Middle Miocene elasmotheriine Rhinocerotidae from China and Mongolia: taxonomic revision and phylogenetic relationships

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Eight elasmotheriine rhinocerotid species have been described from the Middle Miocene of China and Mongolia. In this paper a revised taxonomy is presented based on direct observation and comparison of the available material. A phylogenetic analysis based on 282 morphological characters has led to the reappraisal of *Procoelodonta* Matthew, 1931, *Caementodon* Heissig, 1972 and *Huaqingtherium* Huang & Yan, 1983. The genus *Procoelodonta* is split into three subgenera: *P.* (*Procoelodonta*) Matthew, 1931, *P.* (*Begertherium*) Beliaeva, 1971, and *P.* (*Pasalarhinus* subg. n). The genus *Caementodon* is split into two subgenera: *C.* (*Caementodon*) Heissig, 1972 and *C.* (*Beliajevina*) Heissig, 1974. Four species are assumed to have occurred in the Middle Miocene within the area studied: *Procoelodonta* (*Procoelodonta*) *mongoliense* (Osborn, 1924), '*P.*' (*Begertherium*) *borissiaki* (Beliaeva, 1971), '*Caementodon*' (*Beliajevina*) *fangxianense* (Yan, 1979) and *Huaqingtherium lintungense* (Zhai, 1978) (= '*Caementodon tongxinensis*' Guan, 1988 = '*Huaqingtherium qiui*' Guan, 1993 = '*Hispanotherium tungurense*' Cerdeño, 1996). *Shennongtherium hypsodontus* Huang & Yan, 1983 is removed from the Elasmotheriina, owing to dental characters which suggest that it is a teleoceratine. The distribution of the main characters later seen in *Elasmotherium* is briefly discussed. The persistence and diversity of the Elasmotheriina throughout the Middle Miocene help explain how minute brachyodont animals gave rise to the mammoth-sized hypsodont *Elasmotherium*.
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Introduction

The elasmotheriines (i.e. Elasmotheriina in the current work) form an extinct group generally acknowledged as having close relationships with extant rhinoceroses within Rhinocerotidae (Heissig 1972, 1976, 1989; Groves 1983; Prothero *et al.* 1986; Fortelius & Heissig 1989; Prothero & Schoch 1989; McKenna & Bell 1997). The elasmotheriines first occur in Eastern Asia in the Early Middle Miocene (MN 5 or MN 6; Neogene Mammal Faunal Unit 6; Qiu *et al.* 1999). Other primitive species have been described in the Early Miocene of Western Europe (Antunes & Ginsburg 1983; Cerdeño 1992; Antoine *et al.* 2000). However, the earliest described so far was discovered in the Aquitanian of Pakistan (Heissig 1972; Antoine & Welcomme 2000). Qiu (1990) pointed out the questionable presence of a primitive elasmotheriine in the Aquitanian locality of Xiejia (China), based on specimens previously attributed to *Brachypotherium* sp. by Li & Qiu (1980). Yet, it shows no affinity with primitive elasmotheriines and actually corresponds to a teleoceratine rhinocerotid, as argued by Antoine & Welcomme (2000).

The first computerized cladistic analysis of the Rhinocerotidae interpreted the elasmotheriines as a polyphyletic group (Cerdeño 1995: 14–15; Figs 1, 2). However, a recent and more extended phylogenetic analysis, based on 282 cranial, dental and postcranial characters and 36 taxa, supports their monophyly within Rhinocerotidae with the North American *Menoceras* and *Diceratherium* as their closest relatives (Antoine 2002; Fig. 288).

Elasmotheriine rhinocerotids are common in the Middle Miocene of Asia (Heissig 1972; Qiu 1990; Guan 1993; Cerdeño 1996; Qiu *et al.* 1999). Eight species have been described in several localities from the so-called 'ante-*Hipparion* faunas' of China and Mongolia (Fig. 2): '*Baluchitherium*

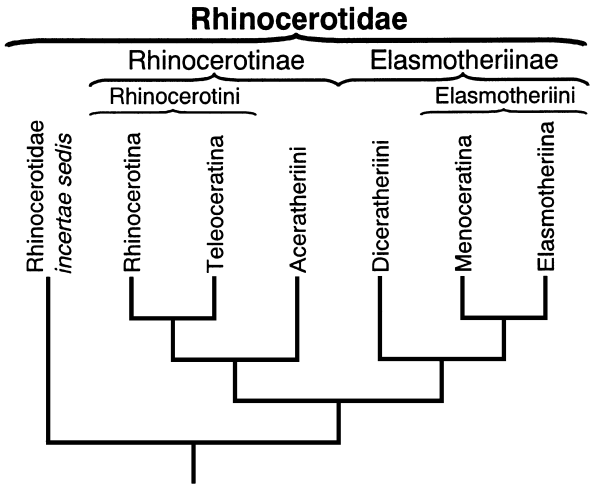

Fig. 1 Phylogenetic relationships between suprageneric taxa within Rhinocerotidae. The Rhinocerotinae include the Aceratheriini (extinct: *Aceratherium* and relatives) and the Rhinocerotini as sister-groups. Within Rhinocerotini, the Rhinocerotina (living rhinoceroses, woolly rhino and relatives) and the Teleoceratina (extinct: *Teleoceras* and relatives) are sister-groups. The Elasmotheriinae include the Elasmotheriini and the Diceratheriini (extinct: *Diceratherium* and relatives). Within Elasmotheriini, the Menoceratina (extinct: *Menoceras* and relatives) are the sister-group of the Elasmotheriina (extinct: 'true' elasmotheriines: *Elasmotherium* and relatives). Modified after Antoine (2002).

Fig. 2 Map of the Middle Miocene localities of China and Mongolia yielding elasmotheriine rhinocerotids, referred to in this work. The Tongxin locality is also known under the name Dingjiaergou. Modified after Qiu *et al*. (1999).

mongoliense' Osborn, 1924, '*Hispanotherium lintungensis*' Zhai, 1978, '*Tesselodon fangxianensis*' Yan, 1979, '*Shennongtherium hypsodontus*' Huang & Yan, 1983, '*Caementodon tongxinensis*' Guan, 1988, '*Begertherium borissiaki*' Beliaeva, 1971, '*Huaqingtherium qiui*' Guan, 1993 and '*Hispanotherium tungurense*' Cerdeño, 1996. The generic attribution of these elasmotheriine taxa has been problematic for decades and defining their precise phylogenetic relationships was therefore necessary before making any taxonomic revision. Most of the specimens were directly observed by the author in 1999. The Middle Miocene Elasmotheriina from East Asia yield key information about the evolution towards grass-eating exhibited by the later elasmotheriines *Elasmotherium*, *Sinotherium* or *Iranotherium*, as is clear from their unique cranial and dental pattern.

Materials and methods

The remains attributed to '*Baluchitherium mongoliense*' Osborn, 1924 and '*Hispanotherium tungurense*' Cerdeño, 1996 are housed in the American Museum of Natural History (AMNH, New York). These specimens were unearthed during the Central Asia Expeditions of the AMNH in the years 1921–30. The hypodigms of '*Hispanotherium lintungensis*' Zhai, 1978; '*Tesselodon fangxianensis*' Yan, 1979 and *Shennongtherium hypsodontus* are deposited in the Institute for Vertebrate Paleontology and Paleoanthropology (IVPP), in Beijing, while the specimens identified as '*Caementodon tongxinensis*' Guan, 1988 and '*Huaqingtherium qiui*' Guan, 1993 are stored in the Beijing Natural History Museum (BNHM). The hypodigm of '*Begertherium borissiaki*' Beliaeva, 1971 is in the Palaeontological Institute of the Russian Academy of Sciences (PIN), in Moscow. The holotype of '*Beliajevina tekkayai*' Heissig, 1974 is stored in the Bayerische Staatssaamlung für Paläontologie (BSP) in Munich.

Capital letters are used for upper teeth (I, C, D, P, M), while lower case letters indicate lower teeth (i, c, d, p, m). The drawings and photographs were made by the author, except where indicated.

The inclusion of intraspecifically variable characters (sexual dimorphism, individual and ontogenetic variations) in a cladistic analysis has been debated for decades. Because they can 'contain useful phylogenetic information' (Wiens 2001: 690), I have included such characters in the current analysis. I have treated them in the same way as character 264 (Table 1), which corresponds to the presence/absence of a fibula-facet on the calcaneus. This facet is always absent in several taxa (in 29 specimens of the recent *Diceros bicornis*; Guérin 1980: 131), always present in others (in 14 specimens of '*Aegyrcitherium beonense*' Antoine, 1997) and absent in 9/11 specimens of *Hispanotherium matritense* (Lartet *in* Prado 1864). Therefore, I have replaced the binary states ('0, absence; 1, presence') by multistate quantitative states based on frequency ('0, always absent (100%); 1, generally absent (50–99%); 2, generally present (50–99%); 3, always present

Table 1 Distribution of nonambiguous apomorphies at each node of the consensus tree (Fig. 3). Apomorphic character states are only mentioned for multistate characters. The reversions are preceded by the sign '-'. Reliable characters (RI ≥ 0.80) are in bold-face. Capital letters indicate the most robust nodes, thus justifying generic distinctions.

Node B: 23, 44, **79**, **81**, **82**, **110**^{1}, **–154**, **184**, –212, 220, 230, 252^{1}, 253
Node C: 15^{1}, 35^{1}, 42^{1}, **74**, 75, –94^{1}, 107^{1}, **110**^{2}, 111^{2}, 120
Node D: 22, **67**^{1}, **70**^{1}, 103^{1}, **115**^{2}, 129, **133**, 151^{2}, **161**^{1}, 247, 264^{1}, **265**^{2}
Controlled Teleoceratina (node E): 42^{2}, 54, **134**, 142, **168**, **202**, **205**, **206**, **224**, **229**, 232, 241, 242, **249**, **251**, 252^{2}, 262, 264^{2}, **279**
Node F (*Teleoceras fossiger, Prosantorhinus douvillei, Shennongtherium hypsodontus*): 39, 50, 77, 95, 97, 109^{3}, **114**^{2}, **115**^{3}, 130, –179, **182**^{1}, 193, 204, 226^{1}, –230^{0}, 234, 260, –263^{0}, 264^{3}, 272
Elasmotheriinae (node G): **–23**, **65**, **110**^{3}, 122, 143, 151^{3}, 172, 201, **207**, 212, 248, 263^{3}, 274
Elasmotheriini (node H): –18^{0}, 19^{1}, 45, **59**^{1}, 72^{2}, 88, –97, 140^{2}, **146**, **154**, **176**, **234**, **235**, 244, 256, 266, **278**
Elasmotheriina (Node I): 89^{1}, 102^{3}, 116
Kenyatherium bishopi: 66, –103^{0}, –121
Node J: –83^{2}, 85^{1}, **114**^{1}
Bugtirhinus praecursor: –83^{0}, –85, 87^{3}, –101^{1}, 204
Node K: **114**^{2}, 124, 157^{2}, **211**
Caementodon (*Caementodon*) *oettingenae*: –72^{1}, 128^{2}, –130
Node l: 97, 109^{1}, 209,
Caementodon (*Beliajevina*) *fangxianense* (node m): 87^{3}, 109^{3}, –116
Caementodon (*Beliajevina*) *caucasicum*: –85, 95^{2}, –10^{1}, 108^{1}, –118
Node N: –87^{2}, **101**^{3}, 125, **198**, 208, 261^{1}, **280**
Hispanotherium grimmi: 77, 78, 100, 105^{3}, 204, 217
Node p: –57, 62, –118, –122, –172, 199^{3}
Hispanotherium matritense: 85^{2}, 167, 181, 212, –219^{0}, –221, –271, –274, –275
Node q: –87^{1}, –223^{1}, 271^{2}
Hispanotherium matritense from Córcoles: –83^{1}, 107^{2}, 180^{1}, 191, 255
Node r: 77, –97, 261^{2}, 264^{3}
Hispanotherium beonense: 37, –55, –56, 98, 104, 122, 222^{1}, 226^{1}, 252^{2}, 255, 270
Node S: –85^{0}, **114**^{3}, –124, 167, 173
Procoelodonta (*Pasalarhinus* subg. n) *tekkayai*: –87, –88, –103, –147^{2}, 156^{2}
Node t: 87^{3}, 118
Procoelodonta (*Begertherium*) *borissiaki*: 100, 103^{2}, 105^{3}
Node u: 126^{2}
Procoelodonta (*Procoelodonta*) *mongoliense*: 1, 11^{2}, 26^{2}, 39, –83^{0}
Node V: 24^{1}, **33**, **66**, 83^{3}, 109^{2}
Huaqingtherium lintungense: 85^{1}, 97, –103^{0}, 108, –118
Node W: 7^{1}, **21**, 25^{1}, 47^{2}, 54^{1}, 57, 63^{2}, **64**^{1}, **69**^{1}, 76, 109^{3}, 119, **123**^{1}, 127, –263^{0}
Iranotherium morgani: 11, 34, 105^{3}, 128^{2}, 226^{2}, 239, 252^{2}
Node X: 2, 3, 4, 25^{2}, –40, –45, 46, 48, –49, –111^{2}, –112^{2}, –130, **136**, 137
Parelasmotherium schansiense: 24^{2}, –120, 123^{2}, 132
Node Y: 37, **64**^{2}, **69**^{2}, –102^{2}, 107^{3}, –111^{1}, 112^{3}, –12^{1}, –126
Sinotherium lagrelii: –63^{1}, –127, –161^{0}
Elasmotherium (node Z): **59**^{2}, **64**^{3}, **69**^{3}, 89^{2}, **90**^{3}, **93**, –111^{0}, 117, 153^{2}, **161**^{2}
Elasmotherium caucasicum: 100, 105^{3}
Elasmotherium sibiricum: –120, 222^{2}

(100%)'), as detailed by Antoine (2002). The corresponding characters are additive (morphoclines).

Lower level systematics within Elasmotheriina is deduced from the current cladistic analysis (Fig. 3), on the basis of both the topology of the strict consensus tree and the reliability of the corresponding nodes: some of them are strongly supported by reliable synapomorphies (i.e. Retention Index [RI] higher than 0.80), which are set in boldface in Table 1 and illustrated in Fig. 3. I have split the elasmotheriines into distinct genera using these robust and reliable nodes (Fig. 3: nodes J, K, N, S, V–Z), although other dichotomies of the consensus tree (Fig. 3: nodes l, m, p, q, r, t, u) are weaker since they are exclusively supported by recurrent synapomorphies (homoplastic: RI lower than 0.80). However, the corresponding terminal taxa can be differentiated by autapomorphies, even on the few available specimens. Therefore, in order to avoid generating a large number of new generic names whose relationships are weakly supported, I have restricted the elasmotheriine genera to monophyletic groups and used double quotes (e.g. '*Procoelodonta*' *tekkayai*) to indicate where association of the remaining species with these genera is doubtful. In addition, some monophyletic subgenera have been erected within such genera.

For each genus or subgenus revised in this work, the emended diagnosis is established according to the apomorphies listed at corresponding nodes (Table 1; Fig. 3). The specific diagnoses further reflect the autapomorphies listed in Table 1.

Systematics

The suprageneric systematics of the Rhinocerotidae follows Antoine (2002), where two subfamilies are recognized within the family, as summarized in Fig. 1: Rhinocerotinae Owen, 1845 and Elasmotheriinae Bonaparte, 1845. The Rhinocerotinae include Aceratheriini Dollo, 1885 (extinct: *Aceratherium* and relatives) and Rhinocerotini Owen, 1845 as sister-groups. Within Rhinocerotini, Rhinocerotina Owen, 1845 (living rhinoceroses and woolly rhino) and Teleoceratina Hay, 1902 (extinct: *Teleoceras* and relatives) are sister-groups. The Elasmotheriinae include Elasmotheriini Bonaparte, 1845 and Diceratheriini Dollo, 1885 (extinct: *Diceratherium* and relatives). Within Elasmotheriini, Menoceratina Prothero, Manning & Hanson, 1986 (extinct: *Menoceras* and relatives) is the sister-group of Elasmotheriina Bonaparte, 1845 (extinct: 'true' elasmotheriines, *Elasmotherium* and relatives).

