

THE ORIGIN OF CHALICOTHERES (PERISSODACTYLA, MAMMALIA)

by J. J. HOOKER *and* D. DASHZEVEG

ABSTRACT. Description of a new genus of perissodactyl, *Protomoropus*, for the species '*Hyracotherium*' *gabunia* Dashzeveg and its inclusion with a diversity of other primitive perissodactyls in a cladistic analysis results in the following higher order changes to our knowledge of perissodactyl phylogeny. *Protomoropus* is sister taxon to the Chalicotheriidae plus Lophiodontidae, which themselves are confirmed as sister groups. The previously monofamilial superfamily Chalicotherioidea is extended to include all three taxa. *Paleomoropus* and *Lophiaspis* are shown to be primitive lophiodontids. Various genera of the Isectolophidae are shown to be stem members of a clade that includes chalicotheres and lophiodonts. The infraorder Ancylopoda is extended to include them. Inclusion of isectolophids in the Ancylopoda rather than as stem tapiromorphs results in the break up of the clade Tapiromorpha. Instead, the modern perissodactyl groups, comprising the horse superfamily Equoidea and that of the rhinos and tapirs, the Ceratomorpha (here reduced in rank to parvorder), form a new clade which is here named infraorder Euperissodactyla nov. The Brontotheriidae form the sister group to Ancylopoda plus Euperissodactyla. The clade comprising Ancylopoda plus Euperissodactyla is named suborder Lophodontomorpha nov. The Chalicotherioidea and Chalicotheriidae evolved in Asia. The Lophiodontidae arose following dispersal from Asia to North America. Dispersal continued to Europe, where the family radiated.

KEY WORDS: Mongolia, cladistics, systematics, Lophiodontidae, Ancylopoda, palaeobiogeography.

CHALICOTHERES are bizarre extinct members of the order Perissodactyla. They are usually ranked as a family or superfamily within an extinct higher rank taxon called Ancylopoda. The Ancylopoda has variably been expanded to include the family Lophiodontidae. It is the Neogene chalicotheres that are best known, with their huge fissured claws instead of hooves and in the case of the subfamily Chalicotheriinae, greatly elongate forelimbs and reduced hindlimbs, representing an extreme adaptation for bipedal high browsing (Zapfe 1979; Coombs 1983, 1989), and giving a gorilla-like stance. One genus of Schizotheriinae even flaunted a high-domed skull (Coombs 1979). In the Eocene, mainly dental remains are known (Radinsky 1964) and members are usually referred to the Eomoropidae (McKenna and Bell 1997; Colbert and Schoch 1998), even though Coombs (1989) found this family to be paraphyletic. Here, Eomoropidae is regarded as synonymous with Chalicotheriidae.

Chalicotheres have in the past been considered to be, together with the brontotheres, closest to horses (Superfamily Equoidea) in the suborder Hippomorpha (e.g. Simpson 1945; see also Schoch 1989 for a full history of perissodactyl classification). However, Radinsky (1964, 1969) judged that they had mixed characters of the two modern suborders Hippomorpha and Ceratomorpha and placed them as a third independent group. Hooker (1984, 1989) divided these mixed characters into primitive and derived states and showed that the derived ones linked chalicotheres with ceratomorphs rather than with hippomorphs. For this larger clade, he resurrected Haeckel's term Tapiromorpha (Moropomorpha of Schoch 1984; Prothero and Schoch 1989; Colbert and Schoch 1998). The chalicothere-brontothere link has recently been resurrected without explanation by McKenna and Bell (1997), although possibly based on *Danjiangia*, described as a chalicothere with characters linking it to brontotheres (Wang 1995). Arguments for establishing *Danjiangia* as a brontothere rather than as a chalicothere are given by Hooker and Dashzeveg (2003) and summarized here. *Danjiangia* lacks the complete high upper premolar and upper molar metaloph joining the ectoloph typical of chalicotheres, and bears an upper molar mesostyle lacking in a primitive chalicothere such as *Litolophus* or in other ancylopods such as *Paleomoropus* and *Lophiaspis*

(Depéret 1910; Radinsky 1964; Savage *et al.* 1966). In contrast, it has the strong dilambdodonty (especially the buccally deflected upper molar preparacrista) of *Lambdotherium* (e.g. Osborn 1929).

A character of the upper molars, the presence of a mesostyle, was critical to the original referral of chalicotheres to the Hippomorpha, ceratomorphs always lacking this feature. Reliance on a single character, however, has not proven parsimonious with the advent of cladistic analyses, but even before this, Radinsky (1964) described two genera without mesostyles that he considered to be chalicotheres. The first is *Litolophus* from the middle Eocene of China and unequivocally a chalicothere in all other features (see Appendix). The second is *Paleomoropus* from strata of early Eocene age in North America. It is strongly bilophodont and known only from three associated upper molars. A slight lingual tilt to its metacone is typical of ceratomorphs and in detailed morphology *Paleomoropus* was recognized to be very closely related to European Eocene *Lophiaspis*. *Lophiaspis* had long been accepted as a member of the extinct endemic European family Lophiodontidae (e.g. Fischer 1977), classified then with the Ceratomorpha. Because of the similarity to *Paleomoropus*, Radinsky (1964) and Savage *et al.* (1966) classified *Lophiaspis* in the Eomoropidae, but retained the family Lophiodontidae for *Lophiodon* and a few other genera. Cladistic analyses have subsequently linked Lophiodontidae with chalicotheres in the Ancylopoda (Hooker 1984, 1989; Froehlich 1999), these together being sister group to the Ceratomorpha. In contrast, on cranial (non-dental) and postcranial characters, Holbrook (2001) found no evidence to relate Ancylopoda more closely to one rather than any other group of perissodactyls.

New finds of early Eocene age from the Bumban Member, Naran Bulak Formation, in the vicinity of Naran Bulak, Nemegt Basin, southern Gobi, Mongolia (see Russell and Zhai 1987 for location and details of the stratigraphy), are here shown to represent the oldest known chalicotherioid. They are placed in the new genus *Protomoropus*, but in an existing species, '*Hyracotherium*' *gabunia*, that was until now poorly known. A combination of derived chalicothere-like characters plus more primitive character states than previously encountered in this group allow the problems of the relationships of the chalicotheres and lophiodonts to be better resolved and Ancylopoda to be more securely related within the order Perissodactyla, via stem members.

Terminology and abbreviations. Dental terminology follows Hooker (1994, fig. 2). Institutional abbreviations: BMNH, The Natural History Museum, London; FSL, Faculté des Sciences, Lyon; MNHN, Muséum National d'Histoire Naturelle, Paris; PIN, Paleontological Institute, Moscow; PSS, Geological Institute, Mongolian Academy of Sciences, Ulaanbaatar; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; YPM, Yale Peabody Museum, New Haven.

SYSTEMATIC PALAEOLOGY

Order PERISSODACTYLA Owen, 1848

Suborder ANCYLOPODA Cope, 1889

Superfamily CHALICOTHERIOIDEA Gill, 1872

Family uncertain

Genus PROTOMOROPUS nov.

Type species. *Hyracotherium gabunia* Dashzeveg, 1979a.

Derivation of name. Greek, *protou*, formerly, before now, plus *Moropus*, a genus of derived chalicothere, indicating a forerunner of chalicotheres.

Diagnosis. Small ancylopod, upper and lower first molar length about 8 mm (see Table 1 for other measurements). Molars with relatively short upper trigon and lower talonid basins. Marked wear gradient from M1 to M3. Upper molars with essentially vertically implanted paracone and metacone, with only slightly buccally flexed centrocrista, well-developed protoloph and metaloph with weak paraconule and variably developed metaconule, parastyle not distally recurved, no mesostyle, and strong lingual cingulum around protocone. M³ ectoloph elongate compared to M¹⁻² and with prominent metastyle. Lower molars

TABLE 1. Maximum lengths and widths, in millimetres, of cheek teeth of *Protomoropus gabunia*, *?Orientolophus namadicus* and *Cardiolophus* sp.; md, mesiodistal length; ect, length of ectoloph measured parallel with the buccal margin and involving only upper molars. Width is taken transversely from parastyle to protocone on uppers and across the talonid in M_{1-2} and across trigonid in M_3 . PIN specimens measured from casts.

Species	No.	Tooth	length (md)	length (ect)	width
<i>P. gabunia</i>	PSS.20-55	RDP ⁴	7.20		7.35
	PSS.20-56	LDP ⁴	7.00		6.90+
	PIN.3104-323	RP ⁴	6.65		8.55
		RM ¹	8.10	8.25	(10.00)
		RM ²	9.15	9.55	11.50
		RM ³	9.50	10.20	11.70
	PSS.20-220	RM ¹	8.20	(8.40)	(10.10)
	PSS.20-9	RM ₁	8.05		5.25
		RM ₂	8.85		6.00
		RM ₃	(12.5)		—
	PIN.3104-480	LM ₂	8.50		6.45
	PIN.3104-481	RM ₃	—		6.35
<i>?O. namadicus</i>	PSS.20-10	RM ^{1/2}	7.35	7.70	9.90
<i>Cardiolophus</i>	PSS.20-224	LP ⁴	(6.90)		—
	PSS.20-223	LM ³	9.45	10.10	11.70

with straight cristid obliqua (metalophid) whose mesial end is low, joining the back of the trigonid approximately at the midpoint between protoconid and metaconid, ectocingulid strong round hypoconid, metaconid buttress present, paracristid making angle of *c.* 40 degrees to tooth long axis, and twinned metaconid cusps close together. M_{1-2} with prominent median cusped hypoconulid and faint remnant of entoconulid developed close to entoconid. M_3 bearing well-developed hypoconulid lobe with sloping distal wall and main hypoconulid cusp buccally and subterminally situated. DP⁴ with large mesially protruding parastyle.

Protomoropus gabunia (Dashzeveg, 1979a) comb. nov.

Text-figures 1A-F, 3A-I

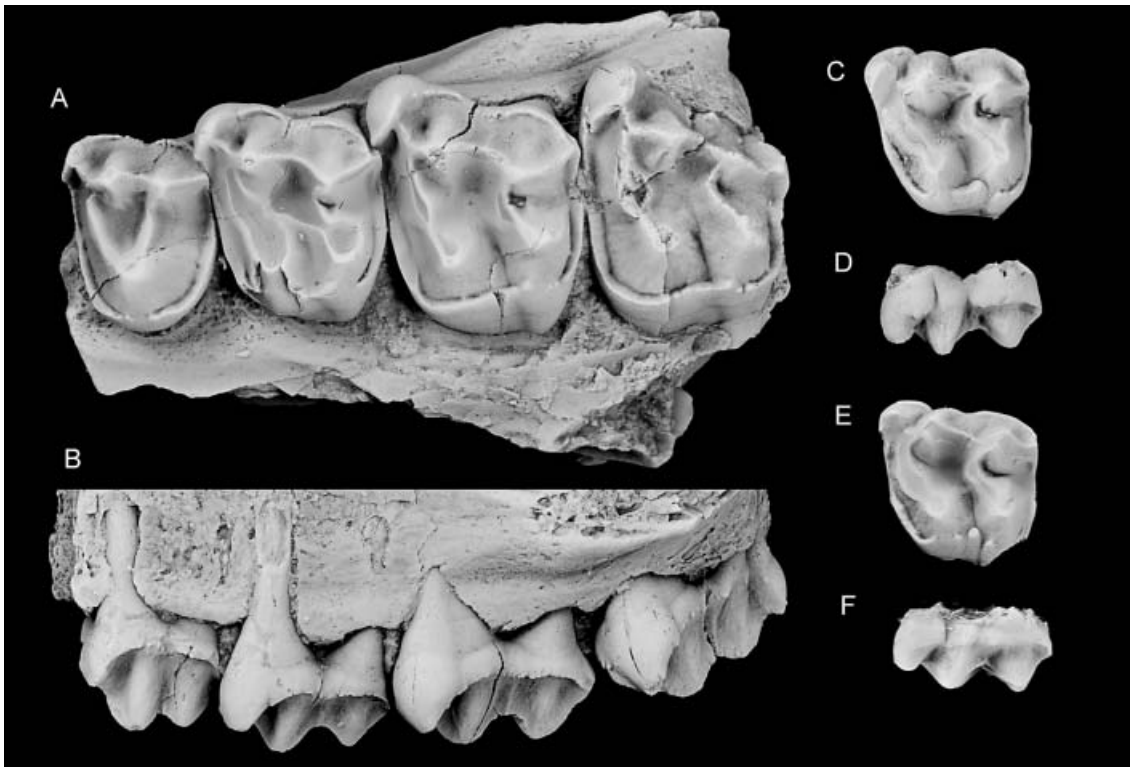
- vp*1979a *Hyracotherium gabunia* Dashzeveg, pp. 109–112, fig. 1a–b.
 vp 1979b *Homogalax namadicus* Dashzeveg, pp. 108–110, fig. 2.
 v. 1993 *?Orientolophus gabunia* (Dashzeveg); Ting, p. 205.
 v. 1998 *?Orientolophus gabunia* (Dashzeveg); Ting, p. 140.

