

A primitive ceratomorph (Perissodactyla, Mammalia) from the early Tertiary of Europe

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Hyracotherium cuniculus Owen, 1842, from Palaeocene–Eocene boundary strata in NW Europe, was formerly considered to be an equoid. It is here placed in *Cymbalophus gen. nov.*, in the perissodactyl suborder Ceratomorpha, which comprises tapiroids and rhinocerotoids, as one of its most primitive and earliest members. This revised classification is based on an evaluation of its advanced versus primitive character states, and comparison with a variety of other primitive perissodactyls. Check tooth occlusal relationships in the early stages of ceratomorph evolution are discussed and contrasted with the fundamental perissodactyl morphotype as represented in *Hyracotherium*. It is suggested that the Lophiodontidae (formerly considered to be ceratomorphs) may be more closely related to chalicotheres; that the Isectolophidae may be the sister-group of chalicotheres and lophiodonts plus ceratomorphs; and that *Cymbalophus* is the most primitive known member of the newly restricted Ceratomorpha. *Cymbalophus* is placed tentatively in the family Helaletidae.

KEY WORDS:—Phylogeny – *Hyracotherium* – *Cymbalophus gen. nov.* – Lophiodontidae – Isectolophidae – teeth.

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INTRODUCTION

The relationships and evolutionary history of English species of *Hyracotherium* have recently been tentatively interpreted in terms of a single lineage, according

to the documentation of a stratigraphical morphocline in the London Basin (Hooker, 1980). The succession consists of at least three species from a total of four horizons. The earliest species, *H. cuniculus* Owen, 1842, from the Suffolk Pebble Beds, based on isolated teeth and two jaw fragments, is redescribed here as *Cymbalophus* **gen. nov.**, distinct from *Hyracotherium* and interpreted instead from outgroup comparison of its characters as a very primitive ceratomorph perissodactyl. Its relationships with other early perissodactyls are considered and its bearing on some perissodactyl subordinal subdivisions evaluated. Following MacFadden (1976) the extinct condylarth family Phenacodontidae is chosen as the outgroup. It is generally considered to be very close phenetically to perissodactyls and to contain their ancestor, in the form of *Tetraclaenodon* or a related unknown taxon (Radinsky, 1966a).

ABBREVIATIONS

BMNH, Department of Palaeontology, British Museum (Natural History), London. MNHN, Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris.

SYSTEMATICS

Order Perissodactyla Owen, 1848
Suborder Ceratomorpha Wood, 1937
Family ?Helaletidae Osborn, 1892

Cymbalophus **gen. nov.**

TYPE-SPECIES: *Hyracotherium cuniculus* Owen, 1842.

OTHER SPECIES: *C.* sp. indet. from Try (see below).

ETYMOLOGY: From Latin, 'cymba', meaning ferry boat, with reference to Ferry Cliff, one of the localities at which material has been found; and Greek, 'lophos', meaning crest, a common perissodactyl generic suffix, referring to the transverse ridges of the cheek teeth. Masculine.

RANGE: Early Sparnacian (Palaeocene/Eocene boundary time), S England, Belgium and N France.

DIAGNOSIS: Small primitive ceratomorph perissodactyl (astragalus and orbit unknown), length of M_2 , 7.3 mm. Dental formula

$$\frac{?3 \quad ?1 \quad ?4 \quad 3}{3 \quad 1 \quad 4 \quad 3}$$

Upper and lower molars low crowned and moderately lophodont. Premolars nonmolariform. M^{1-3} : paracone and metacone weak and centrocrista straight; P^3 , M^{1-3} paracone and metacone slightly displaced buccally (the former more than the latter), weakening or interrupting buccal cingulum adjacent to paracone and giving preparacrista an oblique mesiolingual orientation. Metaloph weak but recurving up lingual wall of metacone on M^{1-3} , absent on P^3 . M^3 very slightly tapered distally. Lower molars and distal premolars with nearly longitudinal, buccally positioned paralophid and metalophid, the latter curving slightly lingually to join distal trigonid wall at

lingual side of protoconid. Lower molars with protolophid well developed and unnotched; hypolophid weak and notched; metaconid and metastylid fused in more than 85% of individuals (e.g. in Fig. 8 but not Fig. 9); buccal and lingual walls of protoconid and metaconid, and hypoconid and entoconid respectively, tending to be only slightly convergent occlusally; distal walls of main cuspids usually steep. Preultimate lower molars with prominent hypoconulid. M_3 hypoconulid lobe relatively short and narrow. Moderate length postcanine diastema ($c.$ = length of M_2).

Cymbalophus cuniculus (Owen, 1842) **comb. nov.**

1970 *Hyracotherium* Owen; Quinet & Verlinden: 1-10, pls 2-3. (For earlier synonymy see Hooker, 1980.)

MATERIAL: The lectotype is an M^3 (BNMH. 36569) (Fig. 4); secondary types and other material are listed in Hooker (1980) and some are figured here (Figs 1-4, 8-9). Additional subsequently collected specimens are a left DP^3 (BNMH. M43288) (Fig. 5) and a right DP^4 (BNMH. M43289). A new fragment of jaw with M_1 has been found to fit BNMH. M36494, making this now a right mandibular fragment with M_{1-3} (Figs 7, 10, 11). The left mandibular ramus, with P_3-M_2 and alveoli for I_{1-3} , C, P_{1-2} and M_3 , from Erquelines, Belgium, is referred to this species herein; it provides the only undoubted lower premolars known to date (see Quinet & Verlinden, 1970).

