

ZOOLOGICAL JOURNAL OF THE LINNEAN SOCIETY

EDITOR

Dr J. P. Thorpe

Port Erin Marine Laboratory, Port Erin, Isle of Man IM9 6JA

ASSOCIATE EDITORS

Dr R. Bieler (North American authors), Field Museum of Natural History, Roosevelt Road at Lakeshore Drive, Chicago IL 60605-2496, U.S.A.

Dr N. Bruce, Zoologisk Museum, Universitetsparken 15, DK 2100, København, Denmark

Prof. S. L. Chown, Department of Zoology and Entomology, Faculty of Biological and Agricultural Science, University of Pretoria, Pretoria 0002, South Africa

Dr M. E. Christiansen, Zoological Museum, University of Oslo, Sars Gt. 1, Oslo, N-0562, Norway

Prof. M. Edmunds, Department of Applied Biology, University of Central Lancashire, Preston PR1 2HE

Dr P. L. Forey, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

Dr P. J. Hayward, School of Biological Sciences, University of Wales Swansea, Singleton Park, Swansea SA2 8PP

Dr A. G. Knox, Buckinghamshire County Museum, Tring Road, Halton, Buckinghamshire HP22 5PJ

Dr A. Lister, Department of Biology, University College London, Gower Street, London WC1E 6BT

Dr C. Nielsen, Zoologisk Museum, Universitetsparken 15, DK 2100, København, Denmark

Dr D. B. Norman, Sedgwick Museum, University of Cambridge, Downing Street, Cambridge, CB2 3EQ

Dr W. F. Ponder, Division of Invertebrate Zoology, The Australian Museum, 6 College Street, Sydney South, N.S.W. 2000, Australia

Prof. J. D. Pye, Department of Biosciences, Queen Mary College, 327 Mile End Road, London E1 4NS

Dr O. Rieppel, Department of Zoology, Field Museum of Natural History, Roosevelt Road at Lakeshore Drive, Chicago IL 60605-2496, U.S.A.

Dr A. D. Rogers, Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB

Dr M. J. Scoble, Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD

Dr A. M. Solé-Cava, Departamento de Genética-Inst Biología-CCS, UFRJ, Caixa Postal 21941, 590 Rio de Janeiro, Brazil

Prof. Dr J. W. Wägele, Fakultät für Biologie, Universität Bielefeld, Postfach 100131, 33615 Bielefeld, Germany

Dr M. H. Wake, Department of Integrative Biology, University of California, Berkeley, CA 94720-3140, U.S.A.

The *Zoological Journal* publishes original papers on systematic and evolutionary zoology and comparative, functional and other studies where relevant to these areas. Studies of extinct as well as living animals are included. Reviews are also published; these may be invited by the Editorial Board, but the submission of uninvited reviews is welcomed. The Journal has a wide circulation amongst zoologists and although narrowly specialized papers are not excluded, potential authors should bear that readership in mind.

Manuscripts may be sent to the editor or to any member of the editorial board. North American authors should, in the first instance, send their manuscripts to Dr Rüdiger Bieler. Brief instructions to authors are published in each issue. Books for review should be sent to Professor Brian Fox, The Linnean Society of London, Burlington House, Piccadilly, London W1V 0LQ.

Academic Press journals do not levy page charges.

ZOOLOGICAL JOURNAL OF THE LINNEAN SOCIETY; ISSN 0024-4082. Volumes 119-121, 1997, published monthly by Academic Press at 24-28 Oval Road, London NW1 7DX, U.K. Annual worldwide subscription price including postage: £525. Buyers in Canada should add GST at the current rate of 7%. Subscription orders should be sent to Journals Subscription Department, Harcourt Brace and Company Ltd., Foots Cray High Street, Sidcup, Kent DA14 5HP, U.K. (Tel: +44 (0) 181 300-3322). Subscribers should send notices of change of address to the publisher at least 6-8 weeks in advance including both old and new addresses.

All members of the Linnean Society should send changes of address to Academic Press Limited (address above) and to the Linnean Society of London, Burlington House, Piccadilly, London W1V 0LQ.

Periodicals postage rate paid at Jamaica, NY 11431, U.S.A.

Air freight and mailing in the U.S.A. by Publications Expediting Inc., 200 Meacham Avenue, Elmont, NY 11003, U.S.A.

U.S.A. POSTMASTERS: Send changes of address to ZOOLOGICAL JOURNAL OF THE LINNEAN SOCIETY, Publications Expediting, Inc., 200 Meacham Avenue, Elmont, NY 11003, U.S.A.



New ceratomorph perissodactyls (Mammalia) from the Middle and Late Eocene of Mongolia: their implications for phylogeny and dating

D. DASHZEVEG

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

J. J. HOOKER

Palaeontology Department, Natural History Museum, Cromwell Road, London SW7 5BD, UK

Received March 1996; accepted for publication August 1996

Eight species rank taxa are described from Eocene sites in the Gobi Desert, Mongolia. *Irdinolophus* gen. nov. is erected for *Desmatotherium mongoliense* Osborn and for *Irdinolophus? tuiensis* sp. nov. The genus is placed at the stem of the family Deperetellidae. Intraspecific variation in *Teleolophus magnus* is documented for the first time; *Pachylophus* is synonymized with *Teleolophus*; and *Deperetella* cf. *birmanica* is recorded far north of its previously known range in Burma. The first known lower teeth of *Colodon inceptus* support referral of *Desmatotherium fissum* to *Colodon*. The stratigraphic range of the hyracodontid *Ardynia* is extended back from the late Eocene to the early middle Eocene. A range of primitive tapiroids and rhinocerotoids are analysed cladistically to resolve the problematic affinities of the extinct families Deperetellidae and Rhodopagidae. The Deperetellidae are shown to belong to a monophyletic superfamily Tapiroidea, whilst the Rhodopagidae belongs to the Rhinoceroidea, but is distinct from the Hyracodontidae. *Veragromovia*, previously synonymized with the tapiroid *Helaletes*, is resurrected as a valid genus within the Rhodopagidae. Tsagan Khutel and other sites in the Kholbolchi Formation may be older than Irdinmanhan faunas in Asia, equating with those from the Arshanto Formation of China of probable early Lutetian or latest Ypresian age. The Irdinmanhan Mergen fauna may be slightly older than that from Irdin Manha, because of the primitive aspect of its *Lophialetes*.

© 1997 The Linnean Society of London

ADDITIONAL KEY WORDS:—tapiroids – rhinocerotoids – Deperetellidae – Rhodopagidae.

CONTENTS

Introduction	106
Systematics	107
Gladistic analysis of primitive tapiroids and rhinocerotoids	124
The problems	124

Correspondence to Dr J. J. Hooker. e-mail: jjh@nhm.ac.uk.

Character definitions	128
Results of the analysis	129
Relative dating of the Kholbolchi and Mergen Formations	135
Kholbolchi Formation	135
Mergen Formation	136
Acknowledgements	136
References	136

INTRODUCTION

The material described here was collected by the first author (D.D.) when leading field teams from the Mongolian Academy of Sciences to the localities of Mergen, Khoer Dzan and Ergilin Dzo in the eastern Gobi Desert (Dornogobi Province) and Tsagan Khutel in the Valley of the Lakes (Obor Khangay Province), Mongolia, between 1967 and 1982.

The locality of Tsagan Khutel was discovered by the American Museum Central Asiatic Expedition of 1925 (Berkey *et al.*, 1929), but received its formal name much later (Dashzeveg, 1979). The mammal-bearing strata belong to the Kholbolchi Formation (Badamgarav *et al.*, 1975), which is generally accepted to be of middle Eocene age (Russell & Zhai, 1987: 145–148). More detailed relative dating is proposed below.

The locality of Mergen, in the Dolodoi Lake Basin, was discovered by D.D. and has been described by Dashzeveg (1991: 5). There are two distinct sequences of strata at this locality (Russell & Zhai, 1987: 149), the upper of which contains the mammalian fossils and has been dubbed the Mergen Suite (=Formation) by Dashzeveg (1991: 8, Fig. 3).

The strata exposed at Khoer Dzan and Ergilin Dzo cover the timespan from late Eocene to early Oligocene, but all the specimens described here come from the late Eocene Sevkhul Member of the Ergilin Dzo Formation, except one, which is from the early Oligocene Ergilin Member of the same formation. Khoer Dzan and Ergilin Dzo have been described by Dashzeveg (1991: 6–7) and Russell & Zhai (1987: 268–278) and the correlation and dating of the various levels have been discussed by Dashzeveg (1993).

The dental terminology used herein is detailed in Fig. 24 and essentially follows Hooker (1989, 1994). Abbreviations of taxa used in Table 3 and the cladograms (Figs 24–27) are as follows: HYPANC = hypothetical ancestor; HYRACH = *Hyrachyus eximius*; HEPT = *Heptodon*; HELALE = *Helaletes nanus*; DESMAT = *Desmatotherium intermedium*; DILOPH = *Dilophodon*; COLOCC = *Colodon occidentalis*; COLINC = *Colodon inceptus* and *C. fissus*; PLESIO = *Plesiocolopirus*; PROTAP = *Protapirus*; IRDMON = *Irdinolophus mongoliensis*; IRDTUI = *Irdinolophus? tuiensis*; TELEOL = *Teleolophus*; RHORAD = '*Rhodopagus radinskyi*'; TRIPCU = *Triplopus cubitalis*; VERAGR = *Véragromovia*; RHODOP = *Rhodopagus sensu stricto*; PATAEC = *Pataecops*.

Material described here is housed in the Geological Institute of the Mongolian Academy of Sciences, Ulaanbaatar, whose numbers are prefixed PSS. Other institutional abbreviations are as follows: AMNH = American Museum of Natural History, New York; AS.GSSR = Institute of Paleobiology, Georgian Academy of Sciences, Tbilisi; BMNH = Natural History Museum, London; FSL = Faculté des Sciences, Université de Lyon; IVPP = Institute of Vertebrate Paleontology & Paleoanthropology, Beijing; ONG = Oil & Natural Gas Commission, Dehra Dun; PIN = Palaeontological Institute of the Russian Academy of Sciences, Moscow.

SYSTEMATICS

Infraorder Ceratomorpha
 Family Lophialetidae Matthew & Granger, 1925c
 Genus *Lophialetes* Matthew & Granger, 1925c

Type species. *Lophialetes expeditus* Matthew & Granger, 1925c, from the Irdin Manha Formation, middle Eocene, of Irdin Manha, Inner Mongolia, China.

Included species. Unnamed and open nomenclature forms of doubtful status, including *L. expeditus?* (see Radinsky, 1965) from the Ulan Shireh Formation, middle Eocene, of the Shara Murun region, Inner Mongolia, China.

Diagnosis. See Radinsky (1965).

Discussion. Radinsky was unsure of species distinctions within this genus, but documented in the type assemblage of *L. expeditus*, coefficients of variation for tooth measurements higher than were to be expected in a single species. Moreover, he could find no consistent morphological differences which could be used to divide the assemblage. In the similar-aged Ulan Shireh Formation at North Mesa, Shara Murun region, Radinsky recorded *Lophialetes* specimens that averaged slightly smaller size than those from Irdin Manha, but with much overlap. He named them *L. expeditus?* and was unsure whether they represented a distinct species or whether slight temporal differences between the Irdin Manha and Ulan Shireh assemblages were responsible for the size variation.

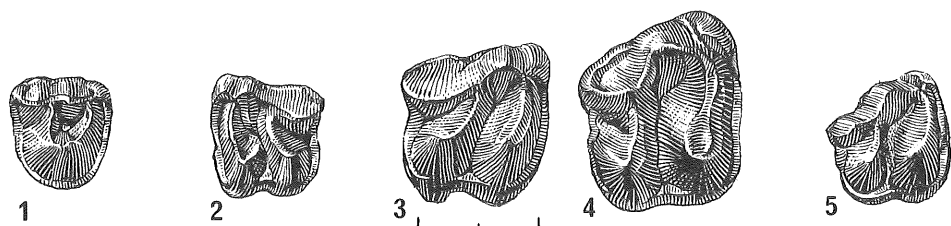
Skull and articulated skeletal material was recovered from the similar-aged Khaychin Ula Formation at Khaychin Ula III, Zaaltay Gobi Province, Mongolia by Reshetov (1979) and referred to *L. expeditus*. Reshetov gave no individual tooth measurements of his material, but measurements of the unworn M¹ in the scale drawing in his fig. 12 fit well within those of the type assemblage of *L. expeditus*.

The new material from Mergen consists of only a few isolated teeth. It thus adds little to solving the problem of species discrimination with *Lophialetes*, but it is noteworthy that the available teeth differ considerably in size at the same site and stratigraphic horizon. What is more interesting is that thanks to the nearly unworn state of the molars, it is possible to measure their crown height. This is slightly lower than in either *L. expeditus* or *L. expeditus?*; in fact, it is intermediate between these 'species' and the closely related genus *Schlosseria* (see Radinsky, 1965). They can be distinguished morphologically from *Schlosseria* by the presence of a cingulum around the lingual end of the mesial arm of the lower molar paralophid, where the latter recurves slightly distally. The material is categorized here as *Lophialetes* sp.

Overall, the *Lophialetes* represented at Mergen appears slightly more primitive morphologically as well as in crown height than its counterparts in the Irdin Manha, Ulan Shireh and Khaychin Ula Formations, which may indicate a slightly older age for deposition of the Mergen Formation.

Lophialetes sp. (Figs 1–3, 5–7)

Material. Right P^{3/4} (PSS.41-4); right M^{1/2} (PSS.41-5); right M³ (PSS.41-6); 2 left DP⁴ (PSS.41-7, 41-60); left M_{1/2} (M₁?) (PSS.41-61); right M_{1/2} (M₂?) (PSS.41-62); 3 right



Figures 1-5. Occlusal views of upper cheek teeth from Mergen. Figs 1-3, 5, *Lophialetes* sp., right $P^{3/4}$ (PSS.41-4); 2, left DP^1 (PSS.41-7); 3, right $M^{1/2}$ (PSS.41-5); 5, right M^3 (PSS.41-6). Fig. 4, *Indinolophus mongoliensis* (Osborn) **comb. nov.**, right $M^{1/2}$. Scale bar = 10mm.

DP_4 (PSS.41-63, 41-64, 41-65). All from the Mergen Formation, middle Eocene, of Mergen, Dornogobi Province, Mongolia.

Description. The length-width proportions of the upper premolar (Fig. 1) are more like that of P^3 than P^4 when compared with the holotype of *Lophialetes expeditus* (see Radinsky, 1965, fig. 2A). In this respect the tooth is unlike either P^3 or P^4 of *Schlosseria magister* Matthew & Granger.

The $M^{1/2}$ length and width measurements plot within either M^1 of *L. expeditus* or M^1 or M^2 of *L. expeditus?*, but length coincides with the mean of M^1 and width with M^2 of the latter. Although slightly worn, crown height seems less than in *L. expeditus* and *L. expeditus?*, because of less distal flaring of the postmetacrista (metastylar wing) (Fig. 3).