Diagnosis. As for genus.

Holotype. Right DP⁴ (PSS.20-55) from the base of the Bumban Member, Naran Bulak Formation, Quarry 1, Tsagan Khushu, Naran Bulak area, southern Gobi, Mongolia (Text-fig. 1C–D).

Paratype. Left DP⁴ (PSS.20-56) from the base of the Bumban Member, Naran Bulak Formation, Quarry 1, Tsagan Khushu, as above (Text-fig. 1E–F). NB: the second described paratype (PSS.20-57) is removed from the species (see below).

New material. Right maxilla with P⁴–M³ (PIN.3104-323) (Text-fig. 1A–B), right M¹ (PSS.20-220), mesial fragment of left M¹ (PSS.20-221), damaged right DP⁴ (PSS.20-222), right dentary fragment with M_{1-3} (PSS.20-9, originally paratype of *Homogalax namadicus*) (Text-fig. 3A–C), left M₂ (PIN.3104-480) (Text-fig. 3D–F), right M₃ damaged mesially (PIN.3104-481) (Text-fig. 3G–I). All from Quarry 1, base of the Bumban Member, Tsagan Khushu.



TEXT-FIG. 1. *Protomoropus gabuniaei* (Dashzeveg, 1979a) comb. nov., base of the Bumban Member, Naran Bulak Formation (Bumbanian, early Eocene), Quarry 1, Tsagan Khushu, southern Gobi, Mongolia; upper cheek teeth, shown as from left side, coated with ammonium chloride. A–B are epoxy casts. Views are occlusal (A, C, E) and buccal (B, D, F). A–B, right maxilla with P^4 – M^3 (reversed), PIN.3104-323. C–D, holotype right DP^4 (reversed), PSS.20-55. E–F, paratype left DP^4 , PSS.20-56. All $\times 3$.

Interpretation of type material and reasons for referral of new material. The holotype and the paratype listed above are upper cheek teeth identified originally as M^2 (Text-fig. 1C–F). The new referred material includes maxillary and mandibular specimens with associated molars in the lower dentition and fourth premolar plus molars in the upper (Text-figs 1A–B, 3A–I). M^2 of the maxilla (PIN.3104-323) does not match the holotype or paratype for identity of tooth type.

The holotype and paratype are low-crowned teeth with an outline that narrows in a lingual direction, with a resultant acute mesiobuccal corner with large parastyle. The teeth are wider distally than mesially and the hypocone is better developed than the protocone. In addition, there is a papillate lingual cingulum. All of these features are typical of milk premolars, especially the large hypocone, which is often precocious in its development over the protocone (Butler, 1952a).

These two teeth are similar morphologically to the first and second molars of the referred maxilla in details of cusps and loph angle and orientation, but differ in being slightly lower crowned, having thinner enamel, an outline (described above) that tapers mesially instead of distally, and a larger, more mesially protruding parastyle. The combination of similar cusp and loph pattern but thinner enamel of the holotype and paratype upper teeth is even stronger evidence that these are upper deciduous premolars, which are reidentified here as DP^4 .

There are, however, two other perissodactyls in the basal Bumban fauna of the Naran Bulak area that need to be eliminated from the equation. One is described (*Homogalax namadicus* Dashzeveg, 1979b)

(Text-fig. 4A–B), whilst the other is so far undescribed, but referable to the isctolophid genus *Cardiolphus* (Text-fig. 4C–E). The single upper molar in each case, like PIN.3104-323, has a pattern that can broadly be termed bilophodont. However, the *H. namadicus* holotype $M^{1/2}$ is much wider than long, whereas length and width are nearly equal in the ‘*H.*’ *gabunia*i type upper teeth. Moreover, the metaloph joins the ectoloph only tenuously, whereas in both PIN.3104-323 and type ‘*H.*’ *gabunia*i the metaloph is high, with a strong link to the ectoloph nearly reaching to the tip of the metacone. In fact, a more direct comparison can be made with *Orientalophus* Ting, 1993, to which genus *H. namadicus* has been tentatively referred (Ting 1998). The DP^4 of the type species of *Orientalophus*, *O. hengdongensis* Ting, 1993 (identified reliably by being associated with molars in two maxillae), is more transverse than type ‘*H.*’ *gabunia*i and has a weaker metaloph like its molars. Whether or not *H. namadicus* belongs to the genus *Orientalophus*, it is morphologically closer to the latter than to ‘*H.*’ *gabunia*i. It is therefore judged that *H. namadicus* and ‘*H.*’ *gabunia*i are not synonymous.

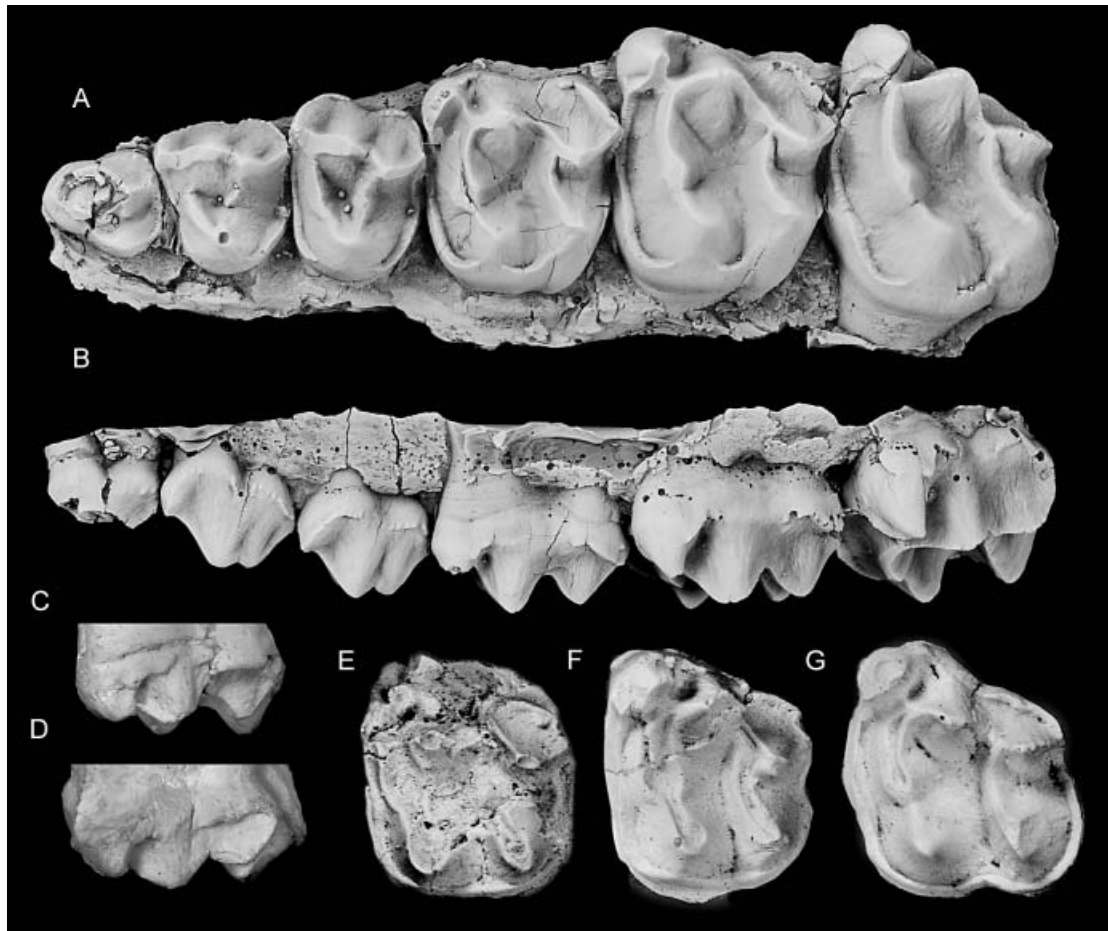
The *Cardiolphus* M^3 from Tsagan Khushu (Text-fig. 4D–E) is close to that of *C. radinskyi* Gingerich, 1991 (UM.68548) (Text-fig. 4F–G). It is, however, slightly shorter and broader with a slightly stronger metaloph and deeper buccal notch between the parastyle and paracone. A P^4 , also from Tsagan Khushu (Text-fig. 4C) is nearly identical to the same tooth of *C. radinskyi* (UM.68548). It is distinctly less lophodont than the P^4 of the maxilla (PIN.3104-323), with a distinct metaconule that is lacking in the latter. It is thus unlikely that the type uppers of ‘*H.*’ *gabunia*i belong to *Cardiolphus*.

A second paratype, now lost, a lower first or second molar (PSS.20-57), was originally described for ‘*Hyracotherium*’ *gabunia*i (Dashzeveg 1979a, fig. 1v). At 6.5 mm long, it is too small to belong to *P. gabunia*i now that the holotype and paratype upper teeth are re-identified as DP^4 rather than M^2 . It has a slightly buccally convex cristid obliqua (metalophid) that meets the back of the trigonid buccal of the midline, a complete but notched hypolophid, a rounded mesiobuccal angle in crown view, and an untwinned metaconid. In all these characters it is like M_1 of *Orientalophus hengdongensis*. It is also of appropriate size and morphology to be a lower $M_{1/2}$ of *Homogalax namadicus*, displacing the paratype lower dentition of this species (Text-fig. 3A–C), which is here referred instead to *Protomoropus gabunia*i. In terms of occlusal relationships, the untwinned metaconid and notched hypolophid of PSS.20-57 match the complete protoloph, uninterrupted by a paraconule, and low recurved metaloph of the holotype $M^{1/2}$ of *H. namadicus* (the occlusal relationships of *P. gabunia*i are discussed below). The similarities of PSS.20-57 to *O. hengdongensis* give further support for referring *H. namadicus* to the genus *Orientalophus* as Ting (1993, 1998) has already tentatively proposed.

Description and comparisons

Upper dentition. The right maxilla (PIN.3104-323) shows four well-preserved teeth in variable states of dietary wear (Text-fig. 1A–B). P^4 and M^2 are lightly worn, whereas M^1 is quite heavily worn, a large area of exposed dentine involving the metaloph and metacone nearly reaching the protoloph. It does in fact merge with the protoloph on the more worn isolated M^1 (PSS, cast M45259). M^3 on the other hand is essentially unworn although fully erupted. This gradient of wear is more marked than in other primitive ancylopods (e.g. *Eomoropus*, *Lophiaspis*) but similar to the state encountered in some more derived ones like *Schizotherium* (e.g. Butler 1965, fig. 1A).