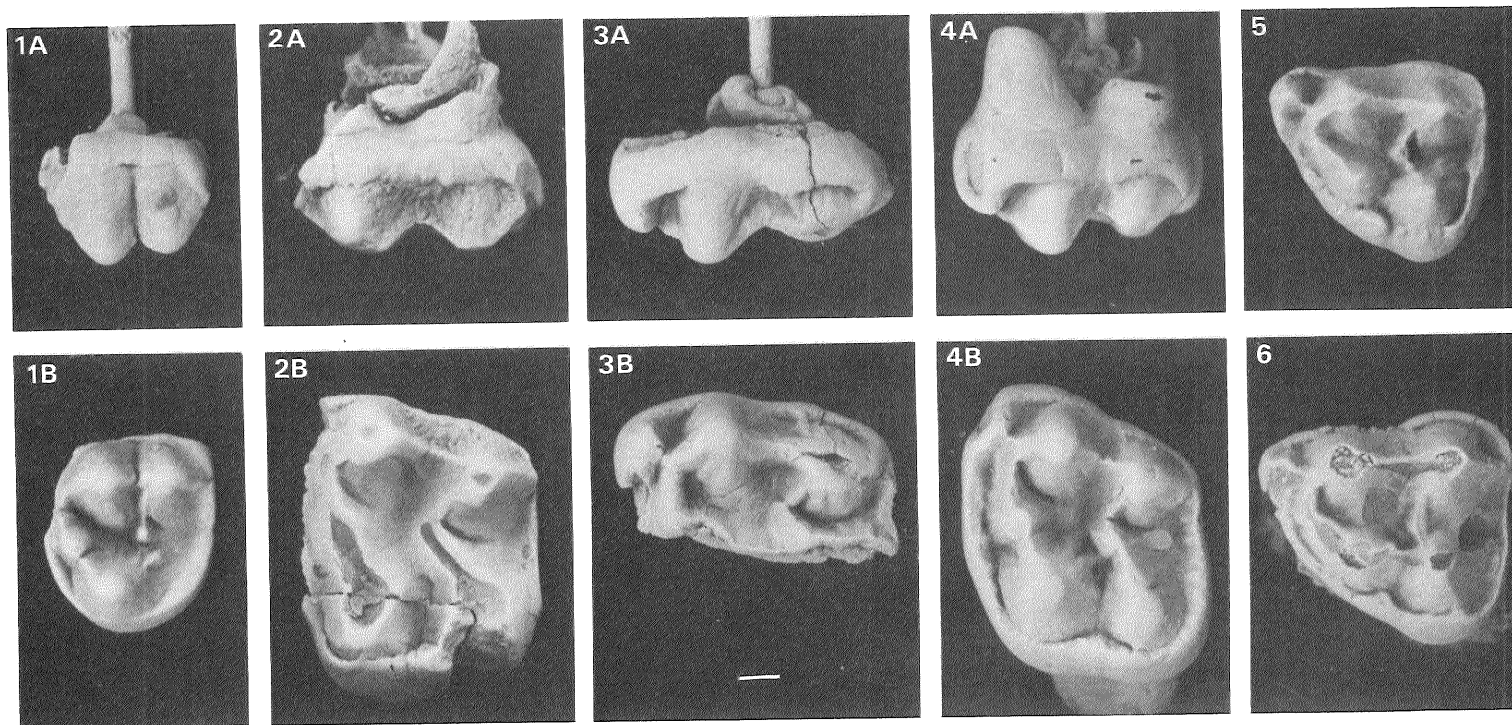
HORIZONS AND LOCALITIES: Suffolk Pebble Beds of Kyson, Ferry Cliff and Bramford, Suffolk, England; and Sables d'Erquelines, levels E? and F(base) (see Heinzelin, 1979: 8), of Erquelines, French-Belgian border. Early Sparnacian (= late Thanetian) (Palaeocene/Eocene boundary time).

DIAGNOSIS: As for genus, only named species.

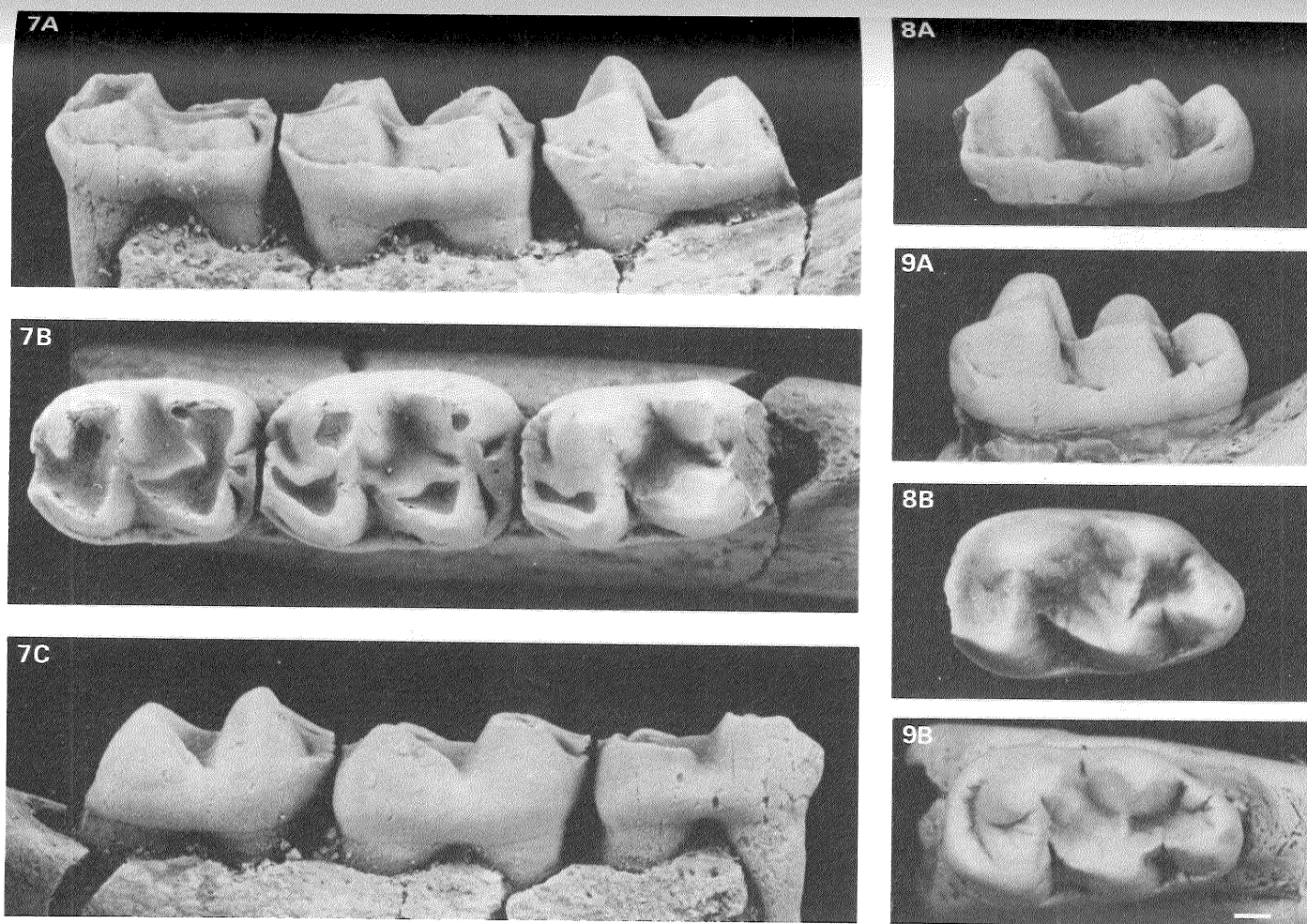
INDIVIDUAL VARIATION: Variation exists in important features such as angle of the metalophid (e.g. Figs 7B, 8B, 9B); fusion of the metaconid/metastylid complex; development of the hypolophid; distal angle of slope of the protolophid (e.g. Figs 7A, 8A, 9A); occlusal convergence angle of buccal and lingual lower molar cuspids (e.g. Figs 11-12); and buccal tilt of the paracone. All nevertheless show greater or lesser development of the diagnostic states of these characters. Other more minor variation is described by Cooper (1932).

