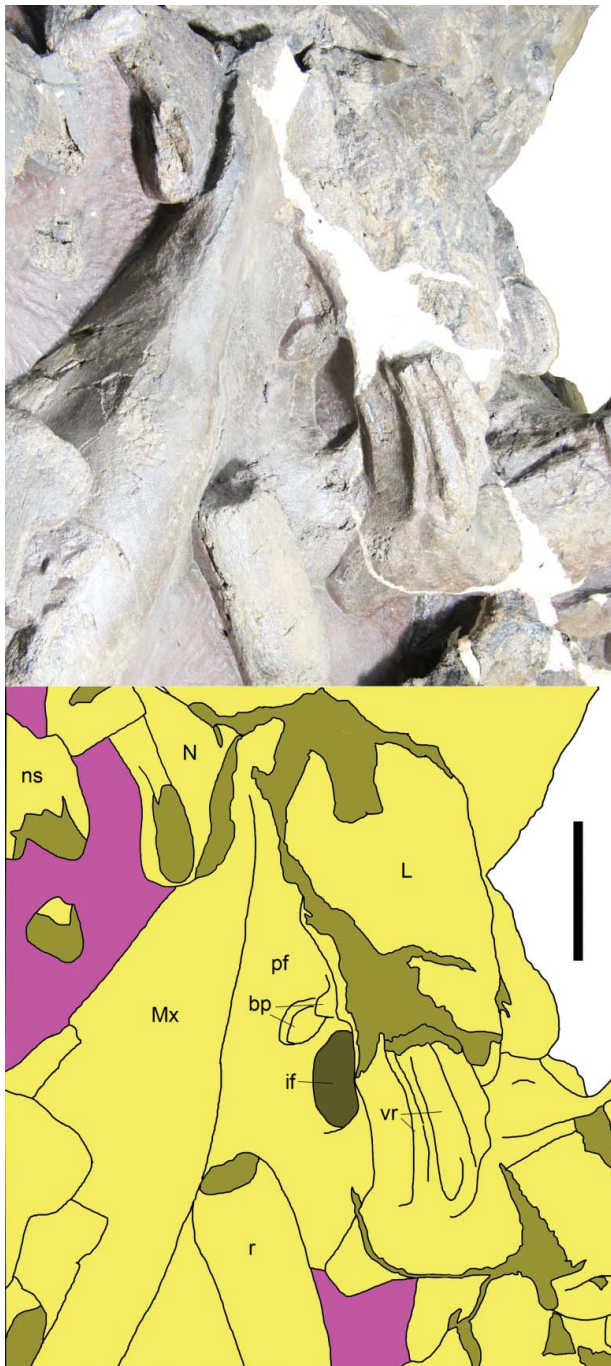


Figure 6. *Cadurcodon maomingensis* sp. nov., left orbital region in anterior view showing detail of preorbital fossa (SYSU-M-3, holotype). Maoming Basin, Guangdong Province, China; Youganwo Formation, middle–upper Eocene. Abbreviations: bp, bump-like projections above the infraorbital foramen; if, infraorbital foramen; L, lacrimal; Mx, maxilla; N, nasal; ns, neural spine; pf, preorbital fossa; r, rib; vr, vertical ridges on lacrimal. For the key to the explanatory drawing see Figure 2. [See online version of paper for coloured figure.] Scale bar = 5 cm.

The nasals are almost completely preserved, but the bone surface is damaged anteriorly (Figs 3, 6). The nasals are not fused collaterally, and the right bone partially

overlaps the left one (Fig. 3). The nasals have a wide posteriorly convex posterior margin, half as wide as the anterior margin, and deeply concave side margins. The nasal is short; its anterior end is at the level of the distal margin of the canine alveolus. The anterior margin of the nasal is concave, and the medial end of the collateral nasals form an anteriorly projecting process. There is a distinct naso-maxillary suture preserved on the left side (Figs 3, 6). The posterolateral process of the nasal is incomplete, and it is not clear whether the naso-lacrimal contact was present. The transverse nasal-frontal suture is mostly damaged.

The frontals are slightly wider than long on the dorsal side (Fig. 3). The anterior margin contacting the nasals is mostly damaged. The anterior margin of the each frontal is concave, and the anteriorly projecting medial process of the frontals is intruded between the nasals. There are prominent temporal ridges extending from the sagittal crest, approximately to the postorbital process. Near the junction of the temporal ridges there are pocket-like depressions beneath the ridges. The frontal postorbital process is small and positioned just posterior to the fronto-lacrimal contact. The dorsal surface of the frontals is remarkably flat. The fronto-parietal suture cannot be discerned, and likely it was outside the preserved braincase fragment. Within the temporal cavity there is a clear fronto-maxillary suture which extends along the sphenopalatine fissure (Fig. 3).

The jugal is visible on the left side anterior and posterior to the maxillary postorbital process (Fig. 3). Anteriorly, the jugal contacts the lacrimal.

Mandible. The mandibular body and base of the coronoid process are complete on the right side, and the mandibular symphysis is preserved on the left side (Figs 2, 3). The mandibles are firmly fused at the symphysis, the posterior end of which is placed at the level between p3 and p4. The anterior end of the mandible is somewhat downturned, allowing antero-dorso-lateral projection of the canine. There is a small diastema between the lower incisor and canine. The lower postcanine diastema is distinctly longer than the upper diastema and equal in size to the length of the lower premolars plus m1. The dorsal margin of the mandible is sharp along the postcanine diastema and flanked laterally by a distinct depression. There is a large mental foramen closer to the ventral margin of the mandible and just anterior to the level of p3. The dorsal margin of the mandible is concave along the cheek teeth. The curve of this concavity continues posteriorly onto the coronoid process. The ventral margin of the mandible is concave anteriorly and convex beneath the cheek teeth up to the missing angular process. The mandibular body thickness is 34% of the body depth at m3. There is a shallow masseteric fossa partially preserved on the coronoid process. At the base of the coronoid process anteriorly there is a shallow depression similar to that in

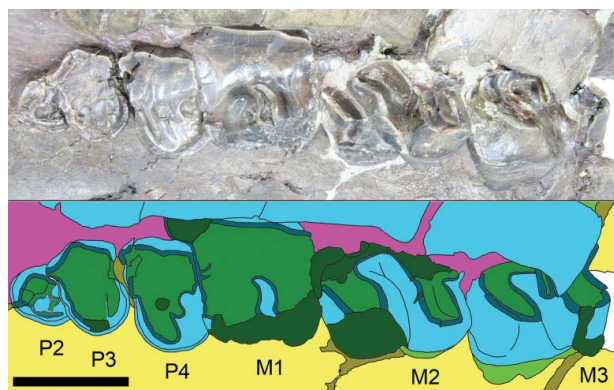


Figure 7. *Cadurcodon maomingensis* sp. nov., left upper cheek teeth (P2–4 and M1–3) in occlusal view (SYSU-M-3, holotype). Maoming Basin, Guangdong Province, China; Youganwo Formation, middle–upper Eocene. For the key to the explanatory drawing see Figure 2. [See online version of paper for coloured figure.] Scale bar = 5 cm.

‘*Gigantamynodon*’ *cessator* from the late Eocene of Mongolia (Gromova 1954, fig. 22).

Dentition. The dental formula is I 2/1, C 1/1, P 3/2, M 3/3. The right I2, left I3 and both lower incisors are in place in their alveoli (Fig. 5). The right I3 is displaced and preserved separately (Figs 2, 3). The crowns of all incisors are conical. The mesial upper incisors (I2; L = 24.1 mm,

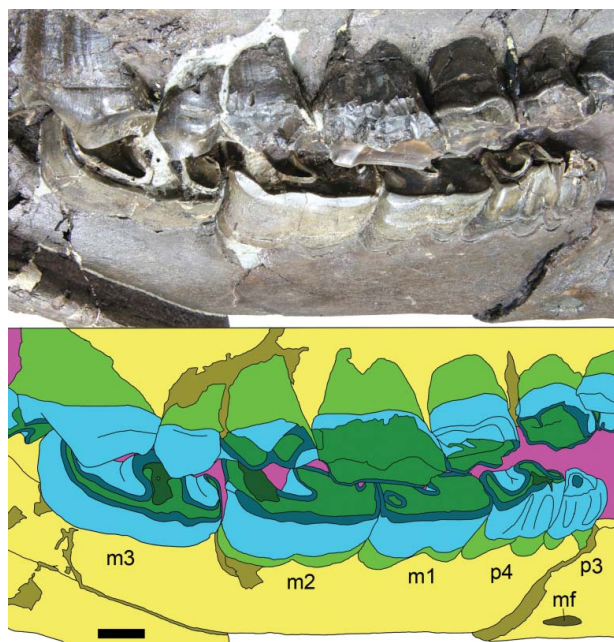


Figure 8. *Cadurcodon maomingensis* sp. nov., right lower cheek teeth (p3–4 and m1–3) in labioocclusal view (SYSU-M-3, holotype). Maoming Basin, Guangdong Province, China; Youganwo Formation, middle–upper Eocene. Abbreviation: mf, mental foramen. For the key to the explanatory drawing see Figure 2. [See online version of paper for coloured figure.] Scale bar = 5 cm.