The upper molars have a large parastyle which projects essentially mesially in M^1 , mesiobuccally in M^2 and strongly buccally in M^3 . Its position is mirrored by the orientation of the adjacent segment of the preparacrista. The centrocrista is nearly straight, the very slight lingual tilting of the metacone with respect to the paracone resulting in a slight buccal curvature, evident only with wear on M^1 and M^2 . The centrocrista plus the preparacrista and postmetacrista form a moderately developed ectoloph. There is no mesostyle, although a very faint ridge on the buccal wall of the centrocrista and, in the case of M^3 , a tiny cuspule arising from the ectocingulum just distal of its midpoint could be construed as incipient or vestigial mesostyle homologues. The protoloph and metaloph are strong. The paraconule is well marked even in heavy wear as on M^1 and not much smaller than the protocone. There is a weak metaconule on M^2 , none on M^3 and wear has removed the evidence from M^1 . The protoloph joins the preparacrista midway along its length, the distal half of the latter being essentially mesiodistally orientated. The metaloph recurves to join the front of the metacone, extending right to its tip. The postmetacrista is deflected somewhat buccally on M^{1-2} , but on M^3 it is mesiodistal and elongate, terminating in a prominent metastyle, which makes the ectoloph of this tooth more elongate than that of the others. This last is an autapomorphy of *P. gabunia*i. Cingula are generally

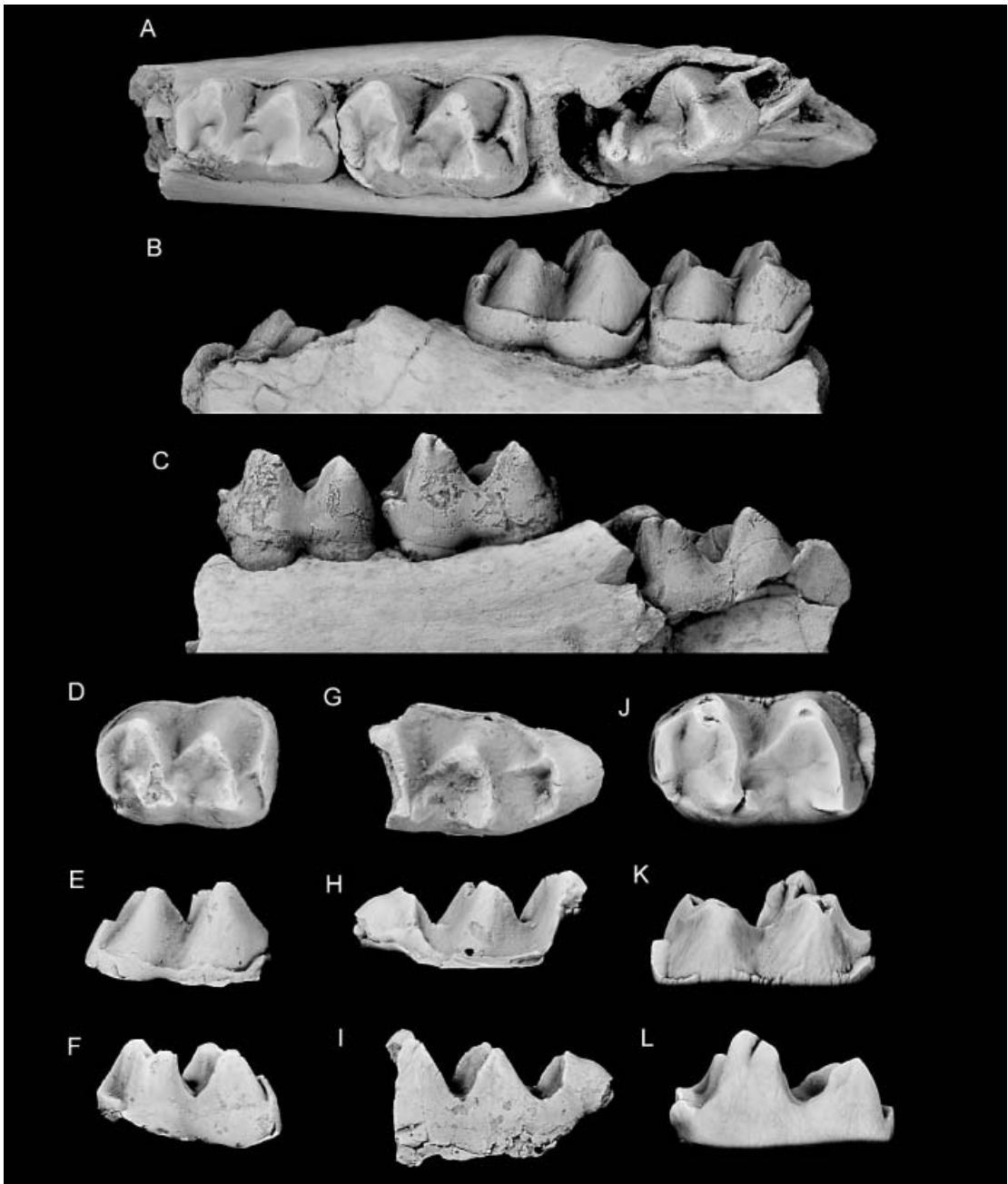


TEXT-FIG. 2. Ancylopod upper cheek teeth, shown as from left side. A–B are epoxy casts; C–G are plaster casts; all $\times 2$. Views are occlusal (A, E–G) and buccal (B–D). A–B, *Lophiaspis maurettei* Depéret, 1910; holotype right P^2 – M^3 (reversed), FSL.2084, base of the Montaiguët Limestones (Neustrian, early Eocene), Palette, France. C–G, *Paleomoropus jepseni* Radinsky, 1964, holotype, Willwood Formation (Wasatchian, early Eocene), Clarks Fork Basin, Wyoming, USA. E, left M^1 . C, F, right M^2 (reversed). D, G, left M^3 , YPM-PU13254.

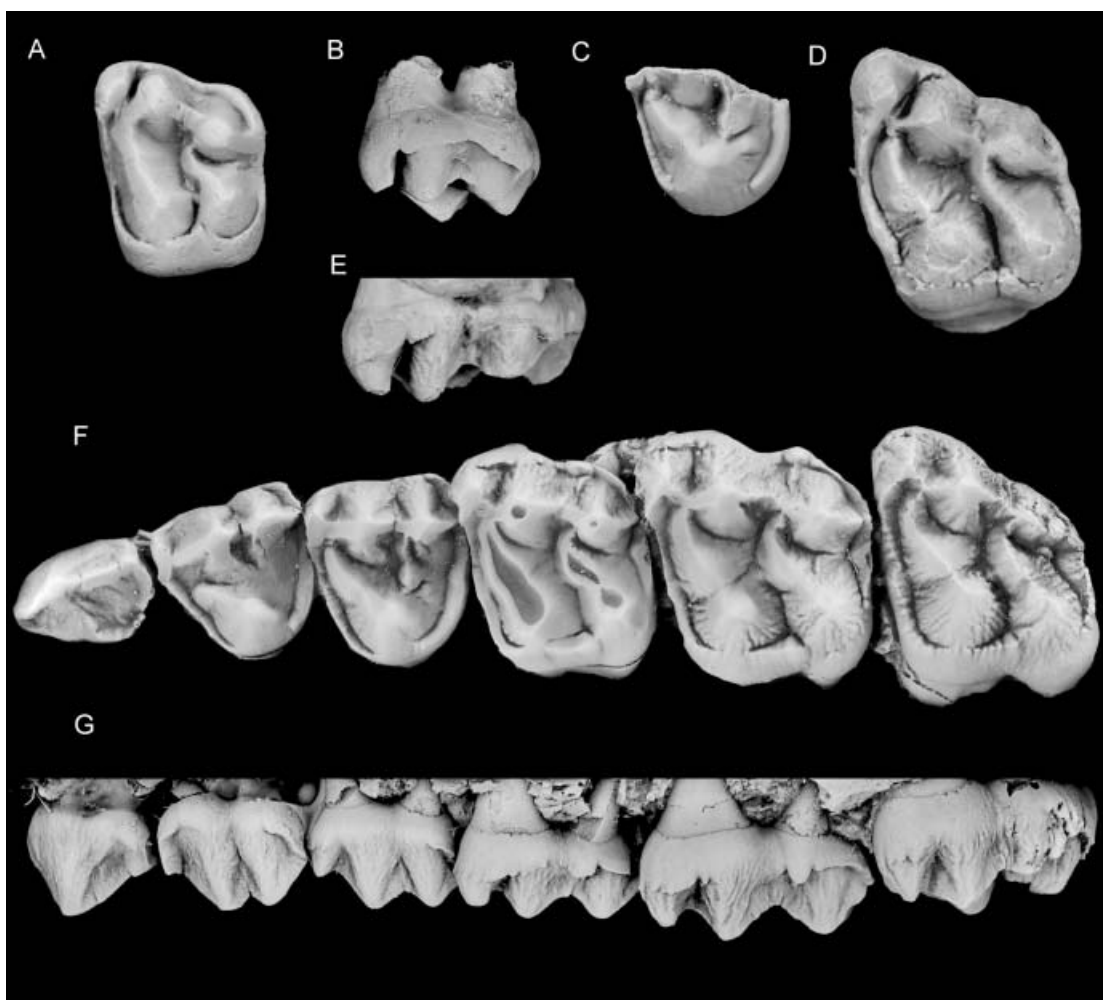
well-developed, especially lingually, but they are reduced or broken round the metacone and midway along the buccal wall on M^{1-2} and along most of its length on M^3 .

P^4 is premolariform. The lophoid crests arising from the protocone form a V-shape, the mesial branch composed of the protoloph, the distal branch composed of aligned postprotocrista and premetacrista. The protoloph just fails to meet the preparacrista. It has a faint swelling midway along its length, but is not developed into a discrete structure that could be termed a paraconule. There is no metaconule on the lophoid crest that joins the metacone right at its tip as the metaloph does on the molars. The cingula are strong, but broken around the protocone and in the middle of the buccal wall.

In overall cusp and crest pattern, this upper dentition has many similarities with *Paleomoropus*, *Lophiaspis* and *Litolophus*. In particular, it is very similar to *Lophiaspis* except that the latter is larger, the paraconule is slightly more lingually situated, there is a marked tilt of the metacone lingually and of the paracone buccally, and the cingula show greater interruption (Text-fig. 2A–B). Otherwise, the orientation of the transverse lophs and the parastyle are remarkably similar in the two taxa. *Paleomoropus* is also similar in being very like *Lophiaspis* but here the tilting of the paracone and metacone is less marked and thus less different from *Protomoropus* (Text-fig. 2C–G).



TEXT-FIG. 3. Ancylopod lower cheek teeth, shown as from right side, coated with ammonium chloride; D-L are epoxy casts. Views are occlusal (A, D, G, J), buccal (B, E, H, K) and lingual (C, F, I, L). A-I, *Protomoropus gabuniai* (Dashzeveg, 1979a) comb. nov., base of the Bumban Member, Naran Bulak Formation (Bumbanian, early Eocene), Quarry 1, Tsagan Khushu, southern Gobi, Mongolia. A-C, right dentary with M_{1-3} , PSS.20-9. D-F, left $M_{1/2}$ (reversed), PIN.3104-480. G-I, right M_3 , PIN.3104-481. All $\times 3$. J-L, *Lophiaspis maurettei* Depéret, 1910; left $M_{1/2}$ (reversed), MNHN.Mu-194-Louis, Argiles à Lignites d'Épernay (Neustrian, early Eocene), Mutigny, France; $\times 2$.



TEXT-FIG. 4. Ancylopod upper cheek teeth, shown as from left side, coated with ammonium chloride; F-G are epoxy casts. Views are occlusal (A, C-D, F) and buccal (B, E, G). A-B, *Orientolophus? namadicus* (Dashzeveg, 1979b); holotype right $M^{1/2}$ (reversed), PSS.20-10, base of the Bumban Member, Naran Bulak Formation (Bumbanian, early Eocene), Quarry 1, Tsagan Khushu, southern Gobi, Mongolia. C-E, *Cardiolophus* sp., base of the Bumban Member, Naran Bulak Formation (Bumbanian, early Eocene), Tsagan Khushu, southern Gobi, Mongolia. C, left P^4 , PSS.20-224, Quarry 1. D-E, left M^3 , PSS.20-223, Quarry 5. F-G, *Cardiolophus radinskyi* Gingerich, 1991; left P^2 - M^3 , UMMP.68548, Willwood Formation (Wasatchian, early Eocene), locality SC-87, Clarks Fork Basin, Wyoming, USA. All $\times 3$.

Litolophus is even more like *Protomoropus* in the orientation of its paracone and metacone, but differs in a more mesial position of the ectoloph attachment of the metaloph, mesiodistal elongation of the protocone on the molars, more closely approximated paracone and metacone on P^4 , and autapomorphic elongation of the molars and reduction in size of the premolars. The pattern of wear on M^2 of the holotype of *L. gobiensis* is very like that on M^1 of the *P. gabuniaii* maxilla in the mesial expansion of the metaloph dentine to encompass part of that of the ectoloph (Radinsky 1964, fig. 3).

Lower dentition. The best lower dentition is that preserved in the right dentary fragment which formed the paratype of *Homogalax namadicus* (PSS.20-9) (Text-fig. 3A-C). However, M_3 is unerupted and the hypoconulid lobe damaged, so

an isolated M_3 (PIN.3104-481) provides the missing information (Text-fig. 3G-I). An isolated M_2 (PIN.3104-480) also gives some idea of individual variation (Text-fig. 3D-F). PSS.20-9 shows a similar wear gradient to the maxilla, but at an earlier wear stage. Thus, on M_1 , wear is moderate, on M_2 it is slight and on M_3 it is entirely within the crypt and unworn. The protolophid and hypolophid are well-developed, the former distinctly notched, the latter only slightly so. The cristid obliqua (metalophid) is straight and oblique in orientation, joining the back of the trigonid approximately at the midpoint and low on the crown. The buccal branch of the paracristid is only slightly less oblique than the cristid obliqua. The metaconid is twinned with the distal twin slightly smaller than the mesial one. Their degree of separation varies a little on the only tooth type showing this structure in more than one specimen, the M_3 . The buttress-like ridge that forms distobuccally on the distal metaconid is close to the postmetacristid, the valley between the two being narrow. The protoconid bears a sharp lingual rib. Cingula where present are mainly strong, but completely missing lingually and weak or interrupted round the protoconid. A cingulum is present lingual of the hypoconulid on M_{1-2} . The entocristid has a break in slope near the tip of the entoconid, which represents the remnant of the entoconulid. The M_3 hypoconulid lobe is large, with a distally protruding bulge. The ectocingulid does not continue round its distal margin, but rises up the side of a small buccal cusp that is best interpreted as the hypoconulid. The hypoconulid lobe is encircled by a crest, which buccally mirrors the cristid obliqua for shape and orientation, and lingually curves low to meet the back of the entoconid. Distally, it bears two tiny cusps. The talonid basins in all three lower molars are short and the buccal and lingual tooth walls converge at a very acute angle.