The name Elasmotheriinae Bonaparte, 1845 is older than the names Diceratheriinae Dollo, 1885 and Menoceratinae Prothero, Manning & Hanson, 1986, and there is no prevailing usage of Diceratheriinae or Menoceratinae as synonyms of Elasmotheriinae in the literature. Therefore, according to the International Code of Zoological Nomenclature (ICZN, 1999), the available family group names are Elasmotheriinae for (Diceratheriini + Elasmotheriini) and Elasmotheriini for (Menoceratina + Elasmotheriina).

Order Perissodactyla Owen, 1848

Family Rhinocerotidae Owen, 1845

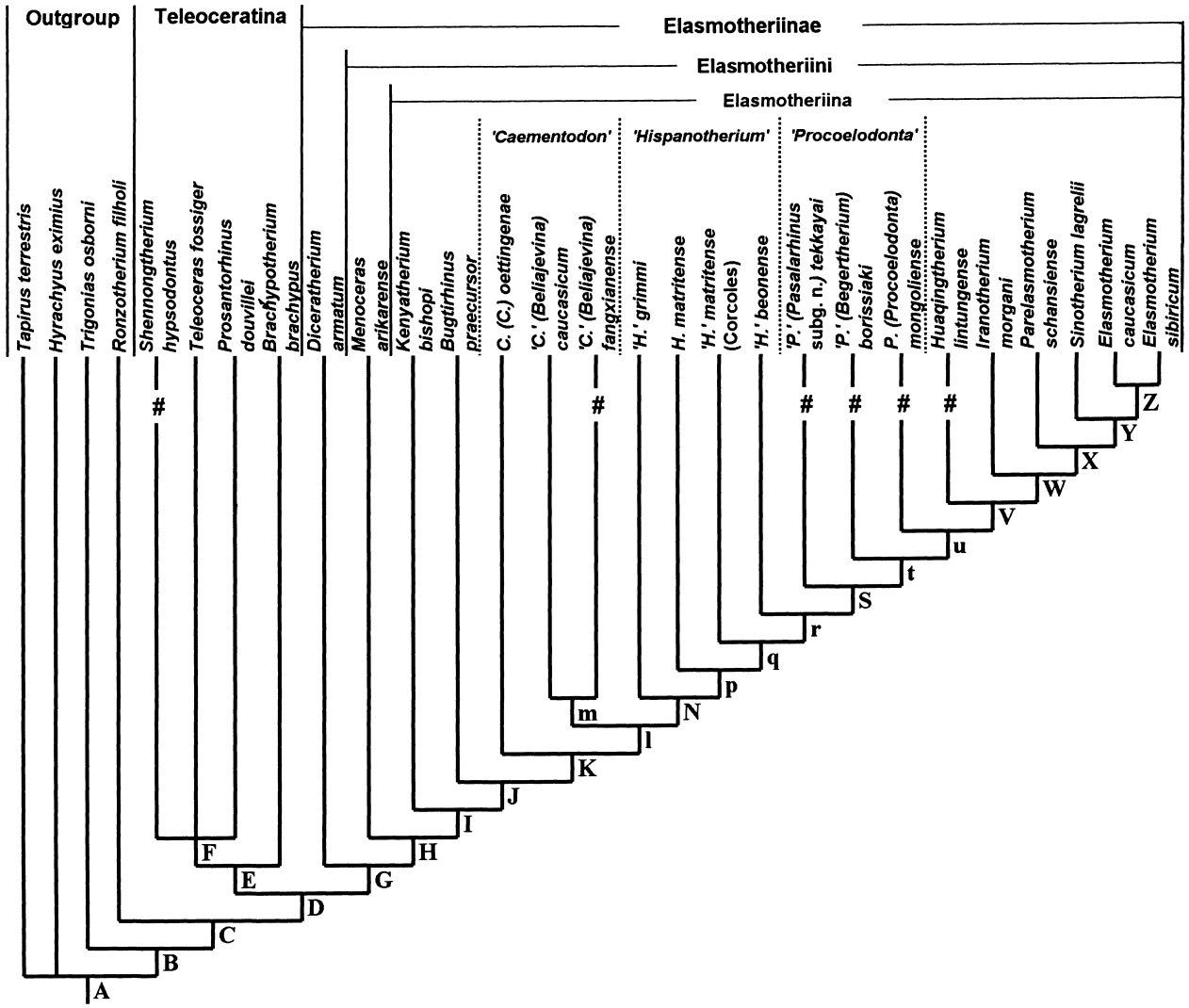

Fig. 3 Cladogram of the Elasmotheriina (Mammalia, Rhinocerotidae). Consensus of two equally parsimonious trees (860 steps; CI = 0.42; RI = 0.61); 282 characters analysed in 28 taxa. Results given by the heuristic 'mh*bb' command (Hennig86, ver. 1.5; Farris 1988). Taxa revised in the current work indicated by #. The distribution of unambiguous synapomorphies at each node is further detailed in Table 1. Capital letters are used for well-supported nodes justifying generic distinctions within Elasmotheriina. Distribution of main synapomorphies at selected nodes: node E (selected Teleoceratina), M3 with a triangular cross section, secondary folds on D2, weak gutter for the *m. extensor carpi* on the radius, straight magnum-facet on the McII, robust distal end on the fibula, brachypod limbs; node F (*Teleoceras fossiger*, *Prosantorhinus douvillei*, *Shennongtherium hypsodontus*), transverse metaloph and reduced protocone on P2; node I (Elasmotheriina), wide postfossette on upper premolars, lingual wall on P4, strong constriction on the protocone of M1-2; node K, posterior cingulum low on M1-2, lingual cingulum usually absent on M1-2 and lower molars, semilunate and ulna articulated; node l, protocone reduced on P2, labial cingulum usually present on upper molars, magnum-facet straight on the scaphoid; node m ('*Caementodon*' (*Beliajevina*)), lingual cingulum always lacking on P2-4, as the labial cingulum on upper molars; weak constriction of the protocone on M2; node N, constricted hypocone on P3-4 and M1, concave medial border on the radius, low and smooth intermediate relief on the metapods, expansion of the calcaneus-facet 1 usually wide and low on the astragalus, straight posterior tuberosity on the magnum, small-sized trapezium-facet on the scaphoid and proximal radius-ulna facets usually distinct; node S, no lingual cingulum on the upper molars, strong and continuous posterior cingulum on M1-2, simple and sagittal crochet on P4; node t, no lingual cingulum on P2-4, weak paracone fold on M1-2; node u, antecrochet and hypocone always joined on M1; node V, nasals broadened rostrally, orbits laterally projected, cement very abundant, labial cingulum always absent on the upper premolars and generally absent on the upper molars; node W, anterior shifting of the cheekteeth series, nasals at least partly fused, huge post-tympanic process, noticeable enamel foldings, partial hypsodonty, cristella generally present and metacone fold absent on M1-2; node X, partially ossified nasal septum, indented protocone on M3; node Y, developed enamel foldings on cheekteeth, subhypsodonty; *Elasmotherium* (node Z), intense enamel foldings on cheekteeth, hypsodonty completed, antecrochet always present on P3, P2 always lacking, hypolophid almost sagittal on lower molars.

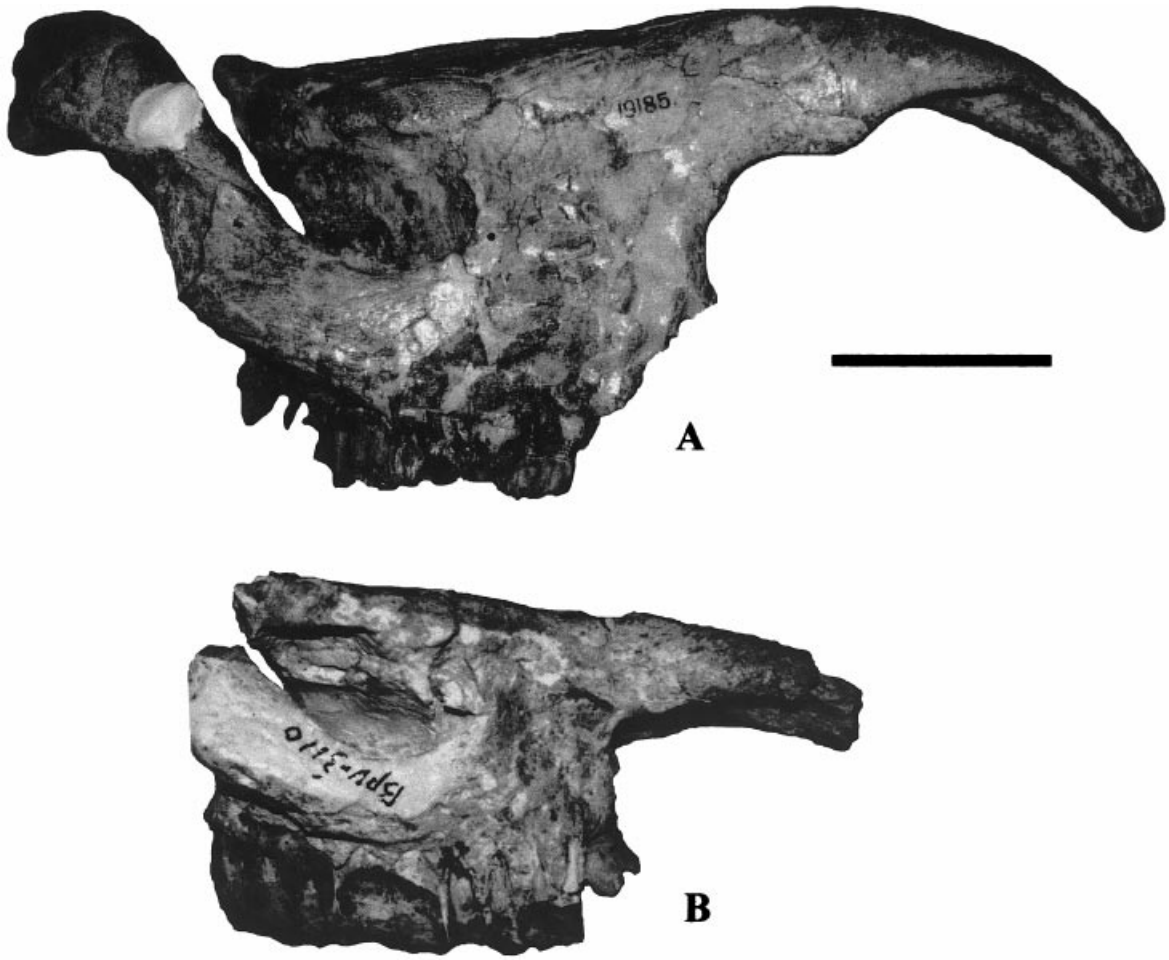

Fig. 4 A, B. *Procoelodonta* (*Procoelodonta*) mongoliense. —A. Incomplete skull AMNH 19185 (holotype), Loh (Mongolia, Early Middle Miocene). —B. Incomplete crushed skull BNHM BVP-3110, Tongxin (Ningxia, China, Early Middle Miocene). Both are lateral views. Scale bar = 10 cm.

Subfamily Elasmotheriinae Bonaparte, 1845
Tribe Elasmotheriini Bonaparte, 1845
Subtribe Elasmotheriina Bonaparte, 1845

***Genus Procoelodonta* Matthew, 1931**
Gobitherium Kretzoi, 1943: 268–270, text-figs 1, 2.

Type species. *P. mongoliense* (Osborn, 1924).

Diagnosis. Elasmotheriina lacking any lingual cingulum on the upper molars, with strong and continuous posterior cingulum on M1-2, simple and sagittal crochet on P4. Less advanced than *Huaqingtherium*, *Iranotherium*, *Parelasmotherium*, *Sinotherium* and *Elasmotherium* in having nasals not broadened rostrally, orbits without lateral projection, little cement, labial cingulum usually present on the upper cheek teeth.

Included species. Type species, plus (doubtfully) '*P.*' *borissiaki* (Beliaeva, 1971), '*P.*' *tekkayai* (Heissig, 1974).

Subgenus *Procoelodonta (Procoelodonta)* Matthew, 1931
Type species. *P.* (*P.*) *mongoliense* (Osborn, 1924).

Diagnosis. That of the type species, by monotypy.

***Procoelodonta (Procoelodonta) mongoliense* (Osborn, 1924)**
(Figs 4 and 5A, B)
Baluchitherium mongoliense nov. sp. Osborn, 1924: 3–5, text-fig. 2.
'*Baluchitherium mongoliense*' Matthew, 1924: 5.
'*Baluchitherium*' *mongoliense* Wood, 1927: 10.
Procoelodonta mongoliense nov. gen. Matthew, 1931: 1–9, text-figs 1, 2.
Procoelodonta Forster-Cooper, 1934: 575, text-fig. 1.

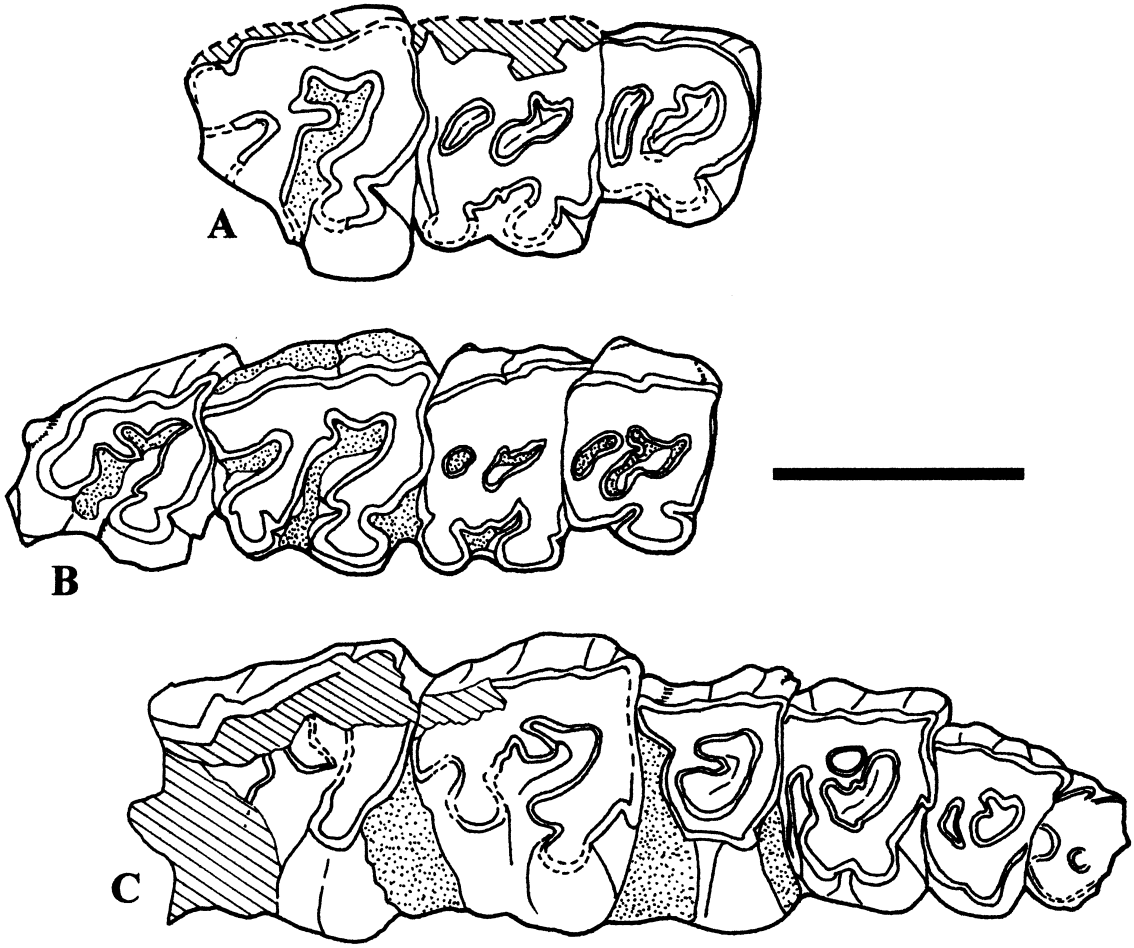

Fig. 5 A–C. *Procoelodonta* (*Procoelodonta*) *mongoliense*. —A. Right upper series P4-M2 from the holotype skull AMNH 19185, Loh (Mongolia, Early Middle Miocene). —B. Right upper series P4-M3 from the skull BNHM BVP-3110, Tongxin (Ningxia, China, Early Middle Miocene). —C. '*Procoelodonta*' (*Begertherium*) *borissiaki*. Right upper series P1-M2 from the holotype skull PIN 2737–1, Beger Nur (Western Mongolia, Middle Miocene). Redrawn after Beliaeva (1971: 83, Fig. 4). All are occlusal views. Scale bar = 5 cm.