W = 21.8 mm for the right tooth) are larger than the distal incisors (I3; L = 18.0 mm for the left tooth). The lower incisors (i3; L = 26.1 mm, W = 21.7 mm for the right tooth and L = 25.5 mm, W = 20.9 mm for the left tooth) are somewhat larger than I2. The roots of the lower incisors are mesiodistally constricted. The upper incisors are planted vertical to the jaw, while the lower incisors are semiprocumbent. There are no cingula or cingulids on the incisors. The apical wear facets are much more pronounced on the lower incisors than on the upper ones.

The canines are very large. The upper canine (L = 45.0 mm for the left tooth) is longer proximodistally and curved, with the tip pointed ventrally. The lower canine is shorter proximodistally and more robust (L = 49.0 mm; W = 41.0 mm for the right tooth), with an almost straight crown directed antero-dorso-laterally. The crown of the lower canine is angled laterally to the root, while on the upper canine the crown and root are in the same plane. There is a prominent strip-like wear facet along the most of the crown mesially on the lower canine. On the upper canine, the wear facets are present on both mesial and distal sides. They are much wider mediolaterally and confined to the apical part of the crown. The mesial of these facets is deeper than the distal facet.

The upper cheek teeth are completely preserved on the left side (Figs 2, 7; Table 1). The right upper premolars were originally preserved, but were almost completely destroyed subsequently. One lower molar and one upper molar of a different rhinocerotoid taxon were glued to the positions of the right M2 and M3, respectively, by a local collector (Fig. 2). The upper premolars (L = 85.0 mm) are 39.5% of the upper molar series (L = 215.0 mm). The upper premolars are short anteroposteriorly and drastically decrease in width from P2 to P4. The width of P3 is 153% of the width of P2, and the width of P4 is 118% of the width of P3. The W/L ratio for the upper premolars is 113% (P2), 146% (P3) and 153% (P4), respectively. The upper premolars are submolariform. P2 is oriented obliquely to the tooththrow. It is little worn. The ectoloph is destroyed. The protoloph is long and mesially convex. The metaloph is shorter and directed towards the protocone. There is a very short crista between the transverse lophes. There is a complete cingulum along the exposed lingual and mesial sides. The occlusal surface of P3 is completely worn. On P4 the labial half is completely worn, but the parastyle and anterior rib are still recognizable. The lingual ends of the protoloph and metaloph can

Table 1. Measurements (in mm) of the upper cheek teeth of SYSU-M-3, the holotype of *Cadurcodon maomingensis* sp. nov.

	P2	P3	P4	M1	M2	M3
L	25.4	30.2	34.0	68.0	68.0	81.5
W	28.8	44.0	51.9	65.0	58.5	52.5

be recognized. The metaloph is distinctly smaller and shorter than the protoloph. There is a complete lingual cingulum. M1 is the widest tooth in the molar series, with W/L ratio 96%. Its crown is completely worn, with the protoloph and metaloph separated lingually by a narrow slit. The ectoloph is labially convex. The parastyle is very large, distinctly projecting labially beyond the labial side of P4. There is no trace of an anterior rib. M2 is less worn, with the protoloph and metaloph separated by a wide sinus. The bases of the protocone and hypocone are adjacent. The W/L ratio for M2 is 86%. The ectoloph is labially concave. The metastyle is distally directed. M3 is longest in the upper molar series, with W/L ratio 64%. The ectoloph is straight. The metastyle is directed distolabially and, together with the metaloph, forms a border for the large posterior valley. The transverse lophs, as well as the bases of the paracone and hypocone, are widely separated. The antecrochet of M3 is smaller than those of M2. There is a mesial cingulum extending lingually onto the base of the protocone.

The lower cheek teeth are preserved only on the right side, where they are exposed from the labial view (Figs 2, 8; Table 2). The occlusal side of the lower cheek teeth is mostly obscured by the upper cheek teeth (Fig. 8). The lower premolars (L = 64.0 mm) are 32% of the lower molar series (L = 197.5 mm). The p3 is double-rooted and little worn. The tooth is premolariform with a talonid missing and most of the crown formed by the protoconid. p4 is molariform with distinct paralophid, metalophid and hypolophid (W/L ratio 74%). On the labial side of the lower premolars, there is a vertical ridge at the protoconid-talonid junction flanked by mesial and distal depressions. There is a faint labial cingulum on p4. The lower molars are narrow, with W/L ratio 46% (m1), 41% (m2) and 39% (m3), respectively. The wear progressively decreases from m1 to m3. The paralophid and metalophid are united on m1 and widely separated on m3. There is a dentine island on the hypolophid of m1. The hypolophid of m3 is very long and the entoconid is high, extending beyond the occlusal level of the crown. The labial crown side is flat, without a groove separating the trigonid and talonid. There is a distinct complete labial cingulid which is placed progressively lower on the crown from m1 to m3.

Vertebrae. There are six opisthocoelous vertebrae buried together with the skull. Two vertebrae, exposed in lateral view on the left skull side (Fig. 3), are posterior thoracic

Table 2. Measurements (in mm) of lower molar teeth of SYSU-M-3, the holotype of *Cadurcodon maomingensis* sp. nov.

	p3	p4	m1	m2	m3
L	26.2	34.5	47.8	68.0	79.0
W	24.5	25.5	22.0	28.0	31.0

vertebrae. They have centra with strong ventral keels and relatively narrow, subtriangular articular surfaces. The neural spines are posteriorly inclined in both these vertebrae. On the first of these vertebrae (Fig. 3), the ventral centrum length is smaller than the dorsal centrum length and centrum articulation surfaces are skewed. Another thoracic vertebra (Fig. 3) has a longer centrum, small sub-horizontal prezygapophyses and large vertical postzygapophyses. This change in orientation of zygapophyseal surfaces suggests that it is the last thoracic (diaphragmatic) vertebra. Two other vertebrae with preserved neural spines are lumbar vertebrae (Fig. 3). They have a wide cordiform anterior articulation surface of the centrum and vertical semilunar prezygapophyseal facets with a distinct metapophysis above. One of these vertebrae preserves a rather long transverse process (a fused lumbar rib). The neural spine of this vertebra is posteriorly inclined and transversely expanded at the tip. The last two vertebrae are exposed only by their cordiform anterior articular surfaces of the centrum (Fig. 3). By similarity in the shape of articular surface with those in lumbar vertebrae, these two vertebrae are also likely lumbar. Thus, at least four lumbar vertebrae were present in this taxon.

Phylogeny of Amynodontidae

Previous phylogenetic hypotheses of Amynodontidae

The first described amynodontid was the Oligocene *Cadurcotherium cayluxi* from France (Gervais 1873; Noutlet 1876; Roman & Joleaud 1909). Soon after this, three amynodontid genera (*Amynodon*, *Orthocynodon* and *Metamynodon*) were established in the Eocene and Oligocene of the USA (Marsh 1877; Scott & Osborn 1882, 1883, 1887). The diagnosis of Amynodontidae was refined by Osborn (1898), who recognized such important amynodontid characters as presence of a preorbital fossa, shortening of the nasals and the quadratic shape of M3. The first Asiatic Amynodontidae were described from the Oligocene of Pakistan and Eocene of Myanmar (Pilgrim 1912, 1925; Forster Cooper 1922; Matthew 1929). Subsequently, amynodontids were found in Mongolia and China (Osborn 1923, 1924, 1936; Zdansky 1930).

The sequence of North American amynodontids (*Orthocynodon* *Amynodon* *Megalamynodon* *Metamynodon*) was considered a “made-to-order example to prove orthogenetic evolution” (Wood 1941, p. 88). Wood further noted that he knew of “no similar authentic case so completely devoid of side lines, in the whole field of palaeontology, in which an internal perfecting principle seems so clearly at work.” However, then-known Mongolian amynodontids showed an “entirely different evolutionary pattern”, “a complex, polyphyletic type of

evolution diverging into numerous lines, which frequently parallel each other and the American amynodonts, forming five main autochthonous lines [...] during the upper Eocene and the Oligocene” (Wood 1941, pp. 88–89). Wood intended to revise Asiatic amynodontid taxa based on the abundant materials collected by the Central Asiatic expedition of AMNH (Simpson 1945, p. 257), but this task was never completed.