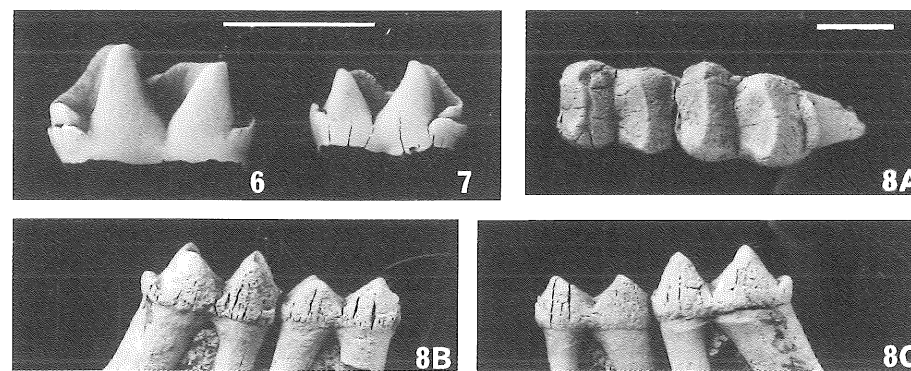
The size of M^3 lies outside the range for either *L. expeditus* or *L. expeditus?*, but the width is only 0.5 mm less than the minimum for the latter. The proportions give a relatively short broad tooth somewhat intermediate between *Lophialetes* and *Schlosseria*. Also anomalous is the metacone, which has a slight buccal rib like *Schlosseria* and unlike *Lophialetes* (Fig. 5). The height of both the metacone and paracone are only 47% of the tooth width. In the holotype of *L. expeditus*, the height of the metacone is 60% of the tooth width.

As in the $M^{1/2}$, the Mergen DP^1 's (Fig. 2) show less distal flaring than does *Lophialetes expeditus?* (cf. Radinsky, 1965, fig. 3). The state of this character is more like that of a DP^1 in *Schlosseria* from Irdin Manha (AMNH.81764).

The left $M_{1/2}$ is unworn (Fig. 7). Its length and width measurements plot around the middle of the range for M_1 and very near the bottom end for M_2 in *L. expeditus?* Only the length overlaps with the very bottom of the range of M_1 in *L. expeditus*. The height of the protoconid is 103% of the tooth width. On an unworn M_3 of *L. expeditus?* (AMNH.26109) the same height percentage is 107%.

The right $M_{1/2}$ is also unworn (Fig. 6). Its length measurement plots towards the upper end of the range of variation for M_2 of typical *L. expeditus* (Radinsky, 1965: 193, table 1). Its width measurements match either M_1 or M_2 of this 'species'. The height of the protoconid is 8.6mm, which is 105% of the width of the tooth, thus closer to AMNH.26109 than the smaller left $M_{1/2}$.

Of the three DP_4 's, one has measurements that plot well within the range for this tooth type in typical *L. expeditus* (Radinsky, 1965: 194, table 2). The other two are smaller and plot near the mean for *L. expeditus?* and outside the range for *L. expeditus*. They differ in length from each other by only 0.2 mm, whereas the larger tooth is 1.7-1.9 mm (18-20%) longer. Unfortunately, deciduous premolars tend to be more size variable than molars, so the differences cannot be used as evidence for the existence of two species.



Figures 6-8. Figs 6, 7, *Lophialetes* sp., lower molars in lingual view from Mergen; 6, right $M_{1/2}$ (PSS.41-62); 7, left $M_{1/2}$ (PSS.41-61). Fig. 8, *Colodon inceptus* Matthew & Granger, associated right $M_{2,3}$ (PSS.27-34) from Khoer Dzan; A, occlusal view; B, buccal view; C, lingual view. Coated with ammonium chloride. Scale bars = 10 mm.

TABLE 1. Length, width and height measurements in millimetres of *Lophialetes* sp. from Mergen. W1 and W2 represent two width measurements at trigonid and talonid respectively, only possible on lower molariform teeth

Tooth	No.	Length	W1	W2	Height prof'd	Height para/metacone
$P^{3/4}$	41-4	8.4	9.2			
$M^{1/2}$	41-5	11.2	12.6			
M^3	41-6	9.8	10.7			5.0
DP^1	41-7	9.2	10.1			
DP^1	41-60	—	9.7			
$M_{1/2}$	41-61	10.3	6.2	6.3	6.5	
$M_{1/2}$	41-62	13.6	8.2	8.4	8.6	
DP_4	41-63	9.4	5.2	5.7		
DP_4	41-64	9.2	5.0	5.4		
DP_4	41-65	11.1	6.7	6.6		

Superfamily Tapiroidea Burnett, 1830
Family uncertain
Genus *Colodon* Marsh, 1890

Type species. *Lophiodon occidentalis* Leidy, 1868.

Included species. *C. kayi* (Hough, 1955), *C. woodi* (Gazin, 1956), *C. angulatus* Douglass, 1901, *C. stovalli* Wilson & Schiebout, 1984, *C. inceptus* Matthew & Granger, 1925a, *C. fissus* (Matthew & Granger, 1925c) **comb. nov.**; doubtfully *C. orientalis* Borissiak, 1918.

Excluded species. *C. hodsimai* Takai, 1939 and *C? grangeri* (Tokunaga, 1933) are poorly substantiated species (see Radinsky, 1965). *C? kushiroensis* Tomida, 1983 from the early Oligocene of Japan, should probably belong to another genus (pers. comm., Tomida, 1985).

Distribution. Middle Eocene to late Oligocene of North America; middle Eocene to early Oligocene of Asia.

Diagnosis. See Radinsky (1963: 57).

Discussion. *Desmatotherium fissum* Matthew & Granger, 1925c is transferred here tentatively to the genus *Colodon*. It was referred to *Helaletes* by Radinsky (1965:230), although he noted that the relatively short broad P^{3-4} with slightly divided protocone and hypocone were similar to *Colodon*. He recognized nevertheless that they differed from *Colodon* in having less prominent metalophs which joined the protocones rather than the hypocones as in *Helaletes* (presumably referring to '*H. intermedius*', which has been referred back to *Desmatotherium* by Schoch, 1989). The orientation of the P^{3-4} metalophs is in fact somewhat intermediate between *Desmatotherium* and *Colodon* and additional derived similarities with *Colodon* can be seen in the relatively wider P_{3-4} talonids (also shared with other tapiroids) and shorter P_3 trigonid (Fig. 24Q).

Haagella peregrina Heissig, 1978, from the early Oligocene (MP22) of Haag 2, southern Germany, was described from a small sample of isolated teeth as the only European deperetellid. The single $M^{1/2}$ is heavily worn, the horizontal abrasion on the transverse lophs producing a pattern of exposed dentine like that on M^1 of the larger, unique holotype of *Colodon? orientalis*. However, the orientation of the metaloph is rather oblique and appears to have joined the ectoloph mesially of the metacone as recognized by Heissig. This primitive feature is unlike *Colodon*, *Helaletes*, or any deperetellid (even the low crowned *Indinolophus*). Heissig mentioned the steeply shearing longitudinal ridge of the $P_{2/3}$ as being deperetellid-like, but the paraconid is broken away and it is thus not possible to judge whether or not this was tall as in deperetellids (see below). In accordance with Heissig's recent opinion (Schoch, 1989: 310–311), *Haagella* is best regarded as a possible relative of *Colodon* until it becomes better known.

Colodon inceptus Matthew & Granger, 1925a (Figs 8–9)

v* 1925a *Colodon inceptus* Matthew & Granger: p. 4, fig. 5.

1925a *Paracolodon curtus* Matthew & Granger: p. 4, fig. 4.

v. 1965 *Colodon inceptus* Matthew & Granger; Radinsky, p. 232, fig. 19.

Holotype. Left maxilla with P^3 – M^3 (AMNH.20357), from the Ergilin Dzo Formation ('Ardyn Obo beds'), late Eocene/early Oligocene of Ergil Obo (= 'Ardyn Obo' of Matthew & Granger), eastern Gobi, Mongolia.

Material. Left dentary fragment with M_{2-3} (M_3 has metaconid and entoconid broken away) (PSS.27–33) and associated right M_2 and M_3 (PSS.27–34) from the Sevkhul Member, Ergilin Dzo Formation, late Eocene, of Khoer Dzan, Mongolia.

Diagnosis. See Radinsky (1965).

Description and discussion. So far, only upper teeth have been described, so referral of the lower molars described here requires justification. They are strongly bilophodont and relatively low crowned. The paralophid and metalophid are very weak, short and slightly lingually (obliquely) orientated. The protolophid is nearly transverse, whereas the hypolophid is somewhat oblique as in *Colodon occidentalis*. The M_3

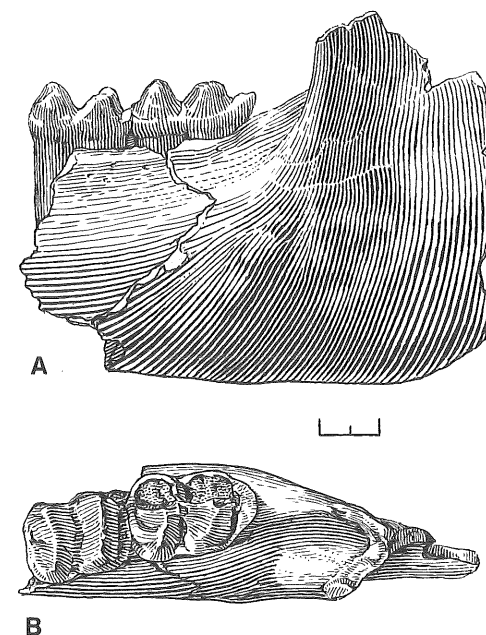


Figure 9. *Colodon inceptus* Matthew & Granger, fragment of left dentary with M_{2-3} (PSS.27–33) from Khoer Dzan; A, lateral (buccal) view; B, dorsal (occlusal) view. Scale bar = 10 mm.

hypoconulid lobe is reduced to little more than a cingular bulge. It is variable in size on the two specimens, projecting more distally and occlusally in PSS.27–33 (Fig. 9) than in PSS.27–34 (Fig. 8). The former development is similar in degree to that of *C. occidentalis* figured by Scott (1941, pl.81, fig. 2). In contrast to this species, the Khoer Dzan teeth are slightly narrower relative to their length and have slightly better marked ectoflexids and hypoflexids.

The teeth are somewhat corroded and it is possible to see some trace of Hunter–Schreger bands in the enamel near the loph and cusp tips of the M_3 of PSS.27–34. Along the worn edge of the protolophid these are nearly vertical but slightly divergent occlusally. They can be seen to curve around the metaconid to assume a horizontal orientation and can thus be described as horizontal–concave. This pattern is similar to that found in modern *Tapirus indicus* and the primitive rhinocerotoid *Hyrachyus*, and contrasts with the vertical orientation found in *Deperetella* (Fortelius, 1985: 60).

The obliquity of the hypolophid in the new specimens, resulting in convergence buccally of the two transverse lophs, means that these lower molars occlude well with the similarly orientated transverse lophs of the holotype upper molars of *C. inceptus*. This contrasts with the essentially parallel lophs of *C. occidentalis* and ?*C. orientalis*. The latter, which is from slightly younger strata in Kazakhstan (early Oligocene), is likewise known only from the upper dentition, and is another species with which the Khoer Dzan teeth could potentially be identified.

The exact level in the Ergilin Dzo Formation at which the holotype of *C. inceptus* was found is not recorded. However, it seems most likely that it came from the same level as the new specimens, namely the late Eocene Sevkhul Member.

The small primitive species *C. fissus* (Matthew & Granger, 1925c) **comb. nov.** shares the following characters with *C. inceptus*: premolars showing only incipient molarization (the beginning of splitting of the lingual cusp) and lacking a lingual cingulum; lower molars relatively narrow (primitive); and M_3 hypoconulid reduced to a cingular bulge (derived) (Fig. 24L). Although the character of the M_3 hypoconulid is slightly variable in *C. inceptus* as described here, the same degree of development in both *C. fissus* (AMNH.81802) (Radinsky, 1965: 231) and one of the *C. inceptus* specimens (PSS.27-34) in contrast to the generally better development of this cusp in the North American species, suggest a close relationship between *C. fissus* and *C. inceptus*.

Family Deperetellidae Radinsky, 1965

Type genus. *Deperetella* Matthew & Granger, 1925b.

Included genera. *Teleolophus* Matthew & Granger, 1925c; *Irdinolophus* gen. nov.

Excluded genera. *Pachylophus* Tong & Lei, 1984 is here synonymized with *Teleolophus* (q.v.). *Haagella* Heissig, 1978 is more likely to be related to *Colodon* (see above).

Emended diagnosis. Tapiroidea whose upper molars have protoloph and metaloph parallel and slightly oblique, and metacone displaced far lingually and reduced or lost on M^3 . M_3 hypoconulid reduced to cingular bulge. Premolars, particularly anterior ones, tend to be elongate, the lowers with tall paraconids and trenchant notched paralophids on P_{2-3} . Derived members characterized by moderately high crowned, strongly bilophodont, molars, with transverse lophs of uppers joined buccally by U-shaped ectoloph.

Discussion. Matthew & Granger (1925c) considered *Teleolophus* and *Deperetella* closely related to *Colodon* and placed them together in the Helaletidae. Radinsky (1965: 214) considered the similarities to *Colodon* to be convergent and stressed features of the incisors, canines and premolars shared with members of the Lophialetidae. He thus erected the family Deperetellidae for these two genera to reflect their distinctive molar morphology. The recognition of derived molar and premolar features shared between species here placed in the new genus *Irdinolophus* on the one hand and *Teleolophus* and *Deperetella* on the other, indicates remoteness from the Lophialetidae and supports Matthew & Granger's ideas of a sister group relationship with *Colodon* and its relatives. The family Deperetellidae is nevertheless retained here as a well characterised, albeit small, monophyletic group. *Colodon* is removed from the paraphyletic family Helaletidae, but its exact status with respect to the families Tapiridae and Deperetellidae is currently unresolved (see cladistic analysis below).

Irdinolophus gen. nov.

Type species. *Desmatotherium mongoliense* Osborn, 1923.

Tentatively referred species. *Irdinolophus?* *tuiensis* sp. nov.

Etymology. From the type locality of the type species, plus *lophos*, Greek for yoke, referring to the lophoid crests, a common tapiroid suffix. Masculine.

Diagnosis. Deperetellid with low-crowned cheek teeth. P^{3-4} nonmolariform, P^2 as long as broad, semimolariform, with protocone and hypocone distinct but connate. P_{3-4} with talonids broader than trigonids; P_3 with tall paraconid, the paracristid forming a notched shearing edge. Upper molars with: lingual paracone rib tilted slightly distally; centrocrista almost aligned with the metaloph; metacone a distinct small cusp; and postmetacrista well developed (weakening on M^3). Lower molars with slightly oblique hypolophid. M_3 with tiny hypoconulid.

