

The phylogeny and classification of the Dinocerata (Mammalia, Eutheria)

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The Dinocerata (uintatheres), an extinct order of Paleocene-Eocene mammals, are known from Asia and western North America. This paper clarifies the distribution, genus-level taxonomy and phylogenetic relationships of the uintatheres. There are six valid uintathere genera: *Prodinoceras* Matthew, Granger & Simpson 1929 from the late Paleocene-early Eocene of North America and Asia (= *Probathyopsis* Simpson 1929, = *Bathyopsoides* Patterson 1939, = *Mongolotherium* Flerov 1952, = *Prouintatherium* Dorr 1958, = *Jiaoluotherium* Tong 1978, = *Houyanotherium* Tong 1978, = *Pyrodon* Zhai 1978, = *Phenaceras* Tong 1979, = *Ganatherium* Tong 1979), *Gobiotherium* Osborn & Granger 1932 from the middle Eocene of Asia, *Bathyopsis* Cope 1881 from the early-middle Eocene of North America, *Uintatherium* Leidy 1872 from the middle Eocene of North America and Asia, *Tethyopsis* Cope 1885 from the middle Eocene of North America, and *Eobasileus* Cope 1872b from the middle Eocene of North America. The six genera form a monophyletic order Dinocerata that shares a close common ancestry with the South American order Xenungulata (= *Carodnia*). The mirorder Uintatheriamorpha (Dinocerata plus Xenungulata), in turn, shares a close common ancestry with the Asian "anagalid" *Pseudictops*. Thus, uintatheres and xenungulates do not have a condylarthran ancestry. South American pyrotheres, via *Carolozittelia*, may share a close common ancestry with the xenungulates. The common ancestor of uintatheres arose in Asia, achieved a trans-Pacific distribution and gave rise to uintatheres in Asia and North America and the divergent xenungulates in South America because of a vicariance event that separated the two New World continents.

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Introduction

The Dinocerata ("uintatheres") is an extinct order of large mammals known from fossils collected in Paleocene-Eocene continental deposits in Asia and western North America (Figs. 1, 2; Marsh, 1885b; Wheeler, 1961; Lucas & Schoch, 1982). Wheeler (1961) presented the last comprehensive revision of the Dinocerata, but since his work appeared, several new uintathere genera from the People's Republic of China have been proposed. Tong and Lucas (1982) reviewed these new uintatheres, but made no attempt at a taxonomic revision or a revision of the Dinocerata. In this paper, we revise the genus-level taxonomy of the uintatheres and present a phylogenetic classification of the Dinocerata. The following abbreviations are used: AMNH-Department of Vertebrate Paleontology, American Museum of Natural History, New York; FMNH-

Field Museum of Natural History, Chicago; IVPP-Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; PIN-Paleontological Institute of the U.S.S.R. Academy of Sciences, Moscow; PST-Paleontologic-Stratigraphic Section of the Geological Institute of the Mongolian Academy of Sciences, Ulan Bator; PU-Princeton University, Princeton, New Jersey; UCM-University of Colorado Museum, Boulder, Colorado; UM-University of Michigan, Ann Arbor, Michigan; YPM-Division of Vertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven, Connecticut. Chinese place names are given in the Pinyin romanization except for the often-used place names in Inner Mongolia (Nei Monggol Province). Terminology of the cusps of uintathere cheek teeth follows Wheeler (1961, Figs. 2, 3) and Zhou et al. (1975, Figs. 1, 3, Table 1).

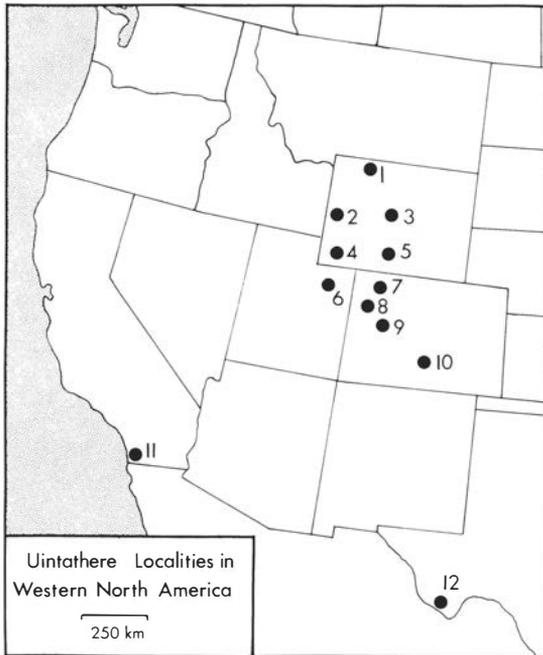


Fig. 1. Principal uintathere localities in western North America: 1. Bighorn basin, Wyoming; 2. Hoback basin, Wyoming; 3. Wind River basin, Wyoming; 4. Green River – Bridger basin, Wyoming; 5. Washakie basin, Wyoming; 6. Uinta basin, Utah; 7. Sand Wash basin, Colorado; 8. Piceance Creek basin, Colorado; 9. Plateau Valley, Colorado; 10. Huerfano basin, Colorado; 11. Rose Canyon Formation, California; 12. Buck Hill Group, Agua Fria area, Texas.

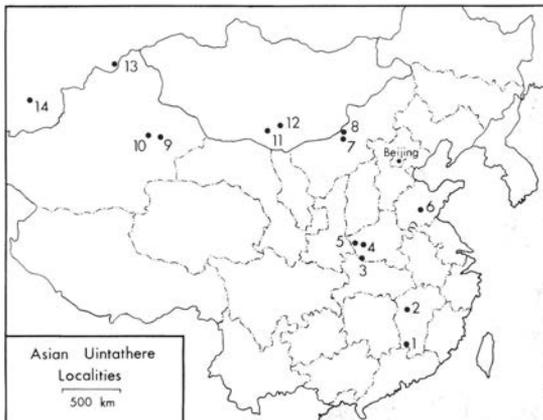


Fig. 2. Asian uintathere localities; 1. Chijiang basin, Jiangxi; 2. Yuanshui basin, Jiangxi; 3. Liguangquiao basin, Henan; 4. Tantou basin, Henan; 5. Lushi basin, Henan; 6. Xintai basin, Shandong; 7. Ailigemiao vicinity, Inner Mongolia; 8. Iren Dabasu vicinity, Inner Mongolia; 9. Turpan basin (Taizicun Formation), Xinjiang; 10. Turpan basin (Dabu Formation), Xinjiang; 11. Ulan Bulak and Naran Bulak, Nemegt basin; 12. Khashaat (Gashato); 13. Tshaibulak, Zaisan basin, Kazakhstan; 14. Torujayyr, Kirgiziya.

Previous studies

The early history of research on the Dinocerata has been reviewed by Simpson (1945), Flerov (1957) and Wheeler (1961). Tong and Lucas (1982) summarized recent discoveries in Asia. Here we consider the superordinal relationships of the Dinocerata.

Marsh (1871, p. 35–36) first described fragmentary uintathere remains (YPM 11030: two skull-fragments, a left tibia and four incomplete thoracic vertebrae; see Wheeler, 1961, pl. 8., fig. 1) from the Eocene of the Bridger basin, Wyoming. He mistook these fragments for the remains of a bronothere, naming them *Titanotherium? anceps*. In the following year (1872) Marsh, Cope and Leidy collected additional uintathere remains from the Eocene deposits of Wyoming. By 1885, competition among these rivals led to the publication of thirteen generic names (see below), and even more specific names, that were applied to the large, derived uintatheres (Uintatheriini of this paper) and precipitated the great Cope-Marsh feud (Wheeler, 1960).

Whereas Cope at first believed that the uintatheres were proboscideans (e.g., Cope, 1872a), Marsh early recognized that they formed a distinct group and coined the name Dinocerata (Marsh, 1873a; replacement name for *Dinocerea* Marsh, 1872a; Simpson, 1945). Later, Cope (e.g., 1875, 1884, 1885) united the Dinocerata and the Pantodonta in his order Amblypoda. This taxonomic concept was more fully developed by Osborn (1898) and found one of its last expressions in Matthew (1937; but written much earlier). Cope (1884) and Osborn (1898) derived the uintathere molar from that of *Pantolambda* by rotation of the ectoloph so that the metacone was placed just posterolabial of the protocone (Simpson, 1929, fig. 4a). Wood (1923), however, reinterpreted the homologies of the cusps of uintathere molars; it is Wood's homologies that are currently accepted. The work of Wood (1923), Simpson (1937) and Patterson (1939) effectively undermined the concept of the Amblypoda (union of the Pantodonta and Dinocerata in a single ordinal-level taxon). However, Simpson (1945) included the Dinocerata with the Pantodonta, Pyrotheria, Proboscidea, Embrithopoda, Hyracoidea and Sirenia in his superorder Paenungulata. The core of Simpson's (1945, p. 240–241) Paenungulata was the Proboscidea and the other groups of African origin listed above, whereas he considered the inclusion of the Pantodonta, Dinocerata and Pyrotheria in this superorder to be "frankly hypothetical", but "reasonable and convenient."