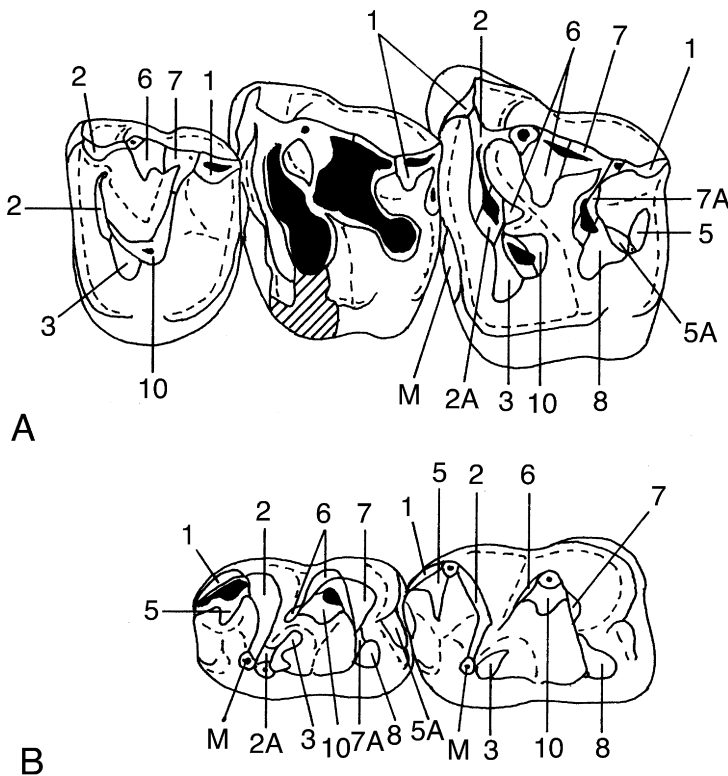
Lower preultimate molars of *Lophiaspis maurettei* Depéret, 1910 (Text-fig. 3J-L) are very similar to those of *P. gabuniai*. However, the cristid obliqua is concave buccally, not straight, the paracristid buccal branch is nearly longitudinal, the metaconid buttress and postmetacristid are nearly lacking, the cingula, lingual protoconid rib and hypoconulid are weaker, and the buccal and lingual tooth walls are parallel. The M_3 hypoconulid lobe is broken away in all known specimens, but it would clearly have been much smaller than in *Protomoropus* (e.g. Savage *et al.* 1966, fig. 27).

Lower molars of *Litolophus* (Radinsky 1964, fig. 3) diverge more from *Protomoropus* in overall appearance than do those of *Lophiaspis*. Thus, the cristid obliqua joins the distal metaconid high on the crown and, together with the paracristid buccal branch, is more oblique in orientation; the hypoconulid is indistinguishable on the distal cingulum of M_{1-2} and much smaller and lower on M_3 ; and the buccal and lingual walls converge occlusally at a greater angle.

OCCLUSION

The occlusal relationships of *Protomoropus* cheek teeth (Text-fig. 5) are important for an understanding of derived chalicothere occlusion in general (see Butler 1952a, b, 1965; Hooker 1984, 1994, for background). Although at slightly different wear stages, the first and second molars of the maxillary and mandibular dentitions occlude reasonably well. The paraconule slides obliquely down the notch between the twinned metaconid cusps. This shows that PSS.20-9 cannot belong to *Homogalax namadicus* because the upper molar of this taxon has a straight uninterrupted protoloph with no paraconule. A lingual phase facet on the lower molar between the protoconid lingual rib and the buccal branch of the paracristid occludes with a well-developed posthypocrista on M^1 and M^2 and, probably at the stage of wear of PSS.20-9, with that of DP^4 , as P^4 of PIN.3104-323 has no homologous facet. None of the cheek teeth shows evidence of buccal phase facets 4 or 9 (Text-fig. 6), which indicates an emphasis on shear of the transverse lophs, mesially on uppers and distally on lowers.

Normally, moderate obliquity of the lower molar cristid obliqua is associated with moderate flexing of the upper molar centrocrista. In the case of *Protomoropus*, the cristid obliqua is oblique but the centrocrista is straight. On the upper molars, however, a blunt lingual paracone rib extends basally across the central valley, almost meeting the back of the paraconule. It is the large facet on the paracone extending between this lingual rib and the postparacrista that makes contact with the distal half of the cristid obliqua; and a small facet on the back of the paraconule that has a comparably small area of contact with the mesial end of the cristid obliqua. For the purposes of occlusion with the cristid obliqua, this lingual paracone rib functions like a more lingually positioned paracone cusp. It may have foreshadowed the more derived chalicothere dilambdodonty with sharp W-shaped ectoloph and large mesostyle. Here, shifting of the sizes and spatial relationships of the cusps (Radinsky 1964, p. 26) includes a reorientation distad for the lingual paracone rib, shifting its large facet buccally and reducing it. Thus, with increased buccal flexing of the centrocrista, contact with the lower molar cristid obliqua is made by the postparacrista alone (Butler 1965, figs 2, 6).



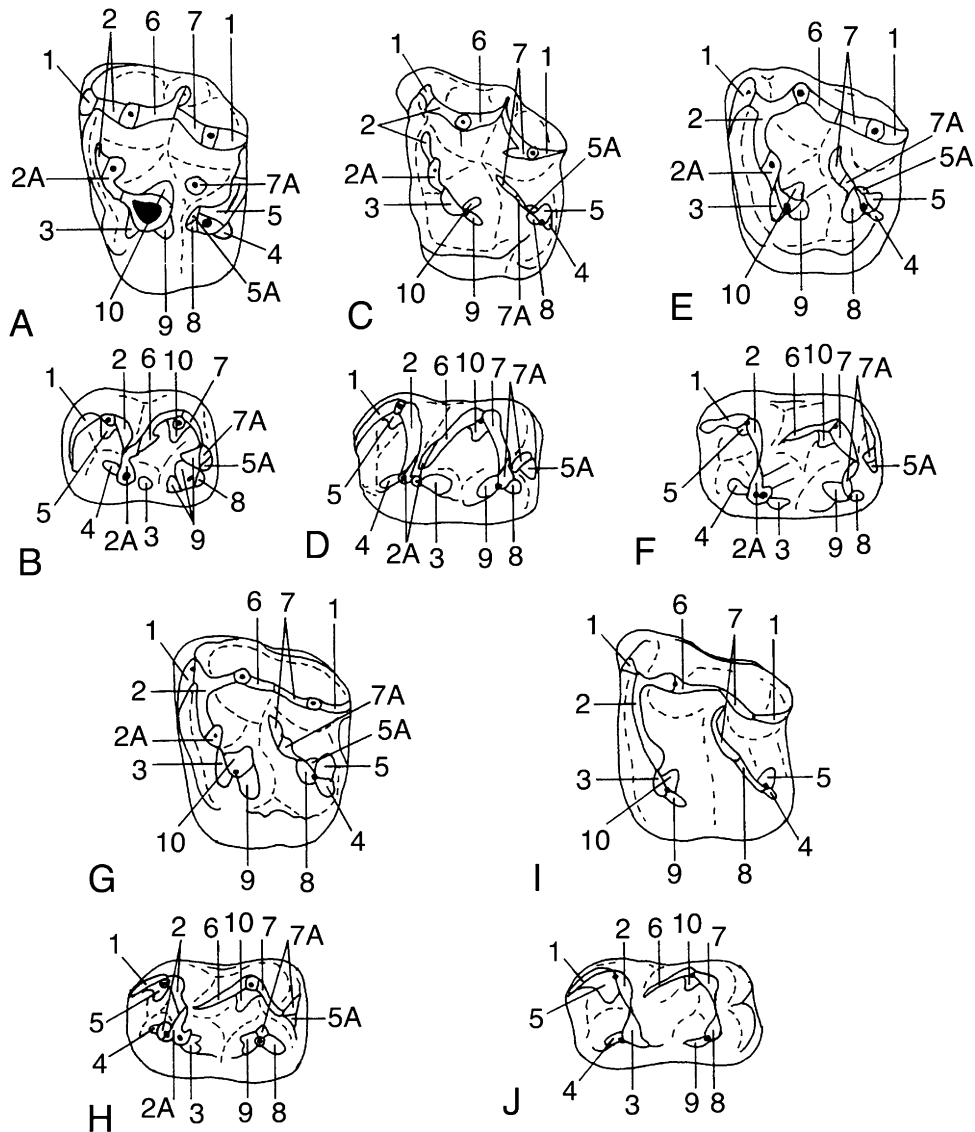
TEXT-FIG. 5. Crown views, showing occlusal relationships of *Protomoropus gabuniai* cheek teeth. Wear facets are numbered according to Butler (1952*a, b*), with additions from Hooker (1984) and herein. A, upper left P4–M2 (reversed from original PIN.3104-323). B, lower right M1–2 (PSS.20-9).

Two lingual phase facets of different orientation exist on the buccal face of the M² hypocone of *Protomoropus* (Text-fig. 5A). The more distal one is facet 5, which contacts the lingual face of the M₃ protoconid. The more mesial one has a different orientation and contacts the lingual face of the M₂ hypoconulid (Text-fig. 5B). This facet, here labelled 5A, occurs widely in primitive perissodactyls and *Ectocion* (Text-fig. 6). It appears not to have been distinguished previously from facet 5 (Hooker 1984, figs 19B, 21B; 1994, fig. 2E–F). In late buccal phase, a near-horizontal facet on the mesial cingulum of the upper molar is made by the more mesial metaconid cusp of the opposing lower molar (M in Text-fig. 5).

RELATIONSHIPS OF *PROTOMOROPUS* AND ANCYLOPODS

Given the mixture of derived ancylopod plus primitive perissodactyl characters of *Protomoropus*, it was deemed important to analyze its characters cladistically in the context of both typical chalicotheres and a variety of primitive members of other perissodactyl groups, to see if this could shed light on ancylopod relationships.

A data matrix (Appendix, section 1) was constructed for 20 taxa, including *Protomoropus* and three phenacodontids. One of the latter, *Phenacodus*, was chosen as outgroup following previous arguments (Hooker 1994; Hooker and Dashzeveg 2003). Because so many of the relevant taxa are poorly known, characters are mainly dental, although supplemented by a few cranial and postcranial ones, where these could be scored for enough taxa to be significant. Many of the characters used are the same as in Hooker and Dashzeveg (2003), but in some cases with fewer or more states and in other cases with new characters added, reflecting the different taxonomic composition of the matrix. The 54 characters are listed and described in the Appendix (section 2). Text-figure 6 illustrates some of the states of these characters. All the multistate characters but three were treated as fully ordered as they were judged to form simple



TEXT-FIG. 6. Diagrammatic crown views of molars showing wear facets (numbered as Text-fig. 5) of a range of primitive perissodactyls and a phenacodontid, to demonstrate homologous cusps and crests and to illustrate characters in Appendix, section 2. A-B, *Ectocion osbornianus*; C-D, *Lambdaotherium popoagicum*; E-F, *Cymbalophus cuniculus*; G-H, *Pliolophus vulpiceps*; I-J, *Karagalax mamikhelensis*. A, C, E, G, I are upper left first or second molars; B, D, F, H, J are lower right first or second molars. Not to scale.

transformation series and two of the remainder (characters 3 and 37) were entered as stepmatrices (Swofford 1990) to reduce or avoid duplication and consequent potential undesirable weighting of primitive states (Lipscomb 1992). They are shown in the Appendix (section 3). Character 27 was treated as unordered because interpretation of the relationships of the states could not be assessed *a priori*. Characters linked by the occlusal relationships of upper and lower tooth partners were treated as single, thus reducing inadvertent weighting of certain tooth characters over others. This involves characters 1, 3,

7, 23, 25 and 39. Letters rather than numbers are used for states other than zero in multistate characters to facilitate understanding of character state transformations on the cladogram.