Baluchitherium mongoliense Teilhard de Chardin & Leroy, 1942: 62.
Gobitherium mongoliense Kretzoi, 1943: 268–270, text-figs 1, 2; Beliaeva 1971: 81, fig. 1; Cerdeño 1995: 25–26, text-figs 18, 19.
Gobiatherium Orlov & Gromova, 1962: 333; Orlov & Gromova 1968: 456.
Iranotherium mongoliense Heissig, 1974: 26–27; Heissig 1976: 21; Fortelius & Heissig 1989: 227–233, figs 1, 2; Cerdeño 1996: 2.

Holotype. MONGOLIA, Loh (Field n°67; Osborn 1924). AMNH 19185, fragmentary skull with right P4-M2. Figured by Osborn (1924), Beliaeva (1971) and in the current work (Figs 4A and 5A).

Geographic range. Mongolia (Loh, Field n°67; Osborn 1924) and China (Ningxia).

Stratum typicum. Loh Formation, Mongolia, Early Middle Miocene (Early Tunggurian; Qiu *et al.* 1999).

Stratigraphic range. Early Middle Miocene (Early Tunggurian; Qiu *et al.* 1999).

Emended diagnosis. Procoelodonta with lateral apophyses on nasal bones; zygomatic arch very high; nasal bones very long and arched; articular tubercle high on the squamosal; labial cingulum always present on upper molars. More advanced than '*P.*' (*Begertherium*) *borissiaki* in having the antecrochet and the hypocone joined on M1.

Material examined. Fragmentary skull from Loh, Mongolia (holotype, AMNH 19185). In the original description, Osborn (1924) mentions the discovery of a pes found (AMNH 19151) in the same horizon as the skull. This pes could not be recovered from the collections of the AMNH during my visit in spring 1999; dorso-ventrally crushed fragmentary skull with right and left P4-M3, from Dingjiaergou (locality also known as Tongxin), China (BNHM, BPV-3110).

Description

Skull. Medium-sized, with very long (250–300 mm), narrow, unfused and regularly arched nasal bones. Lateral apophyses on the nasal bones (much weaker on BPV-3110; Fig. 4). Nasal septum unossified, but nasal bones strongly curved in anterior view, forming a high axial vertical ridge. Smooth vascular impressions on the median part of the nasal bones attesting to the presence of a small nasal median horn. Nasal notch above P2-3; anterior border of the orbit above the posterior half of M1. Processus lacrymalis present. Zygomatic arch very high, with a low anterior end (at the level of the neck of M2). No trace of any frontal horn, nor lateral projection of the orbits. Fronto-parietal crests smooth and well separated. Zygomatic width narrow with respect to the frontal width. Processus postorbitalis present on the squamosal. Suture between maxilla and squamosal smooth. Articular tubercle high on the squamosal.

Dentition. No secondary folds (Fig. 5A,B). Cement abundant on the ectolophs and in the valleys (partly removed during preparation in AMNH 19185). Enamel wrinkled at the neck and corrugated at the top of the crown. Teeth high-crowned but without trace of hypsodonty (retained roots, conical crowns).

P4. Labial and lingual cingula absent. Crochet simple and sagittal. No constriction on the metaloph, nor antecrochet nor medifossette. Short crista. Wide postfossette. Lingual wall formed by the coalescence of protocone and hypocone. Hypocone posterior to the metacone.

Upper molars. Low labial cingulum. No lingual cingulum. Posterior cingulum strong and continuous. Strong antecrochet and crochet. No crista nor medifossette nor cristella. Deep anterior constriction on the protocone. Deep parastyle. Smooth paracone and metacone folds. Mesostyle smooth (BPV-3110) or thick (AMNH 19185). Metastyle long and metaloph short on M1-2. Undulated ectoloph on M1-2. Base of the hypocone constricted on M1-2. Antecrochet and hypocone joined at early stages of wear on M1, but not on M2 (distinct up to the neck). Postfossette present on M1-2. No lingual groove on the protocone of M2. M3 quadrangular but with metaloph and ectoloph fused into an ectometaloph. Protocone trefoil-shaped and protoloph straight and transverse on M3. Posterior vertical groove on the ectometaloph of M3 present.

Table 2 *Procoelodonta* (*Procoelodonta*) *mongoliense*. Comparative dimensions of the teeth from Loh and Tongxin (mm). Abbreviations: L, length; W, width.

	P4		M1		M2		M3	
	W	L	W	L	W	L	W	L
Loh	29	41	43	(> 50)	(> 45)	53	–	–
Tongxin	26–27	37	32	44	45	48–49	36–37	49–50
Mean	26.5	37	32	44	45	48.5	36.5	49.5

Discussion. Both specimens are very similar, although BNHM BPV-3110 is somewhat smaller (Fig. 4; Table 2) and has a smoother mesostyle on M2 (Fig. 4A,B). They share several unambiguous dental synapomorphies which place this taxon within Elasmotheriina: lingual wall and wide postfossette on P4, strong constriction on the protocone of M1-2 (Table 1, Appendix 2; Fig. 3, node I). The species from Loh and Tongxin is more derived than *Kenyatherium* Aguirre & Guérin, 1974, *Bugtirhinus* Antoine & Welcomme, 2000, *Caementodon* Heissig, 1972, and *Hispanotherium* Crusafont & Villalta, 1947 (the latter including *Aegyrcitherium* Antoine, 1997, in possessing five dental synapomorphies: no lingual cingulum on the upper molars, strong and continuous posterior cingulum on M1-2, simple and sagittal crochet on P4 (Fig. 3, node S). These synapomorphies are shared by '*Begertherium borissiaki*' Beliaeva, 1971 and '*Beliajevina tekkayai*' Heissig, 1974, which appear to be close to the specimens from Loh and Tongxin, and more derived Elasmotheriina. On the other hand, the more derived Elasmotheriina (i.e. *Elasmotherium* Fischer, 1808; *Parelasmotherium* Killgus, 1923 [= '*Ninxiatherium*' Chen, 1977] *Sinotherium* Ringström, 1923, *Iranotherium* Ringström, 1924 and *Huaqingtherium* Huang & Yan, 1983) share at least five synapomorphies: nasals broadened rostrally, orbits laterally projected, cement very abundant, labial cingulum always absent on the upper premolars and generally absent on the upper molars (Fig. 3, node V). These derived characters are absent in the skulls AMNH 19185 and BPV-3110. These skulls further differ from the closest taxa ('*Begertherium borissiaki*' Beliaeva, 1971 and '*Beliajevina tekkayai*' Heissig, 1974) in having an antecrochet/hypocone junction on M1 (Fig. 3, node u). Finally, the very long and arched nasal bones, with lateral apophyses, the very high zygomatic arch and the salient articular tubercle on the squamosal separate the skulls described here from other Elasmotheriina (Table 1), including the skull PIN 2737–1, holotype of '*Begertherium borissiaki*' Beliaeva, 1971.

Osborn (1924) originally identified as '*Baluchitherium mongoliense* nov. sp.' the skull AMNH 19185 from Loh, owing to some naso-frontal similarities with the giant hyracodont *Baluchitherium grangeri*. For the same specimen, Matthew (1924) assumed close relationships with the Pleistocene woolly rhinoceros, *Coelodonta*, from dental features (undulated ectoloph, high crowned teeth, constricted protocones). Thus, he renamed it *Procoelodonta mongoliense* (Matthew, 1931). Kretzoi (1943) considered the name '*Procoelodonta*' as a *nomen nudum*, because the skull from Loh cannot be the ancestor of *Coelodonta*. This argument is not valid according to the International Code of Zoological Nomenclature (ICZN 1999). Nevertheless, Kretzoi (1943) gave the new genus name *Gobitherium* to '*B*'. *mongoliense*, which was for the first time put together with *Iranotherium* in the new subfamily Iranotheriinae (here considered to be included within Elasmotheriina; Antoine 2002). Later, the skull AMNH 19185 has alternately been identified as *Iranotherium mongoliense* (Heissig 1974, 1976, 1989; Cerdeño 1995) or *Gobitherium mongoliense* (Beliaeva 1971; Cerdeño 1996). The name *Gobitherium* Kretzoi, 1943 is a junior synonym of *Procoelodonta* Matthew, 1931.

Thus, according to the morphological peculiarity of the remains described above, the valid binomen is *Procoelodonta mongoliense* (Osborn, 1924). Its hypodigm is so far restricted to the partial skulls described above (AMNH 19185, holotype; BNHM BPV-3110).

Subgenus *'Procoelodonta'* (*Begertherium*) Beliaeva, 1971

Type species. '*P.*' (*B.*) *borissiaki* (Beliaeva, 1971), by monotypy.

Diagnosis. That of the type species. See below.

***'Procoelodonta'* (*Begertherium*) *borissiaki* (Beliaeva, 1971)**
(Fig. 5C)

Begertherium borissiaki nov. gen. nov. sp. Beliaeva, 1971: 78–97, figs 1, 3–6.

Begertherium borissiaki Heissig, 1974: 26; Heissig 1976: 20; Fortelius & Heissig 1989: 227–233, figs 1, 2; Cerdeño 1995: 2; Cerdeño 1996: 25–26.

'*Begertherium borissiaki*' Cerdeño, 1996: 25, 27.

Holotype. MONGOLIA, Beger Nur. PIN 2737–1, partial skull with right P1-M3. Figured by Beliaeva (1971).

Geographic range. Restricted to the locality of Beger Nur (Mongolia).

Stratum typicum and stratigraphic range. Middle Miocene ('ante-*Hipparion* deposits').

Emended diagnosis. '*Procoelodonta*' usually lacking medifossette on P3-4; hypocone anterior to metacone on P3-4; crista present on P3. More advanced than '*P.*' (*Pasalarhinus* subg. n.) *tekkayai* in having no lingual cingulum on P2-4 but having a weak paracone fold on M1-2. Less advanced than *P.* (*Procoelodonta*) *mongoliense* in bearing no junction between the antecrochet and the hypocone on M1.

Material examined. Beliaeva (1971) described the holotype skull (PIN 2737–1), a mandible and some isolated teeth. I have not examined the material directly.

Discussion. The scant material attributed to '*Begertherium borissiaki*', together with the uncertain age of the Beger Nur locality, has always generated taxonomic problems. According to Heissig (1974, 1976, 1996, 1999), Fortelius & Heissig (1989) and Antoine (1997), *Begertherium* is a valid genus, distinct from other Early and Middle Miocene elasmotheriines. Cerdeño 1995, 1996) considers this genus to be a junior synonym of *Hispanotherium*, as are *Beliajevina* and *Caementodon*.

Like *P.* (*P.*) *mongoliense*, this taxon bears morphological features that distinguish it both from primitive Elasmotheriina (*Kenyatherium*, *Bugtirhinus*, *Caementodon and Hispanotherium*) and from more derived elasmotheriines, such as *Huaqingtherium*, *Iranotherium*, *Parelasmotherium*, *Sinotherium* and *Elasmotherium* (Fig. 3, nodes S and V). The closest relations exist with '*Beliajevina tekkayai*' Heissig, 1974) and *P.* (*P.*) *mongoliense*, which supports including these three taxa within the same distinct genus *Procoelodonta*. '*B. borissiaki*' is distinct from *P.* (*P.*) *mongoliense* and '*P.*' *tekkayai* in having a medifossette on P3, the hypocone anterior to metacone on P3-4 and a crista always present on P3 (Fig. 5; Table 1). With respect to *P.* (*P.*) *mongoliense*, the labial cingulum is also lacking on upper molars, the nasal bones are shorter and more angular, with a thick horn insertion and no lateral apophyses. On the other hand, '*B. borissiaki*' further differs from '*P.*' *tekkayai* in having neither a continuous lingual cingulum on P2-4, nor a closed posterior valley on p2 (see below).

Therefore, I propose that *Begertherium* Beliaeva, 1971 be considered as a subgenus doubtfully attributed to *Procoelodonta* Matthew, 1931. This subgenus is so far restricted to the type species '*Procoelodonta*' (*Begertherium*) *borissiaki* (Beliaeva, 1971).

***Subgenus 'Procoelodonta' (Pasalarhinus)* subg. n.**

Type species. '*P.*' (*Pasalarhinus*) *tekkayai* (Heissig, 1974), by monotypy.

Diagnosis. That of the type species, by monotypy (see below).

Derivatio nominis. From 'Pasalar', Middle Miocene locality from Anatolia where all the remains attributed to this taxon have been unearthed (Heissig 1974, 1976), and the Greek *rhis*, *rhinos*, meaning nose.

'*Procoelodonta*' (*Pasalarhinus* subg. n.) *tekkayai* (Heissig, 1974)
Beliajevina tekkayai nov. sp. Heissig, 1974: 23–25, Pl. 2, figs 1–6.
Beliajevina tekkayai Heissig, 1976: 13–18, Pl. 1, figs 1–8, Pl. 2, figs 13–19, Pl. 3, fig. 8; Cerdeño 1996: 25.
Begertherium tekkayai Fortelius & Heissig, 1989: 227–233, figs 1, 2; Fortelius 1990: 490–499, text-figs 1–5; Heissig 1999: 183, 188, figs 16.15 and 16.22, table 16.1.
'*Beliajevina*' *tekkayai* Cerdeño, 1995: 2.

Holotype. TURKEY, Anatolia, Pasalar. BSP 1968 VI 593, right P4. Figured by Heissig (1974, 1976).

Geographic range. Restricted to the locality of Pasalar (Anatolia, Turkey).

Stratum typicum and stratigraphic range. Turgut Formation (Upper part of the MN 5, Middle Miocene).

Diagnosis. '*Procoelodonta*' with lingual cingulum always present and continuous on P2-4; transverse metaloph on P3-4; lingual cingulum usually absent on lower premolars; posterior valley always closed on p2. Less advanced than '*P.*' (*Begertherium*) *borissiaki* and *P.* (*Procoelodonta*) *mongoliense* in having a lingual cingulum on P2-4 and a strong paracone fold on M1-2. Further differs from *P.* (*Procoelodonta*) *mongoliense* in bearing no junction between the antecrochet and the hypocone on M1.

Material examined. From this species only dental remains have been described (Heissig 1974, 1976; Fortelius 1990). The postcranial skeleton is represented by scant and fragmentary specimens, still unpublished (Fortelius 1990).

Discussion. Heissig (1974) considered the elasmotheriine from Pasalar to be different from *Hispanotherium grimmi* Heissig, 1974, both from the Middle Miocene of Anatolia. This author includes the former in a new genus, together with the type species '*Beliajevina caucasica*' (Borissiak, 1935), as '*Beliajevina tekkayai*'. Later, Heissig (1989), Fortelius & Heissig (1989) and Fortelius (1990) placed both Anatolian species within the controversal genus *Begertherium* Beliaeva, 1971.