Paula Couto (1952) proposed the new order, Xenungulata, and new family, Carodniidae, for the

South American genus *Carodnia* Simpson, 1935. Paula Couto (1952; also see Paula Couto 1978) also described a dentition and partial skeleton of *Carodnia vieirai*, noting many similarities between it and *Uintatherium*. Paula Couto (1952, p. 387) concluded that:

“...the similarities between these two lower Tertiary genera, one from the South American Paleocene, the other from the North American Eocene, and the fact that both the Xenungulata and the Dinocerata are distinguished among contemporary groups of mammals by their much larger size, make plausible the hypothesis that these two groups are more or less closely related to each other. They may constitute collateral, phylogenetic lines, emerging side by side from a common ancestral stock which may have been one of the primitive groups of the condylarthran stock from the North American lower Paleocene or perhaps Cretaceous.”

Flerov (1957, 1967, p. 24) suggested that the Dinocerata and Creodonts share a close common ancestry from Late Cretaceous or early Paleogene “Insectivora” (e.g., Leptictidae). Wheeler (1961, p. 73–77) tentatively resurrected the hypothesis that the Pantodonta and Dinocerata share a recent common relationship. On the basis of molar morphology, Wheeler (1961, p. 76–77) also suggested that the South American Xenungulata (= *Carodnia*) may be closely related to the Dinocerata. Romer (1966, p. 385) included the Pantodonta, Dinocerata, Xenungulata and Pyrotheria as suborders of the order Amblypoda.

McKenna (1975) suggested that the Dinocerata might have an arctocyonid ancestry and allied them with the orders Arctocyonia, Tillodontia, Tubulidentata, Embrithopoda and Artiodactyla in his mirorder Eparctocyonia. McKenna (1980) later suggested that *Carodnia* may be an uintathere.

Szalay (1977) included the Dinocerata within the superorder Mesaxonia with the orders Perissodactyla, Embrithopoda, Hyracoidea, Proboscidea, Sirenia, Desmostylia and Meridiungulata. Somewhat similarly, McKenna and Manning (1977, p. 72) included the Dinocerata in an “unnamed taxon, essentially Paenungulata Simpson, 1945, p. 131 minus Pantodonta but with Perissodactyla added.”

Most recently, Tong and Lucas (1982) and Lucas and Schoch (1982) suggested that the Dinocerata and Xenungulata are sister taxa that share a close common ancestry with the “anagalid” *Pseudictops* of the late Paleocene of Mongolia. It is within this framework (that uintatheres are not ungulates in the traditional sense, but an “anagalid” offshoot) that the rest of this paper is written.

Table 1. Classification of the Uintatheriamorpha.

Mirorder Uintatheriamorpha, new
Order Xenungulata Paula Couto 1952
<i>Carodnia</i> Simpson 1935
Order Dinocerata Marsh 1873a
Family Prodinoceratidae Flerov 1952
<i>Prodinoceras</i> Matthew, Granger & Simpson 1929
Family Uintatheriidae Flower 1876 (1873)
Subfamily Gobiatheriinae Flerov 1952
<i>Gobiatherium</i> Osborn & Granger 1932
Subfamily Uintatheriinae Flower 1876 (1873)
Tribe Bathyopsini Osborn 1898
<i>Bathyopsis</i> Cope 1881
Tribe Uintatheriini Flower 1876 (1873)
<i>Uintatherium</i> Leidy 1872
<i>Tethyopsis</i> Cope 1885
<i>Eobasilileus</i> Cope 1872b

Systematic Paleontology

The following classification (Table 1) and diagnoses are based on a cladistic analysis (Fig. 3) of *Pseudictops*, *Carodnia* and the Dinocerata (*sensu* Wheeler 1961 with the addition of new genera briefly discussed by Tong and Lucas 1982 and revised in this paper). As derived character-states are set forth in the diagnoses, the number of the node on Figure 3 to which these character-states correspond is given in parentheses. Note that in order to diagnose some taxa which may be partly or wholly plesiomorphic, retained primitive character-states must be listed. In such cases the letter “p” is placed in parentheses after these character-states.

Mirorder UINTATHERIAMORPHA, new

DISTRIBUTION: Late Paleocene (Tiffanian) – middle Eocene (Uıntan) of western North America;

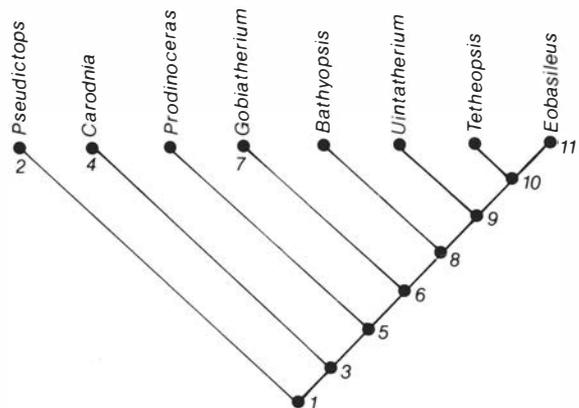


Fig. 3. Cladistic hypothesis of the relationships of *Pseudictops*, *Carodnia* and the Dinocerata. For explanation of the character-states corresponding to the numbered node-points, see text.

Paleocene (Itaboraian) of Brazil and Paleocene (Riochican) of Patagonia; late Paleocene – middle Eocene of China; late Paleocene – early Eocene of the Peoples' Republic of Mongolia; middle Eocene of the U.S.S.R. (Figs. 1, 2; also see Tong and Lucas 1982).

INCLUDED GENERA: *Carodnia*, *Prodinoceras*, *Gobiotherium*, *Bathyopsis*, *Uintatherium*, *Tethyopsis* and *Eobasileus*.

DIAGNOSIS: Eutherian mammals with the following complex of features: incisors broad and, in most cases, multicusped; P3–4/3–4 submolariform to molariform; M1–3/ styler shelves extremely narrow or absent (parastyles small, low and isolated on the anterior cingula); M1–3/ paracones closer to labial margins of teeth than metacones; M1–3/ paralophs and metalophs present, connecting the paracones and metacones to the protocones; P3/ – M3/ possess posterior cingula; P4 – M3/ trigonids compressed anteroposteriorly; and mandibular rami deep (Node 1). M1–2/ protoconules distinct and separated from protocones (the anterior lophs of *Carodnia* here are interpreted as paracone-protococule crests and the posterior lophs as metacone-protococule crests); upper molar outlines subcircular to square; M1/ smaller than M2/ or M3/ and smaller than, or subequal in size to, P4/; M3/ with broad posterior shelf and variably expressed hypocone or hypoconal ridge; M1–3 paralophids very low or absent; M1–3 talonids and trigonids of nearly equal width; M3 hypoconid and hypoconid crest (cristid obliqua) prominent and isolated; neck of astragalus short; naviculoastragalar facet broad, flat and flares (projects) medially; astragalar canal absent; astragalar superior tibial facet and medial tibial facet of trochlea form a smooth, shallow concave surface transversely; astragalar medial and lateral crests sharp (distinct); lateral borders of astragalus elongated relative to medial border; astragalofibular facet well-developed; sulcus astragalii elongated to meet posterior margin of astragalus; astragalar sustentacular facet elongated posteriorly and rides up on anterior portion of base of a distinct ventromedial process; postcranial skeleton relatively large and robust (Node 3).

DISCUSSION: As Tong and Lucas (1982) and Lucas and Schoch (1982) have noted, the Dinocerata, Xenungulata (= *Carodnia*) and the "anagalid" *Pseudictops* appear to possess many synapomorphies (Node 1 of Fig. 3) which unite these groups relative to a primitive therian such as *Kennalestes* or *Asioryctes* (Kielan-Jaworowska, 1977, 1981: note that McKenna 1975, fig. 3 considered *Kennalestes* and *Asioryctes* to be part of a primitive sister taxon

of *Pseudictops* and other erotheres). *Pseudictops* thus can be treated as the primitive sister taxon of the Xenungulata and Dinocerata and can be used to determine some character-state polarities in these groups. Accordingly, the character-states corresponding to Node 1 of Figure 3 listed in the above diagnosis for the Uintatheriamorpha are primitive at the level of Node 3.

Matthew, Granger and Simpson (1929) originally described *Pseudictops lophiodon* from dental material from the late Paleocene Gashato Formation at Khashaat, Peoples' Republic of Mongolia. Sulimski (1968) thoroughly described the known remains of *Pseudictops*, based largely on new materials collected by the Polish-Mongolian Palaeontological Expedition from Naran Bulak and Tsagan Khushu in the Nemegt Basin, People's Republic of Mongolia. Sulimski (1968) also synonymized *Pseudictops arilophiodon* Trofimov, 1952 with *P. lophiodon*.

Matthew, Granger and Simpson (1929) referred *Pseudictops* to ?Insectivora, *incertae sedis* and noted similarities between it, the Leptictidae and *Zalambdalestes*, but did not believe that these indicated any special affinity. They also noted a certain resemblance to the "Amblypoda" (Pantodonta and Dinocerata). Trofimov (1952) added to the description of *Pseudictops*, based on specimens collected by the Mongolian Palaeontological Expedition of the U.S.S.R. Academy of Sciences. He considered *Pseudictops* to be a leptictid, but on the basis of the similarity of its dentition to that of pantodonts, suggested that *Pseudictops* was a herbivore.