Other material attributed to Cymbalophus

Isolated teeth housed in the MNHN from the Paris Basin Sparnacian locality of Try (see Louis *et al.*, 1983, for site and stratigraphic details) include some attributed to a small species of *Hyracotherium* and are here included in *Cymbalophus*. They consist of four upper molars (M-TRY 008, 009, 011 and 023), $M_{1/2}$ (005), distal two-thirds of M_3 (029), DP^3 (010) and DP^4 (008). Size is very close to *C. cuniculus*. Morphological similarities are: the buccal upper molar paracone and metacone associated with weak or interrupted buccal cingulum and oblique preparacrista; weak paracone and metacone; metaloph joining metacone on upper molariform teeth; and a buccal metalophid and paralophid on the lower molar. The DP^3 is almost identical except that the paracone is slightly more buccally tilted, like that of the molars. The only tangible



Figures 1-6. Upper cheek teeth of *Cymbalophus cuniculus* (Owen) and *Hyracotherium* aff. *vulpiceps* (Owen). Views are buccal (A) and occlusal (B or unsuffixed). All specimens sprayed with ammonium chloride. Fig. 1. Left P^3 of *C. cuniculus* from Kyson, BMNH. M14112. Fig. 2. Paralectotype right $M^{1/2}$ (reversed) of *C. cuniculus* from Kyson, BMNH. M29709. Fig. 3. Buccal half of left $M^{1/2}$ of *C. cuniculus* from Bramford, Ipswich Museum, no. 1971.169. Fig. 4. Lectotype left M^3 of *C. cuniculus* from Kyson, BMNH. 36569. Fig. 5. Left DP^3 of *C. cuniculus* from Ferry Cliff, BMNH. M43288. Fig. 6. Left DP^3 of *H. aff. vulpiceps* from the Blackheath Beds of Abbey Wood, BMNH. M29231. Scale bar = 1 mm.



Figures 7-9. Lower molars of *Cymbalophus cuniculus* (Owen). Views are buccal (A), occlusal (B) and lingual (C). All specimens sprayed with ammonium chloride. Fig. 7. Right M_{1-3} (reversed), in place in mandibular fragment, from Ferry Cliff, BMNH. M36494; N.B. M_3 hypoconulid lobe is broken away. Fig. 8. Right M_3 (reversed) from Kyson, BMNH. M14113. Fig. 9. Right M_3 (reversed), in place in mandibular fragment, from Kyson, Ipswich Museum, no. 1951.28.25 (holotype of junior subjective synonym *Macacus eoacenus* Owen, 1846). Scale bar = 1 mm.

differences, which may prevent inclusion of the Try assemblage in the species *C. cuniculus*, are a larger hypoconulid lobe and better developed hypolophid on M_3 . Alternatively, the M_3 fragment may belong to a different kind of perissodactyl, especially as the hypolophid development prevents inclusion in *Cymbalophus* as defined here.

Another early ceratomorph?

Dashzeveg (1979) noted that *Hyracotherium gabunia* Dashzeveg, 1979, from Mongolia, was very advanced in lophodonty. On this basis it should probably not belong in that genus or in the Hippomorpha, but probably in or close to the Ceratomorpha. Dashzeveg's comment that the M_1 protolophid is less developed than the hypolophid is reminiscent of *Homogalax*; whereas the apparent absence of a discrete metastylid in Dashzeveg's figure is more like *Cymbalophus*. The discovery of more material of '*H. gabunia*' is awaited with interest.

Distinction from Hyracotherium

The two genera most similar to *Cymbalophus* are the equid *Hyracotherium* and the isctolophid *Homogalax*. *Hyracotherium* is generally recognized to be the earliest and most primitive representative of the suborder Hippomorpha.

Following Radinsky (1964) and MacFadden (1976), primitive species of *Hyracotherium* (like *H. aff. vulpiceps* (Owen) from Abbey Wood) are considered to have teeth which can be regarded as primitive for the Perissodactyla as a whole (with the possible exception of M^3 hypocone absence or weakness in brontotheres). *H. leporinum* Owen (the type-species) and doubtfully two North American *Hyracotherium* specimens are shown by MacFadden (1976: 8-9) to have the advanced equid pattern of posterior orbital foramina. The orbit of the holotype cranium of *H. vulpiceps* has now been prepared and shows the same equid pattern of foramina as does the type-species. Unfortunately, nothing is known of the orbit of *Cymbalophus*, but virtually all the dental features in which it differs from *Hyracotherium* can be construed as advanced and show ceratomorph trends. *Cymbalophus cuniculus* is more primitive than *H. aff. vulpiceps* in length of M_3 hypoconulid lobe (Hooker, 1980), but some N American specimens of *Hyracotherium* are as primitive as *C. cuniculus* (Savage *et al.*, 1965: fig. 5a, c).