The current cladistic analysis (Table 1, Appendix 2; Fig. 3) shows that '*Beliajevina tekkayai*' Heissig, 1974 is much more derived than both the type species '*B. caucasica*' — here assumed to belong to the genus *Caementodon* Heissig, 1972 — and *Hispanotherium grimmi*. According to the topology of the tree, the elasmotheriine from Pasalar is likely to be included in the genus '*Procoelodonta*' Matthew, 1931 (Table 1; Fig. 3, node S well supported), but not in the subgenus *P.* (*Procoelodonta*), nor in the subgenus '*P.*' (*Begertherium*). Thus, a new monophyletic subgenus is erected, restricted to the type species '*Procoelodonta*' (*Pasalarhinus*) *tekkayai*, Heissig 1974.

Genus *Caementodon* Heissig, 1972
Type species. *C. oettingenae* Heissig, 1972.

Emended diagnosis. Elasmotheriina with low posterior cingulum on M1-2, lingual cingulum usually absent on M1-2 and lower molars, semilunate and ulna articulated. Less advanced than *Hispanotherium*, *Procoelodonta*, *Huaqingtherium*, *Iranotherium*, *Parelasmotherium*, *Sinotherium* and *Elasmotherium* in having no constricted hypocone on P3-4 and M1, having a straight medial border on the radius, high and acute intermediate relief on the metapodials, expansion of the calcaneus-facet 1 (Heissig 1972) always wide and low on the astragalus, curved posterior tuberosity on the magnum, and large trapezium-facet on the scaphoid. Further differs from '*C.*' (*Beliajevina*) in bearing a strong protocone on P2, a lingual cingulum usually lacking on P2-4, a labial cingulum always present on upper molars, a protocone strongly constricted on M2 and a concave magnum-facet on the scaphoid.

Subgenus *Caementodon* (*Caementodon*) Heissig, 1972
Type species. *C.* (*Caementodon*) *oettingenae* Heissig, 1972.

Emended diagnosis. *Caementodon* with an oval I1 in cross section; mesostyle absent on M2; lingual groove always present on the protocone of M2. Further differs from "*Caementodon*" (*Beliajevina*) in always having a lingual cingulum on P2-4, a labial cingulum on upper molars and a strong constriction of the protocone on M2.

Subgenus '*Caementodon*' (*Beliajevina*) Heissig, 1974
Tesselodon Yan, 1979.

Type species. *C.* (*B.*) *caucasicum* (Borissiak, 1935).

Emended diagnosis. '*Caementodon*' with lingual cingulum always absent on P2-4; labial cingulum always absent on upper molars; constriction of the protocone weak on M2. More advanced than *C.* (*Caementodon*) in having a reduced protocone on P2, a labial cingulum usually present on upper molars, a magnum-facet straight on the scaphoid.

'*Caementodon*' (*Beliajevina*) *fangxianense* (Yan, 1979)
(Fig. 6C)
Tesselodon fangxianensis n. g. n. sp. Yan, 1979: 189–200, text-figs 1, 2, Pl. I, figs 2, 3.
Tesselodon fangxianensis Fortelius & Heissig, 1989: 227–233, figs 1, 2; Qiu 1990: 543; Cerdeño 1996: 25, 29.
Tesselodon Cerdeño, 1996: 4.

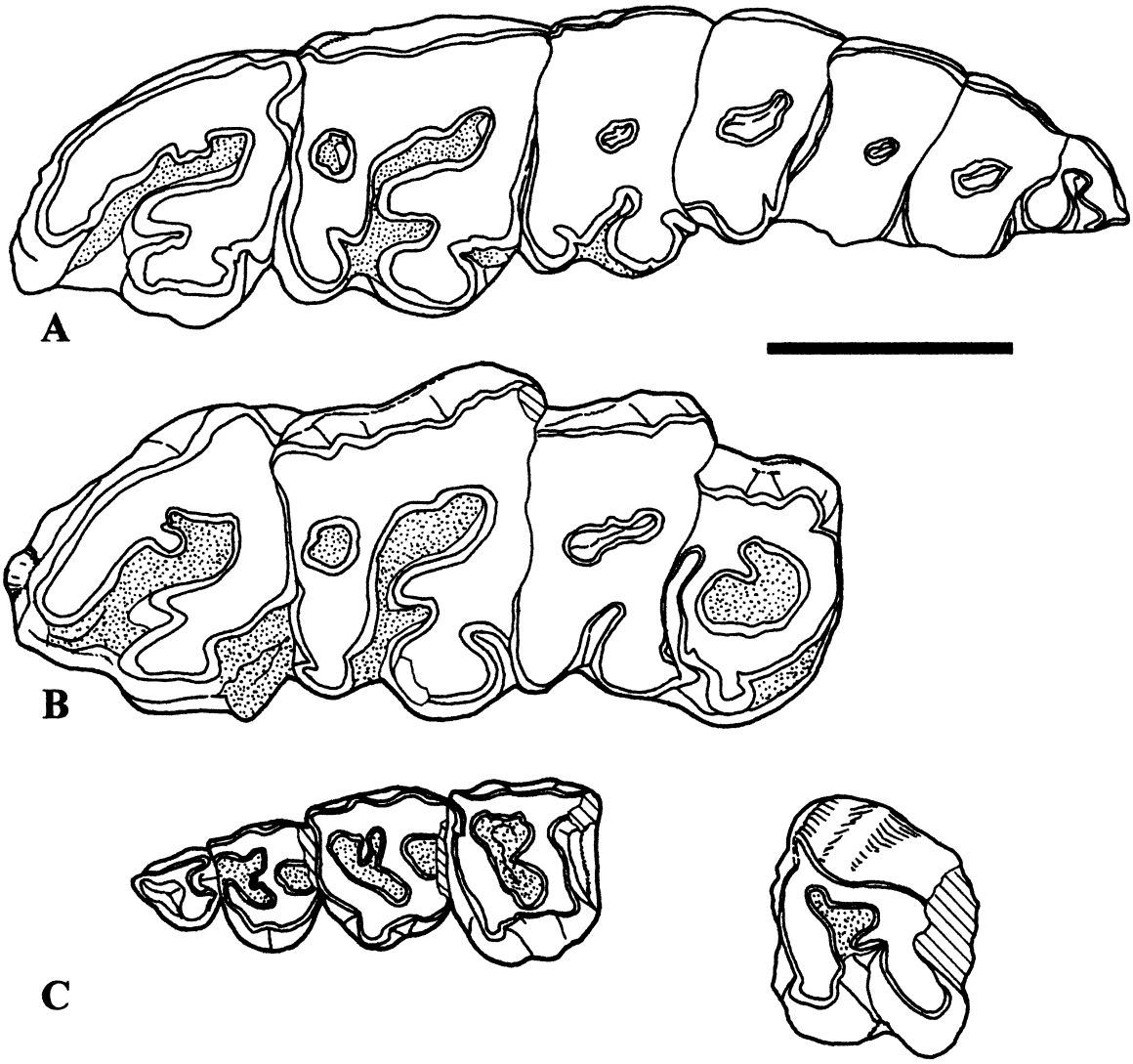

Fig. 6 A–C. *Huaqingtherium lintungense.* —A. Reversed left upper series P1-M1 from the holotype skull IVPP V-3085, Lengshuigou (Shaanxi, China, Middle Miocene). —B. Right upper series P4-M3 from the skull AMNH 26531, Wolf Camp Quarry (Tunggur, Inner Mongolia, China, Middle Miocene). —C. '*Caementodon*' (*Beliajevina*) *fangxianense*. Left upper series P1-P4 + M2 IVPP V-5151 (holotype), Erlanggang (Hubei, China, Middle Miocene). Modified from Yan (1979: 190, fig.1). All are occlusal views. Scale bar = 5 cm.

'*Tesselodon*' Cerdeño, 1996: 26, text-fig. 19.

Holotype. CHINA, Hubei, Fangxian, Erlanggang. IVPP V-5151, left upper series with P1-4 and M2. Figured by Yan (1979).

Geographic range. So far restricted to the Erlanggang locality (Hubei, China).

Stratum typicum and stratigraphic range. Lowermost Tunggurian, Early Middle Miocene (Guan & Made 1993).

Emended diagnosis. That of the subgenus '*Caementodon*' (*Beliajevina*)*:* see above.

Material examined. The only specimen so far attributed to '*C.*' (*B*) *fangxianense* is the holotype (IVPP V-5151). Cranial and postcranial remains are unknown.

Description. The holotype and only specimen has been described by Yan (1979). There is no need for further description, but a more detailed illustration is presented in Fig. 6C.

Discussion. As for *P. mongoliense* (see above), the upper cheek tooth series of IVPP V-5151 (Fig. 5C) shares the synapomorphies characteristic of Elasmotheriina: lingual wall and wide postfossette on P4, strong constriction on the protocone of M1-2 (Fig. 3, node I). The taxon from Erlanggang is more derived than *Kenyatherium* and *Bugtirhinus* in having a crista on P3, a low posterior cingulum and no lingual cingulum on M2 (Fig. 3, node I). The dimensions of V-5151 are small and the dental morphology is very similar to that of *Caementodon oettingenae* (Fig. 5C), although a single synapomorphy, absent in the latter, makes them different (Fig. 3, node l): on P2, the protocone is more reduced than the hypocone (V-5151). The similarity is still more striking with '*Dicerorhinus caucasicus*' Borissiak, 1935 from Belometschetskaya, which Heissig (1974) was the first to include within the elasmotheriines, under the name '*Beliajevina caucasica*' (Borissiak, 1935). The taxon from Erlanggang shares with the latter three exclusive synapomorphies: the lingual cingulum is always lacking on P2-4, as is the labial cingulum on upper molars; the constriction of the protocone is weak on M2 (Table 1; Fig. 3, node m). However, '*B. caucasica*' show some differences, corresponding to autapomorphies, with the series V-5151 (Table 1; crochet always simple on P2-4; P2 with hypocone anterior to metacone; constriction of the protocone usually absent on P3-4; hypocone and metacone separated on P4; M1-2 with a strong paracone fold). On the other hand, '*T. fangxianense*' is short of any autapomorphy (Fig. 3), so this taxon can be considered as the ancestor of '*B. caucasica*' for the checked characters.

More derived Elasmotheriina (*Hispanotherium*, *Procoelodonta*, *Huaqingtherium*, *Iranotherium*, *Parelasmotherium*, *Sinotherium* and *Elasmotherium*) bear at least eight synapomorphies, whose absence is observable in '*B. caucasica*' but generally not preserved in V-5151 (Table 1; Fig. 3, node N): constricted hypocone on P3-4 and M1, concave medial border on the radius, low and smooth intermediate relief on the metapods, expansion of the calcaneus-facet 1 usually wide and low on the astragalus, straight posterior tuberosity on the magnum, small-sized trapezium facet on the scaphoid and proximal radius-ulna facets usually distinct. The absence of any cranial and postcranial remains that can be attributed to '*Tesselodon fangxianensis*' Yan (1979) enhances the uncertainty of its taxonomic status. The distribution of the synapomorphies discussed above (Table 1; Fig. 3) can still be interpreted in taxonomic terms: the generic synonymy between *Beliajevina* Heissig, 1974 and *Tesselodon* Yan, 1979 is supported. Yet, the specimens from Belometchetskaya and Erlanggang appear to be different, even on so scant remains, at a specific level. Besides, *Caementodon oettingenae* Heissig, 1972 is close to the '*Beliajevina–T. fangxianense*' clade (Fig. 3, node m). With respect to other elasmotheriines, these three taxa are very similar to each other. Prior to new findings to come, I propose including all of them in the genus *Caementodon* Heissig, 1972; as three different species (the node l is not well-supported). The '*C. caucasicum–C. fangxianense*' clade (with correct spelling) can be interpreted as a new monophyletic subgenus, '*Caementodon*' (*Beliajevina*) Heissig, 1974. The latter is distinct from the monospecific subgenus *Caementodon* (*Caementodon*) Heissig, 1972.

Genus *Huaqingtherium* Huang & Yan, 1983

Type species. H. lintungense (Zhai, 1978), by monotypy.

Emended diagnosis. That of the type species. See below.

***Huaqingtherium lintungense* (Zhai, 1978)**

(Fig. 6A,B)

Rhinoceros (*partim*) Borissiak, 1948: 20.
Hispanotherium lintungensis Zhai, 1978: 122–126, text-fig. 46, Pl. 14; Cerdeño 1996: 25–27, 30
Huaqingtherium lintungensis Huang & Yan, 1983: 21.
Caementodon tongxinensis sp. nov. Guan, 1988: 1–21; Pl. 2, figs 3, 4; Pl. 3, figs 3–5 and 8–11.
Hispanotherium sp. Guan, 1988: 15.
Huaqingtherium giui Guan, 1988: 3, 15.
Huaqingtheium giui Guan, 1988: 3.
'*Hispanotherium*' Qiu, 1990: 533.
Hispanotherium Qiu, 1990: 542.
Caementodon tongxinensis Guan, 1993: 203–207; Pl. 2; Guan & Made 1993: 153; Cerdeño 1996: 26; Guan *et al.* 1998: 148–150, Pl. 2, fig. 7; Qiu *et al.* 1999: 447.
Huaqingtherium qiui Guan, 1993: 202–207, Pl. 1; Guan *et al.* 1998: 149–150 [partim]; Qiu *et al.* 1999: 447.
Iranotherium cf. *longirhinus* Cerdeño, 1995: 2; Cerdeño 1996: 2.
'*Caementodon tongxinensis*' Cerdeño, 1996: 30, text-fig. 19.
Hispanotherium lintungense Cerdeño, 1996: text-figs 18, 19.
Hispanotherium tungurense nov. sp. Cerdeño, 1996: 1, 2, 18–32; text-figs 10–15, 18, 19.
Hispanotherium tungurense Qiu *et al.*, 1999: 447.

Holotype. CHINA, Shaanxi, Lengshuigou. IVPP V-3085, skull with left and right P1-M3. Figured by Zhai (1978).

Geographic range. China (Shaanxi, Ningxia, Inner Mongolia).

Stratum typicum. Middle Tunggurian (Middle Miocene, MN 7) after Qiu (1990) and Qiu *et al.* (1999).

Stratigraphic range. Tunggurian (MN 6–8; Middle Miocene).

Emended diagnosis. Elasmotheriina with a crochet usually simple on P2-4; hypocone stronger than protocone on P2; transverse metaloph on P3-4; metacone and hypocone separated

Table 3 *Huaqintherium lintungense*. Comparative dimensions of the teeth from Lengshuigou, Tunggur and Tongxin. * After Cerdeño (1996: 37, table 2). Abbreviations: L, length; W, width.

	P1		P2		P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
Lengshuigou	20–22	20–21	25	33–36	26	41	27–28	44	32–33	51–54	48–49	58–60	48	52–54
Mean	21	20.5	25	34.5	26	41	27.5	44	32.5	52.5	48.5	59	48	53
Tunggur*	20.5	18.1	26.2	30.5	34.2	41.8	36.1–39.4	47.2–57.9	42.5–49.2	59.2	64.4	60.9–64.6	46.4–60	59.8–67.5
Mean	20.5	18.1	26.2	30.5	34.2	41.8	37.2	52.7	45.7	59.2	64.4	69.1	52.3	61.3
Tongxin	—	—	27	31	29–30	37.5–40	—	—	—	—	47–49	51–56	40–43	46–52
Mean	—	—	27	31	29.5	38.7	—	—	—	—	48	53.5	41.6	48.4

on P4; paracone fold strong on M1-2. Less advanced than *Iranotherium*, *Parelasmotherium*, *Sinotherium* and *Elasmotherium* in bearing no anterior shifting of the cheek tooth series, unfused nasals, no huge post-tympanic process, no enamel folding, no partial hypsodonty, no cristella but a metacone fold on M1-2.