An earlier attempt to revise amynodontid systematics was made by Kretzoi (1942), who proposed several new generic names and divided the family into four subfamilies: Amynodontinae, Cadurcotheriinae, Metamynodontinae and Paramynodontinae. Gromova (1954) considered this classification unfounded. She provided a new, much expanded diagnosis of Amynodontidae, and did not recognize any suprageneric groups within the family.

The next attempt to refine amynodontid classification was made by Wall (1980, 1982a, b; Wall & Manning 1986). In particular, he proposed the first cladistic phylogeny of Amynodontidae based on manual analysis of the distribution of 22 characters among 11 terminal taxa (Wall 1982a, 1989, 1998). Wall (1989) divided the family into two subfamilies: Rostriamynodontinae, with a single genus *Rostriamynodon*, and Amynodontinae. The latter subfamily was split into three tribes: Amynodontini (*Amy-nodon*), Cadurcodontini (*Sharamynodon*, *Amy-nodontopsis*, *Sianodon* and *Cadurcodon*) and Metamynodontini (*Megalamynodon*, *Paramynodon*, *Zaisanamynodon*, *Metamynodon* and *Cadurcotherium*).

Wall’s characters and 10 amynodontid taxa were included in a broader phylogenetic analysis of Rhinocero-toidea by Prothero *et al.* (1986). Amynodontidae were divided into Cadurcodontinae and Paramynodontinae, with *Amy-nodon* considered *incertae sedis*. The Cadurcodontinae and Paramynodontinae are identical in content with the Cadurcodontini and Metamynodontini of Wall (1989).

New phylogenetic hypothesis of Amynodontidae

The new cladogram shows sequential branching of basal taxa and two sister clades on the top, one including *Megalamynodon*, *Metamynodon* and *Paramynodon*, and another with *Procadurcodon*, *Zaisanamynodon*, *Cadurcotherium* and *Cadurcodon* (Fig. 9). The first clade is similar in content to Wall’s Metamynodontini, but Wall (1989) included also *Zaisanamynodon* and *Cadurcotherium* in this tribe. Wall (1989) linked *Cadurcotherium* with Metamynodontini by two cranial characters, hypertrophy of the zygomatic arches and increased width of the lower jaw. Both these characters are not included in our analysis. The first character is difficult to formalize; the second character is rarely noticed in the literature and its distribution is poorly known. Wall (1989) also mentioned that dental characters also support a metamynodontine

relationship for *Cadurcotherium*, but did not specify these characters. His diagnosis of Metamynodontini, besides the dental formula, which is not different from that of other amynodontids, includes just one dental character, “cheek teeth relatively high crowned” (Wall 1989, p. 348). *Cadurcotherium* was known from limited materials at that time, and after discovery of a skull and partial skeleton of *C. cayluxi* (Bonis 1995), Wall admitted that it is more likely a cadurcodontine than a metamynodontine (Wall & Heinbaugh 1999). In our analysis, *Cadurcotherium* and *Cadurcodon* are sister taxa. The two taxa are united by five unambiguous synapomorphies: 20(1), ventral margin of mandibular ramus convex in lateral view; 22(1), two upper incisors; 23(2), I3 distinctly smaller than I2; 24(2), one lower incisor (in males, females may have two lower incisors); and 27(1) cheek teeth covered in cement. Under accelerated transformation there are five more synapomorphies for the clade *Cadurcotherium* + *Cadurcodon*: 7(0), maxilla-frontal contact on rostrum absent; 14(3), infraorbital foramen above M2; 16(1), orbit low positioned on the skull; 17(1), well-developed rugosities for attachment of strong snout musculature on lacrimal; and 32(0), additional loph distal to metaloph (‘inner cingulum’) on P2–4 absent.

The genus *Cadurcodon* is supported by two unambiguous characters: 2(1), premaxilla fused and thickened; and 9(1), upper postcanine diastema short. One more synapomorphy is added by accelerated transformation: 34(1), crista between metaloph and protoloph on P4 present. *Cadurcodon maomingensis* is the most basal member of the clade. It has one autapomorphy: 48(2), m3 length to width ratio between 2.2–2.8. In other *Cadurcodon* species, m3 is less elongated. The autapomorphy of *C. bahoensis* is a shallow labial groove separating trigonid and talonid on lower molars (character 47(1), considered a reversal under the current phylogenetic hypothesis). The other reversal, P4 protoloph and metaloph of similar length and parallel (character 33(1)), is an autapomorphy for *C. ardynensis* (delayed transformation), or a synapomorphy for *C. ardynensis* and *C. kazakademius* (accelerated transformation; the state of this character is actually unknown for *C. kazakademius*).

The Metamynodontini in our analysis includes *Paramynodon*, *Megalamynodon* and *Metamynodon* with unresolved relationships on the consensus tree (Fig. 9). The tribe Metamynodontini is here defined as a stem-based taxon that includes *Metamynodon planifrons* and all amynodontids closer to it than to *Cadurcodon ardynensis*. This clade is supported by three unambiguous synapomorphies: 12(2), preorbital fossa reduced, typically not extending medial to orbit (unknown for *Megalamynodon*); 19(1), extensive supraglenoid shelf covering the external auditory meatus; and 24(1), two lower incisors (*Paramynodon*, two-three incisors in *Megalamynodon* and one to two incisors in *Metamynodon*). There are two more

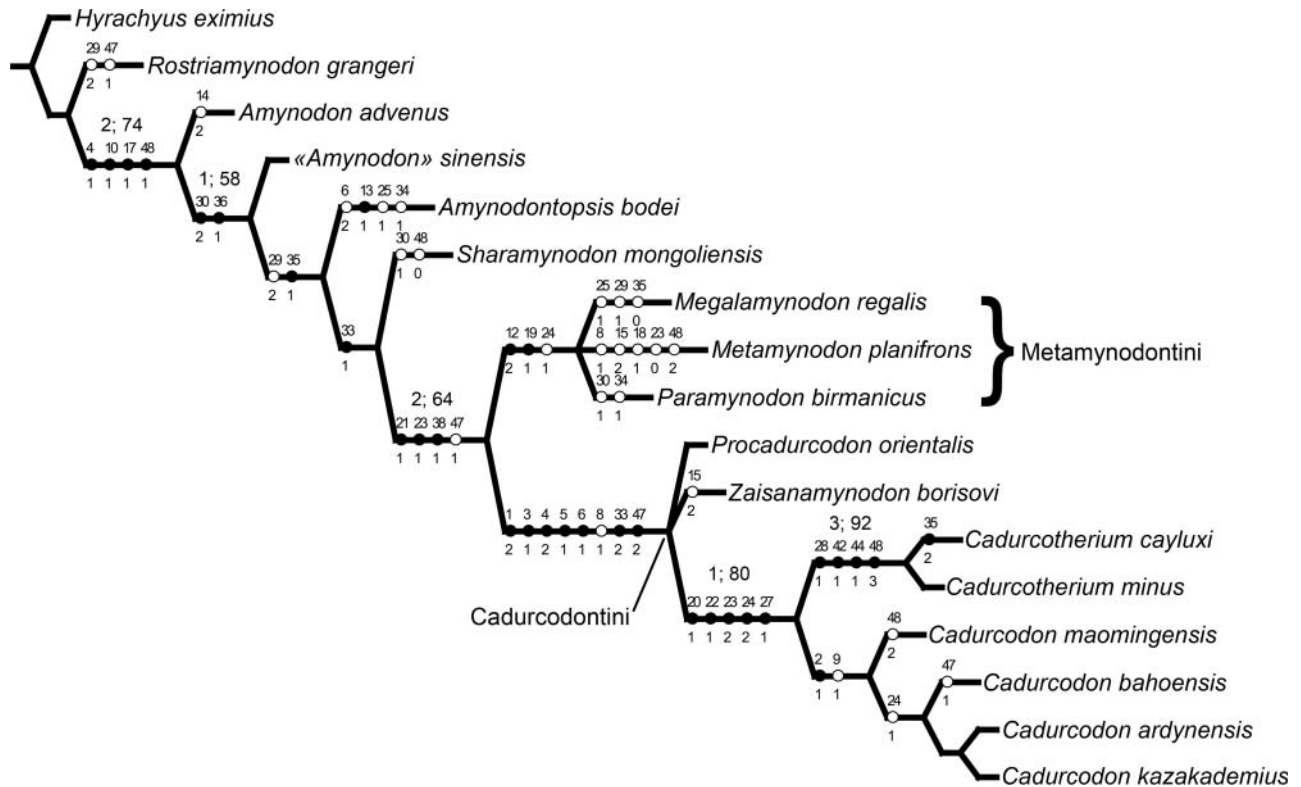


Figure 9. Strict consensus tree of the three NONA most parsimonious trees with a length of 97 steps, a consistency index of 0.66, and a retention index of 0.75. Only unambiguously optimized characters are shown (black circles are nonhomoplasies and white circles are homoplasies). The numbers at the circles are characters (above) and states (below). The numbers at the nodes separated by semicolons are Bremer and bootstrap support values.