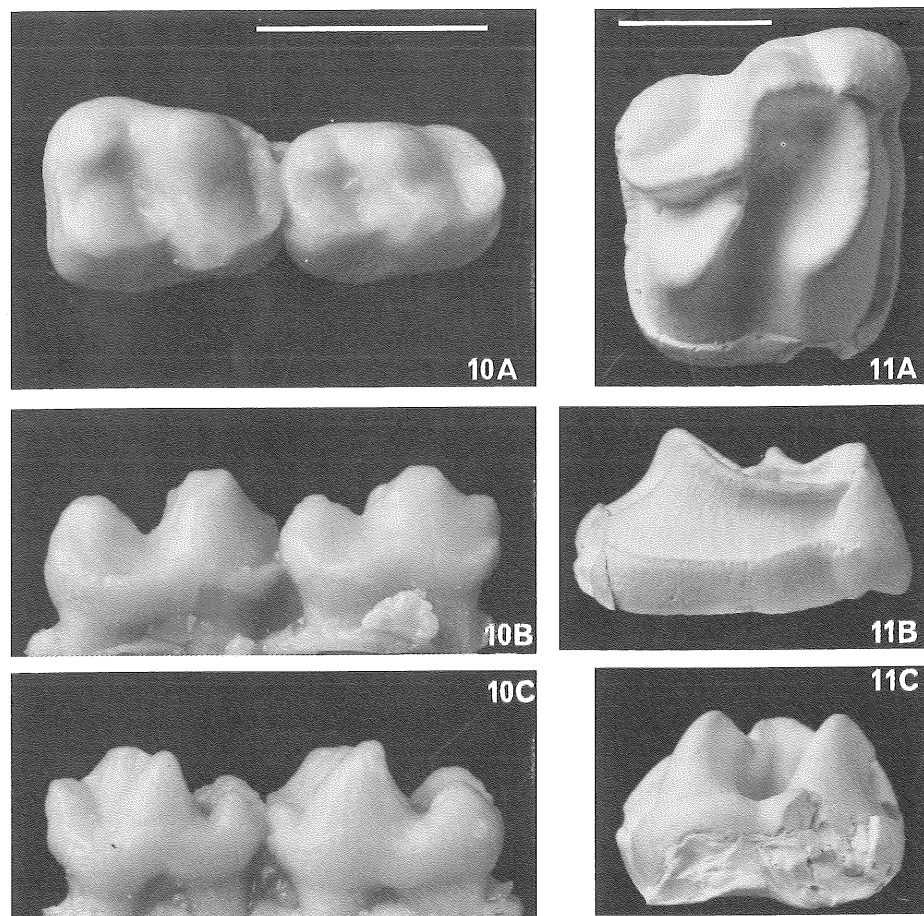
Discussion. Radinsky (1965: 227–231) referred *Desmatotherium mongoliense* to the genus *Helaletes*. He thereby abandoned the genus *Desmatotherium*. He noted that the characters of upper molar metacone reduction and depression and lower cheek tooth width indicated that '*H. mongoliensis*' was closer to *Colodon* than to *Helaletes*, yet premolar molarization was more like *Helaletes*. He also recognized that his generic assignment was subjective. Schoch (1989: 306) resurrected *Desmatotherium* for *Helaletes intermedius* on the basis of metalophs that bypass the hypocones on P^{3-4} and extremely reduced M_3 hypoconulid. However, as only one specimen of *D. intermedius* involves upper premolars and as *H. nanus* has been shown to have such high intraspecific variation for these teeth (Radinsky, 1963: 47, fig. 10), it is doubtful whether the character warrants generic separation for *H. intermedius*. However, it is also present in *Dilophodon* (see Radinsky, 1963, pl. 3, fig. 1; herein Fig. 24S), which is a closely related genus (see cladistic analysis below). Another feature of the upper molars of *D. intermedius* is a parastyle that is compressed against the paracone. This derived state is shared also with *Helaletes? mongoliensis* (Fig. 24I), *Colodon*, *Plesiocolopirus* and members of the families Deperetellidae and Tapiridae. All these are therefore derived with respect to *Helaletes*, and Radinsky's characters linking *H. mongoliensis* with *H. nanus* are primitive.

The relationships of '*H. mongoliensis*' become clearer when its premolars are considered. It differs from both *Helaletes nanus* and *H. intermedius* in P_{3-4} having a slightly wider talonid basin and in P_4 having a shorter trigonid. These characters are also shared with *Colodon*, *Plesiocolopirus*, tapirids and deperetellids, although the state is more extreme in some *Colodon* species (e.g. *C. occidentalis*). P_3 like that of *H. nanus* has a distinct paraconid, but it is distinctly taller than in this species and resembles the development in *Teleolophus* and *Deperetella* (Figs 10, 18, 20C). This paraconid occludes with the distal half of a relatively elongate P^2 . Thus the premolars of '*H. mongoliensis*' are showing the beginnings of elongation that typifies advanced members of the Deperetellidae. Its P_3 also differs from that of the similar-sized *Helaletes fissus*. The latter has greatly reduced the P_3 paraconid and the species is here referred to the genus *Colodon* (q.v.). As '*H. mongoliensis*' shares a derived character with the Deperetellidae, but only primitive characters with *Helaletes nanus*, it is placed in the new genus *Irdinolophus* as the most primitive member of the family Deperetellidae.

Irdinolophus mongoliensis (Osborn, 1923) **comb. nov.** (Figs 4, 10)

Holotype. Right maxilla with P^2 – M^3 (AMNH.19161) from the Irdin Manha Formation, middle Eocene, of Irdin Manha, Inner Mongolia, China.

New material. Right $M^{1/2}$ ($M^2?$) (PSS.41-3) from the Mergen Formation, middle Eocene, of Mergen, eastern Gobi, Mongolia.



Figures 10, 11. Fig. 10, *Irdinolophus mongoliensis* (Osborn) **comb. nov.**, right P_{3-4} (AMNH.81717) from Irdin Manha; A, occlusal view; B, buccal view; C, lingual view. Fig. 11, *Irdinolophus? tuiensis* sp. **nov.**, right $M^{1/2}$ (PSS.13-15) from Tsagan Khutel; A, occlusal view; B, mesial view; C, lingual view. Both casts. Scale bars = 10 mm.

Diagnosis. Small species of the genus. M^1 length 12.1 mm; M^2 length 14.75 mm. Upper molar ectocingulum forms a ridge adjacent to the metacone. Upper molar lingual cingulum weak and interrupted.

Description. Unlike the holotype, this isolated preultimate molar is fairly heavily worn (Fig. 4). Its width dimensions and trapezoidal shape are almost identical to those of the holotype M^2 , but the length dimensions are less. The latter is probably entirely due to the occlusal and interstitial wear which has removed mesial and distal edges of this occlusally splayed molar. Otherwise it is remarkably similar. Only the cingula are slightly stronger, although no more extensive. The parastyle appears separated from the paracone unlike the holotype, but this difference also seems to result from wear.

This is the first record of the taxon for Mongolia. Apart from the type locality, it is otherwise recorded from the middle Eocene Lumeiyi Formation of the Lunan

Basin, Yunnan Province, China; and doubtfully from the middle Eocene middle Obayla Formation, Zaysan Depression, Kazakhstan (Russell & Zhai, 1987).

Irdinolophus? tuiensis sp. **nov.** (Fig. 11)

Holotype. Right $M^{1/2}$ (PSS.13-15) from the Kholbolchi Formation, middle Eocene, of Tsagan Khutel, Valley of the Lakes, Mongolia.

Etymology. From the River Tui which flows close to the type locality and into Orog Nur Lake.

Diagnosis. Large species of the genus, $M^{1/2}$ length = 20 mm. Upper molar ectocingulum forming a rounded bulge adjacent to the metacone. Lingual cingulum complete.

Description. The tooth is almost entirely unworn, except for a very small buccal phase facet along part of the edge of the protoloph. The crown is almost complete except for a small break at the lingual base of the protocone. The transverse lophs show the mesial curvature towards their occlusal edges typical of other deperetellids, although the crown height is scarcely more than half that of a typical member of the family, like *Teleolophus magnus* (Fig. 11B, C). Although the distal loph is composed of metaloph plus centrocrista, it is interrupted by a distinct small metacone with a strong postmetacrasta, both of which are reduced or missing in the higher crowned deperetellids. The ectocingular bulge near the metacone is more prominent than but otherwise similar in nature to that of *Teleolophus medius* and *T. danjiangensis* (Fig. 11A).

The slight distal tilting of the paracone and contribution to the distal transverse loph of the postparacrasta as well as the premetacrasta is a primitive feature, being encountered in *Desmatotherium* and *Helaletes*. In *Deperetella*, *Teleolophus* and some species of *Colodon*, a mesial tilt of the paracone is associated with the broad U-shape produced by the preparacrasta and postparacrasta, linking the two transverse lophs buccally. In this feature, therefore, *I? tuiensis* is more primitive than *Deperetella* or *Teleolophus*.

The low crown height of PSS.13-15 is rather reminiscent of the pattern often encountered in fourth deciduous premolars belonging to perissodactyls with more hypsodont molars. However, the non-salient nature of the parastyle and especially the thickness of the enamel, as seen in cross section in the small break at the base of the protocone, leave no doubt that the specimen concerned belongs to the permanent dentition.

Discussion. The species is attributed tentatively to the genus *Irdinolophus* because it is represented by only a single isolated tooth and because two of its characters, the bulging ectocingulum and complete lingual cingulum, are shared with other deperetellid genera but not with *I. mongoliensis*, making it probable that *Irdinolophus* (*sensu lato*) is paraphyletic. However, this is considered a more rational taxonomic step in the present state of knowledge than erecting a new genus for *I? tuiensis*.

It is possible that *Teleolophus? shandongensis* Chow & Qi, 1982, from the Guanzhuang Formation, Xintai Basin, Shandong Province, China, is closely related to *I? tuiensis*. These authors were doubtful of the generic attribution of their species and noted that it had an S-shaped ectoloph. This structure as interpreted from the illustration (Chow & Qi, 1982, pl. 1, fig. 8) is very similar to that of the larger *Irdinolophus*

tuiensis, where the postmetacrista is relatively strong. The two species might be congeneric, but the poor quality of the illustration means that it is difficult to be sure. *Teleolophus primarius* Qi, 1987, from the Arshanto beds, Inner Mongolia, China, appears from the buccal and lingual (the only) views (Qi, 1987, fig. 41a,b) of the holotype lower molars, if unworn, to be as low crowned as *P. tuiensis*. *T. primarius* could thus be congeneric with *P. tuiensis*, but smaller size of the former (Qi, 1987, table 13) argues against conspecificity.

Genus *Teleolophus* Matthew & Granger, 1925c

Type species. Teleolophus medius Matthew & Granger, 1925c.

Included species. T. magnus Radinsky, 1965; *T. beliajevi* Biryukov, 1974; *T. danjiangensis* Tong & Lei, 1984; *T. ferganicus* (Beliajeva, 1962); *T. daviesi* Dehm & zu Oettingen-Spielberg, 1958.

Doubtful species. T. liankanensis Zheng, 1978; *T. xui* (Tong & Lei, 1984) **comb. nov.**

Emended diagnosis (modified from Radinsky, 1965). Deperetellid with relatively high-crowned cheek teeth and submolariform premolars, the latter forming a series shorter than that of the molars. P^{2-4} with paracone broadly convex, metacone completely merged into ectoloph, but unshortened and only slightly lingually displaced, and protoloph and metaloph equally prominent and in contact lingually. P_{3-4} with small isolated entoconids. Cement present on cheek teeth. Extreme reduction of lower molar longitudinally orientated paralophid. P_3 paraconid with sharp lingual accessory crest independent of parastylid. Upper molar paracone tilted mesially and its crests form inverted U-shaped lophoid structure joining protoloph and metaloph buccally.

Discussion. As diagnosed by Radinsky, *Teleolophus* was based almost entirely on characters that are primitive with respect to the closely related genus *Deperetella*, implying that it is paraphyletic. The characters underlined in the emended diagnosis are derived characters and provide a sounder basis for its definition and distinction from *Deperetella*. The characters shown underlined and in italics are shared with *Deperetella* exclusive of other deperetellids. In addition to the derived characters of elongation and molarization of the premolars used by Radinsky to diagnose *Deperetella*, this genus has more lingually orientated lower molar paralophids and metalophids, which is derived with respect to other deperetellid genera.

The genus *Pachylophus* was erected for the species *P. xui* Tong & Lei, 1984. The holotype consists of a left maxillary fragment with three molariform teeth identified by the original authors as M^{1-3} . The first of the three teeth is significantly lower crowned than the other two and has thinner enamel; and is thus here reidentified as DP^4 . The M^{2-3} are thus reidentified as M^{1-2} . There is a developmental gradient of characters along the tooth row in deperetellids, which involves particularly the strength of the metacone and strength and orientation of the postmetacrista. Both become weaker distally along the row, whilst the orientation of the postmetacrista changes from oblique to longitudinal in the same direction. Thus the relatively strong M^1 postmetacrista and very weak longitudinal M^2 postmetacrista fit well with the development in species of *Teleolophus* (Fig. 24J). The well developed postmetacrista and stronger distobuccal cingulum mentioned in Tong & Lei's diagnosis reflect their misidentification of the teeth in the holotype. The genus *Pachylophus* is thus

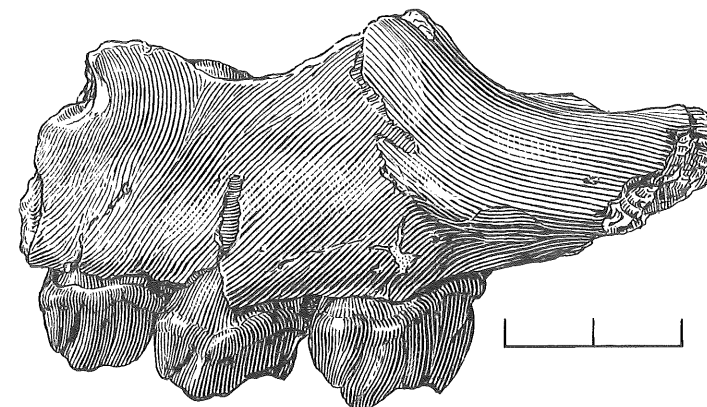


Figure 12. *Teleolophus magnus* Radinsky, left maxilla with P^1-M^2 (PSS.27-22) in lateral (buccal) view, from Khoer Dzan. Scale bar = 20 mm.

synonymized with *Teleolophus* and the species *Pachylophus xui* is recombined as *Teleolophus xui* (Tong & Lei, 1984) **comb. nov.** *T. xui* has upper molars that are very slightly shorter and broader than in *T. medius*, slightly longer and narrower than in *T. magnus*, and intermediate in overall size between the two. The development of its ectocingulum is more like that of *T. medius*. *Teleolophus danjiangensis* Tong & Lei, 1984 is difficult to distinguish from *T. xui* on the basis of the original diagnosis and illustrations. The small differences in the premolars given as distinguishing features appear not to take sufficient account of intraspecific variation and it is likely that the two species are synonymous. If this should be the case, page priority should be invoked to make *T. danjiangensis* the senior synonym as it is based on the more complete specimens.

Teleolophus magnus Radinsky, 1965 (Figs 12-19)

Holotype. Left maxilla with canine, P^1, P^3-M^2 and left and right dentaries with canines, P_2-M_2 (M_3 unerupted) (AMNH.26063) from uncertain level ('Ulan Gochu' beds, Radinsky, 1965), of Irtyn Obo, Inner Mongolia, China.

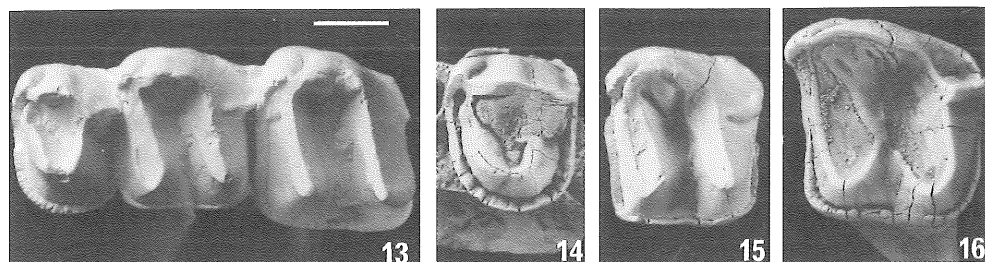
New material. Left maxillary fragment with P^4-M^2 (PSS.27-22); right maxillary fragment with P^4 (PSS.27-25); left P^4 (PSS.27-26); right M^1 (PSS.27-24); left M^2 (PSS.27-128); right M^2 (PSS.27-23); left $M_3?$ (PSS.27-30); fragment of left dentary with damaged M_{1-2} (PSS.27-27); left dentary fragment with P_{3-4} (PSS.27-4). All from the Sevkhol Member, Ergilin Dzo Formation, late Eocene, of Khoer Dzan, Mongolia.

Left dentary fragment with damaged M_3 (PSS.27-28) from the Ergilin Member, Ergilin Dzo Formation, early Oligocene, of Khoer Dzan, Mongolia.

Left dentary fragment with P_4 (distal fragment only) and M_{1-3} (the last unerupted) (PSS.21-36) from the Sevkhol Member, Ergilin Dzo Formation, late Eocene, of Ergilin Dzo, Mongolia.