Material examined. Skull (IVPP V-3085, holotype) from an aged individual, found associated with two astragali and a calcaneus (IVPP V-3086), from the Lengshuigou locality (Shaanxi, China), initially described by Zhai (1978). I could not recover the postcranial remains in the IVPP collections; about 50 cranial, dental and postcranial remains from Dingjiaergou (locality also known as Tongxin). These specimens, previously identified as '*Caementodon tongxinensis*' Guan, 1988; '*Hispanotherium* sp.' and/or '*Huaqingtherium qiui*' Guan, 1993, are deposited in the BNHM; about 60 specimens (skulls, mandibles, isolated teeth and postcranial elements), yet described and listed by Cerdeño (1996; 'type B'). Originating from several localities of the Tung Gur and (Inner Mongolia, China), stored in the collections of the AMNH.

Description. The greatest part of the hypodigm of *H. lintungense* has been described and figured in Zhai (1978), Guan (1988, 1993) and Cerdeño (1996). There is no need for further description. The upper cheek teeth IVPP V-3085 can be compared with the worn series AMNH 26531 in Fig. 6.

Discussion. According to Zhai (1978), the specimens from Lengshuigou are closely related to *Hispanotherium matritense* (Lartet in Prado 1864). The weak development of the crochet and enamel foldings leads this author to consider this taxon as a different species, '*H. lintungensis*' Zhai, 1978. Huang & Yan (1983) assume these specimens from Lengshuigou may belong to a distinct genus, '*Huaqingtherium*' Huang & Yan, 1983, without any further comment. Guan (1993) includes another species in the latter genus ('*Huaqingtherium qiui*'), from some remains found in Tongxin. Contrary to what was first mentioned by Cerdeño (1996), the hypodigm of this taxon (BPV-414, associated broken skull and mandible; BPV-430, mandible) shows typically elasmotheriine features (cement, closed medifossettes on upper premolars). In the same locality (Tongxin = Dingjiaergou), Guan (1988) also named the new species '*Caementodon tongxinensis*'.

Direct examination of most of the remains attributed to '*Hispanotherium lintungensis*' Zhai, 1978; '*Caementodon tongxinensis*' Guan, 1993 and '*Huaqingtherium qiui*' Guan, 1993 did not yield any morphological feature differing from one series to another. I assume their generic and specific synonymy. In the same way, the remains identified as '*Hispanotherium tungurense* nov. sp.' Cerdeño, 1996, stored at the AMNH (New York) are extremely similar to the specimens of *H. lintungense* (Fig. 6A,B). The series from the Tunggur Plateau has the largest dental dimensions, whereas the teeth from Tongxin are the smallest (Table 3). The smallest remains, from the lower level in Tongxin, are somewhat older than the largest ones, from the upper levels of Tunggur. The size increase is a general evolutionary trend in elasmotheriines, also observed at the intraspecific level in *Hispanotherium grimmi* Heissig, 1974 (Antoine 2002).

This distinct elasmotheriine taxon, '*H. lintungensis* Zhai, 1978', is the sister-group of post-Middle Miocene Elasmotheriina (*Iranotherium*, *Parelasmotherium*, *Sinotherium* and *Elasmotherium*; Fig. 3, node W). All of them are more derived than *Kenyatherium*, *Bugtirhinus*, *Caementodon*, *Hispanotherium* (*sensu stricto*) and *Procoelodonta* in possessing nasals broadened rostrally, orbits laterally projected, cement very abundant, labial cingulum always absent on the upper premolars and generally absent on the upper molars (Table 1; Fig. 3, node V). Meanwhile, the anterior shifting of the cheek tooth series, the nasals at least partly fused, the huge post-tympanic process, the noticeable enamel foldings, the partial hypsodonty, the general presence of a cristella and the absence of a metacone fold on M1-2 only characterize the post-Middle Miocene Elasmotheriina (Fig. 3, node W). They are not observed in the series from the Tunggur Tableland (Mongolia), Lengshuigou and Tongxin (China). This series appears

to be well separated both from primitive and derived Elasmotheriina, including the *Hispanotherium* species from western Europe and Anatolia (Cerdeño 1992; Heissig 1996, 1999; Antoine 1997; Antoine *et al.* 2000). I consider this distinction to be at the genus level (Fig. 3, nodes V and W well supported). Therefore, the valid binomen is *Huaqingtherium lintungense* (Zhai 1978).

Phylogenetic relationships

A phylogenetic analysis based on morphological characters originally described by Antoine (2002) has been performed on the elasmotheriines from China and Mongolia. The 282 cranial, dental and postcranial characters and corresponding character states are listed in Appendix 1. The data set, detailed in Appendix 2, includes 28 terminal taxa: four outgroups (*Tapirus terrestris*, *Hyrachyus eximius*, *Trigonias osborni*, *Ronzotherium filholi*), three Teleoceratina (*Teleoceras fossiger* from the Late Miocene of North America, *Brachypotherium brachypus* from the Early and Middle Miocene of Europe, *Prosantorhinus douvillei* from the Early Miocene of Western Europe), 20 Elasmotheriinae (18 Elasmotheriina [exhaustive], *Diceratherium armatum* from the Late Oligocene-Early Miocene of North America, *Menoceras arikarense* from the Early Miocene of North America) and the controversial *Shennongtherium hypsodontus*. All are included in the present analysis.

A branch-and-bound search is impossible because of the high number of terminals. The heuristic 'mh*bb' command (Hennig86 vs. 1.5; Farris 1988) gives two equally parsimonious trees (860 steps; CI = 0.42; RI = 0.61). The consensus tree is illustrated in Fig. 3. The distribution of unambiguous synapomorphies is detailed in Table 1.

Suprageneric taxa such as Teleoceratina, Elasmotheriinae, Elasmotheriini and Elasmotheriina are monophyletic. *Diceratherium armatum* and the Elasmotheriini are sister-groups within Elasmotheriinae, while *Menoceras arikarense* is the sister-group of Elasmotheriina (i.e. elasmotheriines *sensu stricto*). Even if its position is not stated precisely, *Shennongtherium hypsodontus* shares two unambiguous synapomorphies with *Prosantorhinus douvillei* and *Teleoceras fossiger* within Teleoceratina (transverse metaloph and reduced protocone on P2; Table 1; Fig. 3, node F). Therefore, *S. hypsodontus* is removed from the Elasmotheriina, as previously suggested by Fortelius & Heissig (1989).

The Middle Miocene Elasmotheriina from China and Mongolia appear at different levels in the cladogram (Fig. 3). '*Caementodon*' (*Beliajevina*) *fangxianense* is more primitive than '*Procoelodonta*' (*Begertherium*) *borissiaki* and *P.* (*Procoelodonta*) *mongoliense*; *Huaqingtherium lintungense* is the more advanced elasmotheriine encountered in the Middle Miocene. Their respective positions in the tree, their morphological peculiarities and the subsequent taxonomic remarks are precisely detailed above in Materials and methods and Systematics.

Conclusion

The main characters of derived elasmotheres (huge size, frontal horn, ossified nasal septum, enamel folding, hypsodonty, loss of anterior dentition, lengthening of the molar series; Fig. 3) are absent in Middle Miocene Elasmotheriina from China and Mongolia. Most of these features appear somewhat later, during the Late Miocene or the Pliocene, in *Parelasmotherium*, *Sinotherium* and then *Elasmotherium*. Nevertheless, some morphological innovations are first observed in *Huaqingtherium lintungense*. As the most derived elasmotheriine from the Middle Miocene of Eastern Asia, it exemplifies the advanced elasmotheres, with respect to other Elasmotheriina. The body size is greater, the skull has lengthened, the nasals have widened and the nasal horn has strengthened, the orbits begin to project laterally, the cement becomes more and more abundant, the tooth crowns are higher, the enamel folding appears, and the anterior dentition is reduced. Such cranio-dental evolution demonstrates unequivocally the increasing proportion of grass-eating in the elasmotheriine diet throughout the Middle Miocene. This tendency continues throughout the Pliocene and the Pleistocene. These observations conform with the palaeoenvironmental reconstructions of the North-Asiatic Province proposed by Leopold *et al.* (1992) and Qiu *et al.* (1999) for the Late Middle Miocene: savannas with Gramineae and Herbaceae, under temperate climates for which *H. lintungense* was well adapted.

The persistence and diversity of the Elasmotheriina throughout the Middle Miocene in Eastern Asia help explain how minute brachyodont animals (such as *Bugtirhinus* and *Caementodon oettingenae*) gave rise to the mammoth-sized hypsodont *Elasmotherium*.

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Appendix 1

Cranial, dental and postcranial characters and character states used for the cladistic analysis. Five characters are treated as non-additive (NA): 72, 94, 102, 140 and 187. The others are additive. Fourteen characters are non-informative for the 28 terminal taxa included in the present analysis (9, 32, 41, 52, 92, 113, 139, 163, 164, 215, 225, 237, 273, 281, indicated * in the list). They have been retained because alternative character states define other rhinocerotid taxa [within square parentheses] otherwise detailed by Antoine (2002).

SKULL

1 Nasal: lateral apophysis = 0, absent; 1, present
2 Maxillary: *foramen infraorbitalis* = 0 above premolars; 1, above molars
3 Nasal notch = 0, above P1-3; 1, above P4-M1
4 Nasal septum = 0, never ossified; 1, ossified even sometimes
5 Nasal septum: ossified = 0, partially; 1, totally
6 Nasal/lacrymal: contact = 0, long; 1, punctual or absent
7 Orbit: anterior border = 0, above P4-M2; 1, above M3; 2, behind M3
8 Lacrymal: *processus lacrymalis* = 0, present; 1, absent
9* Frontal: *processus postorbitalis* = 0, present; 1, absent [recent African rhinos; *Coelodonta antiquitatis*]
10 Maxillary: anterior base of the *processus zygomaticus maxillari* = 0, high; 1, low
11 Zygomatic arch = 0, low; 1, high; 2, very high
12 Zygomatic arch: *processus postorbitalis* = 0, present; 1, absent
13 Zygomatic arch: *processus postorbitalis* = 0, on jugal; 1, on squamosal
14 Jugal/squamosal: suture = 0, smooth; 1, rough
15 Skull: dorsal profile = 0, flat; 1, concave; 2, very concave
16 Sphenoid: *foramen sphenorbitale* and *f. rotundum* = 0, distinct; 1, fused
17 Squamosal: area between temporal and nuchal crests = 0, flat; 1, depression
18 External auditory *pseudo-meatus* = 0, open; 1, partially closed; 2, closed
19 Occipital side = 0, inclined forward; 1, vertical; 2, inclined backward
20 Occipital: nuchal tubercle = 0, little developed; 1, developed; 2, very developed
21 Skull: back of teeth row = 0, in the posterior half; 1, restricted to the anterior half
22 Pterygoid: posterior margin = 0 nearly horizontal; 1, nearly vertical
23 Skull = 0, dolichocephalic; 1, brachycephalic
24 Nasal bones: rostral end = 0, narrow; 1, broad; 2, very broad
25 Nasal bones = 0, totally separate; 1, anteriorly separate; 2, fused
26 Nasal bones = 0, long; 1, short; 2, very long
27 Median nasal horn = 0, absent; 1, present
28 Median nasal horn = 0, small; 1, developed
29 Paired nasal horns = 0, absent; 1, present
30 Paired nasal horns = 0, terminal bumps; 1, lateral crests
31 Frontal horn = 0, absent; 1, present
32* Frontal horn = 0, small [recent two-horned rhinos]; 1, huge
33 Orbit: lateral projection = 0, absent; 1, present
34 Zygomatic width/frontal width = 0, less than 1.5; 1, more than 1.5
35 Frontal-parietal = 0, sagittal crest; 1, close frontoparietal crests; 2, distant crests
36 Occipital crest = 0, concave; 1, straight; 2, forked
37 Maxillary: *processus zygomaticus maxillari*, anterior tip = 0, progressive; 1, brutal
38 Vomer = 0, acute; 1, rounded
39 Squamosal: articular tubercle = 0, smooth; 1 high
40 Squamosal: transversal profile of articular tubercle = 0, straight; 1, concave
41* Squamosal: *foramen postglenoideum* = 0, distant from the *processus postglenoidalis*; 1, close to it [*Plesiaceratherium mirallesi*]
42 Squamosal: *processus postglenoidalis* = 0, flat; 1, convex; 2, dihedron
43 Basioccipital: *foramen nervi hypoglossi* = 0, in the middle of the fossa; 1 shift antero-externally
44 Basioccipital: sagittal crest on the basilar process = 0, absent; 1, present
45 Squamosal: posterior groove on the *processus zygomaticus* = 0, absent; 1, present
46 Squamosal-occipital: *processus posttympanicus* and *processus paraoccipitalis* = 0, fused; 1, distant
47 Squamosal: *processus posttympanicus* = 0, well developed; 1, little developed; 2, huge
48 Occipital: *processus paraoccipitalis* = 0, well developed; 1, little developed
49 Occipital: *foramen magnum* = 0, circular; 1, subtriangular
50 Basioccipital: median ridge on the condyle = 0, absent; 1, present

51 Basioccipital: medial truncation on the condyle = 0, absent; 1, present
52* Basioccipital: medial truncation on the condyle = 0, present at juvenile stage [*Plesiaceratherium mirallesi*]; 1, still present at adult stage

MANDIBLE

53 Symphysis = 0, very upraised; 1, upraised; 2, nearly horizontal
54 Symphysis = 0, spindly; 1, massive; 2, very massive
55 Symphysis: posterior margin = 0, in front of p2; 1, level of p2-4
56 *Foramen mentale* = 0, in front of p2; 1, level of p2-4
57 *Corpus mandibulae*: lingual groove = 0, present; 1, absent
58 *Corpus mandibulae*: lingual groove = 0, still present at adult stage; 1, present at juvenile stage only
59 *Corpus mandibulae*: base = 0, straight; 1, convex; 2, very convex
60 Ramus = 0, vertical; 1, inclined forward; 2, inclined backward
61 Ramus: *processus coronoideus* = 0, well developed; 1, little developed
62 *Foramen mandibulare* = 0, below the teeth neck; 1, above the teeth neck