McKenna (1963) compared *Pseudictops* to *Anagale*, whereas Van Valen (1964) compared *Pseudictops* to *Eurymylus*. Romer (1966) assigned *Pseudictops* to the Anagalidae. Szalay and McKenna (1971) erected the order Anagalida, including *Pseudictops*, which McKenna (1975) later included as a grandorder in his magnorder Ernotheria, superorder Leptictida. Szalay (1977), however, included the Anagalida as a suborder of the Lagomorpha.

Relative to the Uintatheriamorpha, *Pseudictops* possesses the following autapomorphies: a lagomorph-like astragalus and calcaneum (Szalay, 1977, fig. 16). unlike the "taligrade" astragalus and calcaneum of primitive uintatheres (Pl. 3), and parastylids on M1–3 (Node 2). Relative to *Pseudictops*, the Xenungulata and Dinocerata are united by a number of synapomorphies (Node 3). A close relationship between the Dinocerata and the Xenungulata has been suggested by a number of previous workers (Simpson, 1935; Paula Couto, 1952; Wheeler, 1961; McKenna, 1980; Tong and Lucas, 1982; Lucas and Schoch, 1982). McKenna (1980) even assigned *Carodnia* to the "?Dinocerata." However, both the Xenungulata and the Dinocera-

ta are well-known and well-characterized orders (see diagnoses below) and we find it most satisfactory (causing the least amount of nomenclatural disruption) to retain them as distinct orders and coin a new superordinal term, the mirorder Uintatheriamorpha, to express the close relationship between these forms relative to other eutherian mammals.

Order XENUNGULATA Paula Couto 1952

1952 Xenungulata Paula Couto, p. 370.

DISTRIBUTION: Paleocene (Itaboraian) of Brazil and Paleocene (Riochican) of Patagonia, Argentina.

INCLUDED GENUS: *Carodnia* Simpson, 1935 (= *Ctalecarodnia* Simpson, 1935). *Carolozittelia* Ameghino, 1901, from the Casamayoran (?Lower Eocene) of Patagonia and the pyrotheres may also eventually prove to be uintatheriamorphs; see Paula Couto (1952), McKenna (1980) and the discussion below.

REVISED DIAGNOSIS: Uintatheriamorphs with extremely enlarged P2/2; M1–2/ fully bilophodont; M3/ with hypoconal ridge; M3 lacks distinct paraconid; M1–3 bear postcingulids (Node 4).

DISCUSSION: Recognition that *Carodnia* shares a close common ancestry with the Dinocerata also opens the possibility that *Carolozittelia* and the Pyrotheria (includes *Pyrotherium* Ameghino 1888, *Propyrotherium* Ameghino 1901 [= *Griphodon* Anthony 1924]¹, *Columbitherium* Hoffstetter 1970 and *Proticia* Patterson 1977) should be included in the Uintatheriamorpha. Pyrotheres have either

¹ *Griphodon* Anthony 1924, from probable middle Eocene deposits in Venezuela (Patterson, 1977, p. 421–422), and *Propyrotherium* Ameghino, 1901 from the Mustersan (Middle Eocene: Marshall, 1982) of Patagonia probably are not generically distinct. Comparisons between the two taxa are difficult because of a lack of comparable elements. Nevertheless, AMNH 29394 (Simpson, 1967, pl. 45, fig. 8) referred by Simpson (1967) to *P. ?saxeum* and judged by us to be a lower M/1 (not P/4, contra Patterson 1977, p. 410; note that the external shelf of AMNH 29394 is quite large) is virtually identical to the M/1 of AMNH 17724 (Anthony, 1924, fig. 1; Patterson, 1942, fig. 2), the holotype of *G. peruvianus*, except for a minor size difference (compare Simpson, 1967, table 78 and measurements given by Patterson, 1942, p. 4) and the development of a low cingulid between the lophids on one margin of AMNH 29394. These differences hardly warrant generic distinction though we tentatively consider *P. peruvianum* and *P. saxeum* to be distinct species pending further documentation of dental variation in *Propyrotherium*. *Promoerotherium* Ameghino 1906, rightfully considered by Simpson (1967, p. 237) to be a *nomen dubium*, may, as Simpson (1967) suggested, also be a synonym of *Propyrotherium*.

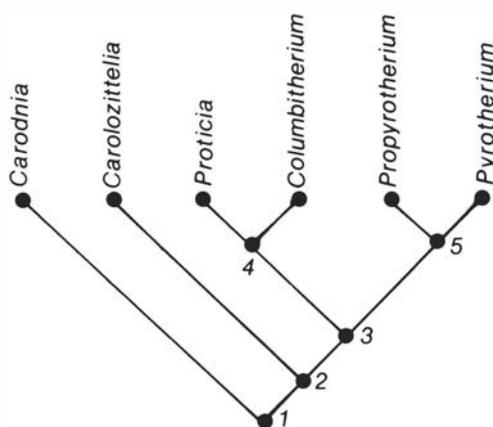


Fig. 4. Tentative cladistic hypothesis of the relationships of *Carodnia*, *Carolozittelia* and the Pyrotheria. Character-states corresponding to the numbered node points are: 1. M1–2/1–2 bilophodont and M/1–3 bear postcingulids. 2. Entoconid-hypoconid cristid present on M/3 and M3/ bilophodont. 3. P/4 bilophodont, hypoconulid lobe present on M/3, large tusk-like incisors present. 4. Molar cusps bulbous and additional cusp(s) present in valleys between lophs. 5. Upper molar lophs canted forward and lower molar lophids canted backward so that loph-lophid wear is abapical; cheek teeth are crown hypsodont.

been explicitly allied with proboscideans (e.g., Ameghino, 1906; Loomis, 1914), with pantodonts and uintatheres (within the Paenungulata: Simpson 1945; also see Matthew 1915), with notoungulates (e.g., Patterson, 1977) or with no other order of mammals (Gaudry, 1909). Recent discussions of pyrothere relationships by Simpson (1978) and McKenna (1980) have dismissed these alliances and McKenna (1975, p. 66) suggested a possible close relationship between pyrotheres and "tethytheres" (e.g., sirenians and desmostylians). Although we have not studied pyrothere relationships in sufficient detail to make a firm judgment, we have (based mostly on information given by Anthony, 1924; Gaudry, 1909; Loomis, 1914; Patterson, 1942, 1977; Paula Couto, 1952; Hoffstetter, 1970 and Simpson, 1935, 1967) constructed a tentative cladistic hypothesis that links the pyrotheres, via *Carolozittelia*, with *Carodnia* (Fig. 4). If this hypothesis cannot be readily refuted, then the Pyrotheria should be included in the Uintatheriamorpha as a suborder of the Xenungulata.

Order DINO CERATA Marsh 1873a

Dinocerata Marsh, 1873a, p. 117.

(For supergeneric terms that have been applied to the Dinocerata, see Wheeler, 1961, p. 17.)

DISTRIBUTION: Late Paleocene (Tiffanian) – middle Eocene (Uintan) of western North America; late Paleocene – middle Eocene of the Peoples' Republic of China; late Paleocene – early Eocene of the People's Republic of Mongolia; middle Eocene of the U.S.S.R. (Figs. 1, 2; also see Wheeler, 1961 and Tong & Lucas, 1982).

INCLUDED GENERA: *Prodinoceras*, *Gobiatherium*, *Bathyopsis*, *Uintatherium*, *Tethyopsis* and *Eobasileus*.

REVISED DIAGNOSIS: Uintatheriamorphs in which P1/1 are extremely small or absent; P2/2 are submolariform; P3–4/3–4 molariform; metastylids present on P/2 – M/3; P/3 – M/3 metalophids oriented obliquely and inclined posteriorly; P/3 – M/3 with large, anteriorly set and isolated hypococonids and hypoconid crests; entoconid crests and hypoconulid crests present on lower molars (lost in derived dinoceratans); inframandibular flange present in most males (Node 5).

DISCUSSION: The Dinocerata were last thoroughly reviewed and revised by Wheeler (1961). But since that time, a number of new Chinese forms have been described by Tong (1978, 1979) and Zhai (1978) and briefly reviewed by Tong and Lucas (1982). Below, we present both a genus-level revision and a supragenetic classification of the Dinocerata. It is beyond the scope of this paper to attempt a species-level revision of the genera.

In reviewing the validity of the genera of uintatheres, it must be kept in mind that in uintatheres, intraspecific variability appears to have been extremely high for some features. As Flerov (1957), Dorr (1952, 1958), Wheeler (1961) and Dashzeveg (1982) have noted, uintatheres are characterized by strong sexual dimorphism in such characters as size of canines, size of the inframandibular flanges, size of sagittal crests, length of diastemata, size of horns, and overall size and robustness of the skull and skeleton.