Diagnosis. See Radinsky (1965).

Description. The original definition of *Teleolophus magnus* was based on a single specimen. Subsequently referred specimens are few: one dentary with worn teeth from the late



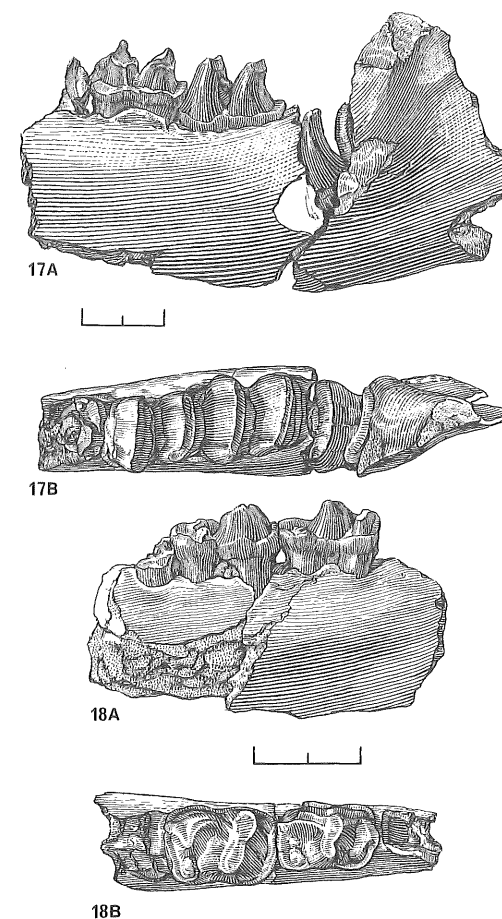
Figures 13–16. *Teleolophus magnus* Radinsky, upper cheek teeth in occlusal view, from Khoer Dzan. 13, left P¹–M² (PSS.27-22); 14, right P¹ (reversed) (PSS.27-25); 15, right M¹ (reversed) (PSS.27-24); 16, left M² (PSS.27-128). Figures 14 and 16 coated with ammonium chloride. Figures 13 and 15 are casts. Scale bar = 10 mm.

Eocene Chaganbulage Formation of Chaganbulage, Inner Mongolia, China (Qi, 1981); a few lower cheek teeth (which probably do not belong to *T. magnus*) from unnamed ?Sharamurian strata at Alag Tsav, Dornogobi Province, Mongolia (Reshetov, 1979: 34, fig. 6.1, who described them incorrectly as coming from the Ergilin Dzo Formation of Djavkhalant Ula); and doubtfully a mandible and maxillary fragment with premolars from the Khaychin Formation of Khaychin Ula II, Mongolia (Reshetov, 1979, pl. 1, figs 5, 6). Consequently the range of intraspecific variation is virtually unknown. The new material provides a slightly richer assemblage mainly from Khoer Dzan, which can begin to address this problem.

Two P¹'s show different protocone structure. PSS.27-25 has a single narrow protocone (Fig. 13) whereas PSS.27-26 has a broader protocone with a lingual fissure (Fig. 14), indicating incipient molarization as in the holotype. PSS.27-25 also has a slightly lingually tilted metacone.

The P₃₋₄ (PSS.27-4) are similar to the same teeth of the holotype, but differ in being slightly larger (Table 1) and in P₃ having a stronger and more lingually extensive paraconid accessory crest (Figs 18, 24O). Presence of this crest is diagnostic of the genus, but it is not certain how significant taxonomically are the differences in its degree of development.

Of the first and second molars preserved in the holotype maxilla, M¹ is damaged. The Khoer Dzan maxilla with P¹–M² (PSS.27-22) in contrast has well preserved teeth and shows well the differences between M¹ and M², allowing isolated preultimate molars to be identified as to jaw position (Fig. 13). The M¹ is nearly rectangular with the long axis transverse. M² is trapeziform, with the buccal margin oblique and with the distal margin shorter than the mesial margin and is slightly less transversely elongate than M¹. The M¹ postmetacrista is distinct, extending from the crown base to the worn metaloph edge. The M² postmetacrista is very weak and restricted to the basal few millimetres of the crown only. The isolated upper molars from Khoer Dzan can be readily identified to M¹ or M² according to outline shape, but the strength of the postmetacrista varies independently of this. For instance, PSS.27-128 has a distinct postmetacrista (Fig. 16). The lower molars are mainly identifiable as to jaw position because they are almost all preserved in dentary fragments. Accordingly, M₁ is distinguished from M₂ by having a slightly better developed paralophid (although the crest is weak in both). However, there is some variation in development of the paralophid, and on M₂ it may be entirely absent

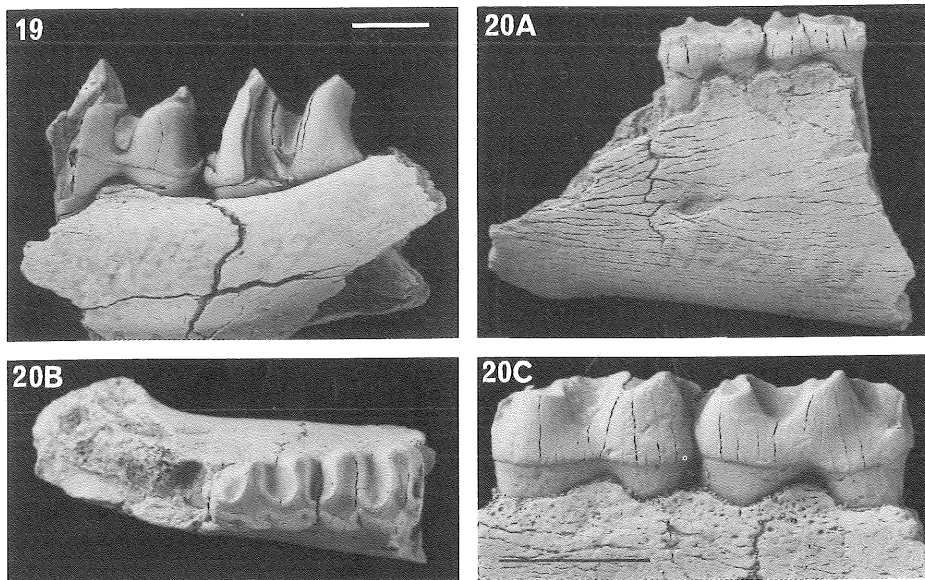


Figures 17, 18. *Teleolophus magnus* Radinsky. 17, left dentary fragment with M₁₋₃ (the last unerupted) (PSS.21-36) from Ergilin Dzo; A, lateral (buccal) view; B, dorsal (occlusal) view. 18, left dentary fragment with P₃₋₄ (PSS.27-4) from Khoer Dzan; A, medial (lingual) view; B, dorsal (occlusal) view. Scale bars = 20 mm.

(Figs 17, 19). The M₂ paralophid occludes with the M¹ postmetacrista in buccal phase mastication and it is thus logical that variation in one should be reflected in equivalent variation in the other. On the larger specimens, the lower molars tend to have a better developed buccal cingulum (Fig. 17) than do the smaller specimens (Fig. 19).

The molars range somewhat in size (Table 2; Figs 13, 15, 16), although nearly all are from the same lithostratigraphic unit (Sevkhul Member). It is thus unlikely that the size differences represent a chronocline. Only the M₃ (PSS.27-28) is from higher strata and it is difficult to judge the significance of its large size in the light of ignorance of the holotype M₃ and the relatively high size variation usually encountered in the third molar of mammals.

What is interesting is that size appears to correlate positively with strength of the upper molar postmetacrista and of the lower molar paralophid. There are insufficient teeth to provide a meaningful coefficient of variation (6.77 for the 4 M²'s), but there is an 11% difference between the smallest and largest M¹ in their maximum width



Figures 19, 20. Fig. 19, *Teleolophus magnus* Radinsky, from Khoer Dzan, left dentary fragment with M_{1-2} (PSS.27-27) in lateral (buccal) view. Fig. 20, *Deperetella* cf. *birmanica* (Pilgrim), from Khoer Dzan, left dentary fragment with P_{3-4} (PSS.27-31); A, lateral (buccal) view; B, dorsal (occlusal) view; C, lingual view. Coated with ammonium chloride. Scale bars = 10 mm.

TABLE 2. Maximum length and width measurements in millimetres of teeth of *Teleolophus magnus* from Khoer Dzan and Ergilin Dzo

		Length	Width
P^1	PSS.27-25	16.5	20.5
	PSS.27-26	16.0	20.3
	PSS.27-22	14.5	20.4
M^1	PSS.27-22	19.3	22.0
	PSS.27-24	21.1	24.5
M^2	PSS.27-22	22.5	24.7
	PSS.27-23	22.7	24.0
	PSS.27-128	26.0	26.6
P_3	PSS.27-4	19.0	12.5
P_4	PSS.27-4	19.5	13.9
M_1	PSS.27-27	22.1	15.0
	PSS.21-36	23.0	15.9
M_2	PSS.27-27	23.5	16.0
	PSS.21-36	24.0	18.0
M_3	PSS.21-36	—	22.2
	PSS.27-30	26.5	18.3
	PSS.27-28	—	21.1

dimension, a 15% difference between the largest and smallest M^2 in their maximum length dimension, and a 12.5% difference between the largest and smallest M_2 in their maximum width dimension. The possibility exists that two different species are represented, a larger one with less reduction of postmetacrista and paralophid (more primitive) and a smaller one with more reduction of these crests (more

derived). These differences are no less in degree than those that distinguish some species of similar sized herbivores of similar age on different continents (e.g. the genera *Palaeotherium* and *Anoplotherium* in Europe). However, more specimens are needed to demonstrate whether the size and morphological differences in this case are part of a continuous spectrum or disparate and thus whether one or two species are represented. A conservative approach in recognizing only one is taken here.

Genus *Deperetella* Matthew & Granger, 1925b

Type species. *Deperetella cristata* Matthew & Granger, 1925b.

Included species. *Deperetella depereti* (Zdansky, 1930) Radinsky, 1965; *Deperetella similis* (Zdansky, 1930) Radinsky, 1965; *Deperetella birmanica* (Pilgrim, 1925) Radinsky, 1965; *Deperetella khaitchinulensis* Reshetov, 1979.

Diagnosis. See Radinsky (1965).

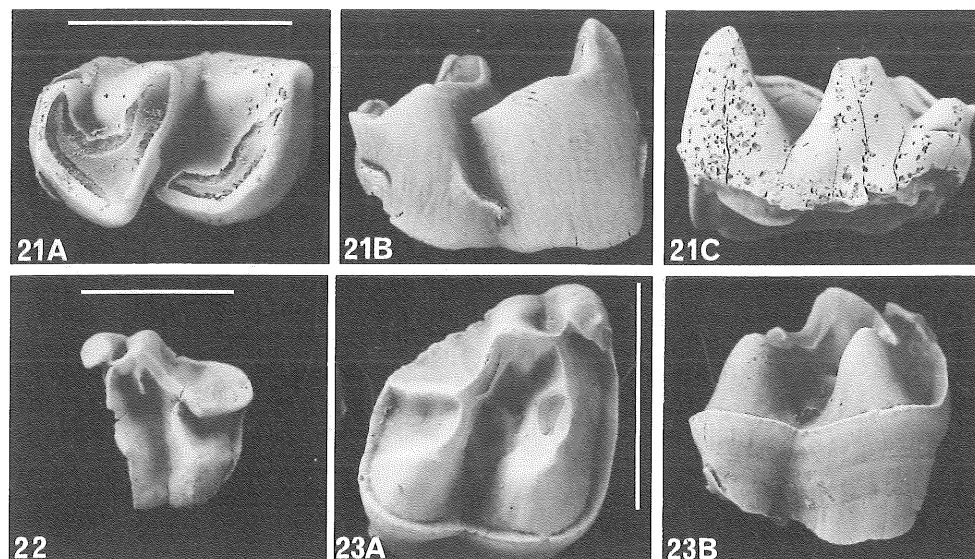
Deperetella cf. *birmanica* (Pilgrim, 1925) (Fig. 20)

Material. Left dentary fragment with P_{3-4} (PSS.27-31) from the Sevkhul Member, Ergilin Dzo Formation, late Eocene, Khoer Dzan, Mongolia.

Description. The jaw fragment is complete to the ventral edge (Fig. 20A); at its anterior end it shows strong medial curvature indicative of the proximity of the symphysis; it bears two heavily worn teeth. The second of the two teeth is fully molariform, whereas the first is nearly so, both having complete hypolophids. That they are both premolars is indicated by the presence of a posthypocristid. According to the degree of molarization and position with respect to the posterior edge of the symphysis of other species of *Deperetella*, the teeth are identified as P_{3-4} . The symphysis is interpreted to begin at the anterior edge of P_2 , which is represented only by alveoli (Fig. 20B).

Although there is some preservational weathering on the buccal walls, there is no evidence of the presence of cingula on either tooth. Both teeth have a protostylid, rather strong and crestiform on P_3 (Fig. 20A,B). P_3 is 14.1 mm long by 10.1 mm wide (maximum at talonid); P_4 is 13.8 mm long by 11.9 mm wide (maximum at talonid). There is some length reduction due to the heavy wear, although this is not likely to be great. The P_3 trigonid has a buccally displaced paraconid and is shorter than the talonid (Fig. 20C).

Discussion. The small size, absence of cingula, the short P_3 trigonid and the presence of protostylids indicates that the specimen cannot be identified with *Deperetella cristata*, *D. depereti* or *D. khaitchinulensis*. *D. similis* is smaller and known only from upper teeth, so is not directly comparable. The closest comparison is with *D. birmanica* (BMNH.M12756), which has a P_4 protostylid and lacks lingual cingula (Pilgrim, 1925). It differs in being slightly smaller and having a partial ectocingulum on P_4 . Unfortunately, the available material (lower jaws) of *D. birmanica* does not include teeth mesial of P_4 . So no positive judgement can be made on the significance of the character of the short P_3 trigonid in PSS.27-31. However, *D. similis* is almost identical in size to *D. birmanica* and like it lacks cingula (Pilgrim, 1925, pl.2, fig. 9). It also has less molariform P^{3-4} . It thus seems that PSS.2731 is part of a group of closely related



Figures 21–23. Fig. 21, *Ardynia* sp., left $M_{1/2}$ (PSS.41-66), from Mergen; A, occlusal view; B, buccal view; C, lingual view. Fig. 22, Rhinoceroidea undet., left $M^{1/2}$ (PSS.41-67) in occlusal view, from Mergen. Fig. 23, *Veragromovia desmatotherioides* Gabunia, cast of holotype right M^3 , from the Zaisan Basin, Kazakhstan; A, occlusal view; B, lingual view. Coated with ammonium chloride. Scale bars = 5 mm.

species (*D. similis*, *D. birmanica*) and is more distant from *D. cristata*, *D. depereti* or *D. khaitchinulensis*. It may be specifically distinct from *D. birmanica*, but there is as yet insufficient material to demonstrate this convincingly. It is thus here identified as *D. cf. birmanica*. *D. birmanica* is a rare species and thus a major range extension from Burma to Mongolia of this or a close relative is of considerable interest.

Superfamily Rhinoceroidea Owen, 1845
 Family Hyracodontidae Cope, 1879
 Genus *Ardynia* Matthew & Granger, 1923

Type species. *Ardynia praecox* Matthew & Granger, 1923, from the late Eocene to early Oligocene of Mongolia.

Included species. *Ardynia mongoliensis* (Beliajeva, 1952) Dashzeveg, 1991, from the late Eocene to early Oligocene of Asia.

Diagnosis. See Dashzeveg (1991).

Ardynia sp. (Fig. 21)

Material. Left $M_{1/2}$ (PSS.41-66) from the Mergen Formation, middle Eocene, of Mergen, Dornogobi Province, Mongolia.