synapomorphies under accelerated transformation: 9(1), short upper postcanine diastema (long in *Paramynodon*); and 32(0), additional loph distal to metaloph ('inner cingulum') on P2–4 absent. Four additional synapomorphies supports this clade under delayed transformation: 14(2), infraorbital foramen above P4 (unknown for *Megalamynodon*); 16(2), high position of orbit on the skull (unknown for *Megalamynodon*); 17(0), well-developed rugosities for attachment of strong snout musculature on lacrimal absent (unknown for *Megalamynodon*); and 39(1), p3 distinctly shorter than p4 and molariform (more derived in *Megalamynodon*).

Zaisanamynodon, placed in Metamynodontini by Wall (1989), indeed shares some characters with that clade: 7(1), maxilla-frontal contact on rostrum present; 14(2), infraorbital foramen above P4; 15(2), anterior border of orbit above M1; 16(2), high position of orbit on the skull; 23(1), I3 much larger than I2; and 39(1), p3 distinctly shorter than p4 and molariform. Wall (1989, fig. 17.2) considered maxilla-frontal contact on the rostrum an important character for Metamynodontini, although the state of this character is not known for *Paramynodon* and *Megalamynodon*. We coded *Zaisanamynodon* as having this contact following Lucas *et al.* (1996), but this character cannot be checked on the illustrated specimens.

On our consensus tree, *Zaisanamynodon* and a similar but poorly known *Procadurcodon* form a polytomy with the clade *Cadurcotherium* + *Cadurcodon* (Fig. 9). *Zaisanamynodon* and *Procadurcodon* share an additional loph distal to the metaloph ('inner cingulum') on P2–4 (character 32(1), present also in *Sharamynodon*). *Procadurcodon* differs from *Zaisanamynodon* by the more derived structure of p3, which is distinctly shorter than p4 and pre-molariform, with talonid reduced or absent (character 39(2)). The tribe Cadurcodontini is defined here as a stem-based taxon that includes *Cadurcodon ardynensis* and all amynodontids closer to it than to *Metamynodon planifrons*. By this definition, *Cadurcodon*, *Cadurcotherium*, *Zaisanamynodon* and *Procadurcodon* are included in Cadurcodontini. This clade is supported by eight unambiguously optimized synapomorphies: 1(2), ascending process of premaxilla absent, maxilla forms part of the external naris border; 3(1), nasals reduced; 4(2), anterior margin of nasals squared; 5(1), nasals do not overhang external nares; 6(1), posterior extension of nasal incision above P4; 8(1), diastema between upper incisors and canine absent (parallelism in *Metamynodon*); 33(2), P4 paraloph and metaloph parallel, metaloph much smaller (reversed in *C. ardynensis*); and 47(2), labial groove separating trigonid and talonid on lower molars absent (reversed in *C.*

bahoensis). Two more synapomorphies unite the group under accelerated transformation: 18(1), postglenoid and posttympanic processes adjacent (present also in *Metamynodon*); and 39(2), p3 distinctly shorter than p4 and pre-molariform, with talonid reduced or absent (present also in *Megalamynodon* and reversed in *Zaisanamynodon*).

Amynodontopsis and *Sharamynodon* were included in Cadurcodontini by Wall (1989). In our analysis these taxa branch off prior to the clade Metamynodontini + Cadurcodontini. The latter clade is supported by the unambiguous synapomorphies: 21(1), posterior end of mandibular symphysis at p4; 23(1), I3 much larger than I2 (further derived in *Cadurcotherium* and *Cadurcodon*); 38(1), p2 absent (polymorphic in *Amynodontopsis* and *C. ardynensis*); and 47(1), labial groove separating trigonid and talonid on lower molars shallow (absent in Cadurcodontini). Wall (1989) recognized suprageneric taxa Amynodontini for *Amynodon* and Rostriamynodontinae for *Rostriamynodon*. These monotypic taxa are redundant and the family Amynodontidae is divided here into two tribes, Metamynodontini and Cadurcodontini.

Biogeographical history of Amynodontidae

In our analysis, the outgroup taxon for the Amynodontidae is the early–middle Eocene North American basal rhinocerotoid *Hyrachyus eximius*. This determines the North American-Asian origin for the Amynodontidae by S-DIVA analysis (Fig. 10). Several less-known species of

Hyrachyus are present in the Eocene of China (Huang & Qi 1982; Qi 1987; Huang & Wang 2002). Some authors consider the poorly known *Caenolophus* from the middle–late Eocene of China the most primitive amynodontid or ancestral form for the amynodontids (Radinsky 1967, 1969; Prothero *et al.* 1989; Wall 1989, 1998; Huang & Wang 2001). *Caenolophus* was attributed originally to the Hyracodontidae (Matthew & Granger 1925). According to Radinsky (1967), one of the originally described species of *Caenolophus* belongs to the hyracodontid genus *Triplopus*, but two others, including the type species *C. promissus*, are amynodontids. Wall & Manning (1986, p. 917) considered *Caenolophus* “anatomically intermediate between amynodontids and more primitive ceratomorphs such as *Hyrachyus*”. Diversity of amynodontid-like rhinocerotoids in the Eocene of Asia and presence on that continent of the most basal and the oldest known amynodontid, *Rostriamynodon grangeri*, make Asia the most probable place of origin of Amynodontidae (Wall 1982a, 1998). Amynodontids diversified mostly in Asia. There are four dispersal events out of Asia implied by our phylogenetic hypothesis, three to North America and one to Europe (Fig. 10). The possible fifth dispersal event from Asia to North America, involving *Procadurcodon*, is not shown on our cladogram or discussed below.

The first amynodontid migrant to North America was *Amynodon*, represented by two species in a number of middle Eocene localities in the USA (Scott & Osborn 1883; Osborn 1890; Troxell 1921; Stock 1939; Wilson & Schiebout 1981; Wall 1982a, b, 1998). The older, smaller and more primitive species, *A. reedi* from California, USA (Stock 1939; Wall 1982b), apparently indicates that its ancestors migrated via Beringia (Wall 1982a), and were first spread along the North American Pacific coast. *Amynodon* has no close relatives in Asia. It is more derived than the Asiatic sister taxon, *Rostriamynodon*, in having a shorter preorbital region of the skull (character 10(1)).

The next dispersal event involved the genus *Amynodontopsis*. The genus is represented by one described species, *A. bodei*, from middle Eocene strata in California, South Dakota and Texas, USA (Stock 1933, 1939; Bjork 1967; Wilson & Schiebout 1981; Wall 1998). Like *Amynodon*, this species may have spread to the North American East from the Pacific coast. A second, undescribed species of *Amynodontopsis* is present in the upper Eocene Ulan Gochu Formation of Nei Mongol, China (Wall 1980, 1989; Meng & McKenna 1998). Although the North American occurrence is older than the Asiatic, the sister taxon for the clade including *Amynodontopsis* is the Asiatic ‘*Amynodon*’ *sinensis*, which suggests migration from Asia to North America.

All previous amynodontid migrants to North America showed a moderate radiation on that continent (two species of *Amynodon* and one species of *Amynodontopsis*). Little more successful there were members of the tribe

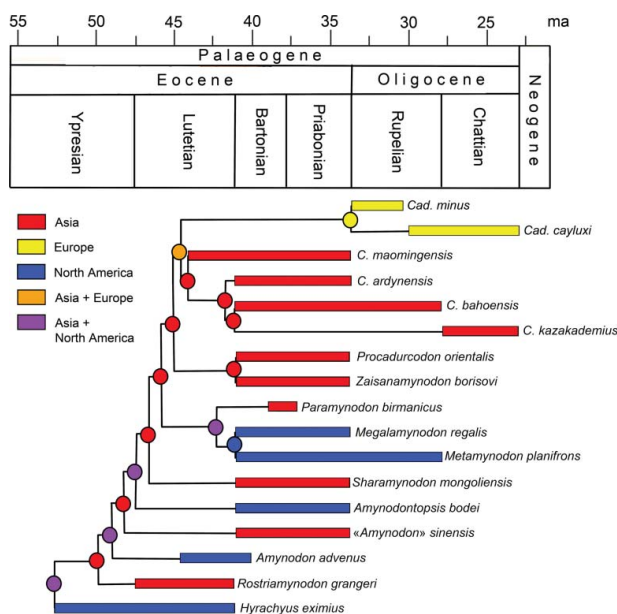


Figure 10. Time-calibrated phylogram of Amynodontidae based on the phylogenetic hypothesis shown in Figure 9. The circles at each node represent the relative probabilities for the ancestral areas inferred using the Statistical Divergence-Vicariance Analysis method (S-DIVA). [See online version of paper for coloured figure.]