The presence/absence of P1/1 is intraspecifically variable in uintatheres. The holotypes of *Bathyopsis fissidens*, *Probathyopsis newbilli*, *Phenaceras lacustris*, and *Houyanotherium primigenum* possess small (vestigial) P1/1's (Wheeler, 1961; Tong, 1978, 1979) as do supposed males of "*Mongolotherium*" *efremovi* (Flerov 1957) and an anomalous specimen of *Uintatherium anceps* (Wheeler, 1961). The holotype of *Prodinoceras diconicus* bears the alveolus for a small P1/ (Tong, 1978). A single specimen of *Gobiatherium* bears a vestigial canine (Osborn & Granger, 1932). As Jepsen (1930, p. 129), Tong (1978, p. 92), Rose (1981, p. 94) and Dashzeveg (1982) have pointed out, and as is also evident from the discussion below, features such as the relative

development of the metacone on P2/ and the protoconules and metaconules on P3/ – M3/; the presence and relative size of the hypocones on M1–3/; the presence of ridges descending posteriorly from the middle of the metalophs of M1–3/; the relative distinctiveness and size of the entoconids; and the form of the posterior portion of the M/3 talonid all vary greatly in uintatheres, both intragenerically and intraspecifically. Thus, these characters must be used cautiously when distinguishing uintathere genera.

We here note that generically-indeterminate specimens of uintatheres have been reported from the lower Eocene Tantou Formation in the Tantou basin, Henan ("Prodinoceratinae": Tong & Wang, 1980) and from a middle Eocene horizon of the Lushi Formation in the Lushi basin, Henan ("Uintatheriinae": Tong & Wang 1980). These specimens have not yet been described. Young and Bien (1935, fig. 5) assigned a partial upper molar from the middle Eocene Guanzhuang Formation (Xintai basin, Shandong) to the chalicothere (*Perissodactyla*) genus *Grangeria*, but this tooth may belong to a uintathere. Tong and Lucas (1982) reported a maxillary fragment with an incomplete M2–3/ from the Eocene of the Turpan basin (Xinjiang) as representing a generically-indeterminate occurrence of an uintathere about the size of the North American species *Bathyopsis fissidens*. Gabuniya (1962, 1977) has reported "Uintatheriidae?" from the ?upper Eocene at Tschaibulak in the Zaissan basin in Kazakhstan.

Family PRODINOCERATIDAE Flerov 1952

1952 *Prodinoceratidae* Flerov, p. 1029.

DISTRIBUTION: Late Paleocene and early Eocene of western North America, the People's Republic of China and the People's Republic of Mongolia.

INCLUDED GENUS: *Prodinoceras*.

DIAGNOSIS: Relatively small to medium-sized dinoceratans with a relatively non-molariform P2/; full set of upper and lower incisors; entoconids moderately to very distinct; entoconid and hypoconid crests present on lower molars; lower molars relatively elongated; skull with single sagittal crest; astragalus bears a short, but distinct, neck (p).

DISCUSSION: The Prodinoceratidae, consisting of the single genus *Prodinoceras*, is the plesiomorphous sister taxon of all other dinoceratans and thus must be diagnosed as possessing a suite of retained primitive characters and lacking the derived characters of the Uintatheriidae.

Prodinoceras Matthew, Granger & Simpson, 1929

- 1929 *Prodinoceras* Matthew, Granger & Simpson, p. 10.
 1929 *Probathyopsis* Simpson, p. 1.
 1939 *Bathyopsoides* Patterson, p. 373.
 1952 *Mongolotherium* Flerov, p. 1030.
 1958 *Prouintatherium* Dorr, p. 507.
 1978 *Jiaoluotherium* Tong, p. 92.
 1978 *Houyanotherium* Tong, p. 95.
 1978 *Pyrodon* Zhai, p. 104.
 1979 *Phenaceras* Tong, p. 395.
 1979 *Ganatherium* Tong, p. 397.

DISTRIBUTION: Same as that for the *Prodinoceratidae*.

REVISED DIAGNOSIS: Same as that for the *Prodinoceratidae*.

DISCUSSION: We consider nine generic names to be junior subjective synonyms of *Prodinoceras*. Although this may seem a surprising taxonomic decision, we draw attention to the following considerations that have influenced our judgment:

1. Many features that have been used to differentiate *Probathyopsis*, *Bathyopsoides*, *Mongolotherium*, *Prouintatherium*, *Jiaoluotherium*, *Houyanotherium*, *Pyrodon*, *Phenaceras*, and *Ganatherium* from each other and from *Prodinoceras* either are features that display evident sexual dimorphism in uintatheres (e.g., size of inframandibular flange) or are features that are variable within a single species (often a single sample) of uintatheres (e.g., size and distinctiveness of the P2/ metacone and metaloph).

2. Since many taxa of primitive uintatheres (examples are *Prodinoceras martyr*, *Probathyopsis newbilli* and *Pyrodon xinjiangensis*) are known from only a few specimens, there has been a tendency to attach taxonomic significance to almost any morphological feature that appears to be unique, regardless of how minor that feature is. In some cases these unique features still remain a minor peculiarity of a single specimen, or, as noted above, can be shown to be a feature variable in a single sample of uintathere specimens.

3. Part of the synonymy of *Prodinoceras* presented here has already been explicitly documented, or at least suggested by previous workers. Thus, Gazin (1956, p. 16) suggested that *Bathyopsoides* may be a synonym of *Probathyopsis*. Rose (1981, p. 96) supported Gazin's suggestion, and Tong and Lucas (1982, p. 552–554) explicitly synonymized *Bathyopsoides* with *Probathyopsis*. Rose (1981, p. 93–96) further noted that "the similarities between *Prodinoceras* and *Probathyopsis* are so close that it seems probable that they are congeneric," and Rose demonstrated that *Prouintatherium* is a junior subjective synonym of *Probathyopsis*. In addition, Dashzeveg (1982) has pre-

sented cogent arguments for synonymizing *Prodinoceras*, *Probathyopsis* and *Mongolotherium*.

4. Within the context of a cladistic analysis of uintathere genera (Fig. 2), we are unable to identify derived character-states that separate *Probathyopsis*, *Bathyopsoides*, *Mongolotherium*, *Prouintatherium*, *Jiaoluotherium*, *Houyanotherium*, *Pyrodon*, *Phenaceras*, and *Ganatherium* from *Prodinoceras* as monophyletic taxa of generic rank.

The following historical resumé and analysis provides more detailed documentation of these considerations and thus further establishes the synonymy of *Prodinoceras* advocated here.

Matthew, Granger and Simpson (1929) named *Prodinoceras* (genotypic species = *P. martyr*) for a crushed palate and lower jaws (AMNH 21714: Pl. 1, Fig. 1; Pl. 2, Fig. 1) from the upper Paleocene Gashato (Khashaat) Formation at Khashaat in the south-central People's Republic of Mongolia (Fig. 2). In naming *Prodinoceras*, Matthew, Granger and Simpson (1929, p. 10–11) made the following observations:

"It [*Prodinoceras*] is very closely comparable with an undescribed genus from the Clark Fork Beds, upper Paleocene, of Wyoming [*Probathyopsis* of Simpson (1929)], and like the latter it is an almost ideal ancestral type of uintathere so far as known. It differs, however from the Clark Fork genus in details of P2/, heel of M/3, and other minor features, which might be interpreted as being very slightly more advanced in the present form and in any event remove it somewhat farther from the later North American genera [of uintatheres]."

Simpson (1929, p. 1), when naming *Probathyopsis* (the undescribed genus from the Clark Fork beds alluded to by Matthew, Granger and Simpson (1929); genotypic species = *P. praecursor*), listed the following detailed differences in the morphology of its cheek teeth that purportedly distinguish it from *Prodinoceras*:

1. The labial and posterior borders of P2/ of *Probathyopsis* are more nearly at right angles to each other than are those of the P2/ of *Prodinoceras*.

2. The P2/ protocone of *Probathyopsis* is less distinct and is united to the middle of the ectoloph by a single crest, instead of the two crests that unite the P2/ protocone to the ectoloph in *Prodinoceras*, and thus enclose a small trigon basin.

3. The P2/ metacone of *Probathyopsis* is less distinct (smaller) than that of *Prodinoceras*.

4. The upper cheek teeth of *Probathyopsis* have complete lingual cingula whereas those of *Prodinoceras* do not.

5. The M1–3/ hypocones of *Probathyopsis* are lingual of the protocones, not labial of the protocones as in *Prodinoceras*.

6. The M/3 “posterior talonid crest” (hypoconulid crest) of *Probathyopsis* is higher than that of *Prodinoceras*.

Wheeler (1961, p. 21) further distinguished *Prodinoceras* from *Probathyopsis* by “P3–4/ with distinct ectoloph” in *Prodinoceras*, i.e., the P3–4/ ectoloph clefts of *Probathyopsis* are slightly deeper than those of *Prodinoceras*. Furthermore, as Matthew, Granger and Simpson (1929, p. 10) noted, in *Prodinoceras martyr*, the P2/ ectoloph is turned inward 45 degrees to the tooth-row whereas Simpson’s (1929, p. 1, fig. 1) reconstruction of the upper tooth-row of *Probathyopsis praecursor* shows P2/ with an ectoloph nearly parallel to the tooth-row. This was used as one of the diagnostic features distinguishing these two genera by Wheeler (1961).