Description. The tooth is 12.8 mm long by 7.5 mm wide at the trigonid and 7.9 mm wide at the talonid. It is fairly worn, exposing confluent areas of dentine (Fig. 21A),

but maintaining considerable crown height (Fig. 21B,C). It is thus significantly more hypsodont than other perissodactyls (e.g. *Lophialetes*) in the Mergen fauna, in fact more so than contemporaneous hyracodontids like *Triplopus* (Dashzeveg, 1991). The trigonid is prominently developed with a high bowed mesial paralophid arm that reaches the lingual margin of the tooth. The entoconid seems much taller than the metaconid, but this is due to much greater wear on the mesial half than the distal half of the tooth. The lingual wall of the metaconid is slightly concave. The enamel on the buccal side of the paralophid, protolophid, metalophid and hypolophid is much thicker than on the lingual side (Fig. 21A).

The relative hypsodonty, overall crown pattern and differential buccal and lingual enamel thicknesses as described above are typical of the first or second molars of the genus *Ardynia*. It is about 30% smaller than an M_1 of *A. praecox* and lower crowned. The crown height is not possible to measure because of wear, but an M_1 of *A. praecox* from the Sevkhul Member at Khoer Dzan, which has about the same degree of wear in terms of dentine exposure, is more hypsodont than the Mergen tooth, and the bases of its trigonid and talonid basins as viewed lingually are at a relatively higher level above the base of the crown.

Discussion. The Mergen tooth is clearly different at species level from either of the currently recognized species of *Ardynia* (Dashzeveg, 1991), but is as yet too poorly represented to be named. It extends the stratigraphical range of the genus from the late Eocene-Oligocene back into the early middle Eocene.

Rhinoceroidea undet. (Fig. 22)

Material. Left $M^{1/2}$ (PSS.41-67), from the Mergen Formation, middle Eocene, of Mergen, Dornogobi Province, Mongolia.

Description. Amongst the assemblage of small isolated teeth from Mergen, one upper molar differs from the associated *Lophialetes* by having the metaloph joined to the ectoloph just in front of the metacone instead of more mesially) so that the central valley is broadly U-shaped when viewed lingually. This indicates clearly that it is a more advanced ceratomorph than *Lophialetes*. Its cusp and crest pattern is rather similar to that of *Hyrachyus*, but it is slightly higher-crowned so that the ectoloph, which lacks a metacone rib, flares more distally. This indicates affinities with the Rhinoceroidea.

The tooth shows only slight natural wear, but is damaged so that much of the mesial border (except the parastyle) is broken away, along with the mesial side of the protoloph. It is 12.0 mm long by 12.3 mm wide.

The metacone is moderately lingually deflected as well as being buccally flattened. It has a large distinct parastyle, a rhinocerotoid crista on the lingual side of the paracone and a buccally strongly convex paracone causing a slight ectoflexus (Fig. 22). Although slightly abraded lingually, there appears to be little evidence of a lingual cingulum. It is similar in structure to '*Rhodopagus radinskyi*', but much larger, slightly higher crowned, with a weaker ectocingulum, more buccally salient paracone, less lingually tilted metacone, and the metaloph is not quite so recurved at the buccal end.

PSS.41-67 compares well with the maxilla (AMNH.81801) from the Irдин Manha

Formation, near Camp Margetts, Inner Mongolia, which Radinsky (1965: 234, fig. 21, pl.4, Fig. 5) referred to as 'cf. *Hyrachyus*'. This specimen was said to differ from typical *Hyrachyus* in having no M^2 metacone rib and an incipiently molariform (split protocone) P^4 . M^1 is about the same size as PSS.41-67, but the latter's postmetacrista (metastylar wing) is slightly more flared. Two Chinese species referred to *Heptodon*, *H. niushanensis* Chow & Li, 1965 and *H. tianshanensis* Zhai, 1978 share the same characteristics. Both have more lingually tilted upper molar metacones than does *Heptodon* and unlike this genus their metacones are ribbed buccally. They are thus closer in structure to *Hyrachyus*. The material from Mergen is clearly too fragmentary to make a definite identification, but the tooth does seem to belong to a primitive rhinocerotoid of '*Hyrachyus*' grade.

CLADISTIC ANALYSIS OF PRIMITIVE TAPIROIDS AND RHINOCEROTIDS

The problems

Hooker (1989) reviewed the relationships of major groups within the Perissodactyla and using a cladistic approach (although analyzing manually) examined the relationships within the Ceratomorpha. He concluded that the Lophialetidae were paraphyletic. He thus separated from this family the genus *Kalakotia*, which he placed in the stem of the Tapiromorpha (= Ceratomorpha + Ancylopoda), and the subfamilies Rhodopaginae and Breviodontinae, which he raised to family rank. The Rhodopagidae, which had been included in the rhinocerotoid family Hyracodontidae by Lucas & Schoch (1981), he placed as sister group to the Deperetellidae. He considered the redefined Lophialetidae, Breviodontidae, Rhodopagidae and Deperetellidae as undifferentiated stem ceratomorphs, thus not belonging to either of the modern superfamilies, Rhinoceroidea or Tapiroidea. He thus also redefined the Rhinoceroidea and Tapiroidea as monophyletic groups, although he could find relatively few characters to support them. *Heptodon* was placed as sister taxon to Tapiroidea plus Rhinoceroidea.

The improvement in knowledge of Asian members of the genus *Colodon* (*C. inceptus* and *C. fissus*) and the discovery and recognition of primitive members of the family Deperetellidae (*Irdinolophus? tuiensis* and *I. mongoliensis*) documented herein have implications for relationships within the Tapiroidea and of this superfamily with the Rhinoceroidea. They result in better definitions of the two groups and of their sister relationships.

The Tapiroidea had long been treated as a paraphyletic group from which the Rhinoceroidea evolved (see Radinsky, 1965; Schoch, 1989; Emry, 1989) until it was redefined monophyletically (with sister relationship to the Rhinoceroidea), comprising the extant family Tapiridae plus its more immediate extinct relatives (Hooker, 1989). The attribution of some fossil ceratomorphs to either the Tapiroidea, the Rhinoceroidea or an undefined stem group has understandably varied according to different authors with different concepts of the groups.

This is particularly true of *Hyrachyus*, which was classified by Radinsky in the Tapiroidea, but thought to have been at the same time ancestral to the Rhinoceroidea (Radinsky, 1966). Several characters were put forward by Prothero *et al.* (1986) in support of *Hyrachyus* being a rhinocerotoid, but all but one (loss of the M_3

hypoconulid) were shown by Emry (1989) to be untenable. The loss of the M_3 hypoconulid occurs within ceratomorphs not just in rhinocerotoids but also in advanced tapiroids, advanced deperetellids and the enigmatic *Dilophodon*, *Selenaletes* and *Fouchia*. Emry (1989) included the last three genera in the Rhinoceroidea close to *Hyrachyus*, based on the M_3 hypoconulid loss character. *Fouchia* is more primitive than any rhinocerotoid or tapiroid in having its upper molar metaloph meeting the ectoloph far mesial of the metacone and retaining vestiges of the lower molar posthypocristid (Emry, 1989, figs 1C-D, 2E-F). *Dilophodon* has an upper molar metaloph joining the ectoloph very close to the metacone and a reduced parastyle closely appressed to the paracone (Radinsky, 1963, pl.3, fig. 1). Both are characters of the Tapiroidea, although the second does not occur in the primitive genera *Heptodon* and *Helaletes*. M_3 hypoconulid loss appears thus not to be a very significant character, being emphasized because, being a total loss feature, it is readily recognized by all workers. However, the M_3 hypoconulid is already partly reduced in e.g. *Helaletes* and greatly so in e.g. *Colodon*; so total loss represents only a minor difference in degree from these states.

Another ceratomorph group of uncertain affinities is the Rhodopagidae. The core members of this family, *Rhodopagus* and *Pataecops*, were originally placed in the Lophialetidae by Radinsky (1965). These two genera were distinguished within the Lophialetidae as subfamily Rhodopaginae by Reshetov (1975). Lucas & Schoch (1981: 50) placed *Rhodopagus* and *Pataecops* in the rhinocerotoid family Hyracodontidae on the basis of: (1) relatively high-crowned teeth; (2) long and flat M^{1-2} ectolophs, resulting from the lengthening of the metacone; (3) protoloph longer than metaloph, both lophs oblique to the transverse axis of the tooth; (4) reduced parastyles on the upper molars; (5) M^3 triangular (or nearly so) due to the lingually depressed and reduced metacone; (6) metaloph confluent with the ectoloph in the upper molars; (7) relatively high paralophids and metalophids on the lower molars; and (8) no hypoconulid on M_3 .

Hooker (1989) raised the subfamily Rhodopaginae to family rank and instead classified it as the sister group of the Deperetellidae, remote from both the Rhinoceroidea and Tapiroidea, on the basis of: (1) advanced convergence of the upper molar metacone and hypocone, causing buccal bending of pre- and postmetacristae; (2) distally situated upper molar paracone and restricted mesial end of lower molar metalophid; and (3) M_3 hypoconulid lost.

A number of the characters used by Lucas & Schoch (1981) to ally *Rhodopagus* and *Pataecops* with the Hyracodontidae (their characters 2, 3, 4 and 6) are found also in various tapiroids. Their characters 1 and 7 are found in all rhinocerotoids except *Hyrachyus*; and their character 5 is found in the families Hyracodontidae and Rhinocerotidae.

Gabunia & Kukhaleishvili (1991) described the species *Rhodopagus radinskyi* on the basis of skull and dental material. They used the characters of low crown height, buccally flat metacone, bordered by a cingulum to restore *Rhodopagus* and *Pataecops* to the stem ceratomorph family Lophialetidae. They logically concluded that crown height had increased independently in *Rhodopagus* and rhinocerotoids. However, the presence of the ectocingulum is a primitive ceratomorph character and the flattening of the metacone is also present in *Colodon*, deperetellids and *Heptodon* as well as in *Lophialetes*.

R. radinskyi differs from other species of the genus in having: lower crown height (equivalent to that of *Hyrachyus*); a lower M^{1-3} metaloph and M_{1-3} hypolophid; less

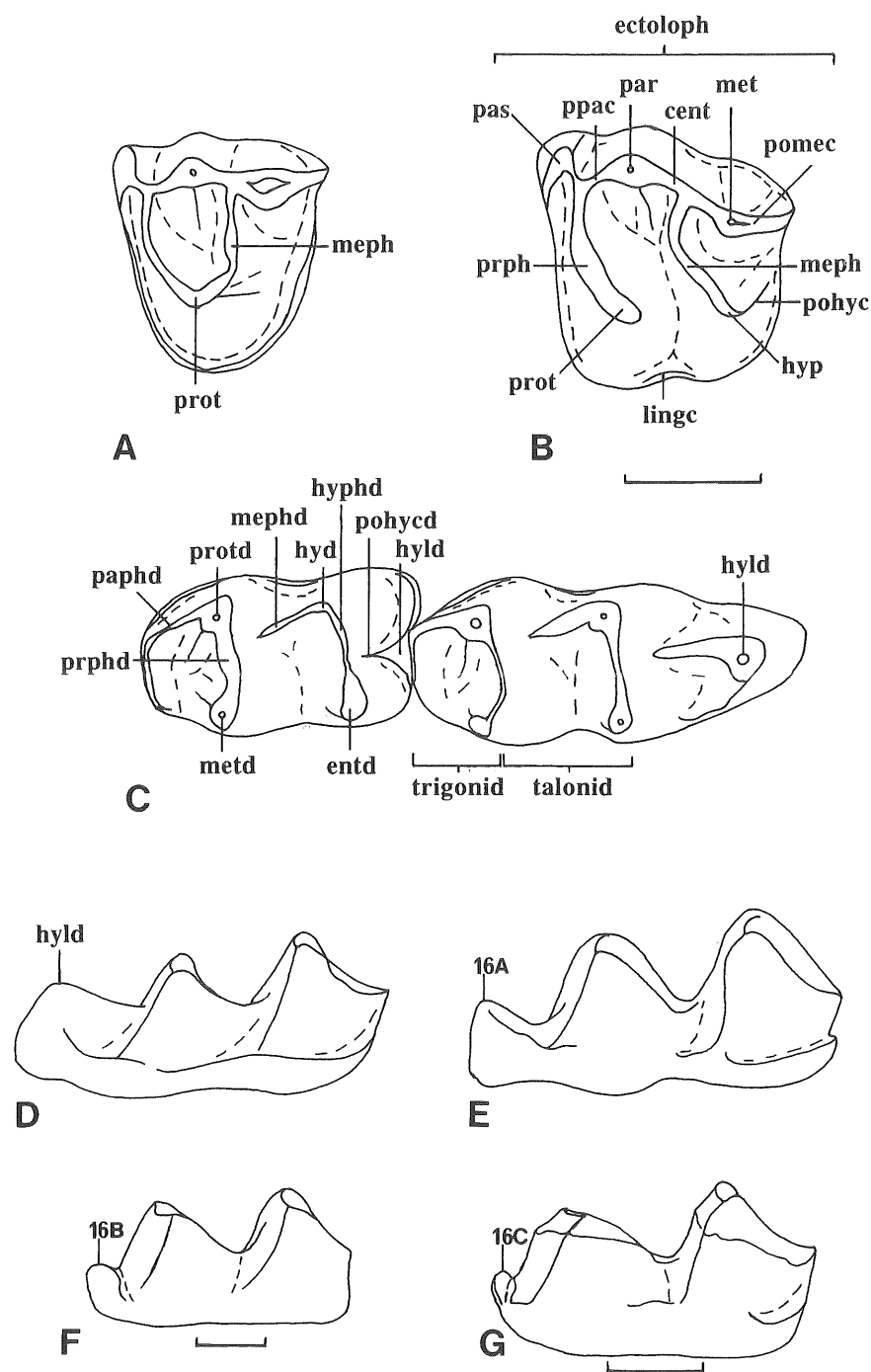
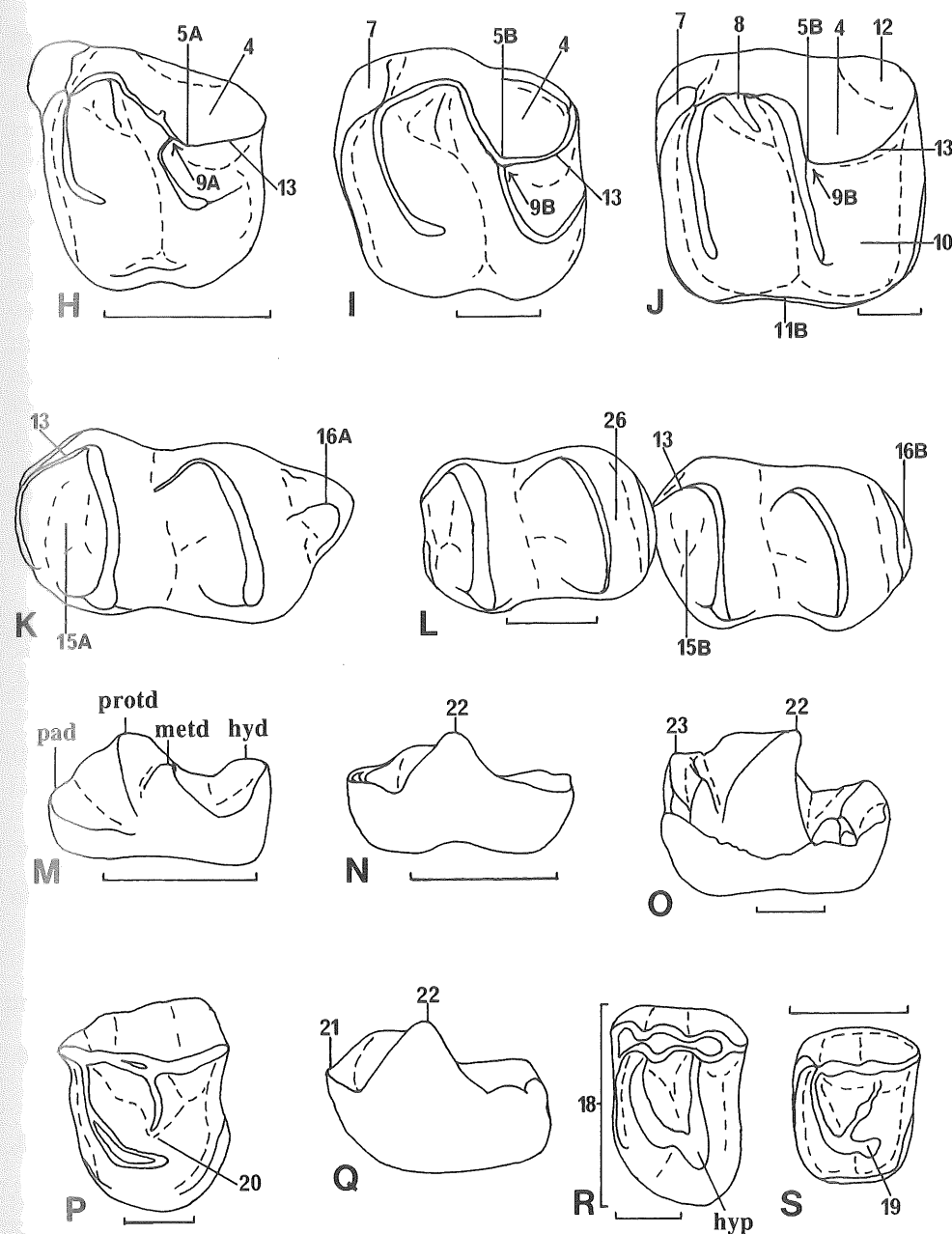