Compared with *Cymbalophus*, a primitive *Hyracotherium* (represented by *H. aff. vulpiceps*) shows few traces of lophodonty; on upper molars, paracone and metacone are strong, there is no evidence of buccal displacement of the paracone or metacone (Fig. 17), the buccal cingulum is essentially complete and the preparacrista is mesiodistally orientated; P^3 conforms to this pattern, but on the holotype of *H. vulpiceps* the paracone is displaced buccally, as in *Cymbalophus*. The upper molar metaloph is rather variable in *H. aff. vulpiceps*, but the metacone is better developed and often there is no connection to the metacone; a connection is, however, present in *H. vulpiceps* and *H. leporinum*. The lower molars and distal premolars have a distinctly oblique metalophid, joining the trigonid at a more lingual position (this also follows for all later equids and palaeotheres); the protolophid is notched; the metaconid and metastylid are distinct twinned cusps; the buccal and lingual walls of protoconid and

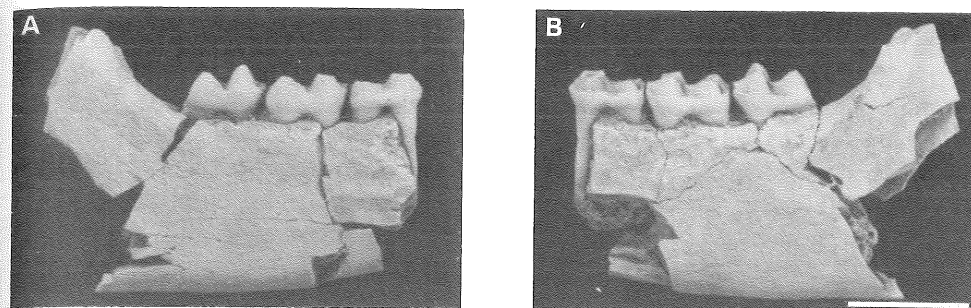


Figure 10. Right mandibular fragment with M_{1-3} (reversed) of *Cymbalophus cuniculus* (Owen), from Ferry Cliff, BMNH. M36494. Sprayed with ammonium chloride. Views are lingual (A) and buccal (B). Scale bar = 1 cm.

metaconid, and hypoconid and entoconid respectively, are more convergent occlusally (Fig. 13); and the distal walls of the main cusps are more sloping.

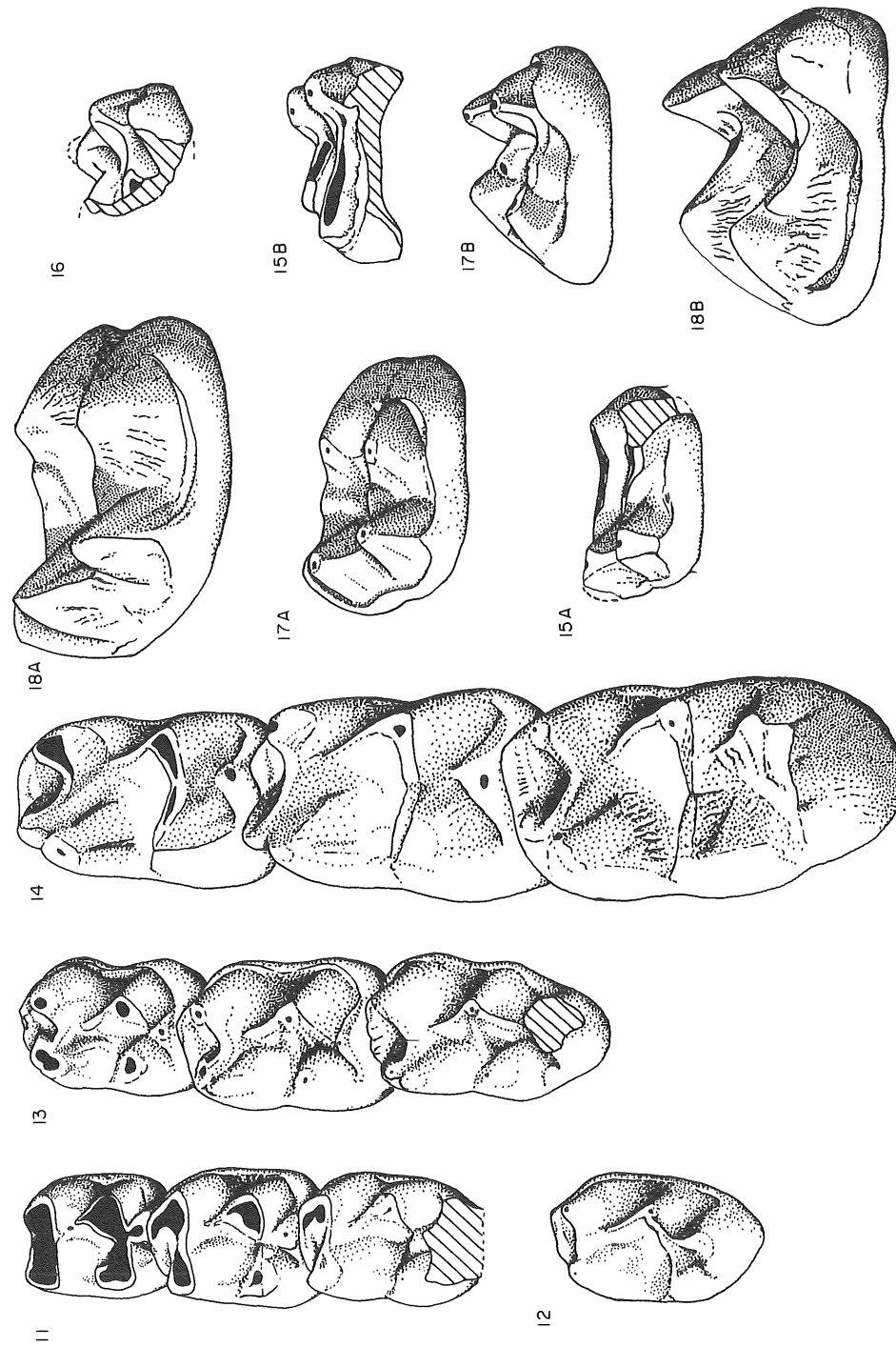
Of the two new specimens of *Cymbalophus* collected, the DP_4 is so worn that no cusp positions can be made out, but the buccal and lingual walls appear to be slightly less occlusally convergent than in *Hyracotherium*. The DP^3 (Fig. 5) is well preserved and like the other upper cheek teeth shows a buccal cingulum interrupted at the paracone and oblique preparacrista, both due to the buccal position of the paracone; a crest loop, consisting of preparacrista and preprotocrista, is projected distinctly mesially and the parastyle is large. A DP^3 of *H. aff. vulpiceps* (BMNH. M29231) (Fig. 6), although more worn, has a buccal cingulum which is not distinctly interrupted, although papillate in the vicinity of the paracone; the preparacrista is mediolaterally orientated; the preparacrista-preprotocrista loop is shorter, the preprotocristal part being more transverse and bearing a very small paraconule; and the parastyle is slightly smaller.