Nevertheless, both Simpson (1929) and Matthew, Granger and Simpson (1929) neglected to point out that, although the right P2/ of the holotype of *Prodinoceras martyr* has “a metacone indicated but not rising free of ectoloph; protocone distinct, lower than metacone, united to paracone by a strong crest and to metacone by a weaker one, enclosing a small basin” (Matthew, Granger and Simpson 1929, p. 10), the left P2/ of the same specimen lacks the distinct metacone-protocone crest that forms the posterior boundary on the small trigon basin of the right P2/. Jepsen (1930, p. 129) first pointed this out when describing the new species *Probathyopsis successor*, and we have confirmed the veracity of his observations by examining AMNH 21714, the holotype of *Prodinoceras martyr*. Thus, one of the characters used by Simpson (1929) to differentiate *Probathyopsis* and *Prodinoceras*, the presence of a protocone-metacone crest on P2/ of *Prodinoceras* and its absence on P2/ of *Probathyopsis*, is not a valid basis for distinguishing these genera.

Jepsen’s (1930) description of *Probathyopsis successor* further weakened the generic distinctions between *Probathyopsis* and *Prodinoceras* listed by Simpson (1929). As Jepsen (1930, p. 128–129) noted, “this species [*Probathyopsis successor*] has many characters in common with both *Probathyopsis praecursor* and *Prodinoceras martyr*, and differs only slightly from each.” Of particular interest here is Jepsen’s (1930, p. 129) observation that “in outline, these two teeth [the P2/’s of *Prodinoceras martyr* and *Probathyopsis successor*] resemble each other more than either one approximates P2/ of *Probathyopsis praecursor*.” It is also worth noting that the M1–3/ hypocones of the holotype of *Probathyopsis successor* (PU 13234) are lingual of, or, on an anteroposterior line with, the protocones

(Jepsen, 1930, pl. 4, fig. 10), as in *Prodinoceras martyr*, not labial of the protocones as in *Probathyopsis praecursor*. Thus, by 1930 it was already obvious that differences in P2/ structure could not be used to differentiate specimens assigned to *Prodinoceras* and *Probathyopsis* and that the position of the M1–3/ hypocones relative to the protocones was somewhat variable in specimens then assigned to *Probathyopsis*.

Subsequent to Jepsen (1930), two additional species of *Probathyopsis* have been proposed. Patterson (1939) named *Probathyopsis newbilli* for a lower jaw (the holotype: FMNH P 15549) and four isolated teeth from the upper Paleocene interval of the Wasatch Formation (also known as “DeBeque Formation”) in the Piceance Creek Basin, Colorado. The isolated M1/ (FMNH P 14939) Patterson (1939, p. 380) assigned to *Probathyopsis newbilli* lacks a complete lingual cingulum and thus in this feature more closely resembles the holotype of *Prodinoceras martyr* than it does the holotype of *Probathyopsis praecursor*.

Probathyopsis lysitensis was named by Kelley and Wood (1954, p. 356) for isolated lower teeth and jaw fragments from the Lysite Member of the Wind River Formation, Wind River Basin, Wyoming. Kelley and Wood (1954, p. 357) noted that *Probathyopsis lysitensis* “is more advanced than any other described species [of *Probathyopsis*], especially in the reduction of the protolophid and the character of the heel of M/3, in which it is approaching *Bathyopsis*.” The known lower teeth of *Probathyopsis lysitensis* differ from the corresponding teeth of *Probathyopsis praecursor* in the following features:

1. There is no swelling of the labial base of the P/4 protoconid in *Probathyopsis lysitensis*, as there is in *Probathyopsis praecursor*.
2. M/3 of *Probathyopsis lysitensis* is larger and has a much better developed hypoconulid crest than does M/3 of *Probathyopsis praecursor*.

When these differences are compared with those enumerated by Simpson (1929; see above) to differentiate *Probathyopsis* from *Prodinoceras*, it seems clear that the lower dentition of *Probathyopsis lysitensis* is as distinct from the lower dentition of *Probathyopsis praecursor* as the lowers of *Prodinoceras martyr* are from those of *Probathyopsis praecursor*. Thus, a taxonomy of primitive uinatheres consistent with the original generic distinctions made by Matthew, Granger and Simpson (1929) should have separated the taxon described by Kelley and Wood (1954) at the generic level from *Probathyopsis*. This, and the fact that some of the features Simpson (1929) originally used to differentiate *Probathyopsis* from *Prodinoceras* (i.e.,

structure of the P2/, position of the M1–3/ hypocones, presence or absence of complete lingual cingula on upper cheek teeth) are variable in the specimens Simpson (1929), Jepsen (1930) and Patterson (1939) assigned to *Probathyopsis* should have rendered the generic distinction of *Probathyopsis* from *Prodinoceras tenuos*.

Nevertheless, to add to the fine (and we believe, somewhat inconsistent) distinctions made between genera of primitive uinatheres in North America, two additional genera were named as distinct from both *Probathyopsis* and *Prodinoceras*. Patterson (1939, p. 373) named *Bathyopsoides* (type species = *B. harrisorum*) for a lower jaw (the holotype: FMNH P 15546), partial skull (a paratype: FMNH P 15552) and dentary fragment plus isolated canine and skeletal fragments (another paratype: FMNH P 15574) from the Wasatch Formation in the Piceance Creek Basin, Colorado. Most of the characters Patterson used to differentiate *Bathyopsoides* from *Probathyopsis* and *Prodinoceras* were later shown by Dorr (1952, 1958) and Wheeler (1961) to be sexually dimorphic in uinatheres. Thus, we agree with Tong and Lucas (1982) that the large canines, large inframandibular flanges, prominent sagittal crest and long diastemata of the holotype and paratypes of *B. harrisorum* suggest that these specimens are males. These features thus cannot be used to diagnose *Bathyopsoides* as a distinct genus as Patterson (1939) did when naming *Bathyopsoides*. Other features used by Patterson (1939) to diagnose *Bathyopsoides* are, once again, minor dental differences that are variable among specimens Simpson (1929), Jepsen (1930) and Patterson (1939) were willing to assign to *Probathyopsis* (e.g., P2/ metacone relatively distinct; M3/ entoconid small) or are not valid differences (e.g., M1/ relatively small, a condition seen in *Probathyopsis* and *Prodinoceras*).

Dorr (1958, p. 507) named *Prouintatherium* (genotypic species = *P. hobackensis*) for a lower jaw and isolated upper teeth (the holotype: UM 27249) that were part of a quarry sample of uinathere specimens he referred to *Prouintatherium hobackensis* from the Hoback Formation in the Hoback River Basin, Wyoming. Previously, Dorr (1952) had referred these specimens to *Probathyopsis successor*. Dorr's (1958, p. 507–508) diagnosis of *Prouintatherium* made no reference to *Prodinoceras* and mostly was concerned with differentiating his new genus from *Probathyopsis*, *Bathyopsoides* and the horned uinatheres (i.e., *Bathyopsis*, “*Elachoceras*”, and *Uinatherium*). As Rose (1981, p. 93–96) pointed out, *Prouintatherium hobackensis* “appears to be dentally indistinguishable from *P[robathyopsis] praecursor*”. The other features cited by Dorr (1958) that supposedly

differentiate *Prouintatherium* from *Probathyopsis* were the following: 1. The mandibular symphysis of *Prouintatherium* is deeper and longer than that of *Probathyopsis*. 2. The lower incisors of *Prouintatherium* have a single or double lingual ridge and strong external (posterior) heels, unlike those of *Probathyopsis successor*. 3. The metastylids of *Prouintatherium* are weaker than are those of *Probathyopsis*. 4. The upper cheek teeth of *Prouintatherium* have incomplete lingual cingula like those of *Prodinoceras martyr* but unlike those of *Probathyopsis*.

Like Rose (1981), we judge these differences either to be due to sexual dimorphism (i.e., deeper and longer mandibular symphysis) or to be differences that are so variable among specimens of primitive uinatheres that they are not of taxonomic significance. We thus concur with Rose (1981) in considering *Prouintatherium hobackensis* Dorr, 1958 to be a junior subjective synonym of *Probathyopsis praecursor* Simpson, 1929. Moreover, we also agree with Rose (1981) that *Probathyopsis successor* Jepsen, 1930 should also be considered a junior subjective synonym of *Probathyopsis praecursor*. Accepting that Dorr's (1958) “*Prouintatherium*” is *Probathyopsis*, comparing the labial view of the P2–4/ of *Prodinoceras* (Matthew, Granger and Simpson, 1929, fig. 7) with that of *Probathyopsis* (Dorr, 1958, Pl. 75, fig. 6) reveals no significant differences in the depths of the ectoloph clefts of P3–4/. If these taxonomic judgments and observations are accepted, then clearly there is no available means to differentiate *Probathyopsis* from *Prodinoceras* as a distinct genus. In other words, those features that Simpson (1929) and Wheeler (1961) used to differentiate *Probathyopsis* from *Prodinoceras* are now known to be variable among North American specimens assigned to *Probathyopsis*, *Bathyopsoides* and/or *Prouintatherium*. Indeed, even if these features could be used consistently to segregate specimens, they still only warrant specific, not generic, distinctions (Dashzeveg, 1982, p. 93). Therefore, we concur with Dasheveg (1982) by considering *Probathyopsis* Simpson, 1929 (= *Bathyopsoides* Patterson, 1939; = *Prouintatherium* Dorr, 1958) to be a junior subjective synonym of *Prodinoceras* Matthew, Granger and Simpson, 1929.