Figure 24. Dental terminology and definitions of states of numbered characters (see text). States are primitive for all characters of *Kalakotia*, on which most of the tooth terms are labelled (A–D, M). Upper teeth shown as left, lower teeth as right (A, B, G, I, L, O, S are reversed). A–D, M, *Kalakotia simplicidentata* Ranga Rao (paratype ONG/K/12 (A,B) and holotype ONG/K/10 (C,D,M) from Sind, India); E, *Heptodon calciculus* (Cope) (holotype AMNH4858, from Wyoming, U.S.A.); F, R, *Colodon inceptus* Matthew & Granger (PSS.27-33 (F), holotype AMNH20357 (R), from Ergilin Dzo, Mongolia); G, *Hyrachyus stehlini* (Depéret) (holotype FSL1983, from the Paris Basin, France); H, *Rhodopagus radinskyi* Gabunia & Kukhaleishvili (AS.GSSR.Z301, from the Zaisan Basin, Kazakhstan); I, *Indinolophus*



mongoliensis (Osborn) (holotype AMNH19161, from Inner Mongolia, China); J, *Teleolophus xui* (Tong & Lei) (holotype IVPP.V7382, from Henan, China); K, N, *Helaletes nanus* (Marsh) (AMNH13124, from Wyoming); L, Q, *Colodon fissus* (Matthew & Granger) (AMNH81802, from Inner Mongolia); O, *Teleolophus magnus* Radinsky (holotype AMNH26063, from Inner Mongolia); P, *Triplopus implicatus* (Cope) (after Radinsky, 1967, fig. 2); S, *Dilophodon leotanus* (Peterson) (after Radinsky 1963, pl. 3, fig. 1). A, P are P¹; R, S P³; B, H–J M^{1/2}; M–O, Q P₃; C, L M₂₋₃; D–G, K M₃. A–C, H–L, P, R, S are occlusal views, D–G buccal views, M–O, Q lingual views. Abbreviations: cent = centrocrista; entd = entoconid; hyd = hypoconid; hyld = hypoconulid; hyp = hypocone; hyhd = hypolophid; meph = metaloph; mephd = metalophid; met = metacone; metd = metaconid; pad = paraconid; paphd = paralophid; par = paracone; pas = parastyle; pohyc = posthypocrista; pohycd = posthypocristid; pomec = postmetacrista; ppac = preparacrista; prot = protocone; protd = protoconid; prph = protoloph; prphd = protolophid. Each scale bar measures 5 mm. That below B applies to A–E, K, Q.

lingually deflected upper molar metacones; virtually no metaconid on P_3 ; and an interrupted upper molar lingual cingulum (Fig. 24H). It nevertheless shares with both *Rhodopagus* and *Pataecops* high straight P^{3-4} ectolophs and occluding continuous longitudinal high buccal crests (metalophid plus paralophid) on P_{3-4} . These characters of *R. radinskyi* warrant its placement in a new rhodopagid genus. The low crown height of *R. radinskyi* removes the specific relationship of the Rhodopagidae with any other rhinocerotoid family as Gabunia & Kukhaleishvili (1991) recognized, but a character of the P^{3-4} indeed warrants their inclusion in the Rhinoceroidea rather than Tapiroidea, as Lucas & Schoch (1981) proposed. This character is the distinct break which occurs between the metaconule and protocone in hyrachyids, hyracodontids, amynodontids and rhinocerotids, when these teeth are nonmolariform (Hooker, 1989: 90, character 39; see Prothero *et al.*, 1986; Hanson, 1989, fig. 20.4; herein Fig. 24P). The character is well marked in *Pataecops* and *R. radinskyi*, but less obvious in *Rhodopagus* (Radinsky, 1965). Rhodopagids also lack (Gabunia & Kukhaleishvili, 1991) any sign of the major narial incision which typifies all tapiroids except *Heptodon* (Radinsky, 1965). This suggests that the characters used by Hooker (1989) to link Rhodopagidae and Deperetellidae as sister taxa are convergent. Moreover, several characters of deperetellids as described above favour return of this family to the Tapiroidea *sensu stricto*.

In order to establish more precisely an hypothesis of relationships between the Tapiroidea and Rhinoceroidea and in particular the allocation of enigmatic groups, we have conducted a phylogenetic analysis of key taxa using PAUP 3.0 (Swofford, 1990). The numbered characters are listed below and largely illustrated by Figure 24. Other illustrations are cited under the individual definitions.

Character definitions

Character 1: Narial incision extending posteriorly no further than P^1 (0); back to P^2 (A); back to P^3 (B).

Character 2: Nasal bones not reduced (0); reduced (1).

Character 3: Manus digit V present (0); absent (1).

Character 4: Upper molar metacone ribbed buccally (0); flat (1).

Character 5: Upper molar metacone not tilted lingually (0); tilted slightly (A) (Fig. 22); tilted markedly (B) (Figs 4, 11).

Character 6: M^2 metacone strong (0); weak (1).

Character 7: Upper molar parastyle large, well separated from paracone (0); small, compressed against paracone (1).

Character 8: Upper molar ectoloph essentially straight, joining vertically implanted or slightly distally tilted paracone (0); ectoloph buccally convex, making U-shaped loph together with protoloph and metaloph, and paracone tilted slightly mesially (1).

Character 9: Upper molar metaloph joins ectoloph near middle (0) (Fig. 3); slightly in front of metacone (A) (Fig. 22); at metacone (B) (Figs 4, 11A, 13).

Character 10: Upper molar posthypocrista present (0); absent (1).

Character 11: Upper molar lingual cingulum incomplete on all teeth (0); complete on M^3 (A); complete on all teeth (B).

Character 12: M^{1-2} ectocingulum adjacent to metacone ridge-shaped and marginal (0); bulbous and encroaching on stylar shelf (1).

TABLE 3. Data matrix of primitive ceratomorphs used in the cladistic analysis. '0' indicates the primitive state. The derived state for binary characters is 1, those for multistate characters are A, B, C. '?' indicates missing data. For explanation of character states, see text.

Characters:	123	456	789	111	111	111	122	222	22
HYPANC	000	000	000	000	000	000	000	000	00
HYRACH	000	0A0	00A	000	100	C10	010	100	01
HEPTOD	000	100	00B	000	10A	A00	000	100	01
HELALE	A00	0B0	00B	000	10A	A00	000	100	01
DESMAT	???	0B0	10B	000	10A	C00	100	101	01
DILOPH	???	0B0	10B	000	00A	C10	100	101	01
COLOCC	B11	1B0	11B	000	10B	A11	001	101	01
GOLINC	B??	1B0	10B	000	10B	B11	001	101	01
PLESIO	B1?	0A0	10B	000	10B	A01	00?	?01	01
PROTAP	B10	000	10B	000	10B	C01	001	101	01
IRDMON	B??	1B1	10B	0A0	10B	A?0	000	111	01
IRDTUI	???	1B1	10B	1B1	11B	???	?0?	???	1?
TELEOL	B?1	1B1	11B	1B1	01B	C10	000	111	11
RHORAD	00?	1B0	00A	000	100	C00	010	000	01
TRIPCU	001	0A0	10A	000	100	C00	010	100	11

Character 13: Upper molar postmetacrista and lower molar paracristid (paralophid) mesiodistally orientated (0); oblique (1).

Character 14: Molar transverse lophs straight in lateral profile (0) (Figs 8B, C, 9A); curved occlusomesially in uppers and occlusodistally in lowers (1) (Figs 17A, 19).

Character 15: Upper molar postmetacrista and lower molar trigonid relatively long (0) (Figs 3, 6, 7, 22); slightly shortened (A); greatly shortened (B) (Figs 4, 11A, 13, 15-17, 19).

Character 16: M_3 hypoconulid lobe large (0); small (A); in the form of a cusped cingulum (B); absent (C).

Character 17: P^1 without hypocone (0); with hypocone (1).

Character 18: P^{3-4} equidimensional or only slightly broader than long (0); transversely elongate (1).

Character 19: P^3 hypocone either absent or connects directly to metaloph (post-protocrista) (0); hypocone independent of metaloph, which joins protocone (1).

Character 20: P^4 metaloph essentially complete (0); broken buccal of protocone (1).

Character 21: P_3 paraconid not reduced (0); reduced (1).

Character 22: P_3 metaconid weak (0); strong (1).

Character 23: P_3 paraconid much lower than protoconid, P^2 not elongate (0); P_3 paraconid nearly as tall as protoconid with trenchant paracristid and P^2 elongate (1).

Character 24: P_{3-4} with talonids no broader than trigonids (0); broader than trigonids (1) (Figs 10A, 18B).

Character 25: Molars brachyodont (0) (Figs 8B,C, 9A); higher crowned (1) (Figs 17A, 19).

Character 26: Lower molar posthypocristid weakly present (0); absent (1).

Results of the analysis

All the characters in the data matrix (Table 3) were treated as ordered and include multiple states. They were polarized using an outgroup (hypanc) based on the

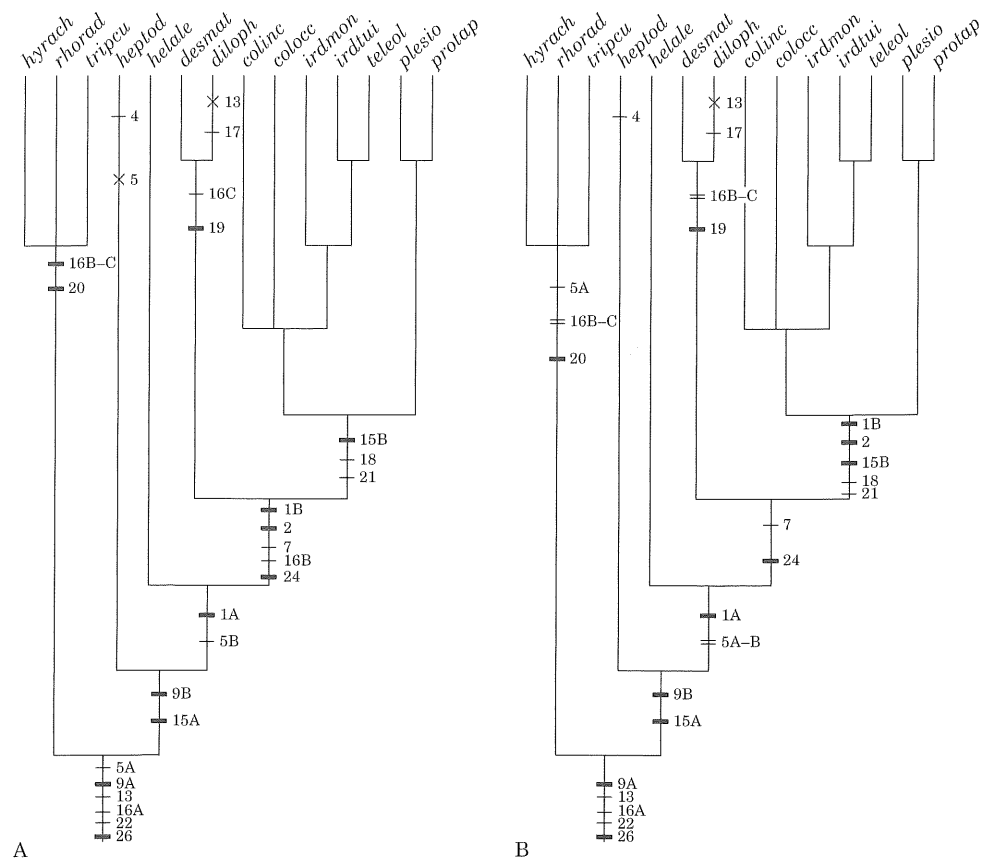


Figure 25. Strict/Adams consensus cladograms from PAUP 3.0 analysis of the data matrix in Table 3. Character states are shown below polytomies and below clades with variable character distributions (see Fig. 26). A, character distributions derived from Acctran optimization; B, from Deltran optimization. N.B. a third cladogram in Deltran differs from B only in having character 22 at the node below *Heptodon* (paralleled in *Hyrachyus* + *Triplopus* in Fig. 27C). Broad bar = synapomorphy; narrow bar = normal polarity homoplasy; X = reversal. For abbreviations of taxa see Introduction.

primitive tapiromorph *Kalakotia* (Fig. 24A–D, M), with the character states unknown in this genus (1, 2, 3) also being coded as 0 (i.e. primitive) based on their representation in other primitive perissodactyls. For the 15 taxa and 26 characters, using a Branch-and-Bound search, PAUP found nine maximum parsimony trees of 57 steps, with a consistency index of 0.571. Deltran versus Acctran optimizations recorded slight differences in character distribution. Although nine different tree topologies were generated, these were based on three alternatives in each of two distinct clades: *Hyrachyus*–*Rhodopagus*–*radinskyi*–*Triplopus* and *Colodon occidentalis*–*C. inceptus/fissus*–*Irdinolphus* + *Teleolophus* (Fig. 26). A consensus cladogram (Strict and Adams were the same) was obtained and is reproduced twice to show the different distributions of character states, for Deltran versus Acctran, below the unresolved nodes (Fig. 25). An Adams consensus of 93 cladograms of 57 and 58 steps shows the relative instability of the relationship between *Plesiocolopirus* and *Protapirus* and the weakness of the *Desmatotherium* + *Dilophodon* – *Colodon* + *Plesiocolopirus* + *Protapirus* + *Deperetellidae*