Choice of taxa

Taxa were chosen for analysis for being: the most primitive unequivocal members of their respective perissodactyl groups, relevant stem perissodactyls of disputed affinities, and phenacodontids. Thus *Hyracotherium* (represented by the type species *H. leporinum*) was chosen as the palaeotheriid, *Pliolophus* as the equid, *Sifrhippus* and *Cymbalophus* as primitive equoids (Hooker 1994), but where the last has alternatively been interpreted as a tapiromorph (Hooker 1984; Froehlich 1999, 2002). *Heptodon* and *Karagalax* were chosen as primitive ceratomorphs. Within Ceratomorpha, *Heptodon* is also regarded as a stem tapiroid (Dashzeveg and Hooker 1997; Holbrook 2001). *Karagalax* was originally described as an isectolophid by Maas *et al.* (2001) but reinterpreted as a stem ceratomorph by Hooker and Dashzeveg (2003). *Pachynolophus* was included because of its conflicting positions as either a primitive tapiromorph (Hooker 1994) or as an equoid (Froehlich 1999). *Litolophus* and *Eomoropus* were chosen as the most primitive undisputed chalicotheres (Coombs 1989), *Paleomoropus* and *Lophiaspis* as either lophiodonts (Fischer 1977; Colbert and Schoch 1998) or primitive chalicotheres (Radinsky 1964; Hooker 1989) and as phenetically very close to *Protomoropus*, and *Lophiodon* as an unequivocal lophiodontid. The isectolophids *Cardiolophus*, *Orientalophus* and *Homogalax wutuensis* were chosen to represent this family of primitive tapiromorphs and particularly because of phenetic similarities to *Protomoropus*. *Lambdotherium* was chosen to represent the Brontotheriidae (Hooker 1989, 1994), notwithstanding claims of palaeothere affinities (Mader 1989). The issue of the relationships of *Lambdotherium* is outside the scope of this paper and will be dealt with elsewhere.

In addition to the outgroup *Phenacodus*, two other phenacodontids, *Ectocion* and *Lophocion* were included in the analysis for having phenetic dental similarities to perissodactyls (Hooker 1994). Arguments for this versus the inclusion of other morphologically more remote 'condylarths' such as *Radinskya* (McKenna *et al.* 1989; Froehlich 1999) are given in Hooker and Dashzeveg (2003).

Analysis

The matrix was analyzed using PAUP 3.1 (Swofford 1990) with the Branch and Bound algorithm. PAUP found five maximum parsimony topologies of 170 steps. The consistency index excluding uninformative characters (CI) is 0.490 and the retention index (RI) is 0.711. Text-figure 7 shows the Strict and Majority Rule consensus cladograms generated from these data, the former with Bremer Support. Text-figure 8 shows the maximum parsimony cladogram whose topology resembles the Majority Rule consensus, together with character state changes.

In all five topologies, the primitive chalicotheres *Litolophus* and *Eomoropus* form a clade, which is sister to another composed of the sister taxa *Lophiodon* and *Lophiaspis* plus a more remote *Paleomoropus*. These two clades are together nested successively with *Protomoropus* and *Homogalax wutuensis*.

This entire clade (referred to as clade A) is nested in four out of the five cases with *Cardiolophus*, and in the fifth with a clade consisting of *Cardiolophus* plus *Orientalophus*. In one of the four cases, *Orientalophus* forms the next branch down.

Another clade that is consistent in all five topologies is *Hyracotherium* and *Pliolophus* (sister taxa) nested successively with *Sifrhippus* and *Cymbalophus*, forming the horse superfamily Equoidea. The nearest relatives to Equoidea are *Heptodon*, *Karagalax* and *Pachynolophus*, whose interrelationships vary, but in three cases form a sister clade to Equoidea, in which *Karagalax* and *Heptodon* are sister taxa.

The clade comprising Equoidea plus *Heptodon*, *Karagalax* and *Pachynolophus* is referred to as clade B. The consistent clade closest to clade B is clade A. *Orientalophus*, in the three cases where it is not part of, or sister taxon to, clade A plus *Cardiolophus*, is sister taxon to clades A and B. In all five topologies, clades A, B, *Cardiolophus* and *Orientalophus* are successively nested with *Lambdotherium* and the phenacodontids *Lophocion*, *Ectocion* and *Phenacodus*.

Topology

The topology of the cladograms differs from that of previous phylogenies of perissodactyls, whether cladistic or pre-cladistic. All five maximum parsimony alternatives are consistent in linking ceratomorphs with equoids (clade B above) rather than with ancylopods. The Tapiromorpha (*sensu* Hooker 1984, 1989 and subsequent authors) is thus paraphyletic. The Chalicotherioidea (*sensu* Radinsky 1964; Savage *et al.* 1966; Hooker 1989) is also paraphyletic as *Paleomoropus* and *Lophiaspis* form a clade with *Lophiodon*, consistent with the classification of Prothero and Schoch (1989). *Paleomoropus* and *Lophiaspis* are thus here included in the family Lophiodontidae. *Protomoropus* is a stem taxon to the Chalicotheriidae (including Eomoropidae) plus Lophiodontidae. With the abandonment of the paraphyletic Eomoropidae (see Coombs 1989; Lucas and Schoch 1989), the superfamily Chalicotherioidea becomes monotypic and, since *Paleomoropus* and *Lophiaspis* have previously been included therein, we propose to extend the superfamily to encompass both families Chalicotheriidae and Lophiodontidae and the genus *Protomoropus*.

Another difference from previous phylogenies is that, with the possible exception of *Orientolophus*, the family Isectolophidae (confirmed as paraphyletic; see Froehlich 1999) breaks its links with the Ceratomorpha and forms a series of stem taxa to the Chalicotherioidea. Of these, *Homogalax wutuensis* shares the most characters with chalicotherioids. In these respects, this species differs from other *Homogalax* species and should therefore be excluded from the genus *Homogalax* to keep the latter monophyletic. Erecting a new genus for it, however, may be premature until it becomes better known.

We propose that the Ancylopoda, previously including only the Chalicotheriidae and Lophiodontidae, be expanded to include the 'isectolophid' genera *Homogalax*, '*Homogalax*' ('*H.*' *wutuensis*), *Isectolophus* and *Cardiolophus* as stem members. The exact position of *Orientolophus* with respect to clade A or B herein may be resolved if it becomes more completely known. For a display of taxonomic groupings higher than genus, see Text-figure 7B.

In all the topologies, *Lambdotherium*, representing the Brontotheriidae, forms the lowest branch of the Perissodactyla, thus sister group to all other perissodactyls.

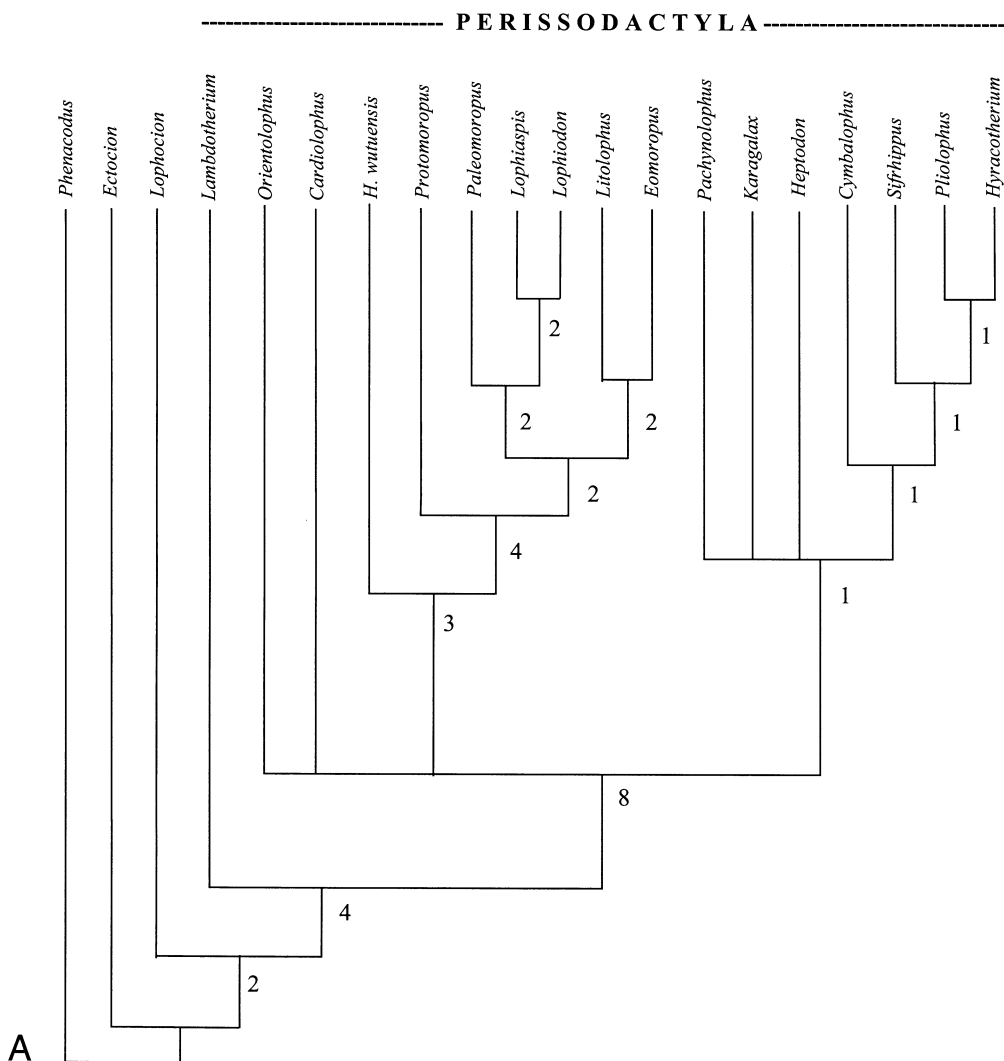
Character state transformations

The character states for all nodes of the Chalicotherioidea as defined here (Text-fig. 8) are consistent in all five maximum parsimony cladograms. They are nearly so also for the next lower node defining the Chalicotherioidea plus '*Homogalax*' *wutuensis*. The Chalicotherioidea are characterized by:

1. Consistent strong buccal projection of the M³ parastyle (43B). This is variably developed in such isectolophids as *Cardiolophus* or *Homogalax* s.s. (43A), but always fully developed in Chalicotherioidea. Unfortunately, M³ is not known for '*H.*' *wutuensis*, so for methodological reasons the Acctran optimization places character 43B at the next lower node.
2. Long M¹⁻² postmetacrista and buccal segment of the lower molar paracristid (23). This is paralleled in clade B.
3. Slight buccal flexing of the upper molar centrocrista (10). This represents a return to the primitive state from a secondarily derived straight centrocrista present in 'isectolophids' (10A).
4. Attachment of the lower molar cristid obliqua to a point on the trigonid backwall midway between protoconid and metaconid (14A). This represents a lingual shift from the 'isectolophid' condition (14B) and signals the beginning of chalicothere dilambdodonty. It is paralleled in the equid-palaeothere clade and in both cases represents a reversal to the condition in the phenacodontid *Ectocion*.
5. Increased obliquity of lower molar paracristid to 30 or 40 degrees (17B or A), the difference depending on Acctran versus Deltran optimization. This represents a reversal from more derived states present in 'isectolophids'. It is also paralleled in *Heptodon* and the equid-palaeotheriid clade.

The Chalicotheriidae plus Lophiodontidae are linked by:

1. Consistent reduction in size of the upper molar metaconule (9B). This is paralleled several times elsewhere on the cladogram.
2. Buccal end of metaloph shifted mesially from metacone (36D). This is paralleled in *Cardiolophus* and *Karagalax*.