Chow (1960) described *Prodinoceras turfanense* from the upper Paleocene Taizicun Formation, Turpan Basin, Xinjiang, People's Republic of China. Chow (1960) distinguished *P. turfanense* from *P. martyr* by the possession of an unbasined P2/ (similar to that of *Probathyopsis*), P4/ relatively shorter than in *P. martyr*, M1–3/ with weaker labial cingula and smaller and slightly more externally placed hypocones, and size slightly smaller than *P. martyr*.

Chow and Tung (1962) described *?Probathyopsis sinyuensis* on the basis of a single maxillary fragment with incomplete M1–2/ from the middle Eocene Ningjiaoshan Member of the Xinyu Group (Yuanshui Basin, Jiangxi). Tong and Lucas (1982) suggested that this species should be reassigned to *Phenaceras*, without justifying this decision. *?P. sinyuensis* is distinguished by prominent ridges extending from the paracones into the basins of M1–2/ – “two crests, one from the metacone and the other from behind the metaloph, extending downwards to meet each other and form a small pit-like depression with a small cusplet rising from the cingular shelf” (Chow and Tung, 1962, p. 371) – and relatively shallow clefts in the M1–2/ ectoloph. Otherwise, the M1–2/ of *?P. sinyuensis* are of the stereotypic uinthere pattern.

On the basis of additional material from the deposits that produced *P. turfanense*, Tong (1978) described *Prodinoceras diconicus*, erected the new genus *Jiaoluotherium* for *P. turfanense* and described *Houyanotherium primigenum* (the genotypic species) and *H. simplum*. *P. diconicus* (Pl. 1, Fig. 2) differs from *P. martyr* in possessing P1/, an unbasined P2/, M1–2/ hypocones set relatively labially, relatively long P3–M3 trigonids, relatively large paralophids, low M3/ entoconid and relatively indistinct lower molar entoconid and hypoconulid crests (Tong, 1978). *Jiaoluotherium* was diagnosed by Tong as follows (free translation of the Chinese in Tong 1978, p. 92–93):

Fairly marked variation in P2/ metacone; with circa 30 percent of the specimens having no well-marked metacone. P3–4/ with strong ectoloph between paracone and metacone; basins shallow; protoconules positioned relatively labially on P3/ – M3/ such that the protoloph and metalophs form a U-shaped ridge. Hypocone on M3/ narrow and small and on a narrow shelf. Lower cheek teeth with very short trigonids, paraconids reduced and medially-placed; except for M1/, paralophids extremely poorly developed; cingulids on posterior margins relatively well-developed and form wide basins. M3/ talonid short, hypoconulid not as wide and as large as in *Prodinoceras*, but usually fairly strong (well-developed). Diastema short. Inframandibular process of jaw not large. Second and third tarsals not fused. Tibia-tarsus with well-marked cone-shaped process and fibular articulation.

It is important to note that *Jiaoluotherium* is known from dental (Pl. 1, Fig. 3; Pl. 2, Figs. 2, 4), cranial and postcranial material, including a partial manus and pes (Pl. 3). Indeed, comparable postcranial elements are not known for other primitive uinthere

and thus cannot be used at present to distinguish *Jiaoluotherium* from other closely related taxa². As in *Prodinoceras*, there is a great amount of dental variability in specimens assigned to *Jiaoluotherium* by Tong (1978). For example, in IVPP V. 4082.2, a palate referred by Tong (1978) to *J. turfanense*, the right P2/ bears a larger metacone and is turned at a greater angle to the tooth-row than the left P2/, and the right M1–2/ bear larger and more distinct hypocones than the left M1–2/ (Tong and Lucas, 1982, Pl. 1, Figs. 3, 4).

Houyanotherium (Pl. 1, Fig. 4; Pl. 2, Fig. 3) was distinguished by its lack of a metacone on P2/ and relatively small hypocones on M1–2/ but well-developed M3/ hypocone, small M3/ entoconid and well developed M3/ hypoconulid (Tong, 1978). A free translation of Tong's (1978, p. 95) diagnosis is as follows:

P2/ with no metacone; M1–2/ hypocone small or absent; M3/ hypocone strongly developed and protruding posteriorly, forming a wide and large talon with an accessory conule on the talon. M3/ entoconid fairly small; hypoconulid well-developed, higher than hypoconid and entoconid; hypoconulid with extremely poorly-developed, or no, ridge.

However, as noted above, these characters are variable and occur in other “genera” discussed above.

Tong (1979) described *Phenaceras lacustris* (Pl. 1, Fig. 5; Pl. 2, Fig. 5) and *Ganatherium australis* from the ?lower Eocene Pinghu Formation, Chijiang Basin, Jiangxi, People's Republic of China. *Phenaceras* was distinguished by a full set of incisors (three on each side, upper and lower); absence of an inframandibular flange; the presence of P1/; a prominent metacone on P2/; metaconules on the upper cheek teeth relatively small to nearly absent; hypocones on M1–2/ very small to absent, but moderately well-developed on M3/; M1–3/ with narrow posterior cingular shelves; and metaconids and metastylids well-separated on the lower cheek-teeth. In bearing extremely small hypocones on M1–2/ but a well-developed hypocone on M3/, *Phenaceras* is identical to *Houyanotherium*.

Ganatherium is known only from a single M3/ which is distinguished by its small entoconid and anteroposteriorly short trigonid. Otherwise, it is nearly identical in size and morphology to M3/'s referred by Tong (1979) to *Phenaceras*. Because the characters that distinguish *Ganatherium* appear to

² All the postcrania Dorr (1958) referred to *Prouintatherium* (UM 34122, 34123, 27523; Dorr 1958, pl. 76, pl. 77, figs. 21–24) pertain to the pantodont genus *Coryphodon* (Lucas 1984).

be relatively minor and variable in other genera and species of uintatheres (e.g., *Prodinoceras*), we here consider *Ganatherium australis* a junior subjective synonym of *Phenaceras lacustris*.

As documented in the preceding paragraphs, there is a fairly marked amount of continuous variation in primitive uintathere cheek tooth morphology in such features as presence or absence of P1/1; P2/ metacone development; depth of P3-4/ ectoloph clefts; position and relative development of hypocones on M1-3/; relative development of cingula on M1-3/; relative development of paralophids, metaconids, metastylids, entoconids and hypoconids on the lower cheek teeth; relative lengths and widths of lower trigonids and talonids; and relative development of hypoconulid crest on M/3. Furthermore, in the sample of *Jiaoluootherium* described by Tong (1978), the same magnitude of variation is seen. Moreover, as described above, the features used by Tong (1978, 1979) to distinguish his *Jiaoluootherium*, *Houyanotherium* and *Phenaceras* from *Prodinoceras* are just such variable features. Therefore, we here also consider the genera *Jiaoluootherium*, *Houyanotherium* and *Phenaceras* to be junior subjective synonyms of *Prodinoceras*.

Flerov (1952) named *Mongolotherium plantigradum* and in 1957 the additional species *M. efremovi*, for medium-sized uintathere specimens from the lower Eocene Naran Bulak Formation at Ulan Bulak and Naran Bulak in the Nemegt Basin, People's Republic of Mongolia. Dentally, *Mongolotherium* is similar to *Prodinoceras*, but was purportedly distinguished by a relatively molariform P2/ in which the protocone is connected to the paracone by a well-developed crest and the smaller metacone is connected to the protocone by a less well-developed crest (thus forming a rudimentary V as in P3/ - M3/); P3-4/ possess well-developed protoconules; hypocones well-separated on M1-3/; M3/ hypocone extremely large and borne on a large posterior talon shelf; and M/1-3 with separate entoconids. Cranially, *Mongolotherium* was purportedly distinguished by very prominent sagittal and occipital crests with the dorsal aspect of the occiput projecting far posterior to, and overhanging, the foramen magnum; a long diastema between C1/1 and P2/1-2 (P/1 apparently was vestigial in some specimens of *M. efremovi*); and horns or arched nasals absent.

Tong (1978) synonymized *Mongolotherium* with *Prodinoceras*, treating it as a subgenus of the latter, on the basis of the close similarity in the dental morphology of the two genera. Dashzeveg (1982) recently argued, on the basis of new specimens of *Prodinoceras* from the People's Republic of Mongolia, that the purported distinctive features of *Mon-*

golotherium either are present on specimens with dentitions unambiguously referable to *Prodinoceras* (especially the prominent sagittal and occipital crest; occiput projecting far posterior to, and overhanging, the foramen magnum) or are variable among specimens of *Prodinoceras* and those specimens Flerov (1952, 1957) referred to *Mongolotherium*. We accept Dashzeveg's (1982) suggestions that this variability either reflects sexual dimorphism, ontogenetic size changes, attritional wear changes on the teeth or represents differences so minor that they could be used for specific, but certainly not generic, distinctions. Therefore, we follow Dashzeveg (1982) in considering *Mongolotherium* Flerov 1952 to be a junior subjective synonym of *Prodinoceras* Matthew, Granger & Simpson 1929.