Metamynodontini, with one species of *Megalamynodon* and three species of *Metamynodon* from the middle–late Eocene of the USA (*Metamynodon* survived until the early Oligocene) (Osborn & Wortman 1895; Troxell 1921; Wood 1937; Scott & Jepsen 1941; Scott 1945; Wilson & Schiebout 1981). The Asiatic member of this tribe, *Paramynodon*, is known from the middle–upper Eocene Pondaung Formation of Myanmar (Pilgrim & Cotter 1916; Matthew 1929; Colbert 1938). The age of the ‘Upper Member’ of the Pondaung Formation, producing remains of *Paramynodon*, is approximately at the Bartonian–Priabonian boundary, ~37 Ma (Maung *et al.* 2005), which is younger than the oldest records of metamynodontines in North America (Wall 1998). However, because the sister taxon for the clade Metamynodontini + Cadurcodontini is the Asiatic *Sharamynodon*, it is more likely that metamynodontines appeared in Asia and dispersed to North America.

The derived amynodontid clade, the Cadurcodontini, radiated mostly in Asia. The only possible migrant of this clade to North America is *Procadurcodon* sp. from the middle Eocene Clarno Formation of Oregon, USA (Hanson 1996; Lucas *et al.* 2004). This was apparently a short-ranged migrant lineage which did not spread outside the North American Pacific coast (Prothero *et al.* 1989). Hanson (1996) noted the possible presence of *Procadurcodon* in the Eocene of Japan. A maxillary fragment of a large amynodontid from the upper Eocene of Japan, identified as cf. *Zaisanamynodon borisovi* (Tomida & Yamasaki 1996), may well belong to *Procadurcodon*. If these attributions are correct, *Procadurcodon* had a circum-North Pacific distribution, while the closely related *Zaisanamynodon* was distributed in mainland Asia.

The two most derived cadurcodontine taxa, *Cadurcodon* and *Cadurcotherium*, had a vicariant distribution. *Cadurcodon* radiated with six to seven species in Central and Eastern Asia. *Cadurcotherium* is the only amynodontid that migrated to Europe, where it had a modest radiation with three species during the early and beginning of the late Oligocene (Gervais 1873; Noulet 1876; Roman & Joleaud 1909; Bonis 1995; Becker 2009; Scherler *et al.* 2013). It appeared in Europe as a result of the ‘Grande Coupure’ event, linked with the closure of the Turgai Strait, when many Asiatic migrants invaded Europe (Stehlin 1909; Prothero 1994).

‘Amynodon’ tuskabakensis, based on a single M3 from the lower Oligocene Kusto Formation of East Kazakhstan (Biryukov 1963), has been subsequently referred to *Hypsamynodon* (Belyaeva 1971), *Cadurcotherium* (Russell & Zhai 1987) and *Cadurcodon* (Lucas & Emry 1996). It is similar to *Cadurcodon* in a number of plesiomorphic characters (parastyle and anterior rib not confluent, rather long metaloph, relatively low crown), but differs in having a posteriorly directed protoloph, which is parallel to the ectoloph. This is a unique derived character, present only

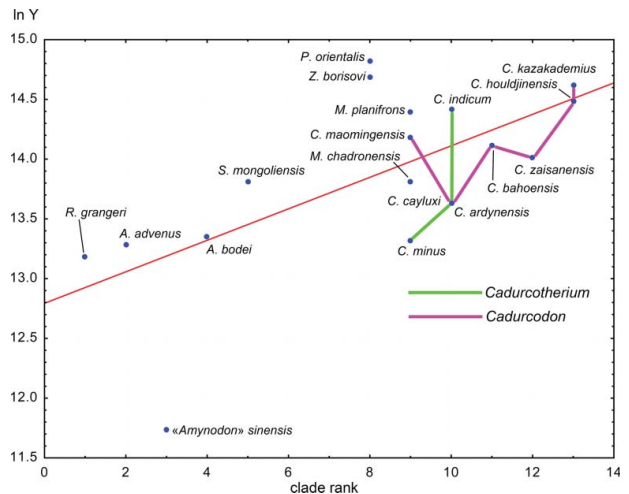


Figure 11. Natural logarithm of body mass (Ln Y) plotted against the clade rank for 18 amynodontid taxa (see Supplemental Table 2 for data). [See online version of paper for coloured figure.]

in *Cadurcotherium*. It is the most plesiomorphic and the only Central Asiatic species of *Cadurcotherium*, which lived near Turgai Strait and might have migrated to Europe after its closure. *Cadurcotherium* also migrated from Central Asia to the South, where it persisted until the late Oligocene in Pakistan (Pilgrim 1912; Antoine *et al.* 2004).

Body size evolution of Amynodontidae

The exact age of most Asiatic records of amynodontids is not certain, and thus we plotted the natural logarithm of the body mass (Ln Y) against the clade rank (Fig. 11). For the taxa not included in the current phylogenetic analysis, we estimate the clade rank according to their most similar taxa included in the analysis. There is a strong positive correlation between the logarithm of the body mass and the clade rank ($0.63, p < 0.05, n = 47$). For *Cadurcodon* this correlation is even greater ($0.78, p < 0.05, n = 15$). *‘Amynodon’ sinensis* is markedly below the regression line. It is the smallest known amynodontid with a body mass estimated as 127 ± 15 kg ($n = 4$). Two taxa reached gigantic size early in the evolution of the family and became the largest known amynodontids: *Zaisanamynodon borisovi* (body mass 2442 ± 257 kg, $n = 4$) and *Procadurcodon orientalis* (body mass 2720 kg, $n = 1$). Two clades of the most derived amynodontids, *Cadurcotherium* and *Cadurcodon*, show marked increase in size during evolution (Fig. 11). In *Cadurcotherium* the smallest species is the early Oligocene *C. minus* with body mass 607 kg ($n = 1$), and the largest is the youngest, late Oligocene species *C. indicum* with body mass 1832 kg ($n = 1$). In *Cadurcodon* the smallest species is the late Eocene *C. ardynensis* with body mass 846 ± 47 kg ($n = 7$). The largest are the last two species, the middle Oligocene *C. kazakademius*

(body mass 2247 kg, $n = 1$) and the upper Eocene *C. houldjiniensis* (body mass 1989 ± 253 kg, $n = 3$). *Cadurcodon maomingensis* is a relatively large species with body mass 1441 kg ($n = 1$). The large body size of *C. maomingensis* does not match its phylogenetic position as the most basal species of *Cadurcodon* (Fig. 11). This species also does not fit a latitudinal gradient variation known as Bergmann's rule (Freckleton *et al.* 2003; Meiri & Dayan 2003; Watt *et al.* 2010), in which body size decreases in increasingly warmer environments. *Cadurcodon maomingensis* is found on the coast of the South China Sea, while *C. ardynensis* lived much farther north in Central Asia. It should be taken into account, however, that the single known specimen of *C. maomingensis* is an adult male and the mean body size of the population could be smaller.


Acknowledgements

We thank two anonymous reviewers for reading the paper and providing useful comments. This study was supported by the National Natural Science Foundation of China (Grant No. 41210001), the Key Project of Sun Yat-sen University for inviting foreign teachers. AA was supported by the Zoological Institute, Russian Academy of Sciences (project 01201351185) and the Russian Foundation for Basic Research (project 16-04-00294).

Supplemental data

Supplemental material for this article can be accessed here: <http://dx.doi.org/10.1080/14772019.2016.1256914>.