TEETH

63 Compared length of the premolars/molars rows = 0, $100 \times L_{P3\text{-}4}/L_{M1\text{-}3} > 50$; 1, $42 < 100 \times L_{P3\text{-}4}/L_{M1\text{-}3} < 50$; 2, $100 \times L_{P3\text{-}4}/L_{M1\text{-}3} < 42$
64 Cheekteeth: enamel foldings = 0, absent; 1, weak; 2, developed; 3, intense
65 Cheekteeth: cement = 0, absent; 1, present
66 Cheekteeth: cement = 0, weak or variable; 1, abundant
67 Cheekteeth: shape of enamel = 0, wrinkled; 1, wrinkled and corrugated; 2, corrugated and arborescent
68 Cheekteeth: crown = 0, low; 1, high
69 Cheekteeth: crown = 0, high; 1, partial hypsodonty; 2, subhypsodonty; 3, hypsodonty
70 Cheekteeth: roots = 0, distinct; 1, joined; 2, fused
71 I1 = 0, present; 1, absent
72 I1: shape of the crown cross section = 0, almond; 1, oval; 2, halfmoon NA
73 I2 = 0, present; 1, absent
74 I3 = 0, present; 1, absent
75 C1 = 0, present; 1, absent
76 i1 = 0, present; 1, absent
77 i1: crown = 0, developed, with a pronounced neck; 1, reduced
78 i2 = 0, present; 1, absent
79 i2: shape = 0, incisor-like; 1, tusk-like
80 i2: orientation = 0, parallel; 1, divergent
81 i3 = 0, present; 1, absent
82 c1 = 0, present; 1, absent
83 Upper premolars: labial cingulum = 0, always present; 1, usually present; 2, usually absent; 3, always absent
84 P2-4: crochet = 0, always absent; 1, usually present; 2, always present
85 P2-4: crochet = 0, always simple; 1, usually simple; 2, usually multiple
86 P2-4: metaloph constriction = 0, absent; 1, present
87 P2-4: lingual cingulum = 0, always present; 1, usually present; 2, usually absent; 3, always absent
88 P2-4: lingual cingulum = 0, continuous; 1, reduced
89 P2-4: postfossette = 0, narrow; 1, wide; 2, posterior wall
90 P2-3: antecrochet = 0, always absent; 1, usually absent; 2, usually present; 3, always present
91 P1 in adults = 0, always present; 1, usually present; 2, always absent
92* P1: antero-lingual cingulum = 0, present; 1, absent [*Rhinoceros sondaicus*]
93 P2 = 0, present; 1, absent
94 P2: protocone and hypocone = 0, fused; 1, lingual bridge; 2, separated; 3, lingual wall NA
95 P2: metaloph = 0, hypocone posterior to metacone; 1, transverse; hypocone anterior to metacone
96 P2: lingual groove = 0, present; 1, absent
97 P2: protocone = 0, equal or stronger than the hypocone; 1, less strong than the hypocone
98 P2: protoloph = 0, present; 1, absent
99 P2: protoloph = 0, joined to the ectoloph; 1, interrupted
100 P3-4: medifossette = 0, always absent; 1, usually absent; 2, usually present; 3, always present
101 P3-4: constriction of the protocone = 0, always absent; 1, usually absent; 2, usually present; 3, always present
102 P3-4: protocone and hypocone = 0, fused; 1, lingual bridge; 2, separate; 3, lingual wall NA
103 P3-4: metaloph = 0, transverse; 1, hypocone posterior to metacone; 2, hypocone anterior to metacone
104 P3: protoloph = 0, joined to the ectoloph; 1, interrupted
105 P3: crista = 0, always absent; 1, usually absent; 2, usually present; 3, always present
106 P3: pseudometaloph = 0, always absent; 1, sometimes present
107 P4: antecrochet = 0, always absent; 1, usually absent; 2, usually present; 3, always present
108 P4: hypocone and metacone = 0, joined; 1, separate
109 Upper molars: labial cingulum = 0, always present; 1, usually present; 2, usually absent; 3, always absent
110 Upper molars: antecrochet = 0, always absent; 1, usually absent; 2, usually present; 3, always present
111 Upper molars: crochet = 0, always absent; 1, usually absent; 2, usually present; 3, always present
112 Upper molars: crista = 0, always absent; 1, usually absent; 2, usually present; 3, always present
113* Upper molars: medifossette = 0, always absent; 1, usually absent [*Diceros bicornis*]; 2, usually present [*Ceratotherium simum*; *Coelodonta antiquitatis*; *Rhinoceros unicornis*]
114 Upper molars: lingual cingulum = 0, always present; 1, usually present; 2, usually absent; 3, always absent
115 M1-2: constriction of the protocone = 0, always absent; 1, usually absent; 2, usually present; 3, always present
116 M1-2: constriction of the protocone = 0, weak; 1, strong
117 M1-2: paracone fold = 0, present; 1, absent
118 M1-2: paracone fold = 0, strong; 1, weak
119 M1-2: metacone fold = 0, present; 1, absent
120 M1-2: metastyle = 0, short; 1, long
121 M1-2: metaloph = 0, long; 1, short
122 M1-2: posterior part of the ectoloph = 0, straight; 1, concave
123 M1-2: cristella = 0, always absent; 1, usually present; 2, always present
124 M1-2: posterior cingulum = 0, continuous; 1, low and reduced
125 M1: metaloph = 0, continuous; 1, hypocone isolated
126 M1: antecrochet-hypocone = 0, always separate; 1, sometimes joined; 2, always joined
127 M1: postfossette = 0, present; 1, usually absent
128 M2: protocone, lingual groove = 0, always absent; 1, usually absent; 2, always present
129 M2: metaloph = 0, continuous; 1, hypocone isolated
130 M2: mesostyle = 0, absent; 1, present
131 M2: mesostyle = 0, weak; 1, strong
132 M2: antecrochet and hypocone = 0, separate; 1, joined
133 M3: ectoloph and metaloph = 0, distinct; 1, fused ectometaloph
134 M3: shape = 0, quadrangular; 1, triangular
135 M3: constriction of the protocone = 0, always absent; 1, usually absent; 2, always present
136 M3: protocone = 0, trefoil-shape; 1, indented
137 M3: protoloph = 0, transverse; 1, lingually elongated
138 M3: posterior groove on the ectometaloph = 0, present; 1, absent
139* p2-3: vertical external roughnesses = 0, absent; 1, present [*Plesiaceratherium mirallesi*]
140 Lower cheekteeth: external groove = 0, developed; 1, smooth, U-shaped; 2, angular, V-shaped (NA)
141 Lower cheekteeth: external groove = 0, vanishing before the neck; 1, developed until the neck

142 Lower cheekteeth: trigonid = 0, angular; 1, rounded
143 Lower cheekteeth: trigonid = 0, obtuse or right dihedron; 1, acute dihedron
144 Lower cheekteeth: metaconid = 0, joined to the metalophid; 1, constricted
145 Lower cheekteeth: entoconid = 0, joined to the hypolophid; 1, constricted
146 Lower premolars: lingual opening of the posterior valley = 0, U-shape; 1, narrow, V-shape
147 Lower premolars: lingual cingulum = 0, always present; 1, usually present; 2, usually absent; 3, always absent
148 Lower premolars: lingual cingulum = 0, reduced; 1, continuous
149 Lower premolars: labial cingulum = 0, present; 1, absent
150 Lower premolars: labial cingulum = 0, continuous; 1, reduced
151 d1/p1 in adults = 0, always present; 1, usually present; 2, usually absent; 3, always absent
152 d1: 0, always two-rooted; 1, usually two-rooted; 2, always one-rooted
153 p2 = 0, always present; 1, usually present; 2, always absent
154 p2: paralophid = 0, isolated, spur-like; 1, curved, without constriction
155 p2: paraconid = 0, developed; 1, reduced
156 p2: posterior valley = 0, lingually open; 1, usually closed; 2, always closed
157 Lower molars: lingual cingulum = 0, always present; 1, usually present; 2, usually absent; 3, always absent
158 Lower molars: lingual cingulum = 0, reduced; 1, continuous
159 Lower molars: labial cingulum = 0, always present; 1, usually present; 2, usually absent; 3, always absent
160 Lower molars: labial cingulum = 0, continuous; 1, reduced
161 Lower molars: hypolophid = 0, transverse; 1, oblique; 2, almost sagittal
162 m2-3: lingual groove of the entoconid = 0, absent; 1, present
163* dI1 = 0, present; 1, absent [*Ceratotherium simum*; *Coelodonta antiquitatis*]
164* dI2 = 0, present; 1, absent [Rhinocerotina]
165 D2: mesostyle = 0, present; 1, absent
166 D3-4: mesostyle = 0, absent; 1, present
167 D2: lingual wall = 0, absent; 1, present
168 D2: secondary folds = 0, absent; 1, present
169 D2: mesoloph = 0, absent; 1, present
170 di1 = 0, present; 1, absent
171 di2 = 0, present; 1, absent
172 Lower milk teeth: constriction of the metaconid = 0, present; 1, absent
173 Lower milk teeth: constriction of the entoconid = 0, absent; 1, present
174 Lower milk teeth: protoconid fold = 0, present; 1, absent
175 d1 (in juveniles) = 0, present; 1, absent
176 d2-3: vertical external roughnesses = 0, absent; 1, present
177 d2-3: ectolophid fold = 0, present; 1, absent
178 d2: anterior groove on the ectolophid = 0, absent; 1, present
179 d2: paralophid = 0, simple; 1, double
180 d2: posterior valley = 0, always open; 1, usually open; 2, usually closed; 3, always closed
181 d3: paralophid = 0, double; 1, simple
182 d3: lingual groove on the entoconid = 0, always absent; 1, usually absent; 2, always present

POSTCRANIAL SKELETON

183 Atlas: outline of the rachidian canal = 0, bulb; 1, mushroom
184 Atlas: alar notch = 0, absent; 1, present
185 Atlas: *foramen vertebrale lateralis* = 0, absent; 1, present
186 Atlas: condyle-facets = 0, comma-like; 1, kidney-like
187 Atlas: axis-facets = 0, straight; 1, sigmoid; 2, transversally concave NA
188 Atlas: *foramen transversarium* = 0, present; 1, absent
189 Atlas: *foramen transversarium* = beside the axis-facet; 1, hidden by the axis-facet
190 Scapula = 0, elongated ($1.5 < H/APD \leq 2$); 1, very elongated ($H/APD > 2$); 2, spatula-shaped ($H/APD \leq 1.5$)
191 Scapula: glenoid fossa = 0, oval; 1, medial border straight
192 Humerus: greater trochiter = 0, high; 1, low
193 Humerus: *fossa olecrani* = 0, high; 1, low
194 Humerus: distal articulation = 0, egg cup (shallow median constriction); 1, diabolo (deep median constriction)
195 Humerus: scar on the trochlea = 0, absent; 1, present
196 Humerus: distal gutter on the epicondyle = 0, absent; 1, present
197 Radius: anterior border of the proximal articulation = 0, straight; 1, M-shaped
198 Radius: medial border of the diaphysis = 0, straight; 1, concave
199 Radius: proximal ulna-facets = 0, always separated; 1, usually separated; 2, usually fused; 3, always fused
200 Radius: insertion of the *m. biceps brachii* = 0, shallow; 1, deep
201 Radius/ulna = 0, independent; 1, in contact or fused
202 Radius: gutter for the *m. extensor carpi* = 0, deep and wide; 1, weak
203 Radius/ulna: second distal articulation = 0, absent; 1, present
204 Radius: posterior expansion of the scaphoid-facet = 0, low; 1, high
205 Ulna: angle between diaphysis and olecranon = 0, open; 1, closed
206 Ulna: anterior tubercle on the distal end = 0, absent; 1, present
207 Scaphoid: postero-proximal facet with semilunate = 0, present; 1, absent or contact
208 Scaphoid: trapezium-facet = 0, large; 1, small
209 Scaphoid: magnum-facet in lateral view = 0, concave; 1, straight
210 Scaphoid: comparison between anterior and posterior heights = 0, equal; 1, Hant < H post
211 Semilunate: ulna-facet = 0, absent; 1, present
212 Semilunate: distal border of anterior side = 0, acute; 1, rounded
213 Semilunate: anterior side = 0, keeled; 1, smooth
214 Pyramidal: distal facet for semilunate = 0, symmetric; 1, asymmetric; 2, L-shaped
215* Pyramidal: distal side = 0, triangular; 1, elliptic [*Ceratotherium simum*; *Diceros bicornis*; *Coelodonta antiquitatis*]
216 Trapezoid: proximal border in anterior view = 0, symmetric; 1, asymmetric
217 Magnum: proximal border of the anterior side = 0, nearly straight; 1, concave
218 Magnum: indentation on the medial side = 0, absent; 1, present
219 Magnum: indentation on the medial side = 0, always shallow; 1, usually shallow; 2, always deep
220 Magnum: posterior tuberosity = 0, short; 1, long
221 Magnum: posterior tuberosity = 0, curved; 1, straight
222 Unciform: pyramidal-facet and McV-facet = 0, always separate; 1, usually separate; 2, always in contact
223 Unciform: posterior expansion of the pyramidal-facet = 0, always absent; 1, usually absent; 2, usually present; 3, always present
224 McII: magnum-facet = 0, curved; 1, straight
225* McII: anterior McIII-facet = 0, present; 1, sometimes absent [*Plesiaceratherium mirallesi*]
226 McII: posterior McIII-facet = 0, always absent; 1, usually absent; 2, always present
227 McII: anterior and posterior McIII-facets = 0, separated; 1, fused
228 McII: trapezium-facet = 0, always present; 1, usually present; 2, always absent
229 McIII: magnum-facet in anterior view = 0, visible; 1, invisible
230 McIV: proximal facet, outline = 0, trapezoid; 1, pentagonal; 2, triangular
231 McV: 0, functional; 1, vestigial
232 Metacarpals: insertion of the *m. extensor carpalis* = 0, flat; 1, salient
233 Coxal: *acetabulum* = 0, oval or circular; 1, subtriangular
234 Femur: trochanter major = 0, high; 1, low
235 Femur: head = 0, hemispheric; 1, medially stiff
236 Femur: surface of epiphysis of the head = 0, flat; 1, crescent-shaped
237* Femur: *fovea capitis* = 0, present; 1, absent [*Diceros bicornis*]
238 Femur: *fovea capitis* = 0, high and narrow; 1, low and wide
239 Femur: third trochanter = 0, developed; 1, very developed
240 Femur: relations between the medial lip of the trochlea and the diaphysis = 0, rupture; 1, ramp
241 Femur: proximal border of the patellar trochlea = 0, curved; 1, straight
242 Tibia: antero-distal groove = 0, present; 1, absent

243 Tibia: medio-distal gutter (tendon *m. tibialis posterior*) = 0, always present; 1, usually present; 2, always absent
244 Tibia: medio-distal gutter = 0, shallow; 1, deep
245 Tibia-fibula = 0, independent; 1, in contact or fused
246 Tibia: posterior apophysis = 0, high; 1, low
247 Tibia: posterior apophysis = 0, acute; 1, rounded
248 Fibula: proximal articulation = 0, low; 1, high
249 Fibula: distal end = 0, slender; 1, robust
250 Fibula: latero-distal gutter (tendon *peronaeus* muscles) = 0, shallow; 1, deep
251 Fibula: position of the latero-distal gutter = 0, posterior; 1, median
252 Astragalus: (Transverse Diameter/Height) ratio = 0, TD/H < 1; 1, 1 ≤ TD/H < 1.2; 2, 1.2 ≤ TD/H
253 Astragalus: (Antero-Posterior Diameter/Height) ratio = 0, APD/H < 0.65; 1, 0.65 ≤ APD/H
254 Astragalus: orientation of the fibula-facet = 0, subvertical; 1, oblique
255 Astragalus: fibula-facet = 0, flat; 1, concave
256 Astragalus: *collum tali* = 0, high; 1, low
257 Astragalus: posterior stop on the cuboid-facet = 0, present; 1, absent
258 Astragalus: caudal border of the trochlea, in proximal view = 0, sinuous; 1, nearly straight
259 Astragalus: orientation trochlea/distal articulation = 0, very oblique; 1, same axis
260 Astragalus: expansion of the calcaneus-facet 1 = 0, always present; 1, usually present
261 Astragalus: expansion of the calcaneus-facet 1 = 0, always wide and low; 1, usually wide and low; 2, always high and narrow
262 Astragalus: calcaneus-facet 1 = 0, very concave; 1, nearly flat
263 Astragalus: calcaneus-facets 2 and 3 = 0, always independent; 1, usually independent; 2, usually fused; 3, always fused
264 Calcaneus: fibula-facet = 0, always absent; 1, usually absent; 2, usually present; 3, always present
265 Calcaneus: tibia-facet = 0, always absent; 1, usually absent; 2, always present
266 Calcaneus: tuber calcanei = 0, massive; 1, slender
267 Calcaneus: insertion of the *m. fibularis longus* = 0, salient; 1, invisible
268 Navicular: cross section = 0, lozenge; 1, rectangle
269 Cuboid: proximal side = 0, oval; 1, triangular
270 Ectocuneiform: postero-lateral process = 0, weak; 1, developed
271 MtIII: proximal border of the anterior side = 0, straight; 1, concave; 2, sigmoid
272 MtIII: posterior MtII-facet = 0, present; 1, absent
273* MtIII: MtIV-facets = 0, distinct; 1, sometimes joined [*Coelodonta antiquitatis*]
274 MtIII: distal widening of the diaphysis (in adults) = 0, absent; 1, present
275 MtIII: cuboid-facet = 0, absent; 1, present
276 MtIII: cuboid-facet = 0, small; 1, large
277 MtIV: postero-proximal tuberosity = 0, isolated; 1, pad-shaped and continuous
278 Phalanx I for MtIII: symmetric insertions = 0, lateral; 1, nearly anterior
279 Limbs = 0, slender; 1, robust (brachypod)
280 Metapodials: intermediate relief = 0, high and acute; 1, low and smooth
281* Central metapodials: postero-distal tubercle on the diaphysis = 0, absent; 1, present [*Plesiaceratherium mirallesi*]
282 Lateral metapodials: insertion of the *m. interossei* = 0, long; 1, short (does not reach distal half of the shaft)

Appendix 2

Data matrix including 282 cranial, dental, and postcranial characters controlled on 28 terminal taxa. The four outgroups are *Tapirus terrestris*, *Hyrachyus eximius*, *Trigonias osborni* and *Ronzotherium filholi*. The characters 72, 94, 102, 140 and 187 are non-additive. Missing observations and nonapplicable characters are, respectively, coded '?' and '–'.