Zhai (1978) described *Pyrodon xinjiangensis* on the basis of three M3/'s (one of which is the holotype) and a M/3 from the lower Eocene Dabu Formation in the Turpan Basin, Xinjiang, People's Republic of China. The M3/ of *Pyrodon* is larger than that of *Prodinoceras* and bears a large hypocone on a large, posterior talon shelf. In this feature *Pyrodon* is very similar to some specimens referred to *Mongolotherium* by Flerov (1952, 1957) and therefore we consider *Pyrodon* to be a junior subjective synonym of *Prodinoceras* (= *Mongolotherium*).

Qi (1979) listed *Mongolotherium efremovi* and *Pyrodon* sp. from the lower Eocene Bayan Ulan Formation, 20 km east of Ailigemiao, Inner Mongolia, People's Republic of China. However, no specimens have been described to substantiate these reports.

Thus, all early and primitive uintatheres are here allocated to a single genus. However, we stress that there may be a number of valid, distinct species of *Prodinoceras*. It is beyond the scope of the present paper to evaluate the species-level taxonomy of the *Dinocerata*.

Family UINTATHERIIDAE Flower 1876 (1873)

1876 Uintatheriidae Flower, p. 387. (see Wheeler 1961, for synonyms).

DISTRIBUTION: Early - middle Eocene of western North America, middle Eocene of the People's Republic of China and the U.S.S.R.

INCLUDED GENERA: *Gobiotherium*, *Bathyopsis*, *Uintatherium*, *Tethyopsis* and *Eobasileus*.

REVISED DIAGNOSIS: Large dinoceratans lacking upper incisors; P/3 - M/2 paraconids and paracristids greatly reduced; lower molars relatively shortened with entoconid crests and hypoconulid crests greatly reduced; lower incisors bilobed; parasagittal crests present; astragalus lacks a neck; some

form of protuberance development or inflation of bone on the skull in the nasal region (Node 6).

DISCUSSION: For many years there has been some confusion over the family name Uintatheriidae which hopefully will be settled here. The first family name applied to the uintatheres was Tinoceridae (Marsh 1872b), but was soon replaced with Tinoceratidae (Marsh, 1873b). Cope later proposed the name Eobasileidae (Cope 1873). Flower (1876), however, used the name Uintatheriidae. Although some authors subsequently used Eobasileidae (Hay, 1929–1930) or coined other terms (e.g. Dinoceratidae Zittel, 1893), Uintatheriidae has been generally accepted (Simpson, 1945; Romer, 1966; Wheeler, 1961; Flerov, 1957; Szalay and McKenna, 1971) and it is generally cited as “Uintatheriidae Flower, 1876”.

Wheeler (1961) demonstrated that *Tinoceras* is a junior subjective synonym of *Uintatherium*; fortunately, the types of *T. grande* (YPM 11040) and that of *U. anceps* (YPM 11030) share common elements (skull parts, vertebrae) so that this synonymy seems beyond doubt and has been well accepted. Thus, according to Article 40 of the International Code of Zoological Nomenclature (Stoll et al. 1964), since the name *Tinoceras* is a synonym of *Uintatherium*, and since the name Tinoceratidae was rejected in favor of the name Uintatheriidae before 1961, the name Uintatheriidae “takes the date of the rejected name [Tinoceratidae] of which it is considered to be the senior synonym” (p. 41). As the senior synonym of Tinoceratidae Marsh 1873b, Uintatheriidae is also the senior synonym of Eobasileidae Cope, 1873. Therefore, Uintatheriidae is the technically valid name of this family of the Dinocerata and common usage is upheld. However, Recommendation 40A of the Code suggests that “a family-group name adopted under the provisions of Article 40 should be cited with its own author and date, followed by the date of the replaced name in parentheses.” Therefore, it seems advisable that the name be cited as “Uintatheriidae Flower 1876 (1873)” not simply as “Uintatheriidae Flower 1876” as is currently being practiced.

Subfamily GOBIATHERIINAE Flerov 1952

1952 Gobiatheriidae Flerov, p. 1032.

DISTRIBUTION: Middle Eocene of China and possibly the middle Eocene of the U.S.S.R. (Fig. 1).

SOLE INCLUDED GENUS: *Gobiatherium*.

REVISED DIAGNOSIS: Uintatheriids without upper canines and with lower canines greatly reduced;

P2/ with a prominent cingular cusp on its anterolabial corner; skull long, thin and shallow with a flat sagittal region; nasals strongly arched with a bony septum connecting their anterior ends to the premaxillae; zygomatic arches broad and flare-out in the region of the glenoid fossae; lower jaw long and shallow with a tall ascending ramus and lacking an inframandibular flange; metacarpals relatively slender and elongate (Node 7).

DISCUSSION: *Gobiatherium*, the sole genus of the subfamily, is discussed below.

GOBIATHERIUM Osborn & Granger 1932

1932 *Gobiatherium* Osborn & Granger, p. 10.

DISTRIBUTION: Same as that for Gobiatheriinae.

REVISED DIAGNOSIS: Same as that for Gobiatheriinae.

DISCUSSION: *Gobiatherium mirificum* was described by Osborn & Granger (1932) from the middle Eocene Irдин Manha Formation, Inner Mongolia, People's Republic of China. The cheek teeth of *Gobiatherium* are extremely similar to those of *Uintatherium*, except that in *Gobiatherium* there is a prominent cingular cusp on the anterolabial corner of P2/, the anterior and posterior cingula are relatively well-developed on P2/ – M3/, P3/ – M3/ bear small metaconules on the metalophs, the hypocoines of M1–3/ are very small and poorly defined, and on M1–3 the metastylids are set distinctly apart from the metaconids. However, *Gobiatherium* lacks not only the upper incisors, but also the upper canines. The three lower incisors on either side are bilobed and the lower canine is incisiform. The skull of *Gobiatherium* is extremely distinctive. It is long, thin and shallow with a broad and flat sagittal region. The nasals are strongly arched and a bony septum connects the anterior ends of the nasals to the premaxillae. Horns on the skull are absent. The zygomatic arches are broad and flare out in the region of the glenoid fossae. The lower jaw is long and shallow, with a tall ascending ramus, and lacks an inframandibular flange. The metacarpals of *Gobiatherium* are relatively elongate and slender compared to those of *Uintatherium*.

Qi (1979) listed *Gobiatherium mirificum* from the middle Eocene Arshanto Formation about 40 km south-southeast of Iren Dabasu, People's Republic of China along with *G. "major"* and *G. "monolobotum"*, both *nomina nuda*. Chow and Tung (1962) described an upper right premolar? (not an incomplete lower cheek tooth as stated by Tong and Lucas 1982) from the ?middle Eocene Yuhuangding Formation (Liguangiao Basin, Henan) as

?*Gobitherium* sp. However, due to the stereotyped nature of uintathere cheek teeth and the damaged condition of the specimen, we regard it as a generically indeterminate dinoceratan. Beliajeva, Trofimov and Reshetov (1974) have also reported *Gobitherium* sp. from the middle Eocene at Torujayr in Kirgiziya, U.S.S.R. without further documentation.

Subfamily UINTATHERIINAE Flower 1876 (1873)

1876 Uintatheriidae Flower, p. 387.

DISTRIBUTION: Early – middle Eocene of western North America; middle Eocene of China.

INCLUDED GENERA: *Bathyopsis*, *Uintatherium*, *Tethyopsis* and *Eobasileus*.

REVISED DIAGNOSIS: Uintatheriids with cranial horns; distinct hypocones on M1–3/ (Node 8).

Tribe BATHYOPSINI Osborn 1898

1898 Bathyopsidae Osborn, p. 182.

DISTRIBUTION: Early and middle Eocene of western North America.

SOLE INCLUDED GENUS: *Bathyopsis*.

REVISED DIAGNOSIS: Relatively small uintatheriines with small horns and a vestigial P/1 present (variable?) (p).

DISCUSSION: *Bathyopsis*, the sole genus of the Bathyopsini, is the plesiomorphous sister-taxon of the higher uintatheres (Uintatheriini) and thus is characterized by the presence of retained primitive characters.

BATHYOPSIS Cope 1881

1881 *Bathyopsis* Cope, p. 75.

DISTRIBUTION: Same as that for the Bathyopsini.

REVISED DIAGNOSIS: Same as that for the Bathyopsini.

DISCUSSION: Cope (1881) described *Bathyopsis fissidens* on the basis of a lower jaw from the early Eocene (Lostcabinian) of the Wind River Basin, Wyoming. Osborn (1913) described a skull from the same area which he provisionally referred to *B. fissidens*. Wheeler (1961) described *B. middleswarti* on the basis of a skull from early Bridgerian (middle Eocene) beds in Sweetwater County, Wyoming.

Bathyopsis is distinguished by relatively high, but anteroposterorly compressed trigonids with extremely small paraconids and paracristids on M/1–3; metastylids that are strong, but closely appressed to the trigonids; entoconids that are not particularly distinct; no hypoconulid crests; no sagittal crest, but rudimentary parasagittal crests and parietal, frontal and maxillary horns present; cranial table slightly basined; skull relatively shallow; and temporal fossae visible in dorsal view. The holotype lower jaw of *B. fissidens* bears alveoli for a complete set of lower incisors, a canine and a small P/1. The skull referred to *B. fissidens* by Osborn (1913) bears a large alveolus for C1/ and lacks P1/. The premaxillae of this specimen are missing. The holotype skull of *Bathyopsis middleswarti* preserves the premaxillae, but lacks upper incisors or a P1/. The holotype lower jaw of *B. fissidens* bears a large inframandibular process; however, this may be due to sexual dimorphism. *B. middleswarti* is distinguished from *B. fissidens* by its larger size, relatively wider occiput and better-developed maxillary, frontal and parietal horns, features that possibly reflect sexual dimorphism. Gazin (1952) reported a mandible of cf. *Bathyopsis fissidens* from the Bridgerian of the Bridger Basin which lacks an inframandibular flange.