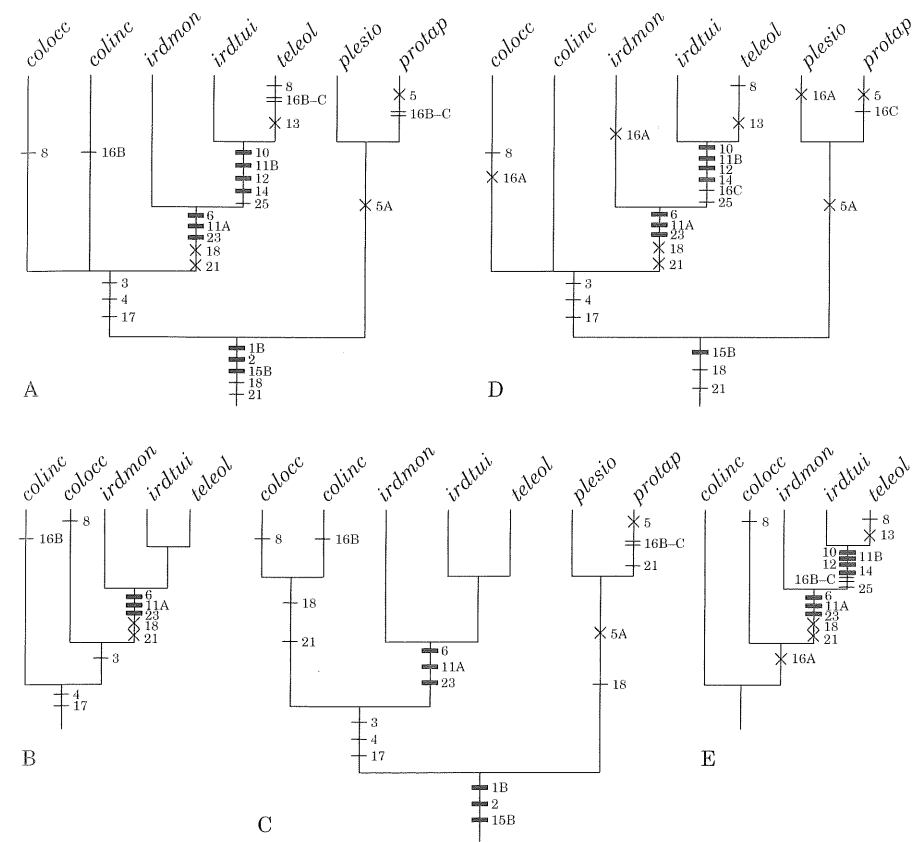


Figure 26. Different maximum parsimony topologies and character distributions for crown part of cladogram shown mainly unresolved in Fig. 25, relating to the Tapiroidea. A–C, Deltran optimization; D–E, Acctran optimization. The PLESIO–PROTAP clade omitted from B and E is as for A and D respectively. See Fig. 25 for explanation of character symbols and the Introduction for abbreviations of taxa.

clade. It maintains discrete Tapiroidea and Rhinoceroidea clades but does not resolve the relationship of *Heptodon* to either.

Differences between the Deltran and Acctran optimizations

On the consensus cladograms (Fig. 25), the different positions of Character 5 depend on whether the moderate lingual tilting of the upper molar metacone (5A) was developed basally and reversed in *Heptodon*, or whether it was evolved independently in rhinocerotoids and tapiroids above the level of *Heptodon* on the cladogram. Characters 1B and 2 either define the clade *Deperetellidae* + *Tapiridae* + *Colodon* or this clade plus *Desmatotherium* + *Dilophodon*. Uncertainty here is because *Desmatotherium* and *Dilophodon* are too poorly known to be scored for these characters. In addition, two slightly different positions for character 22 were produced by Deltran: basally, where this is reversed in *R. radinskyi*, or independently supporting the Tapiroidea and *Hyrachyus* + *Triplopus*.

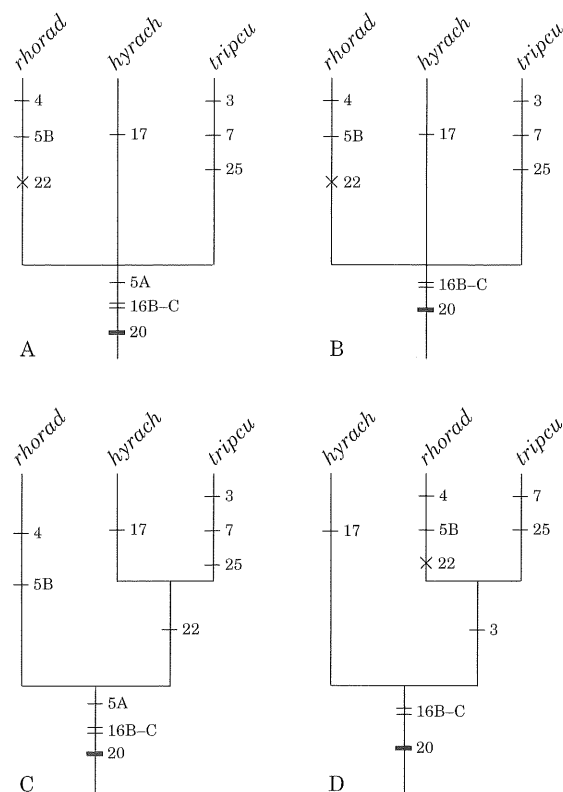


Figure 27. Different maximum parsimony topologies and character distributions for crown part of cladograms shown unresolved in Fig. 25, relating to the Rhinoceroidea. A, C, Deltran optimization; B, D, Acctran optimization. See Fig. 25 for explanation of character symbols and the Introduction for abbreviations of taxa.

Tapiroidea

The tapiroids can be characterized as a monophyletic group by having the upper molar metaloph joining the ectoloph at the metacone and the lower molar trigonid slightly shortened. In addition, a deep narial incision and strongly lingually tilted upper molar metacone characterize all except *Heptodon*.

Colodon + Deperetellidae + Tapiridae

Three different patterns of relationship between *Colodon occidentalis*, *C. inceptus/fissus* and the Deperetellidae were generated by PAUP.

(1) The two *Colodon* species form a clade with the Deperetellidae as its sister group. Here, the clade is defined on the transversely elongate P^{3-4} (18) and reduction of the P_3 paraconid (21). Character 21 is paralleled in *Protapirus* and character 18 in *Protapirus* + *Plesiocolopirus* (Tapiridae) (Fig. 26C).

(2) *Colodon occidentalis* is sister group to the Deperetellidae, this clade being sister group to *Colodon inceptus/fissus*. The *C. occidentalis* + Deperetellidae clade is defined by re-enlargement of the M_3 hypoconulid lobe to the state of being a small distinct cusp (16A) (Fig. 26E) or by loss of digit V in the manus (3) (Fig. 26B). The latter

definition is decidedly weak as the feet are only known in *C. occidentalis*, *Protapirus* and *Deperetella* (the last used here as a proxy for *Teleolophus*).

(3) *C. occidentalis*, *C. inceptus/fissus* and the Deperetellidae form an unresolved trichotomy. Both alternative character positions involve multistate character 16 (the hypoconulid lobe). The Acctran alternative involves reversal to state 16A in parallel in *C. occidentalis* and *Indinolophus mongoliensis* (Fig. 26D). The Deltran alternative involves independent reduction of the M_3 hypoconulid to the cusped cingulum state (16B) in both *C. occidentalis* and *Teleolophus* (being unknown in *Indinolophus? tuiensis*) (Fig. 26A). Both alternatives involve reversal of the transverse elongation of P^{3-4} (18) and of the reduction of the P_3 paraconid (21) in the Deperetellidae.

It is felt that the most likely choice is that shown in Fig. 26C, where *C. occidentalis* and *C. inceptus/fissus* are sister taxa.

Deperetellidae

The nested relationship of *Teleolophus* (representing also *Deperetella*) successively with *Indinolophus? tuiensis* and with *I. mongoliensis* is strongly supported in the analysis, despite poor knowledge of *I? tuiensis* (Fig. 26). The clade was still stable in the 59 step cladograms.

Rhinoceroidea

Both *Hyrachyus* and '*R. radinskyi*' group with the undoubted primitive rhinocerotoid *Triplopus* in all the cladograms as defined by the characters of distinct separation of the P^{3-4} metaconule from protocone (unique) and loss of the M_3 hypoconulid lobe (paralleled remotely elsewhere on the cladogram) (Fig. 25). However, two cladograms do not resolve the relationships of these three taxa (Fig. 27A, B). The problem of homoplasy for character 5A (slight lingual tilting of the upper molar metacone), because of the enigmatic combination of dental character states present in *Heptodon*, means that this character may also independently define the rhinocerotoids and the tapiroids crownward of *Heptodon* (Figs 25, 27).

Other variations are caused by characters 3 and 22. Presence or absence of manus digit V (3) is unknown for any rhodopagid. Absence, the derived state, would suggest a closer link with *Triplopus* than with *Hyrachyus* (Fig. 27D). '*R. radinskyi*' has a weak P_3 metaconid, which is the primitive state of character 22 according to outgroup comparison. The derived strong state has either evolved independently in *Hyrachyus* + *Triplopus* and in tapiroids (Fig. 27C), or basally then reversed in '*R. radinskyi*' (Fig. 27A, B, D). As rhodopagids have short premolar rows compared with the molars and have lost P_1 (character omitted as it is an autapomorphy), it is more likely that the '0' state of character 22 in '*R. radinskyi*' represents a reduction of molarization of P_3 and thus a reversal.

Veragromovia and the Rhodopagidae

The monotypic *Veragromovia desmatotherioides* Gabunia, 1961 was described on the basis of one isolated right M^3 from the middle Obayla Formation, middle Eocene, of the Zaisan Basin, Kazakhstan. Gabunia placed it in the family Helaletidae, which has subsequently been shown to be paraphyletic when used to include more than just *Helaletes* (Hooker, 1989; Schoch, 1989).

Radinsky (1965: 234) synonymized *Veragromovia* with *Helaletes*, on the basis of the "similar size and cusp pattern" of its unique M^3 . His decision has been followed by

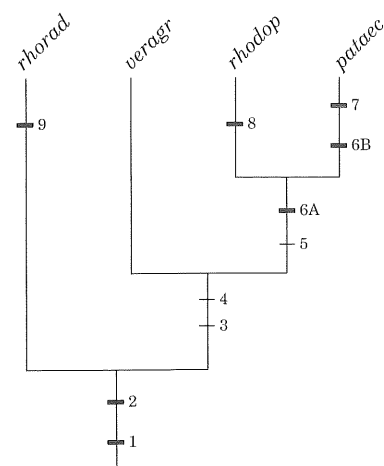


Figure 28. Cladogram (not computer analysed) showing phylogenetic scheme for the Rhodopagidae. Character descriptions: 1=loss of P_1 ; 2=high straight continuous buccal crests on upper and lower P_3-4 ; 3=upper molar lingual cingulum complete; 4=increased crown height (same as character 25 in Table 3); 5=upper molars with markedly lingually tilted metacone (same as character 5B in Table 3); 6=upper molar metaloph and lower molar hypolophid: A, slightly taller than protoloph and protolophid respectively, B, much taller; 7=long upper molar postmetacrista; 8=premolar row shortened relative to molar row; 9=very small size. See Fig. 25 for explanation of character symbols and the Introduction for abbreviations of taxa.

most subsequent authors (e.g. Reshetov, 1979; Prothero & Schoch, 1989). The similarities to *Helaletes*, however, are largely ones that are primitive for the Rhinocerotoida plus Tapiroidea (i.e. excluding more primitive ceratomorphs). The differences: greater crown height, a broad U-shaped central valley, more lingual metacone and presence of a complete lingual cingulum in *Veragromovia* are in combination shared exclusively with the genera *Rhodopagus* and *Pataecops* (Fig. 23). It differs from these genera in having the metaloph no higher than the protoloph and in retaining a large distinct parastyle, both primitive states shared with the much smaller '*Rhodopagus*' *radinskyi*. Figure 28 shows a new phylogenetic scheme for the Rhodopagidae. Although still very poorly represented according to its known derived characters, the genus *Veragromovia* is here resurrected and transferred to the family Rhodopagidae.

The small rhinocerotoid genus *Yimengia* Wang, 1988, from the middle Eocene Guanzhuang Formation, Laiwu County, Shandong Province, China, was considered by its author to be closely related to *Rhodopagus*, as it shares with this genus the premolar row shorter than the molar row, loss of P_1 , and long diastema. However, according to published figures, it appears to lack the continuous buccal cresting of the premolars and the P_3 metaconid appears not to be weak, both of which characterise the Rhodopagidae. Moreover, its degree of upper molar metacone lingual tilt appears to be no greater than in '*Rhodopagus*' *radinskyi*. Its affinities with the Rhodopagidae are thus currently uncertain.

The cladistic analysis conducted here thus resolves the relationships of the Rhodopagidae and Deperetellidae. It strengthens the definition of the Tapiroidea and supports placement of *Heptodon* in that superfamily. No new information from *Lophialetes* alters the position of the Lophialetidae as stem Ceratomorpha. The

characters of metacone attachment position on the ectoloph for the upper molar metaloph (character 9B) and shortening of the lower molar trigonid (character 15A) assume importance for defining the Tapiroidea.

RELATIVE DATING OF THE KHOLBOLCHI AND MERGEN FORMATIONS

Kholbolchi Formation

This formation is bounded by major unconformities. At the locality of Menkhen Teg, it is overlain by the Oligocene Hsanda Gol Formation and rests on unfossiliferous strata which are similar to Palaeocene sediments elsewhere in Mongolia. At Barun Khutsin Tsav, it is overlain by the Miocene Tuin Gol Formation and rests on Palaeozoic basement (see Badamgarav *et al.*, 1975). At Tsagan Khutel, the Kholbolchi Formation is the highest unit at outcrop and rests on possible Palaeocene strata as at Menkhen Teg. The formation is thicker than at the other two localities and in its upper part may include strata higher than any represented at either Menkhen Teg or Barun Khutsin Tsav. In the present context, Tsagan Khutel is important for yielding the type and only known specimen of *Irdinolophus?* *tuiensis*.

The fauna of the Kholbolchi Formation is usually compared with that of the Irдин Manha Formation of Inner Mongolia, thus considered to belong to the middle Eocene (probably early middle, perhaps equating with part of the Uintan North American Land Mammal Age (NALMA), see Russell & Zhai, 1987: 145-148, 403). Most Asian middle Eocene faunas referred to the Irдинmanhan Asian Land Mammal Age (ALMA) by Russell & Zhai consistently include the genus *Teleolophus*. At Tsagan Khutel, however, the only deperetellid is the primitive *Irdinolophus?* *tuiensis*. In the Kholbolchi Formation, this species is associated with the pantodont *Archaeolambda prima* (Dashzeveg). This rather archaic element occurs alongside the uniquely represented perissodactyl genera *Gobihippus* and *Pataecops* as well as the ubiquitous genus *Lophialetes*.

Two other Asian faunas, both in China, that include *Lophialetes* and other typical Irдинmanhan forms, but lack species clearly referable to *Teleolophus*, are those from the Arshanto fauna, Inner Mongolia (Arshanto beds, ex-Arshanto Formation) and from the Xintai Basin, Shandong Province (Guanzhuang Formation). The Guanzhuang Formation has yielded the species *?Teleolophus shandongensis*, which may be closely related to *Irdinolophus?* *tuiensis* and not belong to *Teleolophus* (see above). On the basis of the common occurrence of the species *Hyrachyus modestus*, backed up by similar tillodonts, the Guanzhuang fauna has been correlated with the early Bridgerian NALMA (Qi, 1987: 13), which spans the early/middle Eocene boundary (Woodburne & Swisher, 1995). Moreover, the species *Propalaeotherium sinense* Zdansky, 1930, from the Guanzhuang fauna is almost certainly a brontothere (Hooker, 1994) and shows similarities to North American Lostcabinian (=late Ypresian) *Lambdotherium*.