Comparison with Homogalax

Homogalax (early Eocene) has been considered previously to be the earliest and most primitive ceratomorph. It shares with *Cymbalophus* the upper molar paracone and metacone weakness, straight centrocrista, weak metaloph joining metacone; the slight M^3 distal tapering; the upper molar and distal premolar buccal displacement of the paracone and metacone and associated features (although less marked, Fig. 18); absence of P^3 postprotocrista; the lower molar and distal premolar nearly longitudinal paralophid and metalophid, with a similar trigonid joining position; the acute angle of occlusal convergence of buccal and lingual cusps and the steepness of the main cusp distal walls of the lower molars; the prominence of an M_{1-2} hypoconulid (Fig. 14); and apparently the DP^3 mesially projected preparacrista-preprotocrista loop (the last *vide* Butler, 1952: fig. 5H, where the loop appears broken).

In keeping with its slightly more recent age, *Homogalax* shows the following advances over *Cymbalophus*: slightly greater lophodonty of upper molars; well developed unnotched lower molar hypolophid; and long broad M_3 hypoconulid lobe (Fig. 14).

More interesting are three characters in which *Homogalax* appears to be



Figures 11-18. Molars of *Cymbalophus*, *Hyracotherium* and *Homogalax*. Magnification $\times 3.5$. Views are occlusal (A and unaffixed) and occlusomesial (B). Fig. 11. Right M_{1-3} of *C. canaliculus* from Ferry Cliff, BMNH, M36494; N.B. hypoconulid lobe is broken away. Fig. 12. Right M_3 of *C. canaliculus* from Kyson, BMNH, M14113. Fig. 13. Right M_{1-3} of *Hyracotherium* aff. *vulpiceps* from Abbey Wood, BMNH, M29719-21. Fig. 14. Left M_{1-3} (reversed) of *Homogalax* cf. *protapirinus* (Wortman) from the Wasatchian of the Big Horn Basin, Wyoming, U.S.A., BMNH, M11600. Fig. 15. Paralectotype right $M_{1/2}$ of *C. canaliculus* from Kyson, BMNH, M29709. Fig. 16. Buccal half of left $M_{1/2}$ (reversed) of *C. canaliculus* from Bramford, Ipswich Museum no. 1971. 169. Fig. 17. Right M_2 of *H. aff. vulpiceps* from Abbey Wood, BMNH, M13761. Fig. 18. Left M_3 (reversed) of *H. cf. protapirinus* from the Wasatchian of Burlington, Wyoming, U.S.A., BMNH, M9796.

primitive with respect to *Cymbalophus*; lower molar protolophid weak and notched; distinct twinned metaconid and metastylid (Fig. 14) and short postcanine diastema. Thus the trend in lower molar lophodontology from the primitive state, as seen in *Hyracotherium*, began in *Homogalax* with the hypolophid and in *Cymbalophus* with the protolophid. The presence of a lower molar metastylid is taken to be primitive for the Perissodactyla as it occurs in all members of the outgroup (phenacodontid condylarths). In the latter the metastylid is lower and smaller than the metaconid and the enlargement to twin with the metaconid as in most equoids is an early advancement. Fusion of the two cusps as in nearly all individuals of *Cymbalophus* is a further development.

The function of the twinned metaconid and metastylid in *Hyracotherium* and other equoids is to receive between them buccally a mesially projecting upper molar paraconule, in later stages of buccal phase occlusion. The facets facing lingually on the paraconule and buccally on the metastylid are here labelled 2A (Figs 19-21). They separate and offset facets 2 and 3. Slight lingual migration of the metastylid in *Homogalax* (most marked in advanced species) has flattened the distal face of the protolophid for tapiroid-type occlusion with an almost uninterrupted protoloph (Fig. 21). In more primitive species, facets in the region of the metastylid are more as in *Hyracotherium*. *Cymbalophus* lower molars have responded to a similar but less accentuated upper molar protoloph lophodontology by fusing together the metaconid and metastylid. Facet 2A on the metaconid-metastylid complex is now little shallower in angle than facet 2 or 3, faces mesibuccally and extends some way buccally along the protolophid (Fig. 19B). Similar relationships are displayed between the metaloph and hypolophid (facets 7, 7A and 8) (Figs 19-21).

STEM CERATOMORPH RELATIONSHIPS OF *CYMBALOPHUS* WITHIN THE PERISSODACTYLA

As primitive ceratomorphs share a number of characters with primitive chalicotheres, a consideration of these relationships is relevant to a clear understanding of the limits and nature of the Ceratomorpha as a group. This must precede discussion on the placing of *Cymbalophus* with respect to either group. First, it is necessary to consider briefly how the Perissodactyla have been divided in the past; second, to examine the functional trends in the initial phases of ceratomorph lophodontology; and third to consider possible rearrangements and redefinition of these groups.

Brief history of infraordinal classifications

The order Perissodactyla has been divided by authors in many different ways. The principal schemes are as follows. Soon after the establishment of the order by Owen (1848), the three extant families, Equidae, Tapiridae and Rhinocerotidae, and the two main extinct ones (Chalicotheriidae and Brontotheriidae), plus some minor extinct ones, were usually given equal rank (e.g. Flower & Lydekker, 1891). Later, the Equidae, Chalicotheriidae and Brontotheriidae were combined in the suborder Hippomorpha and the Tapiridae and Rhinocerotidae in the suborder Ceratomorpha, essentially according to the respective dilambdodonty and lophodontology of their cheek teeth

(e.g. Wood, 1934; Simpson, 1945) (Fig. 22A). Within the Hippomorpha, the extinct Palaeotheriidae were combined with the Equidae in the superfamily Equoidea; and the Chalicotheriidae either with the Brontotheriidae in the superfamily Brontotherioidea (= Titanotherioidea) (e.g. Romer, 1945) or separately in the superfamily Chalicotherioidea (e.g. Simpson, 1945) with the additional split of the Eomoropidae (e.g. Viret, 1958). Within the Ceratomorpha, the extinct Isectolophidae, Helaletidae, Lophiodontidae, Lophialetidae and Deperetellidae were combined with the Tapiroidae in the superfamily Tapiroidea (Radinsky, 1963, 1965); and the extinct Hyracodontidae and Aynodontidae with the Rhinocerotidae in the superfamily Rhinoceroidea (Radinsky, 1966b). More detailed accounts are given by Simpson (1945) up to this date.