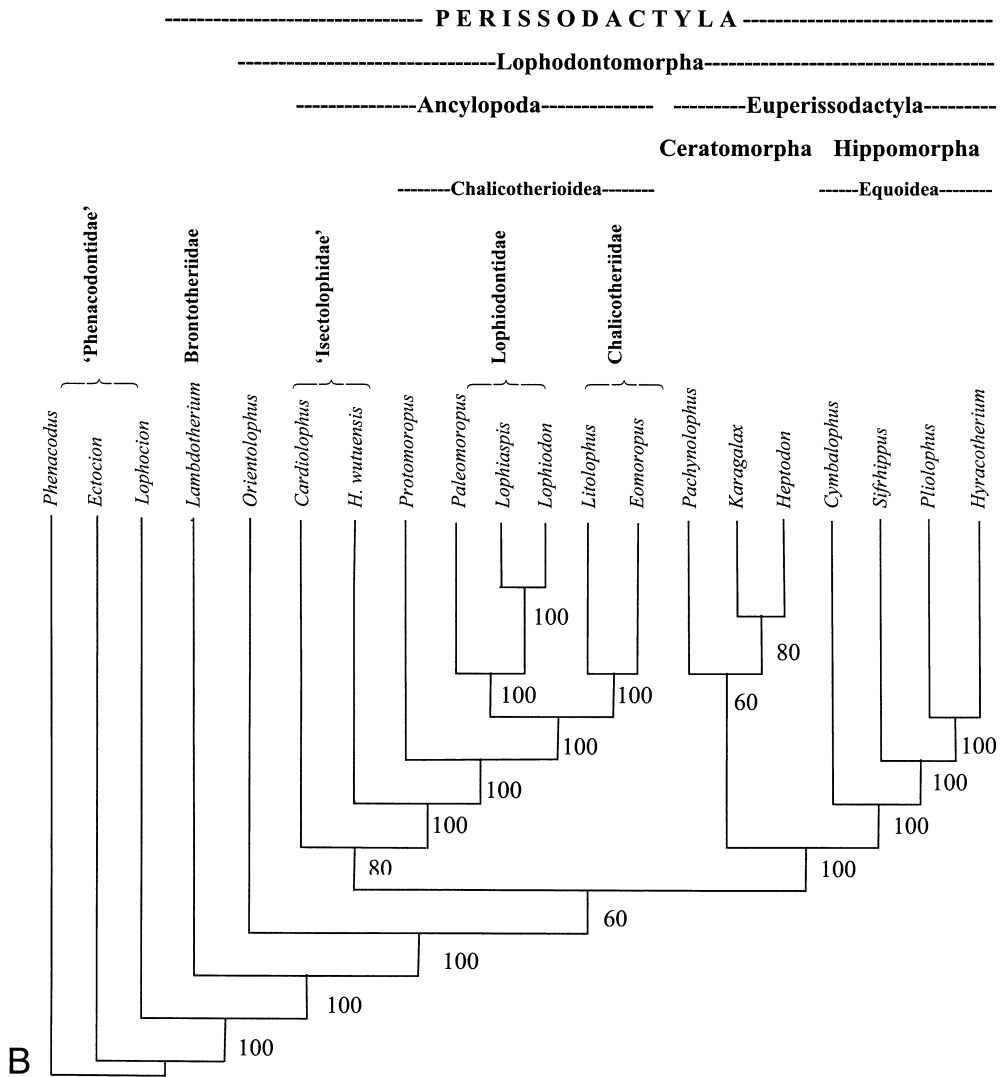
TEXT-FIG. 7. Strict (A) and Majority Rule (B) consensus cladograms from the five maximum parsimony cladograms generated by PAUP 3.1 from the data matrix in the Appendix. The indices on the strict consensus show Bremer Support (Bremer 1994) for the different nodes.

3. Strong distal recurving of the upper molar parastyle (42). This is a typical feature of chalicotheriids and primitive lophiodontids, but not of *Lophiodon* where this character is reversed.
4. Loss of P₁ (32). Because this character is unknown in either *Protomoropus* or '*Homogalax*' *wutuensis*, the Acctran optimization places it two nodes lower down.

The relative weakness of the characters defining this clade compared to the one below probably indicates that *Protomoropus* is close to the ancestry of both families.

The Lophiodontidae are defined by:

1. Loss of P¹ (20). This may define the family or just *Lophiodon*, which is the only genus of the three where the state is known.

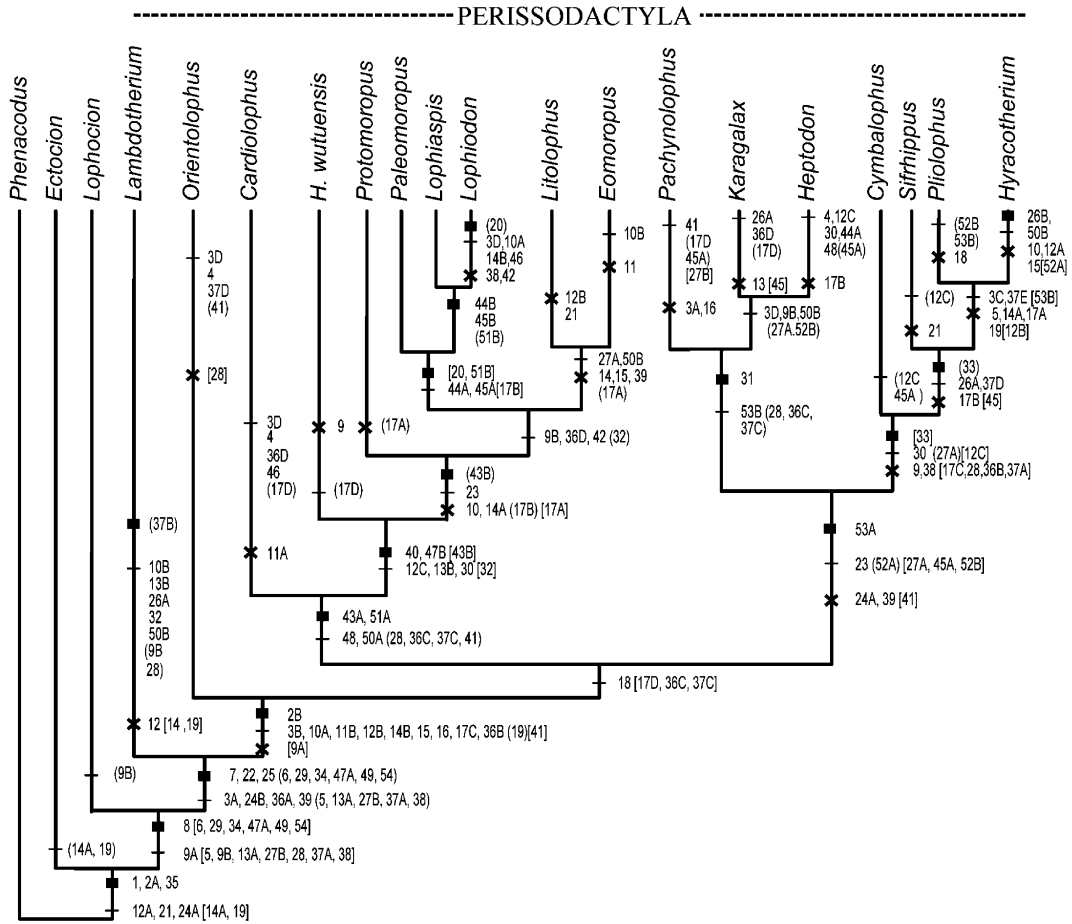


TEXT-FIG. 7. *Continued.*

2. Close approximation of P³ paracone and metacone (51B). This may define the family or just *Lophiaspis* and *Lophiodon*, the tooth type being unknown in *Paleomoropus*.
3. Slight lingual tilting of the upper molar metacone (44A), paralleled in *Heptodon*.
4. Slight buccal tilting of the upper molar paracone (45A), paralleled within clade B.
5. A slight change in the angle of the lower molar paracristid (17B) may take place here or at a lower node (Acctran versus Deltran).

The Chalicotheriidae are defined by:

1. M₃ hypoconulid joining distal margin of post-talonid lobe (27A), paralleled within clade B.
2. Strong P³ postprotocrista (50B), paralleled in the *Karagalax-Heptodon* clade and *Lambdotherium*.
3. Lingual shift of trigonid attachment position of lower molar cristid obliqua (14), representing a reversal to the primitive state and paralleled in *Lambdotherium*.



TEXT-FIG. 8. One of the five maximum parsimony cladograms resembling the Majority Rule one, generated by PAUP 3.1 from the data matrix in the Appendix, showing character state changes; see section 2 of the Appendix for explanation of numbered characters. Broad bar, synapomorphy; narrow bar, normal polarity homoplasy; X, reversal. Characters that vary with different optimizations are enclosed between () for DELTRAN and between [] for ACCTRAN.

4. High level attachment of lower molar cristid obliqua to back of trigonid (15), representing a reversal to the primitive state and paralleled in *Hyracotherium*.
5. Transverse orientation of upper molar metaloph and lower molar hypolophid (39), reversed from the derived oblique state of basal perissodactyls and paralleled in clade B.
6. Increased obliquity of lower molar paracristid to tooth long axis (17A) may take place here or at a lower node (see under Chalicotherioidea).

In maximum parsimony cladogram 3, the Ancylopoda are defined by:

1. M³ parastyle projecting strongly buccally in some individuals (43A).
 2. Incipient approximation of the P³ paracone and metacone (51A).
- These two characters, together with their more derived states (43B, 51B), uniquely define Ancylopoda and demonstrate 'isectolophids' to be their stem members rather than primitive tapiromorphs.
3. P⁴ premetaconule crista strong and extending high on the ectoloph (48), paralleled in *Heptodon*.

4. P³ postprotocrista lost (50A). This structure is regained in Chalicotheriidae (50B).
5. The remaining characters 28, 36C, 37C and 41 may pertain at this or lower nodes, depending on the Acctran versus Deltran optimizations. All are subject to considerable homoplasy and should not be taken as elements of the definition of the Ancylopoda.

Characters common to all five maximum parsimony cladograms that define clade B are:

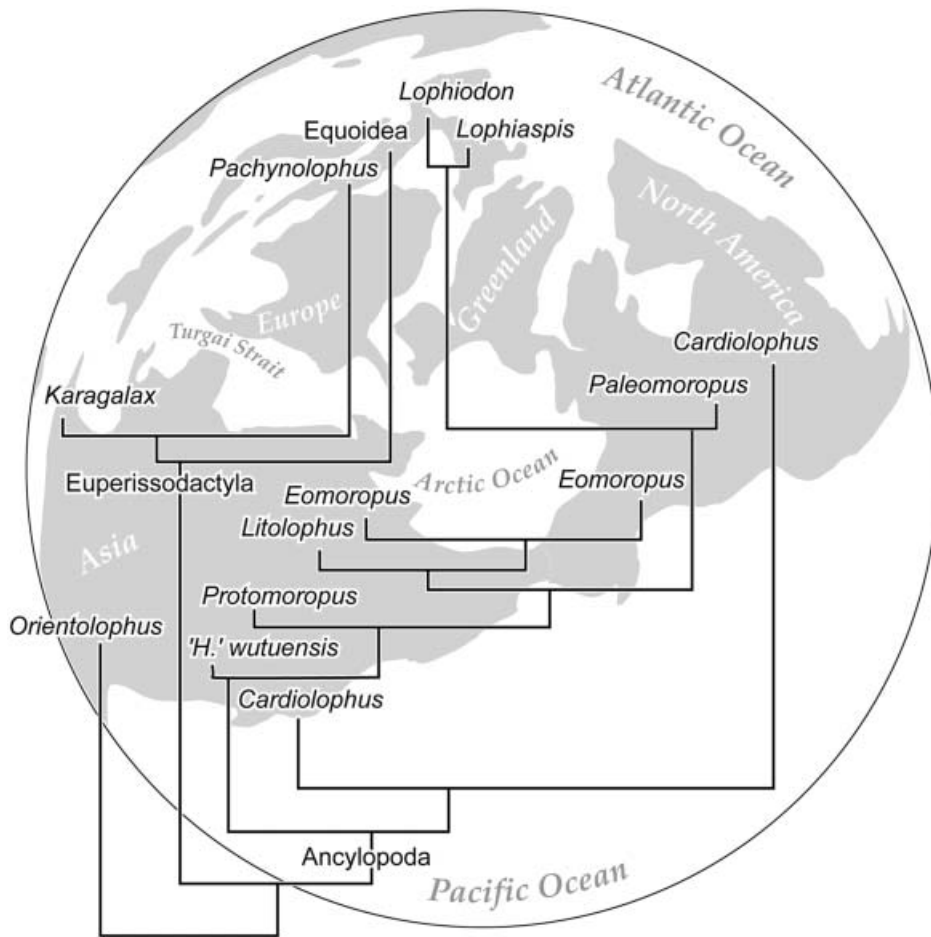
1. Shortening of the post-P₁ diastema (53A), leading to closure (53B) within the clade, is unique to clade B. Although P₁ is lost within the Ancylopoda, there is no evidence that this was preceded by shortening or closure of the P₁₋₂ diastema. Similar shortening and closure of the post-P¹ diastema (52A and B) also occurred, but as this is unknown in primitive *Pachynolophus*, cladograms that place this taxon at the base of clade B put this character at the next higher node rather than at the base.
2. Lengthened M¹⁻² postmetacrista (23), paralleled in Chalicotherioidea.
3. Reduction in size of the upper molar parastyle (24A). Although not reversed to the primitive state, this may be a defining character of clade B. However, an alternative hypothesis is that the parastyle enlarged to the B state independently in brontotheres and ancylopods, rather than that the B state originated with the order Perissodactyla and reduced with clade B. Nevertheless, whether or not it is enlargement that is derived for Ancylopoda or reduction that is derived for clade B (mutually exclusive), the character serves as an important phylogenetic distinction.