The Arshanto beds contain '*Teleolophus*' *primarius*, which may also be closely related to *I?* *tuiensis*. The Arshanto beds underlie the Irдин Manha beds at Arshanto. The Arshantan ALMA has been named for its contained fauna and correlated with the late Bridgerian NALMA, making it slightly younger than the Guanzhuang fauna (Qi, 1987; Holroyd & Ciochon, 1994). However, the faunal similarities between the

Guanzhuang and the Arshanto are more striking than the differences and it is likely therefore that the faunas of not only the Arshanto and Guanzhuang, but also the Kholbolchi Formation belong to a distinct time slice (Arshantan) that predates the Irdinmanhan and belongs to the earliest middle or latest early Eocene. This hypothesis is preliminary, but more intensive collecting at Tsagan Khutel and Barun Khutsin Tsav could provide more compelling evidence.

Mergen Formation

The fauna from this formation at Mergen has been considered typical of the Irdinmanhan (Russell & Zhai, 1987: 149–150), although some of the hyracodonts already described (Dashzeveg, 1991) have proved to belong to species not represented elsewhere. Moreover, the *Lophialetes* is shown herein to be more primitive than typical *L. expeditus* or *L. expeditus?* from the Irdinmanhan Irdin Manha and Ulan Shireh Formations. The Mergen fauna may therefore be slightly older than typical Irdinmanhan faunas.

ACKNOWLEDGEMENTS

We would like to thank Drs D.E. Russell (Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris), M.C. McKenna (Dept of Vertebrate Paleontology, American Museum of Natural History, New York), B.A. Trofimov and the late V.Yu. Reshetov (Palaeontological Institute of the Russian Academy of Sciences, Moscow) for access to collections in their care. Drs D.E. Russell, M.C. McKenna, J. Alexander and Tong Yongsheng kindly provided important perissodactyl casts. Ms G.C. Gould kindly transported casts at short notice. The specimens were prepared by Mr B. Namsrai. The line drawings of specimens were made by Mr V.D. Mogilevskii and the photographs were made by Mr P. Hurst of the Natural History Museum (London) Photostudio. Dr P.L. Forey helped with the production of Figures 25–28. D.D. carried out part of this work while on a Royal Society funded exchange, which is gratefully acknowledged.

REFERENCES

- Badamgarav D, Dashzeveg D, Devyatkin EV, Zhegallo VI, Liskun IG. 1975.** [The stratigraphy of the Paleogene and Neogene in the Valley of Lakes (on the question of separation of stratotypical regions of Paleogene and Neogene in Central Asia)]. In: Kramarenko NN, ed. *Iskopaemaya fauna i flora Mongolii. Trudy sovmestnaya Sovetsko-Mongolskaya Paleontologicheskaya Ekspeditsiya* 2: 250–268. (In Russian)
- Beliajeva EI. 1952.** [Primitive rhinocerotoids of Mongolia] *Trudy Paleontologicheskogo Instituta. Akademiya Nauk SSSR* 41: 120–142. (In Russian)
- Beliajeva EI. 1962.** [The first find of a tapiroid in the Eocene of Middle Asia]. *Byulleten' Moskovskogo Obshchestva Ispytateley Prirody otdel geologicheskij* 5(37): 142–145. (In Russian)
- Berkey CP, Granger W, Morris FK. 1929.** Additional new formations in the later sediments of Mongolia. *American Museum Novitates* 385: 1–12.
- Biryukov MD. 1974.** [A new species of the genus *Teleolophus* from Northern Dzhungaria]. *Teriologiya* 2: 78–82. (In Russian)

- Borissiak A. 1918.** [On the remains of a lophiodontoid ungulate from the Oligocene deposits of Turgai.] *Annales de la Société Paléontologique Russie* 2: 27–31. (In Russian)
- Burnett GT. 1830.** Illustrations of the Quadrupeda, or quadrupeds, being the arrangement of the true four-footed beasts, indicated in outline. *Quarterly Journal of Science, Literature, Arts* 26: 336–353.
- Chow M-C, Li C-K. 1965.** [*Homogalax* and *Heptodon* of Shantung]. *Vertebrata Palasiatica* 9: 15–21. (In Chinese)
- Chow M-C, Qi T. 1982.** [Mammals from the middle Eocene Kuanchuang Formation of Xintai, Shandong]. *Vertebrata Palasiatica* 20: 302–313. (In Chinese)
- Cope ED. 1879.** On the extinct species of the Rhinocerotidae of North America and their allies. *Bulletin of the United States Geological and Geographical Survey of the Territories* 5: 227–237.
- Dashzeveg D. 1979.** [On an archaic representative of the Equoidea (Mammalia, Perissodactyla) from the Eocene of central Asia]. *Trudy sovmestnaya Sovetsko-Mongolskaya Paleontologicheskaya Ekspeditsiya* 8: 10–22. (In Russian)
- Dashzeveg D. 1991.** Hyracodontids and rhinocerotids (Mammalia, Perissodactyla, Rhinocerotidae) from the Paleogene of Mongolia. *Palaeovertebrata* 21: 1–84.
- Dashzeveg D. 1993.** Asynchronism of the main mammalian faunal events near the Eocene-Oligocene boundary. *Tertiary Research* 14: 141–149.
- Dehm R, Oettingen-Spielberg T zu. 1958.** Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 2. Die mitteleocänen Säugetiere von Ganda Kas bei Basal Nordwest Pakistan. *Abhandlungen Bayerische Akademie der Wissenschaften, Mathematische-Naturwissenschaftliche Klasse (NF)* 91: 1–54.
- Douglass E. 1901.** Fossil Mammalia of the White River beds of Montana. *Transactions of the American Philosophical Society (NS)* 20: 237–279.
- Emry RJ. 1989.** A tiny new Eocene ceratomorph and comments on “tapiroid” systematics. *Journal of Mammalogy* 70: 794–804.
- Fortelius M. 1985.** Ungulate cheek teeth: developmental, functional, and evolutionary interrelations. *Acta Zoologica Fennica* 180: 1–76.
- Gabunia LK. 1961.** [The Obayla fauna: the most ancient complex of fossil mammals of the USSR]. *Sobshcheniya Akademii Nauk Gruzinskoy SSR* 27: 711–713. (In Russian)
- Gabunia LK, Kukhaleishvili RE. 1991.** [A Zaysan *Rhodopagus* (Perissodactyla, Tapiroidea)]. *Paleontologicheskii Zhurnal* 25: 107–114. (In Russian)
- Gazin CL. 1956.** The geology and vertebrate paleontology of upper Eocene strata in the northeastern part of the Wind River Basin, Wyoming. Part 2. The mammalian fauna of the Badwater Area. *Smithsonian Miscellaneous Collection* 131(8): 1–35.
- Hanson CB. 1989.** *Teletaceras radinskyi*, a new primitive rhinocerotid from the late Eocene Clarno Formation of Oregon. In: Prothero DR, Schoch RM, eds. *The Evolution of Perissodactyls*. New York, Oxford University Press, 379–398.
- Heissig K. 1978.** Fossilführende Spaltenfüllungen Süddeutschlands und die Ökologie ihrer oligozänen Huftiere. *Mitteilungen Bayerischen Staatssammlung der Paläontologische und historische Geologie* 18: 237–288.
- Holroyd PA, Ciochon RL. 1994.** Relative ages of Eocene primate-bearing deposits of Asia. In: Fleagle JG, Kay RF, eds. *Anthropoid Origins*. New York & London, Plenum Press, 123–141.
- Hooker JJ. 1989.** Character polarities in early perissodactyls and their significance for *Hyracotherium* and infraordinal relationships. In: Prothero DR, Schoch RM, eds. *The Evolution of Perissodactyls*. New York, Oxford University Press, 79–101.
- Hooker JJ. 1994.** The beginning of the equoid radiation. *Zoological Journal of the Linnean Society* 112: 29–63.
- Hough J. 1955.** An upper Eocene fauna from the Sage Creek area, Beaverhead County, Montana. *Journal of Paleontology* 29: 22–36.
- Leidy J. 1868.** Notice of some Eocene remains of extinct pachyderms. *Proceedings of the Academy of Natural Sciences, Philadelphia* 20: 230–233.
- Lucas SG, Schoch RM. 1981.** The systematics of *Rhodopagus*, a late Eocene hyracodontid (Perissodactyla, Rhinocerotidae) from China. *Bulletin of the Geological Institutions of the University of Uppsala (NS)* 9: 43–50.
- Marsh OC. 1890.** Notice of new Tertiary mammals. *American Journal of Science* 39: 523–525.
- Matthew WD, Granger W. 1923.** The fauna of the Ardyn Obo Formation of Mongolia. *American Museum Novitates* 98: 1–5.
- Matthew WD, Granger W. 1925a.** New ungulates from the Ardyn Obo Formation of Mongolia. *American Museum Novitates* 195: 1–12.

- Matthew WD, Granger W. 1925b.** New mammals from the Shara Murun Eocene of Mongolia. *American Museum Novitates* **196**: 1–11.
- Matthew WD, Granger W. 1925c.** The smaller perissodactyls of the Irdin Manha Formation, Eocene of Mongolia. *American Museum Novitates* **199**: 1–9.
- Osborn HF. 1923.** Titanotheres and lophiodonts in Mongolia. *American Museum Novitates* **91**: 1–5.
- Owen R. 1845.** *Odontography; or a treatise on the comparative anatomy of teeth*. London: Hippolyte Bailliere.
- Pilgrim GE. 1925.** The Perissodactyla of the Eocene of Burma. *Palaeontologia Indica* **8**(3): 1–28.
- Prothero DR, Schoch RM. 1989.** Classification of the Perissodactyla. In: Prothero DR, Schoch RM, eds. *The Evolution of Perissodactyls*. New York: Oxford University Press, 530–537.
- Prothero DR, Manning E, Hanson CB. 1986.** The phylogeny of the Rhinoceroidea (Mammalia, Perissodactyla). *Zoological Journal of the Linnean Society* **87**: 341–366.
- Qi T. 1981.** [New materials of the early Oligocene Chaganbulag Fauna from Alxa Zuoqi, Inner Mongolia]. *Vertebrata Palasiatica* **19**: 145–148. (In Chinese)
- Qi T. 1987.** The middle Eocene Arshanto fauna (Mammalia) of Inner Mongolia. *Annals of the Carnegie Museum* **56**(1): 1–73.
- Radinsky LB. 1963.** Origin and early evolution of North American Tapiroidea. *Bulletin of the Peabody Museum of Natural History* **17**: 1–115.
- Radinsky LB. 1965.** Early Tertiary Tapiroidea of Asia. *Bulletin of the American Museum of Natural History* **129**: 181–263.
- Radinsky LB. 1966.** The families of the Rhinoceroidea (Mammalia, Perissodactyla). *Journal of Mammalogy* **47**: 631–639.
- Radinsky LB. 1967.** A review of the rhinocerotoid family Hyracodontidae (Perissodactyla). *Bulletin of the American Museum of Natural History* **136**: 1–45.
- Reshetov VYu. 1975.** [A review of the early Tertiary tapiroids of Mongolia and the USSR]. In: Kramarenko NN, ed. *Iskopaemaya fauna i flora Mongolii. Trudy sovrestnaya Sovetsko-Mongolskaya Paleontologicheskaya Ekspeditsiya* **2**: 19–53. (In Russian)
- Reshetov VYu. 1979.** [Early Tertiary Tapiroidea of Mongolia and the USSR.] *Trudy sovrestnaya Sovetsko-Mongolskaya Paleontologicheskaya Ekspeditsiya* **11**: 1–141. (In Russian)
- Russell DE, Zhai R-J. 1987.** The Paleogene of Asia: mammals and stratigraphy. *Mémoires du Muséum National d'Histoire Naturelle (C)* **52**: 1–488.
- Schoch RM. 1989.** A review of the tapiroids. In: Prothero DR, Schoch RM, eds. *The Evolution of Perissodactyls*. New York: Oxford University Press, 298–320.
- Scott WB. 1941.** Perissodactyla. The mammalian fauna of the White River Oligocene. *Transactions of the American Philosophical Society* **28**: 747–980.
- Swofford DL. 1990.** *PAUP, Phylogenetic Analysis Using Parsimony, Version 3.0*: 1–62. User's manual, Illinois Natural History Survey, Champaign.
- Takai F. 1939.** Eocene mammals found from the Hosan coal-field, Tyosen. *Journal of the Faculty of Science Tokyo* (2) **5**: 199–217.
- Tokunaga S. 1933.** A list of fossil land mammals of Japan and Korea with descriptions of new Eocene forms from Korea. *American Museum Novitates* **627**: 1–7.
- Tomida Y. 1983.** A new helaletid tapiroid (Perissodactyla, Mammalia) from the Paleogene of Hokkaido, Japan, and the age of the Urahoro Group. *Bulletin of the National Science Museum, Tokyo (C)* **9**: 151–163.
- Tong Y-S, Lei Y-Z. 1984.** [Fossil tapiroids from the upper Eocene of Xichuan, Henan.] *Vertebrata Palasiatica* **22**: 269–280. (In Chinese)
- Wang J-W. 1988.** [A new genus of ceratomorphs (Mammalia) from middle Eocene of China]. *Vertebrata Palasiatica* **26**: 20–34. (In Chinese)
- Wilson JA, Schiebout JA. 1984.** Early Tertiary vertebrate faunas, Trans-Pecos Texas: Ceratomorpha less Amynodontidae. *Pearce-Sellards Series, Texas Memorial Museum* **39**: 1–47.
- Woodburne MO, Swisher CC III. 1995.** Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance. In: Berggren WA, Kent DV, Hardenbol JA, eds. *Geochronology, time scales and global stratigraphic correlations: a unified framework for an historical geology*. SEPM Special Publication no. **54**, 335–364.
- Zdansky O. 1930.** Die alttertiären Säugetiere Chinas nebst stratigraphischen Bemerkungen. *Palaeontologia Sinica (C)* **6**: 1–87.
- Zhai R-J. 1978.** [More fossil evidences favouring an Early Eocene connection between Asia and Neartic]. *Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology* **13**: 107–115. (In Chinese)
- Zheng J-J. 1978.** [Description of some late Eocene mammals from Lian-Kan Formation of Turfan Basin, Sinkiang]. *Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology* **13**: 116–125. (In Chinese)



Patterns of growth of the mandibular corpus in spotted hyenas (*Crocota crocuta*) and cougars (*Puma concolor*)

AUDRONE R. BIKNEVICIUS

Department of Biological Sciences, College of Osteopathic Medicine, Ohio University, Athens, OH 45701 U.S.A.

STEVEN R. LEIGH

Department of Anthropology, University of Illinois, Urbana, IL 61801 U.S.A.

Received May 1996; accepted for publication September 1996

Differences in jaw morphology among adult carnivorans are well established, but the ontogenetic mechanisms by which these differences arise are largely unexplored. Mandibular ontogeny in *Crocota crocuta* and *Puma concolor* is analysed biomechanically using principles of beam theory. In each species, the development of cross-sectional properties of the mandibular corpus associated with rigidity under loading follows a biphasic pattern of growth. In early postnatal growth, deposition of cortical bone appears to be constrained by the overall weaker tissue with which juvenile skeletons are constructed and by the need to volumetrically accommodate the developing teeth within their bony crypts. Thus, this stage of growth is characterized by a net periosteal deposition of bone and a swelling of the medullary cavity. In late postnatal growth, the constraints on endosteal deposition of bone are relieved as the permanent teeth erupt; thus, cortical thicknesses increase sharply by periosteal expansion as well as medullary contraction. Finally, it is noted that basic differences in jaw construction between *Crocota* and *Puma* appear to develop prenatally as they are largely in place at birth. Hence, postnatal development enhances, but does not solely contribute to, the biomechanical differences in the jaws of these species.

© 1997 The Linnean Society of London

ADDITIONAL KEY WORDS:—development – feeding adaptations – cross-sectional geometry.

CONTENTS

Introduction	140
Material and methods	141
Reconstruction of corpus cross-sectional shape	141
Scaling analyses	144

Correspondence to: Dr. Audrone R. Biknevičius. e-mail biknevic@ohiou.edu