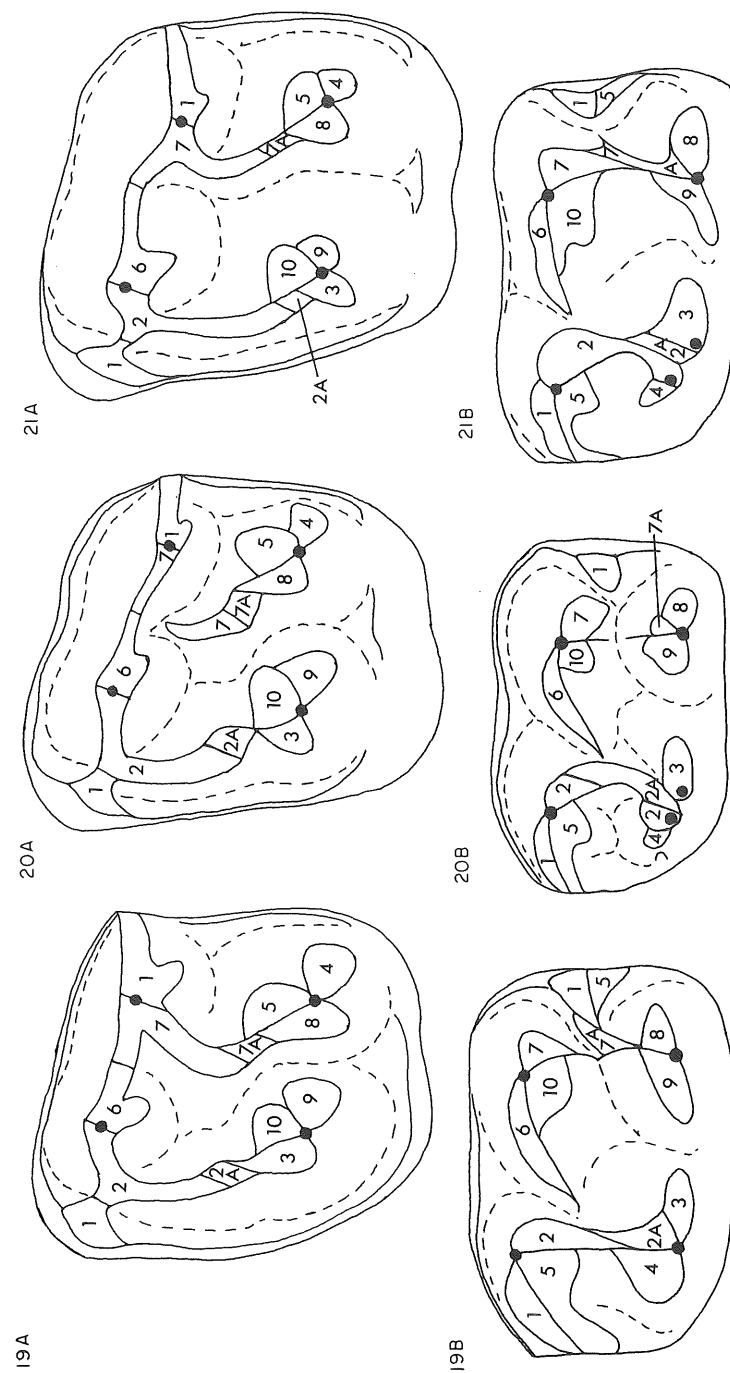
It was soon realized that superfamily division of the Ceratomorpha posed problems when the suspected ancestral rhinocerotoid *Hyrachyus* was considered to fit better within the tapiroid family Helaletidae; and the Aynodontidae were considered to have evolved their rhinocerotoid characters independently of the Hyracodontidae and Rhinocerotidae (Radinsky, 1966b). Thus the Tapiroidea have been shown to be paraphyletic and the Rhinoceroidea polyphyletic, although subordinal level relationships have generally not been in doubt.

Problems with the Hippomorpha proved to be more significant. MacFadden (1976) concluded that the dental characters which linked the three superfamilies of the Hippomorpha were primitive for the Perissodactyla and that the Equoidea could be better separated from all other perissodactyls on the advanced arrangement of the posterior orbital foramina. The weakness of the M^3 hypocone in most Brontotherioidea could be primitive for the Perissodactyla and their metaloph loss sets them apart from all other perissodactyls.

This leaves the Chalicotherioidea in an uncertain position. Radinsky (1964: 25) considered that the molar cusp pattern of this group shared as many characters with the Ceratomorpha as with the Hippomorpha, in which they had usually been included. This gave them an unique combination of characters, together with their own later acquired foot modifications. Radinsky (1964: 6) thus resurrected the suborder Ancylopoda for them, deferring discussion of more specific relationships to either of the other suborders until a better knowledge of early Eocene forms could be gained (Fig. 22B).

Development of ceratomorph occlusal relationships and lophodonty

An important ceratomorph dental feature appears to be the presence of a longitudinal, buccally situated metalophid, which joins the trigonid somewhere in its buccal half, i.e. at or near the protoconid (Wood, 1934: 260; Radinsky, 1964: 4-5). Within the Perissodactyla, this character is widespread in and exclusive to the Ceratomorpha as previously defined. It is considered to have developed originally from the primitive perissodactyl condition (as represented in *Hyracotherium*). Here the metalophid joins the trigonid at a median position on the tooth. Its orientation is oblique (Fig. 13). First, the development would have consisted of a buccal shift of the mesial end, causing the new orientation to be nearly longitudinal and parallel with the long axis of the tooth (e.g. Figs 11, 14, 19B, 21B). As wear facets in this region in *Homogalax* and *Cymbalophus* are