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References

- Aleksandrova, G. N., Kodrul, T. T. & Jin, J. 2015. Palynological and paleobotanical investigations of Paleogene sections in the Maoming basin, South China. *Stratigraphy and Geological Correlation*, **23**(3), 300–325.
- Antoine, P.-O., Shah, S. M. I., Cheema, I. U., Crochet, J.-Y., Franceschi, D. de, Marivaux, L., Metais, G. & Welcomme, J.-L. 2004. New remains of the baluchitherid *Paraceratherium bugtiense* (Pilgrim, 1910) from the Late/latest Oligocene of the Bugti hills, Balochistan, Pakistan. *Journal of Asian Earth Sciences*, **24**, 71–77.
- Averianov, A. O. & Godinot, M. 2005. Ceratomorphs (Mammalia, Perissodactyla) from the early Eocene Andarak 2 locality in Kyrgyzstan. *Geodiversitas*, **27**, 221–237.
- Averianov, A. O. & Potapova, O. R. 1996. The oldest known amynodontid (Perissodactyla, Ceratomorpha), from the early Eocene of Kyrgyzstan. *Comptes Rendus de l'Académie des Sciences. Série IIA, Earth and Planetary Science*, **323**, 1059–1065.
- Averianov, A. O., Obratsova, E. A., Danilov, I. G., Skutschas, P. P. & Jin, J. 2016. First nimravid skull from Asia. *Scientific Reports*, **6**, 25812.
- Becker, D. 2009. Earliest record of rhinocerotoids (Mammalia: Perissodactyla) from Switzerland: systematics and biostratigraphy. *Swiss Journal of Geosciences*, **102**, 489–504.
- Belyaeva, E. I. 1962. [Marsh rhinoceros *Cadurcodon zaisanensis* sp. nov.]. *Paleontologicheskii Zhurnal*, **4**, 116–123. [In Russian.]
- Belyaeva, E. I. 1971. [New data on the amynodonts of the USSR]. *Trudy Paleontologicheskogo Instituta AN SSSR*, **130**, 39–61. [In Russian.]
- Biryukov, M. D. 1961. [Marsh rhinoceros (Amynodontidae) from the middle Oligocene of Turgai Depression]. *Materialy po Istorii Fauny i Flory Kazakhstana*, **3**, 20–29. [In Russian.]
- Biryukov, M. D. 1963. [A new species of amynodont (Amynodontidae) from the Paleogene of Kazakhstan]. *Materialy po Istorii Fauny i Flory Kazakhstana*, **4**, 34–41. [In Russian.]
- Bjork, P. R. 1967. Latest Eocene vertebrates from northwestern South Dakota. *Journal of Paleontology*, **41**, 227–236.
- Bloch, J. I., Rose, K. D. & Gingerich, P. D. 1998. New species of *Batodonoides* (Lipotyphla, Geolabididae) from the Early Eocene of Wyoming: smallest known mammal? *Journal of Mammalogy*, **79**, 804–827.
- Bonis, L. de. 1995. Le garouillas et les sites contemporains (Oligocène, MP25) des phosphorites du Quercy (Lot, Tarn-Et-Garonne, France) et leurs faunes de vertébrés. 9 Perissodactyles: Amynodontidae. *Palaeontographica, Abteilung A: Palaeozoologie, Stratigraphie*, **236**, 157–175.
- Chow, M.-C. & Liu, C.-L. 1955. A new anosternine turtle from Maoming, Kwangtung. *Acta Palaeontologica Sinica*, **3**, 275–282.
- Chow, M.-C. & Xu, Y.-X. 1965. Amynodonts from the upper Eocene of Honan and Shansi. *Vertebrata Palasiatica*, **9**, 190–203.
- Chow, M.-C. & Ye, H.-K. 1962. A new emydid from Eocene of Maoming, Kwangtung. *Vertebrata Palasiatica*, **6**, 225–229.
- Chow, M.-C., Xu, Y.-X. & Zhen, S.-N. 1964. *Amynodon* from the Eocene of Lunan, Yunnan. *Vertebrata Palasiatica*, **8**, 355–360.
- Claude, J., Zhang, J.-Y., Li, J.-J., Mo, J.-Y., Kuang, X.-W. & Tong, H. 2012. Geoemydid turtles from the late Eocene Maoming Basin, Southern China. *Bulletin de la Société géologique de France*, **183**, 641–651.
- Colbert, E. H. 1938. Fossil mammals from Burma in the American Museum of Natural History. *Bulletin of the American Museum of Natural History*, **74**, 255–436.
- Conroy, G. C. 1987. Problems of body-weight estimation of fossil primates. *International Journal of Primatology*, **8**, 115–137.
- Damuth, J. 1990. Problems in estimating body masses of archaic ungulates using dental measurements. Pp. 229–253 in J. Damuth & B. J. MacFadden (eds) *Body size in mammalian paleobiology: estimation and biological implication*. Cambridge University Press, Cambridge.
- Danilov, I. G., Syromyatnikova, E. V., Skutschas, P. P., Kodrul, T. T. & Jin, J. 2013. The first 'true' *Adocus*

- (Testudines, Adocidae) from the Paleogene of Asia. *Journal of Vertebrate Paleontology*, **33**, 1071–1080.
- Emry, R. J.** 1989. A tiny new Eocene ceratomorph and comments on 'tapiroid' systematics. *Journal of Mammalogy*, **70**, 794–804.
- Forster Cooper, C.** 1922. *Metamynodon bugtiensis*, sp. n., from the Dera Bugti deposits of Baluchistan. Preliminary notice. *Annals and Magazine of Natural History, Series 9*, **9**, 617–620.
- Fortelius, M.** 1990. Problems with using teeth to estimate body sizes of extinct mammals. Pp. 207–228 in J. Damuth & B. J. MacFadden (eds) *Body size in mammalian paleobiology: estimation and biological implication*. Cambridge University Press, Cambridge.
- Freckleton, R. P., Harvey, P. H. & Pagel, M.** 2003. Bergmann's rule and body size in mammals. *The American Naturalist*, **161**, 821–825.
- Gervais, P.** 1873. Du *Cadurcotherium cayluxi*, nouveau genre de la famille des Rhinocéridés. *Journal de Zoologie*, **10**, 362–368.
- Gill, T.** 1872. Arrangement of the families of mammals. With analytical tables. *Smithsonian Miscellaneous Collections*, **11** (230), 1–98.
- Gingerich, P. D.** 1974. Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. *Journal of Paleontology*, **48**, 895–903.
- Gingerich, P. D., Smith, B. H. & Rosenberg, K.** 1982. Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. *American Journal of Physical Anthropology*, **58**, 81–100.
- Goloboff, P. A.** 1999. *NONA (ver. 1.9)*. Software published by the author, S. M. de Tucuman, Argentina [updated at www.cladistics.org, accessed 18 November 2003].
- Goloboff, P. A., Farris, J. S. & Nixon, K. C.** 2008. *TNT (Tree analysis using New Technology) (BETA)*. Published by the authors, Tucumán, Argentina.
- Gray, J. E.** 1825. An outline of an attempt at disposition of Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. *Annals of Philosophy, London*, **26**, 337–344.
- Gromova, V.** 1954. [Mars rhinoceroses (Amynodontidae) of Mongolia]. *Trudy Paleontologicheskogo Instituta AN SSSR*, **55**, 85–189. [In Russian.]
- Gromova, V.** 1960. [First finding of amynodont in the Soviet Union (new genus *Procadurcodon*)]. *Trudy Paleontologicheskogo Instituta AN SSSR*, **77**, 128–151. [In Russian.]
- Hanson, C. B.** 1996. Stratigraphy and vertebrate faunas of the Bridgerian-Duchesnean Clarno Formation, northcentral Oregon. Pp. 206–239 in D. R. Prothero & R. J. Emry (eds) *The terrestrial Eocene–Oligocene transition in North America*. Cambridge University Press, Cambridge.
- Holbrook, L. T.** 1999. The phylogeny and classification of tapiromorph perissodactyls (Mammalia). *Cladistics*, **15**, 331–350.
- Huang, X. & Qi, T.** 1982. Notes on late Eocene tapiroids from the Lunan Basin, eastern Yunnan. *Vertebrata Palasiatica*, **20**, 315–326.
- Huang, X. & Wang, J.** 2001. New materials of tapiroid and rhinocerotoid remains (Mammalia, Perissodactyla) from the middle Eocene of Yuanqu Basin, central China. *Vertebrata Palasiatica*, **39**, 197–203.
- Huang, X. & Wang, J.** 2002. Notes on *Hyrachius* (Mammalia, Perissodactyla, Tapiroidea) from the Middle Eocene of Yuanqu Basin, Shanxi Province. *Vertebrata Palasiatica*, **40**, 211–218.
- Jin, J.** 2008. On the age of the Youganwo Formation in the Maoming Basin, Guangdong Province. *Journal of Stratigraphy*, **32**, 47–50.
- Kretzoi, M.** 1942. Ausländische Säugetierfossilien der ungarischen Museen. *Földtani Közlemény*, **72**(1–3), 139–148.
- Legendre, S.** 1989. Les communautés de mammifères du Paléogène (Éocène supérieur et Oligocène) d'Europe occidentale: structures, milieux et évolution. *Münchener Geowissenschaftliche Abhandlungen. Reihe A: Geologie und Paläontologie*, **16**, 1–110.
- Li, Q.** 2003. New materials of *Sianodon* from Shaanxi, China. *Vertebrata Palasiatica*, **41**, 203–210.
- Linnaeus, C.** 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale. Editio decima, reformata*. Laurentii Salvii, Stockholm, 824 pp.
- Liu, H.-T.** 1957. A new fossil cyprinid fish from Maoming, Kwangtung. *Vertebrata Palasiatica*, **1**, 151–153.
- Lucas, S. G.** 2006. A new amynodontid (Mammalia, Perissodactyla) from the Eocene Clarno Formation, Oregon, and its biochronological significance. *PaleoBios*, **26**(2), 7–20.
- Lucas, S. G. & Emry, R. J.** 1996. Biochronological significance of Amynodontidae (Mammalia, Perissodactyla) from the Paleogene of Kazakhstan. *Journal of Paleontology*, **70**, 691–696.
- Lucas, S. G. & Emry, R. J.** 2001. *Sharamynodon* (Mammalia: Perissodactyla) from the Eocene of the Ily Basin, Kazakhstan and the antiquity of Asian amynodonts. *Proceedings of the Biological Society of Washington*, **114**, 517–525.
- Lucas, S. G., Emry, R. J. & Bayshashov, B. U.** 1996. *Zaisamynodon*, a late Eocene amynodontid (Mammalia, Perissodactyla) from Kazakhstan and China. *Tertiary Research*, **17**, 51–58.
- Lucas, S. G., Foss, S. E. & Mhlbachler, M. C.** 2004. *Achaenodon* (Mammalia, Artiodactyla) from the Eocene Clarno Formation, Oregon, and the age of the Hancock quarry local fauna. *New Mexico Museum of Natural History and Science Bulletin*, **26**, 89–96.
- Marsh, O. C.** 1877. Notice of some new vertebrate fossils. *American Journal of Science, Series 3*, **14**, 249–256.
- Matthew, W. D.** 1929. Critical observations upon Siwalik mammals (exclusive of Proboscidea). *Bulletin of the American Museum of Natural History*, **56**, 437–560.
- Matthew, W. D. & Granger, W.** 1923. The fauna of the Houldjin Gravels. *American Museum Novitates*, **97**, 1–6.
- Matthew, W. D. & Granger, W.** 1925. New mammals from the Shara Murun Eocene of Mongolia. *American Museum Novitates*, **196**, 1–11.
- Maung, M., Htike, T., Tsubamoto, T., Suzuki, H., Sein, C., Egi, N., Win, Z., Maung Thein, Z. M. & Aung, A. K.** 2005. Stratigraphy of the primate-bearing beds of the Eocene Pondaung Formation at Paukkaung area, Myanmar. *Anthropological Science*, **113**, 11–15.
- Meiri, S. & Dayan, T.** 2003. On the validity of Bergmann's rule. *Journal of Biogeography*, **30**, 331–351.
- Meng, J. & McKenna, M. C.** 1998. Faunal turnovers of Palaeogene mammals from the Mongolian Plateau. *Nature*, **394**, 364–367.
- Nan, Y. & Zhou, G. Q.** 1996. *Stratigraphy (lithostratic) of Guangdong Province. Multiple Classification and Correlation of the Stratigraphy of China. Vol. 44*. China University of Geosciences Press, Wuhan, 264 pp.