Ch 1–71	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	
Tapirus terrestris	0	0	1	0	–	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
	0	1	0	–	0	–	0	–	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	0	0	0	–	0	0	1	0	0	0	0	0	0	0	0	0	0	–	–	0	–	0	0	
Hyrachyus eximius	0	0	0	0	–	0	0	?	0	1	1	0	0	0	0	0	0	1	0	2	0	0	0	0
	0	0	0	–	0	–	0	–	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
	0	0	0	–	0	0	0	1	0	0	0	1	0	0	1	0	0	–	0	0	–	0	0	
Trigonias osborni	1	0	0	0	–	1	0	0	0	0	1	0	0	0	0	?	0	1	0	2	0	0	1	0
	0	0	0	–	0	–	0	–	0	0	0	0	0	?	0	0	0	0	0	1	0	0	1	0
	1	0	0	–	2	0	1	1	0	0	0	0	0	?	1	0	0	–	0	0	–	?	0	
Ronzotherium filholi	0	1	0	0	–	?	0	0	0	0	0	1	–	0	1	1	0	0	0	0	0	0	1	0
	0	0	0	–	0	–	0	–	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	0
	0	0	0	–	0	0	0	0	0	1	0	0	1	0	0	0	0	–	0	0	–	0	0	
Bugtirhinus praecursor	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	1	0	–	1	0	
'*Caementodon*' *caucasicum*	1	?	0	0	–	?	0	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	0
	0	0	1	0	0	–	0	–	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	0	1	1	1	–	1	0	?	?	1	0	1	0	1	1	0	?	?	
'*Caementodon*' *fangxianense*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	?	1	0	?	?	

Ch 1–71	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	
Caementodon oettingenae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	0	1	0	
Elasmotherium caucasicum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	2	?	1	?	?	2	2	?	?	2	3	1	1	2	1	3	–	?	
Elasmotherium sibiricum	0	1	1	1	1	?	1	–	0	0	0	1	–	?	1	1	0	0	2	2	1	0	0	0
	2	0	0	–	0	–	1	1	1	0	2	2	1	1	0	0	0	2	1	1	0	1	2	1
	0	0	1	1	1	2	1	1	1	–	2	2	0	0	2	3	1	1	2	1	3	–	1	
'*Hispanotherium*' *beonense*	0	0	0	0	–	?	0	0	0	1	1	0	1	0	1	1	1	0	2	2	0	0	0	0
	0	0	1	0	0	–	0	–	0	0	1	0	1	?	0	?	0	1	0	1	1	0	0	0
	1	0	1	1	1	0	0	0	0	1	1	0	?	1	1	0	1	0	1	1	0	2	0	
'*Hispanotherium*' *corcolense*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	1	0	?	?	0	1	1	?	?	?	1	0	1	0	1	1	0	2	?	
'*Hispanotherium*' *grimmi*	?	0	?	0	–	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
	0	?	1	0	0	–	?	?	?	?	2	0	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	1	0	1	1	1	–	1	0	?	0	1	0	1	0	1	1	0	2	?	
Hispanotherium matritense	0	?	?	0	–	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
	?	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	1	0	1	1	0	1	1	0	0	1	1	0	1	0	1	1	0	2	0	
Huaqingtherium lintungense	0	0	0	0	–	0	0	0	0	0	1	0	–	0	1	1	1	0	2	2	0	0	0	1
	0	0	1	1	0	–	0	–	1	0	2	0	0	1	0	1	0	1	0	1	1	0	0	0
	1	0	0	–	1	0	1	1	0	1	1	0	0	1	1	0	1	1	2	1	0	2	?	
Iranotherium morgani	0	0	0	0	–	?	1	0	0	1	2	1	–	?	1	1	1	0	2	2	1	0	0	1
	1	0	1	1	0	–	0	–	1	1	2	?	0	?	0	1	?	1	0	1	1	0	2	0
	1	0	1	1	1	1	1	1	1	–	1	?	?	1	2	1	1	1	2	1	1	2	?	
Kenyatherium bishopi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	1	1	0	?	?	
Parelasmotherium schansiense	0	1	1	1	0	?	2	1	0	0	1	0	1	?	1	?	1	0	2	2	1	0	0	2
	2	0	1	1	0	–	0	–	1	0	2	0	0	1	0	0	0	1	?	1	0	1	2	1
	0	0	1	1	?	?	?	?	?	?	?	?	?	?	2	1	1	1	2	1	1	2	1	
'*Procoelodonta*' *borissiaki*	0	?	0	0	–	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	0	1	1	0	–	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	?	1	0	?	?	
Procoelodonta mongoliense	1	0	0	0	–	?	0	0	0	1	2	0	0	0	?	?	?	?	?	?	?	?	?	0
	0	2	1	0	0	–	0	–	0	0	2	?	0	?	1	?	?	?	?	?	1	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	2	1	0	?	?	
'*Procoelodonta*' *tekkayai*	?	0	1	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	0	?	?	
Sinotherium lagrelii	?	1	1	?	?	?	2	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	1	?	?	?	1	2	1	1	2	1	2	2	?	
Diceratherium armatum	0	0	0	0	–	?	0	1	0	1	1	0	0	0	1	?	1	2	0	2	0	1	0	0
	0	0	0	–	1	1	0	–	0	0	0	0	0	1	1	0	0	1	0	1	0	?	?	?
	0	0	0	?	2	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	–	1	0	
Menoceras arikarense	0	0	0	0	–	?	0	0	0	1	1	0	0	0	1	1	0	0	1	2	0	1	?	0
	0	0	0	–	1	0	0	–	0	0	?	0	0	1	0	1	0	2	0	1	1	1	0	1
	1	0	0	?	1	0	1	1	1	–	1	0	0	0	0	0	1	0	1	0	–	2	0	
Brachypotherium brachypus	0	0	1	0	–	?	0	?	0	0	0	1	0	0	1	1	?	1	?	?	0	?	1	0
	0	0	0	–	0	–	0	–	0	0	2	0	0	0	0	?	0	2	0	1	?	1	1	1
	1	0	0	?	2	2	1	1	1	–	0	0	0	1	0	0	0	–	1	0	–	1	0	
Prosantorhinus douvillei	1	?	0	0	–	?	0	?	?	1	?	?	?	1	1	?	0	1	0	?	?	?	1	0
	0	0	0	–	1	0	0	–	0	?	0	1	0	?	1	1	0	2	0	?	1	1	0	0
	?	1	0	–	1	1	1	1	1	–	0	?	?	0	0	0	0	–	1	0	–	0	0	

Ch 1–71	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	
Teleoceras fossiger	0	1	1	0	–	0	0	0	0	1	1	1	–	0	1	1	0	1	1	1	0	1	1	0
	1	0	0	–	0	–	0	–	0	1	1	0	0	1	1	1	0	2	0	0	0	1	1	1
	1	1	0	–	1	1	1	0	1	–	1	1	0	0	1	0	0	–	1	1	0	1	0	
Shennongtherium hypsodontus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	–	?	1	0	?	?	

Ch 72–142	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119
	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	
Tapirus terrestris	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	2	0
	–	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0
	0	0	0	0	0	0	–	0	0	0	0	–	0	0	0	0	–	0	–	0	–	–	1	
Hyrachyus eximius	0	0	0	0	0	0	0	0	0	0	0	1	0	–	0	0	0	0	0	0	0	0	0	–
	–	–	1	–	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	0	–	0	0	0
	0	1	0	0	0	0	–	0	0	0	0	–	0	0	0	0	–	0	–	0	0	0	0	
Trigonias osborni	1	0	0	0	0	0	0	1	0	1	1	0	0	–	0	0	0	0	0	0	0	0	2	0
	–	0	0	1	0	0	2	0	0	0	0	0	1	0	1	0	0	0	0	0	–	0	1	0
	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	–	0	0	0	0	0	0	
Ronzotherium filholi	0	0	1	1	0	?	0	1	0	1	1	0	0	–	0	0	0	1	0	0	0	0	1	0
	–	0	0	1	0	0	3	0	0	2	0	1	0	1	2	2	2	0	0	0	–	0	0	1
	1	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	–	0	0	0	0	0	0	
Bugtirhinus praecursor	2	?	?	?	?	?	0	1	?	?	?	0	2	0	0	3	–	1	0	0	?	0	3	1
	0	0	0	1	0	1	3	1	0	0	0	0	0	0	3	3	0	0	1	3	1	0	1	?
	?	1	1	0	0	?	?	?	0	1	1	0	0	1	0	2	0	0	?	0	2	0	0	
'*Caementodon*' *caucasicum*	?	?	?	?	0	0	0	1	0	1	1	2	2	0	0	3	–	1	0	0	0	0	3	2
	0	1	0	1	0	1	3	1	0	0	0	0	1	3	3	3	0	0	3	3	0	0	0	0
	1	1	1	0	1	0	0	0	0	?	1	0	0	1	0	2	0	0	?	0	2	0	0	
'*Caementodon*' *fangxianense*	?	?	?	?	?	?	?	?	?	?	?	3	2	1	0	3	–	1	0	?	?	0	3	1
	0	1	0	0	0	2	3	1	0	3	0	0	0	3	3	3	0	0	3	3	0	0	1	?
	?	1	?	0	1	?	?	?	0	0	?	?	0	?	?	?	?	?	?	?	?	?	?	
Caementodon oettingenae	1	?	?	?	?	?	0	1	?	?	?	2	2	1	0	0	1	1	0	0	?	0	3	1
	0	0	0	1	0	2	3	1	0	0	0	0	0	0	3	3	0	0	2	3	1	0	1	0
	1	1	1	0	1	0	0	0	2	1	0	–	0	1	0	2	0	0	1	0	2	0	0	
Elasmotherium caucasicum	?	?	?	?	1	–	1	–	–	1	1	3	0	–	0	3	–	2	3	?	–	1	–	–
	–	–	–	–	1	3	2	1	0	3	1	3	0	3	3	0	3	0	3	3	1	1	–	1
	1	0	0	1	0	1	0	1	?	1	0	–	0	1	0	2	0	0	1	0	2	0	0	
Elasmotherium sibiricum	–	1	1	1	1	–	1	–	–	1	1	3	0	–	0	3	–	2	3	2	–	–	–	–
	–	–	–	1	0	3	2	1	0	2	0	3	0	3	3	0	3	0	3	3	1	1	–	1
	0	0	0	1	–	1	0	1	?	1	0	–	0	1	0	2	1	1	0	0	1	–	1	
'*Hispanotherium*' *beonense*	2	1	1	1	0	1	0	1	0	1	1	2	2	1	0	1	1	1	0	0	0	0	3	1
	0	0	1	–	0	3	3	1	1	0	0	0	0	1	3	3	0	0	2	3	1	0	0	0
	1	1	1	0	1	1	0	0	2	1	1	0	0	1	0	2	0	0	0	0	2	0	0	
'*Hispanotherium*' *corcolense*	?	?	?	?	0	0	0	1	0	1	1	1	2	1	0	1	1	1	0	0	0	0	3	1
	0	1	0	1	0	3	3	1	0	0	0	2	0	1	3	3	1	0	2	3	1	0	0	0
	1	1	0	0	1	1	0	0	0	1	1	0	0	1	0	2	0	0	0	0	2	0	0	
'*Hispanotherium*' *grimmi*	?	?	?	?	0	1	1	–	–	1	1	2	2	1	0	2	1	1	0	0	0	0	3	1
	0	1	0	1	1	3	3	1	0	3	0	0	0	1	3	3	0	0	3	3	1	0	1	0
	1	1	1	0	0	1	0	0	0	1	1	0	0	1	0	2	0	0	0	0	2	0	0	
Hispanotherium matritense	?	?	?	?	0	0	0	1	0	1	1	2	2	2	0	2	1	1	0	0	0	0	3	1
	0	1	0	1	0	3	3	1	0	1	0	0	0	1	3	3	1	0	2	3	1	0	0	0
	1	1	0	0	1	1	0	0	1	1	1	0	0	1	0	2	0	0	0	0	2	0	0	
Huaqingtherium lintungense	?	?	?	1	0	1	1	–	–	1	1	3	2	1	0	2	1	1	0	0	0	0	3	1
	0	1	0	0	0	3	3	0	0	2	0	0	1	2	3	3	1	0	3	3	1	0	0	0
	1	1	0	0	1	1	2	0	0	1	1	1	0	1	0	2	0	0	0	0	2	1	1	
Iranotherium morgani	?	?	?	1	1	–	1	–	–	1	1	3	2	0	0	3	–	1	0	?	?	0	?	?
	?	?	?	?	0	3	3	1	0	3	0	0	0	3	3	3	2	0	3	3	1	0	1	1
	1	1	0	1	0	1	2	1	2	1	1	0	0	1	0	2	0	0	0	0	2	1	1	

Ch 72–142	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119
	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	
Kenyatherium bishopi	?	?	?	?	?	?	?	?	?	?	?	3	2	2	0	0	1	1	0	?	?	?	?	?
	?	?	?	?	0	3	3	0	0	0	0	?	?	?	3	3	0	0	0	3	1	?	?	?
	1	0	?	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Parelasmotherium schansiense	–	1	1	1	?	?	?	?	?	?	?	3	0	–	0	3	?	1	?	2	–	0	?	?
	?	?	?	?	0	3	3	1	?	?	?	0	0	3	3	2	2	0	3	3	1	0	1	1
	0	1	0	2	0	1	2	1	0	1	0	–	1	1	0	2	1	1	?	?	?	?	?	
'Procoelodonta' borissiaki	?	?	?	?	?	?	0	1	0	1	1	?	2	0	0	3	–	1	0	0	?	0	3	1
	?	?	0	1	1	3	3	2	0	3	0	0	0	?	3	3	0	0	3	3	1	0	1	0
	1	1	0	0	?	1	0	0	2	?	?	?	0	?	?	?	?	?	?	?	2	?	0	
Procoelodonta mongoliense	?	?	?	?	?	?	?	?	?	?	?	0	2	0	0	3	–	1	?	?	?	?	?	?
	?	?	?	?	0	3	3	1	?	?	?	0	0	1	3	3	2	0	3	3	1	0	1	0
	?	?	0	0	0	1	2	0	0	?	1	1	0	?	0	2	0	0	?	?	?	?	?	
'Procoelodonta' tekkayai	?	?	?	?	?	?	?	?	?	?	?	1	2	0	0	0	0	1	0	?	?	0	3	1
	0	0	0	1	0	3	3	0	0	?	?	0	0	1	3	3	0	0	3	3	1	0	0	0
	1	1	0	0	0	1	0	0	?	?	1	0	0	1	0	2	0	0	0	0	2	0	0	
Sinotherium lagrelii	?	?	?	?	?	?	?	?	?	?	?	3	1	0	0	3	–	1	2	2	–	0	3	0
	1	0	0	1	0	3	2	1	0	2	1	3	0	3	3	1	3	0	3	3	1	0	1	1
	1	0	0	1	0	1	0	0	0	1	0	–	0	1	0	2	1	1	0	?	2	1	1	
Diceratherium armatum	1	0	1	1	0	0	0	1	0	1	1	3	0	–	0	0	0	0	0	0	0	0	1	0
	–	0	0	1	0	0	1	1	0	0	0	0	0	0	3	1	0	0	0	2	0	0	1	0
	0	0	1	0	0	0	0	0	0	1	0	–	0	1	0	0	–	0	1	0	0	0	0	
Menoceras arikarense	2	1	1	0	1	–	0	1	0	1	1	3	2	2	0	0	1	0	0	0	0	0	1	0
	–	0	0	1	2	3	2	1	0	3	0	0	0	0	3	3	2	0	0	3	0	0	0	0
	1	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	–	0	0	0	2	0	0	
Brachypotherium brachypus	0	?	?	1	0	0	0	1	0	1	1	1	2	1	0	0	0	0	0	0	0	0	2	0
	–	0	0	1	0	0	2	1	0	0	0	1	0	1	2	3	0	0	0	2	0	0	1	0
	1	0	0	0	0	1	0	0	0	1	0	–	0	1	1	0	–	0	1	0	1	0	1	
Prosantorhinus douvillei	0	?	?	1	0	1	0	1	0	1	1	3	1	2	0	0	0	0	0	0	0	0	1	1
	–	1	0	1	0	0	2	1	0	0	0	3	0	3	2	3	0	0	2	3	0	0	0	0
	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	–	0	1	0	0	0	1	
Teleoceras fossiger	0	1	1	1	0	1	0	1	1	1	1	3	2	2	0	2	1	0	0	2	–	0	1	1
	–	1	0	1	0	1	1	1	0	0	0	3	0	3	3	3	0	0	3	3	1	1	–	1
	1	1	0	0	0	1	1	0	1	1	1	0	0	1	1	2	0	0	1	0	0	0	1	
Shennongtherium hypsodontus	?	?	?	?	?	?	?	?	?	?	?	3	2	2	1	0	0	1	0	?	?	0	3	1
	0	1	0	?	0	0	1	1	0	0	0	0	1	?	?	3	0	0	?	?	–	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	