Figures 19-21. Diagrammatic occlusal views of upper left (A) and lower right (B) preultimate molars, showing distribution of homologous wear facets. Facet numbers follow Butler (1952) except 2A and 7A which are introduced here. Fig. 19. *Cymbalophus canaliculus*; A is based mainly on BMNH. M29709 and 36569 and Ipswich Museum no. 1971.169; B is based mainly on BMNH. M36494. Fig. 20. *Hyracotherium aff. vulpiceps*; A is based mainly on BMNH. M13761 and M25129; B is based mainly on BMNH. M29719-21 and M15143. Fig. 21. *Homogalax cf. protapirinus*; A is based mainly on BMNH. M9795 and M9796; B is based mainly on BMNH. M9795 and M11600.

identical to those of *Hyracotherium*, a corresponding change in orientation must have taken place in the upper molars. This consists of a buccal shift and tilt of the upper molar paracone with a consequent buccal slant of the preparacrista and centrocrista towards the paracone (Figs 15, 16, 18), and interruption of the buccal cingulum at the paracone (Figs 2, 3). The reason for this modification may be related to the concomitant buccolingual splaying of the transversely opposite lower molar cuspids, which effectively increases the lengths of the shearing edges of both protolophid and hypolophid. In a similar way, the buccal tilting of the upper molar paracone slightly increased the length of the protoloph by incorporating within it the reorientated preparacrista (Figs 19A–21A). The lesser buccal shift and tilt of the upper molar metacone accompanies likewise the buccal longitudinal orientation of the lower molar paralophid. In more advanced ceratomorphs like *Helalestes*, the upper molar metacone is shifted lingually so that the premetacristal part of the centrocrista is incorporated into the metaloph, thus lengthening this transverse crest too (see also Radinsky, 1963; Butler, 1952). The postmetacrista thus becomes distobuccally oblique, showing that the lingual metacone position is secondary, as is the mesiolingual obliquity of the occluding lower molar paralophid.

The buccal metalophid, although widespread in the Ceratomorpha, does not occur in modern *Tapirus* molars or in M_3 of *Lophiodon*, where instead the metalophid has the primitive oblique orientation. (In *Tapirus*, the paralophid too is oblique.) This apparent anomaly appears to be related to the progressive incorporation of the centrocrista into the transversely shearing metaloph mentioned above. Distal wear on the paracone is thereby reduced and the result in the lower molar is a distal restriction of the buccally situated metalophid. Reorientation or neoformation (probably the former in *Lophiodon* and the latter in *Tapirus*) in the mesial part of the talonid of an oblique metalophid, not affected by buccal phase wear, appears to result in more effective lingual phase wear against a distobuccally oblique (and therefore opposing) upper molar postprotocrista. (In *Tapirus*, the same lingual phase contact also occurs between the paralophid and the posthypocrista.)

Ancylopoda and Ceratomorpha

From the above evidence, the oblique metalophid in *Tapirus* molars and in M_3 of *Lophiodon* can be construed as a reversal to the primitive state. If the same modification of functions is applied to primitive chalicotherioids such as *Lophiaspis*, the apparent anomaly of mixed hippomorph and ceratomorph characters can be resolved. *Lophiaspis*, originally (Depéret, 1911) and subsequently (Fischer, 1964) regarded as closely related to *Lophiodon* (in the ceratomorph family Lophiodontidae), has been placed in the chalicotherioid Eomoropidae by Radinsky (1964: 4, 7–9) and Savage *et al* (1966: 31–35). The characters given by these authors for classifying *Lophiaspis* as a chalicothere are, (1) high uninterrupted metaloph, (2) large parastyle on upper molars, in combination with (3) upper molar paraconule, (4) lower molar twinned metaconid-metastylid, and (5) oblique metalophid. As discussed above, character (1) is a typical ceratomorph character; (3) and (4) are primitive perissodactyl characters; and (2) occurs sporadically in different groups of perissodactyls. Character (5) may be primitive too, but it is associated with

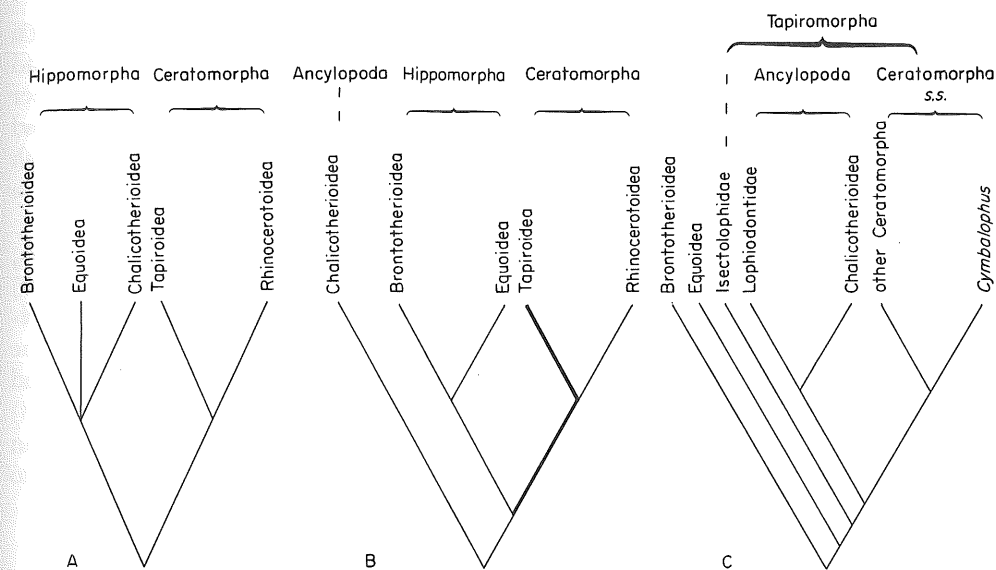


Figure 22. Concepts of relationship within the Perissodactyla according to A, Simpson (1945); B, Radinsky (1964); C, herein. The thickened line in B indicates the view that the Tapiroidea are partly ancestral to the Rhinocerotioidea. The phylogenetic diagram in C is offered purely as a visual explanation for the ideas and suggested use of higher taxa discussed in the text. The suggested modifications of higher taxa involve restriction of Ceratomorpha and extension of Ancylopoda and Tapiomorpha.

incorporation of part of the buccal phase wear on the centrocrista into the metaloph and concomitant distal restriction of its occlusion with the metalophid. It is thus more logical to associate it functionally with the situation in *Tapirus* and, distally, in *Lophiodon* and regard it as a reversal from the advanced buccal to the primitive oblique lingual orientation. Butler's (1939) field theory could be invoked to account for incipient development of the chalicothere trend in *Lophiodon*. To attain the typically dilambdodont later chalicothere molars, further reversals, however, are necessary (as Radinsky, 1964: 5, envisaged): lingual migration of upper molar paracone, accompanied by completion of the buccal cingulum and reorientation of the preparacrista; and oblique lingual orientation of the lower molar paralophid. These would thus result in their strong equoid similarities.