Characters common to all five maximum parsimony cladograms that define clade B, suborder Ancylopoda and *Orientalophus* are:

1. Upper molar preparaconule crista constantly joining preparacrista (2B). This uniquely defines the clade. The character is at the origin of bilophodonty in perissodactyls, which is not present in brontotheres.
2. The variable joining of the metaconal fold to the metaconule (36B), the first stage in development of a full metaloph and unique to this clade.
3. Straightening of the centrocrista (10A) is a feature of loss of dilambdodonty, regained and relost more than once within the group.
4. Loss of upper molar mesostyle (11B), regained within Chalicotheriidae.
5. Reduction in convergence angle of buccal and lingual outer walls of lower molars to *c.* 10 degrees (12B). This often accompanies bilophodonty to lengthen the transverse crests. It is reversed in *Hyracotherium*.
6. Buccal shift of the trigonid attachment position of the lower molar cristid obliqua to join the protoconid (14B), reversed in the equid-palaeotheriid clade and in the Chalicotherioidea, regained in *Lophiodon*.
7. Reduction in height of the mesial end of the lower molar cristid obliqua where it joins the trigonid (15), reversed in chalicotheriids and *Hyracotherium*.
8. Reduction of the lower molar entoconulid (16), reversed in primitive *Pachynolophus*. As a gradual loss character, it is difficult to define and minor in phylogenetic inference. Although less parsimonious, it is possible that it was retained rather than regained in *P. hookeri*.
9. Reduction in obliquity of lower molar paracristid to *c.* 20 degrees to tooth long axis (17C). Subject to reversal in chalicotheriids and within equoids.

Higher taxonomic innovations

Inclusion in the analysis of *Karagalax* and *Pachynolophus* (based mainly on its most primitive species *P. hookeri*) and the recognition of key characters linking isectolophids to chalicotherioids show that some of the defining characters of the Tapiromorpha have evolved independently in Ancylopoda and Ceratomorpha, whilst others are relatively primitive perissodactyl adaptations that reversed independently in equoids and chalicotherioids. We propose the infraorder Euperissodactyla nov. (Text-fig. 7B) for clade B, which encompasses the parvorders Hippomorpha (new rank) (*s.s.* for Equoidea) and Ceratomorpha (new rank) (superfamilies Tapiroidea and Rhinoceroidea). This corresponds essentially to the modern perissodactyl groups. We propose also the suborder Lophodontomorpha nov. (Text-fig. 7B) for Ancylopoda plus Euperissodactyla, which is sister group to the family Brontotheriidae (monotypic suborder Titanotheriomorpha Hooker, 1989). This study does not support the monophyly of the infraorder Selenida McKenna and Bell, 1997 for brontotheriids plus chalicotheriids (the latter *sensu* herein), or of the sub- or infraorder Tapiromorpha Haeckel, 1866 (*sensu* either Hooker 1984 or 1989 for ceratomorphs



TEXT-FIG. 9. Early Eocene polar projection Northern Hemisphere palaeogeographic shoreline map, with superimposed cladogram from Text-figure 8, representing the Ancylopoda plus their immediately related clades. Map from unpublished work by Paul Markwick (see Markwick *et al.* 2000, with minor modifications to North Sea–Arctic Ocean link following Iakovleva *et al.* 2001).

plus ancylopods), or of McKenna and Bell's (1997) Ceratomorpha, expanded to include all perissodactyls except Hippomorpha.

Geographical origins

Text-figure 9 places the ancylopod part of the Text-figure 8 cladogram on an early Eocene Northern Hemisphere palaeogeographic map. It is indicative of an Asian origin for Chalicotherioidea and Chalicotheriidae. The latter did not appear in North America until the Middle Eocene, when *Eomoropus* and *Grangeria* arrived from Asia (Lucas and Schoch 1989). Chalicotheriids did not reach Europe until the middle of the Oligocene, following the closure of the Turgai Straits (Remy *et al.* 1987). The Lophiodontidae, on the other hand, appear to have arisen in North America, following dispersal via the Bering Straits of a primitive chalicotherioid from Asia, and thence moved on to Europe via the North Atlantic–Greenland land bridge. In Europe, they underwent a significant radiation but with relatively little morphological diversity. One species became the largest European Eocene mammal. Lophiodontids

survived in isolation in Europe until the end of the Middle Eocene. One anomalous feature is the apparent lateness of dispersal to Europe. The oldest European lophiodontid is *Lophiaspis* with a first occurrence in the Zone PE IV French sites of Mutigny and Palette, dated at around 52 Ma (Hooker 1998) and thus at least 1 myr after the probable opening of Denmark Strait between Greenland and Europe. Mammal faunas from these sites were already showing some European endemism, indicative of a loss of land connection across the North Atlantic. On the other hand, it is possible that rarity is giving a falsely late European appearance date for *Lophiaspis*. The fossil evidence certainly indicates that lophiodontids occurred only in Europe and North America, with the most primitive taxon in the latter continent. The most primitive chalicotherioid, *Protomoropus*, and its nearest 'isectolophid' relative, '*Homogalax*' *wutuensis*, support an Asian origin for Chalicotherioidea. However, the picture is less clear for ancylopod origins, as the stem ancylopod genus *Cardiolphus* is known from both Asia and North America. In fact, although the evidence is meagre, the unnamed Asian species appears more derived than those from North America in the depth of the buccal notch between the parastyle and paracone and in the strength of the metaloph on the upper molar. This would suggest a North American origin for Ancylopoda. On the other hand, because of missing data, *Orientalophus* was unstable in the cladistic analysis. Thus, although three of the five maximum parsimony results show it to be stem Lophodontomorpha, one shows it as sister taxon to the Ancylopoda and another as sister taxon to *Cardiolphus*, suggesting an Asian origin for Ancylopoda. A better knowledge of *Orientalophus* would probably resolve this issue.

Acknowledgements. We thank the following for access to collections in their care: Drs J. Alexander, M. Novacek (American Museum of Natural History, New York), R. Purdy, R. Emry (United States National Museum, Washington), P. D. Gingerich (UMMP), M. Godinot (University of Montpellier II), M. Hugueney (FSL) and D. E. Russell (MNHN). We are particularly grateful to Drs P. D. Gingerich, S. G. Lucas (New Mexico Museum of Natural History) and S.-Y. Ting (Louisiana State University Museum of Natural Science) for providing casts. Dr A. B. Smith gave help with the Bremer support, Dr P. Markwick permitted us to reproduce an outline of one of his unpublished palaeogeographic maps, Prof. P. M. Butler critically read the manuscript, and Mr P. Crabb of The Natural History Museum, London, Photostudio made the photographic illustrations. We thank the Royal Society for funding visits to Mongolia and England under their international exchange programme. Comments by Dr G. Gunnell and an anonymous referee improved the manuscript. This is a contribution to the NHM Human Origins Programme, Project 297.

REFERENCES

- BREMER, K. 1994. Branch support and tree stability. *Cladistics*, **10**, 295–304.
- BUTLER, P. M. 1952a. The milk-molars of Perissodactyla, with remarks on molar occlusion. *Proceedings of the Zoological Society of London*, **121**, 777–817.
- 1952b. Molarization of the premolars in the Perissodactyla. *Proceedings of the Zoological Society of London*, **121**, 819–843.
- 1965. Fossil mammals of Africa no. 18: east African Miocene and Pleistocene chalicotheres. *Bulletin of the British Museum (Natural History), Geology Series* **10**, 163–237.
- COLBERT, M. W. and SCHOCH, R. M. 1998. Tapiroidea and other moropomorphs. 569–582. In JANIS, C. M., SCOTT, K. M. and JACOBS, L. L. (eds). *Evolution of Tertiary mammals of North America, Volume 1: terrestrial carnivores, ungulates, and ungulatelike mammals*. Cambridge University Press, Cambridge, 691 pp.
- COOMBS, M. C. 1979. *Tylocephalonyx*, a new genus of North American dome-skulled chalicotheres (Mammalia, Perissodactyla). *Bulletin of the American Museum of Natural History*, **164**, 1–64.
- 1983. Large mammalian clawed herbivores: a comparative study. *Transactions of the American Philosophical Society*, **73**, 1–96.
- 1989. Interrelationships and diversity in the Chalicotheriidae. 438–457. In PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.
- COPE, E. D. 1889. The Vertebrata of the Swift Current River, II. *American Naturalist*, **23**, 151–155.
- DASHZEVEG, D. 1979a. Discovery of *Hyracotherium* in Mongolia. *Paleontologicheskii Zhurnal*, **1979**, 108–113. [In Russian].
- 1979b. Discovery of *Homogalax* (Perissodactyla, Tapiroidea) in Mongolia and its stratigraphic significance. *Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Geologicheskii*, **54**, 105–111. [In Russian].

- and HOOKER, J. J. 1997. New ceratomorph perissodactyls (Mammalia) from the Middle and Late Eocene of Mongolia: their implications for phylogeny and dating. *Zoological Journal of the Linnean Society*, **120**, 105–138.
- DEPÉRET, C. 1910. Etudes sur la famille des lophiodontidés. *Bulletin de la Société Géologique de France*, **4**, **10**, 558–577.
- 1917. Monographie de la faune de mammifères fossiles du Ludien inférieur d'Euzet-les-Bains (Gard). *Annales de l'Université de Lyon*, **1**, **40**, 1–290, pls 1–25.
- FISCHER, K.-H. 1977. Neue Funde von *Rhinocerotolophiodon* (n. gen.), *Lophiodon* und *Hyrachyus* (Ceratomorpha, Perissodactyla, Mammalia) aus dem Eozän des Geiseltals bei Halle (DDR). 1 Teil: *Rhinocerotolophiodon*. *Zeitschrift für Geologische Wissenschaften*, **5**, 909–919.
- FROELICH, D. J. 1999. Phylogenetic systematics of basal perissodactyls. *Journal of Vertebrate Paleontology*, **19**, 140–159.
- 2002. Quo vadis eohippus? The systematics and taxonomy of the early Eocene equids (Perissodactyla). *Zoological Journal of the Linnean Society*, **134**, 141–256.
- GILL, T. 1872. Arrangement of the families of mammals with analytical tables. *Smithsonian Miscellaneous Collections*, **11** (230, Art. 1), 1–98.
- GINGERICH, P. D. 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. *University of Michigan Papers on Paleontology*, **28**, 1–97.
- 1991. Systematics and evolution of early Eocene Perissodactyla (Mammalia) in the Clarks Fork Basin, Wyoming. *Contributions from the Museum of Paleontology, University of Michigan*, **28**, 181–213.
- GODINOT, M., CROCHET, J.-Y., HARTENBERGER, J.-L., LANGE-BADRÉ, B., RUSSELL, D. E. and SIGÉ, B. 1987. Nouvelles données sur les mammifères de Palette (Eocène inférieur, Provence). *Münchner Geowissenschaftliche Abhandlungen, A*, **10**, 273–288.
- HAECKEL, E. 1866. *Generelle Morphologie der Organismen. Allgemeine Entwicklungsgeschichte der Organismen. Kritische Grundzüge der mechanischen Wissenschaft von der entstehenden formen der Organismen, begründet durch die Descendenz-Theorie*. Georg Reimer, Berlin, 2 vols, clx + 462 pp.
- HOLBROOK, L. T. 2001. Comparative osteology of early Tertiary tapiromorphs (Mammalia, Perissodactyla). *Zoological Journal of the Linnean Society*, **132**, 1–54.
- HOOKER, J. J. 1984. A primitive ceratomorph (Perissodactyla, Mammalia) from the early Tertiary of Europe. *Zoological Journal of the Linnean Society*, **82**, 229–244.
- 1989. Character polarities in early Eocene perissodactyls and their significance for *Hyracotherium* and infraordinal relationships. 79–101. In PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.
- 1994. The beginning of the equoid radiation. *Zoological Journal of the Linnean Society*, **112**, 29–63.
- 1998. Mammalian faunal change across the Paleocene-Eocene transition in Europe. 428–450. In AUBRY, M.-P., LUCAS, S. G. and BERGGREN, W. A. (eds). *Late Paleocene – Early Eocene climatic and biotic events in the marine and terrestrial records*. Columbia University Press, New York, 513 pp.
- and DASHZEVEG, D. 2003. Evidence for direct mammalian faunal interchange between Europe and Asia near the Paleocene-Eocene boundary. 479–500. In WING, S. L., GINGERICH, P. D., SCHMITZ, B. and THOMAS, E. (eds). *Causes and consequences of globally warm climates in the Early Paleogene*. Special Papers of the Geological Society of America, **369**, 614 pp.
- IAKOVLEVA, A. I., BRINKHUIS, H. and CAVAGNETTO, C. 2001. Late Palaeocene–Early Eocene dinoflagellate cysts from the Turgay Strait, Kazakhstan; correlations across ancient seaways. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **172**, 243–268.
- LIPSCOMB, D. L. 1992. Parsimony, homology and the analysis of multistate characters. *Cladistics*, **8**, 45–65.
- LUCAS, S. G. and SCHOCH, R. M. 1989. Taxonomy and biochronology of *Eomoropus* and *Grangeria*, Eocene chalicotheres from the western United States and China. 422–437. In PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.
- MAAS, M. C., HUSSAIN, S. T., LEINDERS, J. J. M. and THEWISSEN, J. G. M. 2001. A new isctolophid tapiromorph (Perissodactyla, Mammalia) from the early Eocene of Pakistan. *Journal of Paleontology*, **75**, 407–417.
- MADER, B. J. 1989. The Brontotheriidae: a systematic revision and preliminary phylogeny of North American genera. 458–484. In PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.
- MARKWICK, P. J., ROWLEY, D. B., ZIEGLER, A. M., HULVER, M. L., VALDES, P. J. and SELWOOD, B. W. 2000. Late Cretaceous and Cenozoic global palaeogeographies: mapping the transition from a 'hot-house' to an 'ice-house' world. *GFF (Geologiska Föreningens i Stockholm Förhandlingar)*, **122**, 103.
- MCKENNA, M. C. and BELL, S. K. 1997. *Classification of mammals above the species level*. Columbia University Press, New York, 631 pp.