Ch 143–212	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166
	167	168	169	170	171	172	173	174	175	176	177	178	79	180	181	182	183	184	185	186	187	188	189	190
	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212		
Tapirus terrestris	1	0	0	0	0	0	0	1	3	–	0	1	0	0	0	0	0	1	0	0	0	0	1	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1		
Hyrachyus eximius	0	1	0	0	3	–	0	0	0	0	0	1	0	0	2	–	0	0	0	0	?	?	0	0
	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	–	0
	0	0	0	0	0	1	0	0	3	0	1	0	0	0	0	0	1	0	0	0	1	1		
Trigonias osborni	0	1	0	0	2	0	1	–	0	0	0	0	0	0	2	–	2	–	0	0	?	?	0	0
	0	0	0	0	0	0	0	1	0	0	?	0	?	?	0	0	1	1	0	?	0	0	0	0
	?	0	?	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	0		
Ronzotherium filholi	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0
	0	0	0	0	?	0	0	0	0	?	0	0	1	0	0	0	0	1	0	0	0	1	–	?
	1	0	0	1	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0		
Bugtirhinus praecursor	1	0	0	1	2	0	1	–	3	?	0	?	?	?	1	0	1	1	1	0	?	?	0	0
	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	0	0	1	?	0	1	0	0	1	0	?		

Ch 143–212	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166
	167	168	169	170	171	172	173	174	175	176	177	178	79	180	181	182	183	184	185	186	187	188	189	190
	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212		
'*Caementodon*' *caucasicum*	1	1	0	1	3	–	1	–	3	?	0	1	0	0	2	–	2	–	1	0	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	1	1	?	?	?	?	1	0	0	1	1	0	0	0	1	0	1	0	1	1	1	0		
'*Caementodon*' *fangxianense*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Caementodon oettingenae	?	0	0	?	?	?	?	?	3	?	0	1	0	0	2	–	2	–	1	0	?	?	0	0
	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	1	0	0	1	1	1		
Elasmotherium caucasicum	0	1	1	?	3	–	1	–	3	?	2	–	–	–	2	–	2	–	2	0	?	?	?	1
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	2	0	0	?
	?	?	?	?	?	?	1	1	3	1	1	?	?	?	?	?	1	1	1	0	1	0		
Elasmotherium sibiricum	0	1	1	?	3	–	1	–	3	?	2	–	–	–	2	–	2	–	2	0	?	?	?	1
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	0	?	?	1	?	?	1	1	3	1	1	0	1	0	1	0	?	?	?	?	1	?		
'*Hispanotherium*' *beonense*	1	1	0	1	3	–	1	–	3	0	0	1	0	0	2	–	2	–	1	0	?	?	0	0
	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	1
	0	1	1	1	1	0	1	1	3	1	1	0	0	0	1	0	1	1	1	1	1	0		
'*Hispanotherium*' *corcolense*	1	1	0	1	3	–	1	–	3	0	0	1	0	0	2	–	2	–	1	0	?	?	0	0
	0	0	0	0	?	0	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0	0	?
	1	?	?	1	?	?	1	1	3	1	?	0	0	0	?	0	1	1	1	1	1	0		
'*Hispanotherium*' *grimmi*	1	0	0	1	3	–	1	–	3	0	0	?	?	?	2	–	2	–	1	0	?	?	0	0
	?	?	?	?	0	1	0	0	0	1	1	1	1	0	0	0	0	1	?	0	?	?	?	?
	0	?	1	1	0	0	1	1	1	1	1	0	0	1	1	?	1	1	1	1	1	?		
Hispanotherium matritense	1	1	0	1	3	–	1	–	3	?	0	1	0	0	2	–	2	–	1	0	?	?	0	0
	1	0	0	?	?	0	0	0	0	1	1	1	1	0	1	0	?	?	?	?	?	?	?	?
	0	1	?	1	0	?	1	1	3	1	1	0	0	0	?	?	1	1	1	1	1	1		
Huaqingtherium lintungense	1	1	1	1	3	–	1	–	3	1	0	1	0	0	2	–	2	–	1	0	?	?	0	1
	1	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0	?	?	?	?	?	?	?	1
	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1		
Iranotherium morgani	1	1	1	1	3	–	1	–	3	?	0	1	0	?	2	–	2	–	1	0	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	2	?	?	?
	?	?	?	1	?	?	?	?	3	?	1	?	?	?	1	?	?	?	?	?	?	?		
Kenyatherium bishopi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Parelasmotherium schansiense	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	1	?	?	1	1	?	1	1	?	?	?	1	?	?	?	?	?	?	?		
'*Procoelodonta*' *borissiaki*	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Procoelodonta mongoliense	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
'*Procoelodonta*' *tekkayai*	1	1	0	1	2	0	1	–	?	0	0	1	0	2	2	–	2	–	1	0	?	?	0	0
	1	0	0	?	0	0	1	0	0	1	1	1	1	0	0	0	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Sinotherium lagrelii	0	1	1	?	3	–	1	–	3	?	0	?	?	?	2	–	2	–	0	0	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Diceratherium armatum	1	0	0	0	0	1	0	0	3	?	0	0	0	0	0	1	0	0	1	0	?	?	0	0
	0	?	0	?	?	1	0	0	0	0	0	0	1	2	0	0	0	1	0	?	0	1	–	?
	?	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	1	0	0	0	0	1		
Menoceras arikarense	1	0	0	1	0	1	0	0	3	?	0	1	0	0	0	0	2	–	1	0	?	?	1	0
	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	0	2	1	–	1
	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1		

Ch 143–212	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166
	167	168	169	170	171	172	173	174	175	176	177	178	79	180	181	182	183	184	185	186	187	188	189	190
	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212		
Brachypotherium brachypus	0	1	0	0	3	–	0	1	2	0	0	0	1	0	2	–	0	0	1	0	?	?	0	0
	0	1	0	1	0	0	0	?	0	0	1	0	1	1	0	0	?	?	?	?	?	?	?	?
	1	0	0	0	0	1	0	0	2	0	0	1	1	0	1	1	0	0	1	1	0	0		
Prosantorhinus douvillei	0	1	0	0	0	0	1	–	2	2	0	0	0	2	0	0	0	1	1	1	?	?	0	0
	0	1	0	?	?	0	0	0	0	0	0	0	0	3	0	2	1	1	?	1	1	0	1	2
	1	0	1	0	0	1	0	0	2	0	1	1	0	1	1	1	0	0	0	1	0	0		
Teleoceras fossiger	0	1	0	1	0	–	1	–	3	?	1	0	0	0	2	–	2	–	1	0	?	?	1	0
	0	1	0	0	0	0	1	0	1	0	1	0	0	3	0	1	1	1	0	1	0	0	1	2
	1	0	1	0	0	0	0	0	2	0	0	1	0	1	1	1	0	1	0	0	0	1		
Shennongtherium hypsodontus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		

Ch 213–282	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236
	237	238	239	240	241	242	243	244	245	246	247	248	249	250	251	252	253	254	255	256	257	258	259	260
	261	262	263	264	265	266	267	268	269	270	272	272	273	274	275	276	277	278	279	280	281	282		
Tapirus terrestris	0	0	0	0	0	0	–	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	–	0	0	0	0	0	0		
Hyrachyus eximius	1	0	0	0	0	1	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	?
	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	3	0	0	0	0	0	0	0	2	1	–	0	1	0	0	0	0	0	0	0		
Trigonias osborni	0	1	0	0	0	1	0	1	0	0	1	0	0	0	–	0	0	?	0	0	0	0	0	?
	?	?	0	0	1	0	1	–	0	0	0	?	0	0	0	1	1	0	0	0	0	0	0	0
	0	0	0	?	?	1	?	0	0	?	0	0	0	0	?	?	?	?	0	0	0	1		
Ronzotherium filholi	0	0	0	0	0	0	–	1	?	?	?	0	0	0	–	2	0	2	?	0	0	0	0	?
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	0	0	0	1	0	0
	2	0	1	0	1	0	0	1	?	0	0	0	0	0	0	–	0	?	0	0	0	0		
Bugtirhinus praecursor	?	?	?	?	?	?	?	1	0	0	0	?	?	?	?	?	?	2	1	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	1	1	1	0	1	?	?	1	0
	0	0	3	?	?	1	?	1	?	0	2	0	0	1	1	0	1	1	0	0	?	0		
'*Caementodon*' *caucasicum*	0	0	0	1	0	1	2	1	0	0	0	0	0	0	–	0	0	2	1	0	?	1	1	?
	0	0	0	1	0	1	?	?	1	?	?	?	?	?	?	1	1	1	0	1	0	0	1	0
	0	0	3	0	2	1	0	1	1	0	1	0	0	0	1	0	1	?	0	0	0	0		
'*Caementodon*' *fangxianense*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Caementodon oettingenae	0	0	0	1	0	1	0	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	1	0	0	1	0
	0	0	3	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	?	?		
Elasmotherium caucasicum	0	?	?	1	0	?	?	?	?	0	0	?	0	?	?	?	0	?	1	1	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	2	0	0	?	1	0	1	?	0	1	?	0		
Elasmotherium sibiricum	?	?	?	?	?	?	?	?	?	2	0	0	0	0	–	0	0	2	1	1	?	?	?	?
	?	?	?	?	?	1	2	–	1	1	1	1	0	1	1	?	?	1	0	1	?	?	1	0
	2	1	0	3	2	0	1	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0		
'*Hispanotherium*' *beonense*	0	1	0	1	0	1	2	1	1	1	2	0	0	1	0	0	0	2	1	0	1	1	1	1
	0	0	0	1	0	1	0	1	1	1	1	1	0	1	1	2	1	1	1	1	0	1	1	0
	2	0	3	3	2	1	1	1	0	1	2	0	0	1	1	0	1	1	0	1	0	0		
'*Hispanotherium*' *corcolense*	0	1	0	1	0	1	1	1	1	0	1	0	0	0	–	0	0	2	1	0	?	1	?	?
	?	?	0	?	?	1	0	1	?	1	1	?	?	?	?	1	1	1	1	1	0	?	1	0
	1	0	3	1	2	1	0	1	0	0	2	0	0	1	1	0	1	1	0	1	0	0		
'*Hispanotherium*' *grimmi*	?	1	0	?	1	1	2	1	1	0	0	0	0	0	–	0	0	2	1	0	?	?	1	?
	0	0	0	?	?	1	0	1	1	1	1	?	?	?	?	1	1	1	0	1	0	1	1	0
	1	0	3	0	2	?	0	1	0	?	?	?	?	?	?	?	1	?	0	1	0	0		
Hispanotherium matritense	0	1	0	1	0	1	0	1	0	0	0	0	0	0	–	0	0	2	?	0	?	1	1	?
	?	?	0	0	?	1	0	1	1	1	1	?	?	?	?	1	1	1	0	1	0	0	1	0
	1	0	3	1	2	1	0	1	0	0	1	0	0	0	0	–	1	1	0	1	0	0		

Ch 213–282	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236
	237	238	239	240	241	242	243	244	245	246	247	248	249	250	251	252	253	254	255	256	257	258	259	260
	261	262	263	264	265	266	267	268	269	270	272	272	273	274	275	276	277	278	279	280	281	282		
Huaqingtherium lintungense	0	1	0	1	0	?	?	1	1	0	3	0	0	0	–	0	0	2	1	0	?	?	?	?
	?	?	0	1	0	1	0	1	1	1	1	?	0	1	1	1	1	1	0	1	0	?	1	0
	2	0	3	?	2	1	0	1	0	0	2	?	?	?	?	?	?	1	0	1	0	0		
Iranotherium morgani	?	?	?	?	?	?	?	?	?	?	?	0	0	2	1	0	?	?	?	0	?	?	?	?
	?	?	1	1	?	1	0	1	1	1	1	?	?	?	?	2	1	1	0	1	?	1	1	0
	2	0	0	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	0	1	?	0		
Kenyatherium bishopi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Parelasmotherium schansiense	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	1	0	1	1	0
	2	0	0	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	0	?	?	?		
'*Procoelodonta*' *borissiaki*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Procoelodonta mongoliense	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
'*Procoelodonta*' *tekkayai*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Sinotherium lagrelii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
Diceratherium armatum	0	1	0	0	0	1	0	1	0	0	0	0	0	0	–	0	0	2	1	0	?	0	0	0
	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0
	0	0	3	1	2	0	0	1	0	0	2	0	0	1	0	–	0	0	0	0	0	1		
Menoceras arikarense	0	1	0	0	0	1	0	1	0	0	3	0	0	2	0	0	0	2	1	0	1	1	1	0
	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	0	1	0	0	1	0
	1	0	3	3	2	1	0	1	1	0	1	0	0	1	1	0	0	1	0	0	0	0		
Brachypotherium brachypus	0	1	0	0	0	1	0	0	0	1	1	1	0	0	–	0	1	1	1	1	0	0	0	0
	0	0	1	0	1	1	2	–	0	0	1	0	1	0	1	2	1	1	0	0	1	0	1	0
	0	1	1	2	2	0	0	0	0	?	1	0	0	0	1	1	0	0	1	0	0	1		
Prosantorhinus douvillei	1	0	0	0	0	0	–	0	0	0	0	1	0	1	1	1	1	0	1	1	0	1	0	0
	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	2	1	0	0	0	1	0	1	1
	2	1	0	3	2	0	0	0	0	0	1	1	–	0	1	0	0	0	1	0	0	1		
Teleoceras fossiger	0	0	0	0	0	1	0	1	0	0	0	1	0	2	1	0	1	0	1	1	0	1	0	?
	0	0	0	0	1	1	2	–	0	0	1	1	1	0	1	2	1	1	0	0	1	1	1	1
	0	1	0	3	2	0	0	1	1	0	1	1	0	0	1	1	0	0	1	0	0	1		
Shennongtherium hypsodontus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		