Ancylopoda, Lophiodontidae and Isectolophidae

Paralophiodon was split from *Lophiodon* and placed in a new monotypic subfamily in the family Isectolophidae by Dedieu (1977). Whereas his generic characters are well supported, those for relationships with the Isectolophidae consist of: (1) complete lower molar metalophid ("branche vestibulaire de l'hypolophide"); (2) narial incision extending only as far as canine; and (3) absence of postcanine diastema. Character (1) is primitive for the Ceratomorpha (as so far construed), (2) is within the range of variation of species of *Lophiodon* and (3) is present in the Isectolophidae only in *Isectolophus* (Radinsky, 1963: 11). In contrast, *Paralophiodon* and *Lophiodon* share similar pointed incisors (Fischer, 1964) and absence of P^1 . *Paralophiodon* and *Lophiodon*

together (as the Lophiodontidae) share with *Lophiaspis* a lingual metastyle and a weak, distally asymmetric upper molar mesostyle, which resembles in shape and orientation the much stronger one found in *Eomoropus* and most other chalicotheres. In view of this, a closer relationship between lophiodontids and chalicotheres is suggested than between either and the other ceratomorph families. This would reconcile the opposing views of *Lophiaspis* as either a lophiodont (Fischer, 1964) or a chalicotheres (Radinsky, 1964).

Except for the well developed lower molar hypolophid and enlarged M_3 hypoconulid lobe, *Homogalax* (the more primitive of the two isectolophid genera) appears to represent the primitive dental morphotype for both the chalicotherelophiodont group and the remaining ceratomorph families. On this basis, the Isectolophidae would be the sister-group of all these. To name this entire related group, it would be possible to extend slightly the concept of Haeckel's (1873) Tapiomorpha, which has been used (as in recent times by Romer, 1945) as an equivalent for the Ceratomorpha. Ancylopoda could be extended likewise to incorporate the Lophiodontidae (Fig. 22C).

CONCLUSIONS

The exact systematic position of *Cymbalophus* is still not easy to locate. Its main advancements of a well developed protolophid and fused metaconid-metastylid have an incongruent distribution with respect to the groups already discussed. The well developed protolophid occurs within the Isectolophidae in *Isectolophus* but not in *Homogalax*; it also occurs throughout the Ancylopoda (new sense, comprising the chalicotherelophiodont group) and the Ceratomorpha (*s.s.*, i.e. less Isectolophidae and Lophiodontidae). The fused metaconid-metastylid likewise occurs within the Isectolophidae in *Isectolophus* but not in *Homogalax*; within the chalicotherelophiodont group in the Lophiodontidae but not in the Chalicotherioidea; and throughout the Ceratomorpha (*s.s.*). The evidence suggests that both characters have arisen more than once. The characters defining the Isectolophidae appear well supported and a series of well stratified, morphologically intermediate forms links late members of a *Homogalax* species with early *Isectolophus* in a seemingly ancestor-descendent relationship (Radinsky, 1963). If the characters linking lophiodonts with *Lophiaspis* are also tenable, then it is likely that the hypolophid became well developed at a stage when the metastylid was still separate from the metaconid and that the latter's fusion in lophiodonts took place later. It is thus suggested that metaconid-metastylid fusion took place a minimum of three times and that, when it took place in *Cymbalophus*, the hypolophid had not developed into a strong lophoid crest. However, the latter development had already occurred when fusion took place in isectolophids and lophiodonts. On this somewhat slender evidence, it is proposed that *Cymbalophus* is the most primitive known member of the Ceratomorpha (*s.s.*). Family attribution for *Cymbalophus* is naturally a problem. It is here tentatively assigned to the Helaletidae as a conservative approach. This Eocene to Oligocene family is dominantly North American, less diverse in Asia and poorly represented in Europe. It should comprise the genera *Heptodon*, *Helaletes*, *Selenaletes*, *Dilophodon*, *Colodon*, *Hyrachyus* and *Chasmotherium*, according to Radinsky (1969). Certain of these genera are considered to be related to the origin of the Tapiridae, while others are closer to the Rhinoceroidea. The

family is therefore paraphyletic in current usage (even if *Hyrachyus* is excluded, as by Schoch, 1982) and is thus little affected by the addition of *Cymbalophus*.

Cymbalophus cuniculus is recorded from early Sparnacian strata (Hooker, 1980) which are correlated with the Clarkforkian land mammal age of western North America (Gingerich & Rose, 1977; Godinot, 1981). If this correlation is accurate, *C. cuniculus* is probably the earliest ceratomorph known. Hickey *et al.*'s (1983) suggestion from magnetostratigraphy of a Clarkforkian age for the Eocene Ellesmere Island mammal fauna would make the ceratomorph *Hyrachyus*, otherwise late early to middle Eocene, contemporaneous with *Cymbalophus*. However, this dating is now in doubt (Kent *et al.*, 1984).

It is therefore likely that the Ancylopoda/Ceratomorpha split, and the Ancylopoda + Ceratomorpha/Equidea split before it, took place at least as early as the Tiffanian. Helaletid dispersal from NW Europe to N America and Asia may have taken place immediately after the Clarkforkian/early Sparnacian.

Although not now construed as part of an evolving lineage of *Hyracotherium*, *Cymbalophus* appears nevertheless to be stratigraphically restricted in its known (admittedly limited) geographic range to early Sparnacian and may thus be a useful biostratigraphic indicator for this time span in NW Europe.

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Collecting isolated microvertebrate fossils

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A review is presented of the techniques currently used in the collection and separation of isolated teeth and bones of fossil vertebrates. These involve the collection and disaggregation of the sediment, its sieving, concentration and sorting of the residue, and curation of the fossils obtained.

KEY WORDS:—Review – techniques – fossil – microvertebrates – sieving.

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