- Nixon, K. C.** 1999. *Winclada (Beta) version 0.9.9*. Software published by the author, Ithaca, NY [updated at www.cladistics.org, accessed 18 November 2003].
- Noulet, J.-B.** 1876. Note sur un gisement nouveau du *Cadurcotherium cayluxi*. *Mémoires de l'Académie royale des sciences, inscriptions et belles-lettres de Toulouse, Série 7*, **8**, 404–405.
- Osborn, H. F.** 1890. The Mammalia of the Uinta Formation. Part III. The Perissodactyla. *Transactions of the American Philosophical Society, New Series*, **16**, 505–530.
- Osborn, H. F.** 1898. The extinct rhinoceroses. *Memoirs of the American Museum of Natural History*, **1**(3), 75–164.
- Osborn, H. F.** 1923. *Cadurcotherium* from Mongolia. *American Museum Novitates*, **92**, 1–2.
- Osborn, H. F.** 1924. *Cadurcotherium ardynense*, Oligocene, Mongolia. *American Museum Novitates*, **147**, 1–4.
- Osborn, H. F.** 1936. *Amynodon mongoliensis* from the Upper Eocene of Mongolia. *American Museum Novitates*, **859**, 1–9.
- Osborn, H. F. & Wortman, J. L.** 1895. Perissodactyls of the lower Miocene White River beds. *Bulletin of the American Museum of Natural History*, **7**, 343–375.
- Owen, R.** 1848. Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the NW coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London*, **4**, 103–141.
- Pilgrim, G. E.** 1910. Notices of new mammalian genera and species from the tertiaries of India. *Records of the Geological Survey of India*, **40**(1), 63–71.
- Pilgrim, G. E.** 1912. The vertebrate fauna of the Gaj Series in the Bugti Hills and the Punjab. *Palaeontologia Indica*, **4**, 1–83.
- Pilgrim, G. E.** 1925. The Perissodactyla of the Eocene of Burma. *Palaeontologia Indica, New Series*, **8**(3), 1–28.
- Pilgrim, G. E. & Cotter, G. P.** 1916. Some newly discovered Eocene mammals from Burma. *Records of the Geological Survey of India*, **47**, 42–77.
- Prothero, D. R.** 1994. *The Eocene–Oligocene transition: paradise lost*. Columbia University Press, New York, 291 pp.
- Prothero, D. R., Guerin, C. & Manning, E. M.** 1989. The history of the Rhinoceroidea. Pp. 321–340 in D. R. Prothero & R. M. Schoch (eds) *The evolution of perissodactyls*. Oxford University Press, New York.
- Prothero, D. R., Manning, E. M. & Hanson, C. B.** 1986. The phylogeny of the Rhinoceroidea (Mammalia, Perissodactyla). *Zoological Journal of the Linnean Society*, **87**, 341–366.
- Qi, T.** 1975. An early Oligocene mammalian fauna of Ningxia. *Vertebrata Palasiatica*, **13**, 217–224.
- Qi, T.** 1987. The middle Eocene Arshanto fauna (Mammalia) of Inner Mongolia. *Annals of Carnegie Museum*, **56**, 1–73.
- Qi, T.** 1992. A new species of *Gigantamynodon* from Yunnan Province. *Vertebrata Palasiatica*, **30**, 229–232.
- Radinsky, L. B.** 1967. A review of the rhinocerotid family Hyracodontidae (Perissodactyla). *Bulletin of the American Museum of Natural History*, **136**, 1–46.
- Radinsky, L. B.** 1969. The early evolution of the Perissodactyla. *Evolution*, **23**, 308–328.
- Roman, F. & Joleaud, L.** 1909. Le *Cadurcotherium* de l'Isle-sur-Sorgues et révision du genre *Cadurcotherium*. *Archives du Museum d'Histoire Naturelle de Lyon*, **10**, 1–52.
- Russell, D. E. & Zhai, R.** 1987. The Paleogene of Asia: mammals and stratigraphy. *Mémoires du Museum National d'Histoire Naturelle, Series C*, **52**, 1–488.
- Scherler, L., Mennecart, B., Hiard, F. & Becker, D.** 2013. Evolutionary history of hoofed mammals during the Oligocene–Miocene transition in Western Europe. *Swiss Journal of Geosciences*, **106**, 349–369.
- Schwartz, G. T., Rasmussen, D. T. & Smith, R. J.** 1995. Body-size diversity and community structure of fossil hyracoids. *Journal of Mammalogy*, **76**, 1088–1099.
- Scott, W. B.** 1945. The Mammalia of the Duchesne River Oligocene. *Transactions of the American Philosophical Society, New Series*, **34**(3), 209–253.
- Scott, W. B. & Jepsen, G. L.** 1941. The Mammalian Fauna of the White River Oligocene. Part V. Perissodactyla. *Transactions of the American Philosophical Society, New Series*, **28**(5), 747–975.
- Scott, W. B. & Osborn, H. F.** 1882. *Orthocynodon*, an animal related to the rhinoceros, from the Bridger Eocene. *American Journal of Science, Series 3*, **24**, 223–225.
- Scott, W. B. & Osborn, H. F.** 1883. On the skull of the Eocene rhinoceros, *Orthocynodon*, and the relation of this genus to other members of the group. *Contributions from the Museum of Geology and Archaeology of Princeton College*, **1**, 3–22.
- Scott, W. B. & Osborn, H. F.** 1887. Preliminary account of the fossil mammals from the White River Formation, contained in the Museum of Comparative Zoölogy. *Bulletin of the Museum of Comparative Zoölogy*, **13**(5), 151–171.
- Simpson, G. G.** 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, **85**, i–xvi + 1–350.
- Skutschas, P. P., Danilov, I. G., Kodrul, T. T. & Jin, J.** 2014. The first discovery of an alligatorid (Crocodylia, Alligatoroidea, Alligatoridae) in the Eocene of China. *Journal of Vertebrate Paleontology*, **32**, 471–476.
- Stehlin, H. G.** 1909. Remarques sur les faunules de mammifères des couches éocènes et oligocènes du Bassin de Paris. *Bulletin de la Société géologique de France*, **9**, 488–520.
- Stock, C.** 1933. An amynodont skull from the Sespe deposits, California. *Proceedings of the National Academy of Sciences USA*, **19**, 762–767.
- Stock, C.** 1939. Eocene amynodonts from Southern California. *Proceedings of the National Academy of Sciences USA*, **25**, 270–275.
- Swofford, D. L.** 2002. *PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4.0*. Sinauer Associates, Sunderland.
- Takai, F.** 1950. *Amynodon watanabei* from the latest Eocene of Japan with a brief summary of the latest Eocene mammalian faunule in Eastern Asia. *Report of the Geological Survey of Japan*, **131**, 1–14.
- Takai, F.** 1962. [On the boundary between the Paleogene and Neogene of Japan from the viewpoint of the mammals]. *Kaseki*, **4**, 30–31. [In Japanese.]
- Tokunaga, S.** 1926. Fossils of Rhinocerotidae found in Japan. *Proceedings of the Imperial Academy of Japan, Tokyo*, **2**, 289–291.
- Tomida, Y. & Yamasaki, T.** 1996. A large amynodontid from Karatsu Coal-field, Kyushu, Japan and the Eocene–Oligocene boundary. *Bulletin of the National Science Museum. Series C, Geology & Paleontology*, **22**(3/4), 117–131.
- Tong, H., Zhang, J.-Y. & Li, J.-J.** 2010. *Anosteira maomingensis* (Testudines: Carettochelyidae) from the Late Eocene of Maoming, Guangdong, southern China: new material and