- CHOW MIN-CHEN, TING SU-YIN and LUO ZHE-XI 1989. *Radinskya yupingae*, a perissodactyl-like mammal from the late Paleocene of China. 24–36. In PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.
- OSBORN, H. F. 1929. The titanotheres of ancient Wyoming, Dakota and Nebraska. *Monographs of the United States Geological Survey*, **55**, 1–953.
- OWEN, R. 1848. Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight; with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London*, **4**, 103–141.
- PROTHERO, D. R. and SCHOCH, R. M. 1989. Classification of the Perissodactyla. 530–537. In PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.
- RADINSKY, L. B. 1964. *Paleomoropus*, a new early Eocene chalicothere (Mammalia, Perissodactyla), and a revision of Eocene chalicotheres. *American Museum Novitates*, **2179**, 1–28.
- 1969. The early evolution of the Perissodactyla. *Evolution*, **23**, 308–328.
- REMY, J.-A. 1972. Etude du crâne de *Pachynolophus lavocati* n. sp. (Perissodactyla, Palaeotheriidae) des Phosphorites du Quercy. *Palaeovertebrata*, **5**, 45–78.
- CROCHET, J.-Y., SIGÉ, B., SUDRE, J., DE BONIS, L., VIANEY-LIAUD, M., GODINOT, M., HARTENBERGER, J.-L., LANGE-BADRÉ, B. and COMTE, B. 1987. Biochronologie des phosphorites du Quercy: mise à jour des listes fauniques et nouveaux gisements de mammifères fossiles. *Münchner Geowissenschaftliche Abhandlungen, A*, **10**, 169–188.
- RUSSELL, D. E. and ZHAI REN-JIE 1987. The Paleogene of Asia. *Mémoires du Muséum National d'Histoire Naturelle, Sciences de la Terre*, **52**, 1–488.
- SAVAGE, D. E., RUSSELL, D. E. and LOUIS, P. 1965. European Eocene Equidae (Perissodactyla). *University of California, Publications in Geological Science*, **56**, 1–94.
- 1966. Ceratomorpha and Ancylopoda (Perissodactyla) from the Lower Eocene Paris Basin, France. *University of California, Publications in Geological Sciences*, **66**, 1–38.
- SCHOCH, R. M. 1984. Two unusual specimens of *Helaletes* in the Yale Peabody Museum collections, and some comments on the ancestry of the Tapiridae (Perissodactyla, Mammalia). *Postilla*, **193**, 1–20.
- 1989. A brief historical review of perissodactyl classification. 13–23. In PROTHERO, D. R. and SCHOCH, R. M. (eds). *The evolution of perissodactyls*. Oxford University Press, New York, 537 pp.
- SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, **85**, 1–350.
- SWOFFORD, D. L. 1990. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.0. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois, 162 pp.
- THEWISSEN, J. G. M. 1990. Evolution of Paleocene and Eocene Phenacodontidae (Mammalia, Condylarthra). *University of Michigan Papers on Paleontology*, **29**, 1–107.
- TING SU-YIN 1993. A preliminary report on an Early Eocene mammalian fauna from Hengdong, Hunan Province, China. *Kaupia*, **3**, 201–207.
- 1998. Paleocene and early Eocene land mammal ages of Asia. *Bulletin of the Carnegie Museum of Natural History*, **34**, 124–147.
- WANG JING-WEN and TONG YONG-SHENG 1997. A new phenacodontid condylarth (Mammalia) from the early Eocene of the Wutu Basin, Shandong. *Vertebrata Palasiatica*, **35**, 283–289, 1 pl.
- WANG YUAN 1995. A new primitive chalicothere (Perissodactyla, Mammalia) from the early Eocene of Hubei, China. *Vertebrata Palasiatica*, **33**, 138–159, 1 pl.
- ZAPFE, H. 1979. *Chalicotherium grande* (Blainv.) aus der miozänen Spaltenfüllung von Neudorf an der March (Devinská Nová Ves), Tschechoslowakei. *Neue Denkschriften des Naturhistorischen Museums in Wien*, **2**, 1–282, 2 pls.

J. J. HOOKER

Department of Palaeontology
The Natural History Museum
Cromwell Road
London SW7 5BD, UK
e-mail j.hooker@nhm.ac.uk

D. DASHZEVEG

Geological Institute
Mongolian Academy of Sciences
Peace Avenue 63
Ulaanbaatar, Mongolia

4. Lower molar cristid obliqua straight (0); bowed buccally (1).
5. Lower molar protolophid notched (0); shallowly indented, lophoid (1).
6. Lower molar metastylid a prominent cusplule (0); weak to lacking (1).
7. Upper molar metaconule situated on a line drawn between the metacone and hypocone, lower molar hypoconulid an integral part of the posteristid (0); upper molar metaconule (or its position if subsumed by metaloph) distinctly mesial of a line drawn between the metacone and hypocone, lower molar hypoconulid separated from and distal of crest joining hypoconid and entoconid (hypolophid) (1).
8. Upper molar metaconule not joined to hypocone by crest (0); joined to hypocone by crest (1).
9. Upper molar metaconule large (0); size variable, some large, some small (A); all small (B).
10. Upper molar centrocrista straight (A); slightly flexed buccally (0); sharply flexed buccally (B).
11. Upper molar mesostyle large (0); small or variably developed (A); lacking (B).
12. Lower molar buccal and lingual cusp outer walls converge at $c. 45^\circ$ (0); $c. 20^\circ$ (A); $c. 10^\circ$ (B); $c. 5^\circ$ (C).
13. Lower molar metaconid buttress (Hooker, 1994, fig. 2E-F) absent (0); present, buccal in position (A); present, lingual in position (B).
14. Lower molar cristid obliqua attaches to trigonid nearer to metaconid than to protoconid (0); midway between protoconid and metaconid (A); nearer to protoconid than to metaconid (B).
15. Lower molar cristid obliqua attaches high (0); low (1) on back wall of trigonid.
16. Lower molar entoconulid a prominent cusplule (0); weak to lacking (1).
17. Lower molar paracristid, when lightly worn, makes angle to tooth long axis of 50° (0); 40° (A); 30° (B); 20° (C); 10° (D).
18. Lower molar paracristid with mesiobuccal angle rounded (0); sharp or bulging (1).
19. Lower molar trigonid back wall shallow (0); steep (1).
20. P^1 present (0); absent (1).
21. M^{1-2} as long as broad (0); broader than long (1).
22. M^3 without hypocone (0); with hypocone (1).
23. M^{1-2} postmetacrasta and lower molar paracristid buccal segment short (0); long (1).
24. Upper molar parastyle small (0); medium (A); large (B).
25. M^3 smaller than M^2 , M_3 not larger than M_2 (0); M^3 not smaller than M^2 , M_3 larger than M_2 (1).
26. M_3 hypoconulid as close to hypoconid as this is to entoconid (0); more distant but closer to hypoconid than this is to protoconid (A); as far or further from hypoconid than this is from protoconid (B).
27. M_3 hypoconulid forming simple terminal cusp (0); distal margin of post-talonid lobe (A); buccally positioned, bearing more distal or distolingual lobe or cusplule (B). Unordered.
28. M_3 hypolophid incomplete (0); complete (1).
29. P^3 metacone smaller than paracone (0); as large as paracone (1).
30. P^3 with trigon relatively narrow, protoloph weak, paraconule and P_3 metaconid very small and poorly defined (0); trigon broader, protoloph stronger, paraconule (unless subsumed by protoloph) and metaconid much larger and better defined, but smaller than protocone and protoconid respectively (1).
31. P_3 paraconid weak and much lower than protoconid (0); strong and approaching height of protoconid (1).
32. P_1 present (0); absent (1).
33. Optic foramen of orbit significantly in front of (0) or close to (1) anterior lacerate foramen. (NB: *Ectocion* recoded following Holbrook 2001, pp. 16–17).
34. Navicular facet of astragalus convex (0); saddle-shaped (1).
35. Astragalar canal present (0); absent (1).
36. Upper molars with no metaloph (0); with metaconal fold (Hooker, 1994, fig. 2A, C) not joined to metaconule (A); some joined to metaconule, some not (B); consistently joined to metaconule forming complete metaloph (C); buccal end of metaloph (homologue of metaconal fold) shifted mesially from metacone (D).
37. Lower preultimate molar without hypolophid (0); hypolophid complete, comprising equal buccal and lingual segments of former posteristid joining in middle at notch in front of hypoconulid (A); buccal segment lengthened at expense of lingual segment with lingual hypoconulid (B); equal buccal and lingual segments joined into strong unnotched loph, hypoconulid median (C); hypolophid notched but complete like state A, some with lingual segment broken (D); hypolophid with lingual segment consistently broken (E). (See Text-fig. 6).
38. Lower M_{1-2} distal cingulum lingual of hypoconulid absent (0); present (1).
39. Upper molar metaloph and lower molar hypolophid (or line drawn between hypoconid and entoconid), especially on M_3 , transverse (0); oblique (1).
40. Distal lower molar metaconid larger than or equal to mesial metaconid (0); distal smaller than mesial (1).
41. Mesial crest of lower molar metaconid present (0); absent (1).
42. Upper molar parastyle pointing essentially occlusally (0); recurved strongly distally (1).

43. M³ parastyle aligned with those on M¹⁻² (0); projecting strongly buccally in some individuals (A); consistently projecting strongly buccally (B).
44. Upper molar metacone vertically implanted (0); tilted lingually slightly (A); tilted lingually markedly (B).
45. Upper molar paracone vertically implanted (0); tilted buccally slightly (A); tilted buccally markedly (B).
46. P⁴ with postprotocrista (0); without (1).
47. P⁴ metaconule present, large (0); weak (A); absent (B).
48. P⁴ premetaconule crista weak (0); strong, high on ectoloph (1). NB: primitive state of 46 plus derived state of 48 make a continuous lophule.
49. P⁴ metaconule and postprotocrista or its position distal of a line drawn between metacone and protocone (0); more mesial (1).
50. P³ postprotocrista absent (A); faint (0); strong (B).
51. P³ paracone and metacone well separated as on P⁴ (0); closer together (A); very close (B).
52. Post P¹ diastema as long as upper postcanine diastema (0); shorter (A); absent (B).
53. Post P₁ diastema as long as lower postcanine diastema (0); shorter (A); absent (B).
54. P₂₋₃ diastema present (0); absent (1).

3. Stepmatrices for characters 3 and 37 of the data matrix

3.	0	A	B	C	D	37.	0	A	B	C	D	E
0	–	1	2	3	3	0	–	1	2	2	2	3
A	1	–	1	2	2	A	1	–	1	1	1	2
B	2	1	–	1	1	B	2	1	–	2	2	3
C	3	2	1	–	2	C	2	1	2	–	2	3
D	3	2	1	2	–	D	2	1	2	2	–	1
						E	3	2	3	3	1	–