- re-description. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **256**, 279–290.
- Troxell, E. L.** 1921. New amynodonts in the Marsh collection. *American Journal of Science, Series 5*, **2**(7), 28–33.
- Van Valkenburgh, B.** 1990. Skeletal and dental predictors of body mass in carnivores. Pp. 181–206 in J. Damuth & B. J. MacFadden (eds) *Body size in mammalian paleontology: estimation and biological implication*. Cambridge University Press, Cambridge.
- Wall, W. P.** 1980. Cranial evidence for a proboscis in *Cadurcodon* and a review of snout structure in the family Amynodontidae (Perissodactyla, Rhinoceroidea). *Journal of Paleontology*, **54**, 968–977.
- Wall, W. P.** 1982a. Evolution and biogeography of the Amynodontidae (Perissodactyla, Rhinoceroidea). Pp. 563–567 in B. Marnett & M. J. Copeland (eds) *Proceedings of the Third North American Paleontological Convention*. McGill University, Toronto.
- Wall, W. P.** 1982b. The genus *Amynodon* and its relationship to other members of the Amynodontidae (Perissodactyla, Rhinoceroidea). *Journal of Paleontology*, **56**, 434–443.
- Wall, W. P.** 1989. The phylogenetic history and adaptive radiation of the Amynodontidae. Pp. 341–354 in D. R. Prothero & R. M. Schoch (eds) *The evolution of perissodactyls*. Oxford University Press, New York.
- Wall, W. P.** 1998. Amynodontidae. Pp. 583–588 in C. M. Janis, K. M. Scott & L. L. Jacobs (eds) *Evolution of Tertiary mammals of North America. Volume 1: Terrestrial carnivores, ungulates, and ungulate-like mammals*. Cambridge University Press, New York.
- Wall, W. P. & Heinbaugh, K. L.** 1999. Locomotor adaptations in *Metamynodon planifrons* compared to other amynodontids (Perissodactyla, Rhinoceroidea). *National Parks Paleontological Research*, **4**, 8–17.
- Wall, W. P. & Manning, E. M.** 1986. *Rostriamynodon grangeri* n. gen., n. sp. of amynodontid (Perissodactyla, Rhinoceroidea) with comments on the phylogenetic history of Eocene Amynodontidae. *Journal of Paleontology*, **60**, 911–919.
- Wang, B.-Y., Qiu, Z.-X., Zhang, Q.-Z., Wu, L.-J. & Ning, P.-J.** 2009. Large mammals found from Houldjin Formation near Erenhot, Nei Mongol, China. *Vertebrata Palasiatica*, **47**, 85–110.
- Wang, J., Li, H., Zhu, Z., Seguin, M. K., Yang, J. & Guomei, Z.** 1994. Magnetostratigraphy of Tertiary rocks from Maoming Basin, Guangdong Province, China. *Chinese Journal of Geochemistry*, **13**(2), 165–175.
- Wang, Y.-Y., Zhang, Z.-H. & Jin, J.** 2007. Discovery of Eocene fossil mammal from Maoming Basin, Guangdong. *Acta Scientiarum Naturalium Universitatis Sunyatseni*, **46**, 131–133.
- Watt, C., Mitchell, S. & Salewski, V.** 2010. Bergmann's rule; a concept cluster? *Oikos*, **119**, 89–100.
- Wilson, J. A. & Schiebout, J. A.** 1981. Early Tertiary vertebrate faunas Trans-Pecos Texas: Amynodontidae. *Texas Memorial Museum Pearce-Sellards Series*, **33**, 1–62.
- Wood, H. E.** 1934. Revision of the Hyrachyidae. *Bulletin of the American Museum of Natural History*, **67**(5), 181–295.
- Wood, H. E.** 1937. A new, lower Oligocene, amynodont rhinoceros. *Journal of Mammalogy*, **18**, 93–94.
- Wood, H. E.** 1941. Trends in rhinoceros evolution. *Transactions of the New York Academy of Sciences, Series 2*, **3**(4), 83–96.
- Xu, Y.-X.** 1961. Some Oligocene mammals from Chuching, Yunnan. *Vertebrata Palasiatica*, **5**, 315–329.
- Xu, Y.-X.** 1965. A new genus of amynodont from the Eocene of Lantian, Shensi. *Vertebrata Palasiatica*, **9**, 83–86.
- Xu, Y.-X.** 1966. Amynodonts of Inner Mongolia. *Vertebrata Palasiatica*, **10**, 123–190.
- Xu, Y.-X. & Chiu, C.-S.** 1962. Early Tertiary mammalian fossils from Lunan, Yunnan. *Vertebrata Palasiatica*, **6**, 313–332.
- Ye, H.-K.** 1958. A new crocodile from Maoming, Kwangtung. *Vertebrata Palasiatica*, **2**, 237–242.
- Ye, H.-K.** 1963. Fossil turtles of China. *Paleontologica Sinica, New Series C*, **18**, 1–112.
- Ye, H.-K.** 1994. *Fossil and Recent turtles of China*. Science Press, Beijing, 112 pp.
- Ye, J., Meng, J., Wu, W.-Y. & Wu, S.-Y.** 2002. The discovery of late Eocene mammal fossils from Burqin of Xinjiang. *Vertebrata Palasiatica*, **40**, 203–210.
- Young, C. C.** 1937. An Early Tertiary vertebrate fauna from Yuanchü. *Bulletin of the Geological Society of China*, **17**(3–4), 413–438.
- Yu, Y., Harris, A. J. & He, X.** 2010. S-DIVA (Statistical Dispersal-Vicariance Analysis): a tool for inferring biogeographic histories. *Molecular Phylogenetics and Evolution*, **56**, 848–850.
- Zdansky, O.** 1930. Die alttertiären Säugetiere Chinas nebst stratigraphischen Bemerkungen. *Palaentologia Sinica, Series C*, **6**(2), 1–87.