Tong (1982) listed “? *Bathyopsis*” from an undetermined horizon in the Turpan basin (Xinjiang, China), and Tong & Lucas (1982, p. 552) noted that the incomplete M2–3/, upon which Tong (1982) based his identification, pertains to “a generically indeterminate occurrence of an uintathere about the size of the North American species *Bathyopsis fissidens*.” At present, there is no evidence that *Bathyopsis* occurs in Asia.

Tribe UINTATHERIINI Flower 1876 (1873)

1876 Uintatheriidae Flower, p. 387.

DISTRIBUTION: Middle Eocene of western North America; middle Eocene of China.

INCLUDED GENERA: *Uintatherium*, *Tethyopsis* and *Eobasileus* (for synonymies see Wheeler, 1961).

DIAGNOSIS: Large uintatheriines with well-developed cranial horns and a deep basin between the temporal crests and anterior to the occipital crest; lower canine incisiform; paracristids on P/3–M/3 virtually absent; entoconids rarely distinct; entoconid crests and hypoconid crests absent; skeleton large and heavy; tail short (Node 9).

DISCUSSION: Wheeler (1961) last revised the then known distribution of the higher uintatheres

and thus it is not necessary to rediagnose formally these genera here. Of the numerous genera and species erected by Leidy, Cope, Marsh, Osborn, Scott, Speir and Cook in the late nineteenth and early twentieth centuries, Wheeler (1961) recognized three genera and four species as valid: *Uintatherium* Leidy, 1872 including the single species *U. anceps* (Marsh, 1871); *Tethyopsis* Cope, 1885 composed of the type species *T. speirianus* (Osborn, 1881) and *T. ingens* (Marsh, 1885a) and *Eobasileus* Cope, 1872b composed of the single species *E. cornutus* (Cope, 1872b).

Wheeler (1961) diagnosed the taxa which he regarded as valid, listed a number of referred specimens for each taxon, but failed to either justify his synonymies or to describe the morphology of the taxa in any detail. For example, Wheeler (1961) considered no less than twenty-eight named species of large North American uintatheres to be synonyms of *Uintatherium anceps* without ever explicitly documenting these synonymies. However, it appears that at a generic level, Wheeler's (1961) revision is valid and we accept the genera that he recognized and defined as valid, although they may be in need of revision at the specific level.

Uintatherium, *Tethyopsis* and *Eobasileus* are all characterized by relatively large, deep skulls with three pairs of horns and a deep basin on the cranium between the temporal crest and anterior to the occipital crest. The upper canine is large and sabre-like and protected by a distinct inframandibular flange. The upper cheek teeth are of the stereotypic uintathere pattern, very similar to those of *Gobiatherium*, but lacking the cingular cusp on the anterolabial corner of P2/ and (variably) with better-developed hypocones on M1-3/. The lower canines are incisiform. The lower molars are relatively short and broad, virtually lack paracristids, entoconid crests and hypoconulid crests. The entoconids are usually not separate from the posterior talonid lophid.

Uintatherium is the most common uintathere in terms of number of specimens which Wheeler (1961) referred to this taxon. *Uintatherium* is known from the upper Bridgerian (middle Eocene) of the Bridger and Washakie Basins, Wyoming (Wheeler, 1961), from the middle Eocene of the Uinta Formation in the Piceance Creek Basin, northwestern Colorado (see Appendix 1), from the middle Eocene Lushi Formation, Lushi Basin, Henan, China (Tong and Wang 1981), possibly from the Uintan (middle Eocene) Rose Canyon Formation, California (cf. *Uintatherium*: Hutchison 1971), possibly from the Bridgerian-Uintan (middle Eocene) Buck Hill Group in the Agua Fria area, Brewster County, Texas (cf. *Uintatherium anceps*: West 1982) and

possibly from the middle Eocene Guanzhuang Formation, Xintai Basin, Shandong, China (Chow & Tung 1962). The last mentioned occurrence consists of a damaged right M3/ and two upper canines which Chow & Tung (1962) originally referred to "cf. *Uintatherium* sp." Tong & Lucas (1982, p. 551), in referring to these specimens, suggested that "the relatively small size of these teeth make it more likely that they pertain to *Gobiatherium*." However, the cheek teeth of *Uintatherium* and *Gobiatherium* overlap in size, whereas those of *Tethyopsis* and *Eobasileus* tend to be larger (cf. Wheeler, 1961, Chart 5 and Osborn & Granger's 1932 measurements of *Gobiatherium*). Furthermore, *Gobiatherium* lacks upper canines (only a small, vestigial canine is known in one specimen: Osborn and Granger 1932) whereas the Chinese specimen includes two moderately large upper canines, as in *Uintatherium*. Also, although broken, the Chinese M3/ appears to bear a better-developed hypocone than is seen on some specimens of *Gobiatherium* (cf. Tong & Lucas, 1982, Pl. 1, Fig. 6). Thus, we here agree with Chow & Tung's (1962) original reference of these teeth to cf. *Uintatherium* sp.

Uintatherium is distinguished by the possession of a relatively broad skull in which the posterodorsal portion of the temporal fossa is very wide; the maxillary horn is set above the diastema and the parietal horn is set well in advance of the occiput. Specimens of *Uintatherium* also tend to be slightly smaller than those of *Tethyopsis* and *Eobasileus*. *Uintatherium* appears to be plesiomorphous relative to *Tethyopsis* and *Eobasileus*.

Relative to *Uintatherium*, *Tethyopsis* and *Eobasileus* are united by the possession of the following shared-derived character-states: skull long and narrow; portion of skull in front of maxillary horns relatively elongate; and parietal horns relatively near the occiput (Node 10).

Tethyopsis is known only from the middle Eocene of the Washakie Formation, Washakie Basin, Wyoming (Wheeler, 1961). This genus is distinguished by a skull in which the portion of the skull in front of the maxillary horns is only moderately elongate, and the maxillary horn is positioned mainly above the diastemata.

Eobasileus is known from the middle Eocene (Uintan) of the Washakie Formation, Washakie Basin, Wyoming and Colorado and from the middle Eocene (Uintan) of the Uinta Formation, Uinta Basin, Utah. *Eobasileus* is distinguished by a skull in which the portion in front of the maxillary horns is extremely elongate, and the maxillary horn is above the premolars (Node 11). Thus, *Tethyopsis* appears to plesiomorphous relative to *Eobasileus*.

Palaeobiogeography of the Dinocerata

If the cladistic hypothesis presented above is accepted, then the following palaeobiogeographical hypothesis (*sensu* Ball, 1975) can be constructed: The common ancestor of uinatheres and xenungulates arose in Asia from an "anagalid" (*Pseudictops*-like) ancestry. This taxon achieved a trans-Pacific distribution and gave rise to uinatheres in Asia and North America. A vicariance event (severing of a previous connection or "sweepstakes route" between North and South America?) explains the divergent origin of xenungulates from this common ancestor in South America and the subsequent austral endemism of the xenungulates. Uinatheres hegemony was of long duration in Asia and North America and terminated in gigantic, horned animals. However, the isolated evolutionary radiation of xenungulates in South America apparently was short-lived and very confined, unless, of course, pyrotheres did originate from a xenungulate close to *Carodnia* and/or *Carolozittelia*. In that case there was a highly divergent evolutionary radiation of xenungulates (*sensu lato*) in South America.

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Appendix 1:

The occurrence of *Uintatherium* in the Piceance Creek Basin, northwestern Colorado.

We here document the occurrence of *Uintatherium* in the Uinta Formation in the Piceance Creek Basin, northwestern Colorado. Recent prospecting (Lucas & Kihm, 1982) located a partial skull (uncatalogued UCM specimen: Fig. 5) here identified as *Uintatherium anceps* in the lower part of the Uinta Formation (formerly "Evacuation Creek Member" of the Green River Formation) in the north-central Piceance Creek Basin along North Barcus Creek (Lucas & Kihm, 1982, pls. 9, 10; Fig. 6). This partial skull is edentulous except for the canines which were broken from their alveoli by erosion. Most of the skull is very poorly preserved, but the rostrum bearing the two maxillary horns is nearly complete except for the tips of the nasals. The size of the uncatalogued UCM specimen and the fact that its parietal horns (not illustrated here) are well in front of the occiput and its maxillary horns are above the postcanine diastemata permit its ready referral to *Uintatherium anceps* as Wheeler (1961, p. 26–28) diagnosed that taxon. The occurrence of *U. anceps* in the Uinta Formation in the Piceance Creek Basin indicates an upper Bridgerian – Uintan age for the stratum in which it occurs. This age assignment is consistent with correlations of the Uinta Formation in the Piceance Creek Basin based on the age and depositional history of the Green River Formation (Grande, 1980) with which the Uinta Formation intertongues.

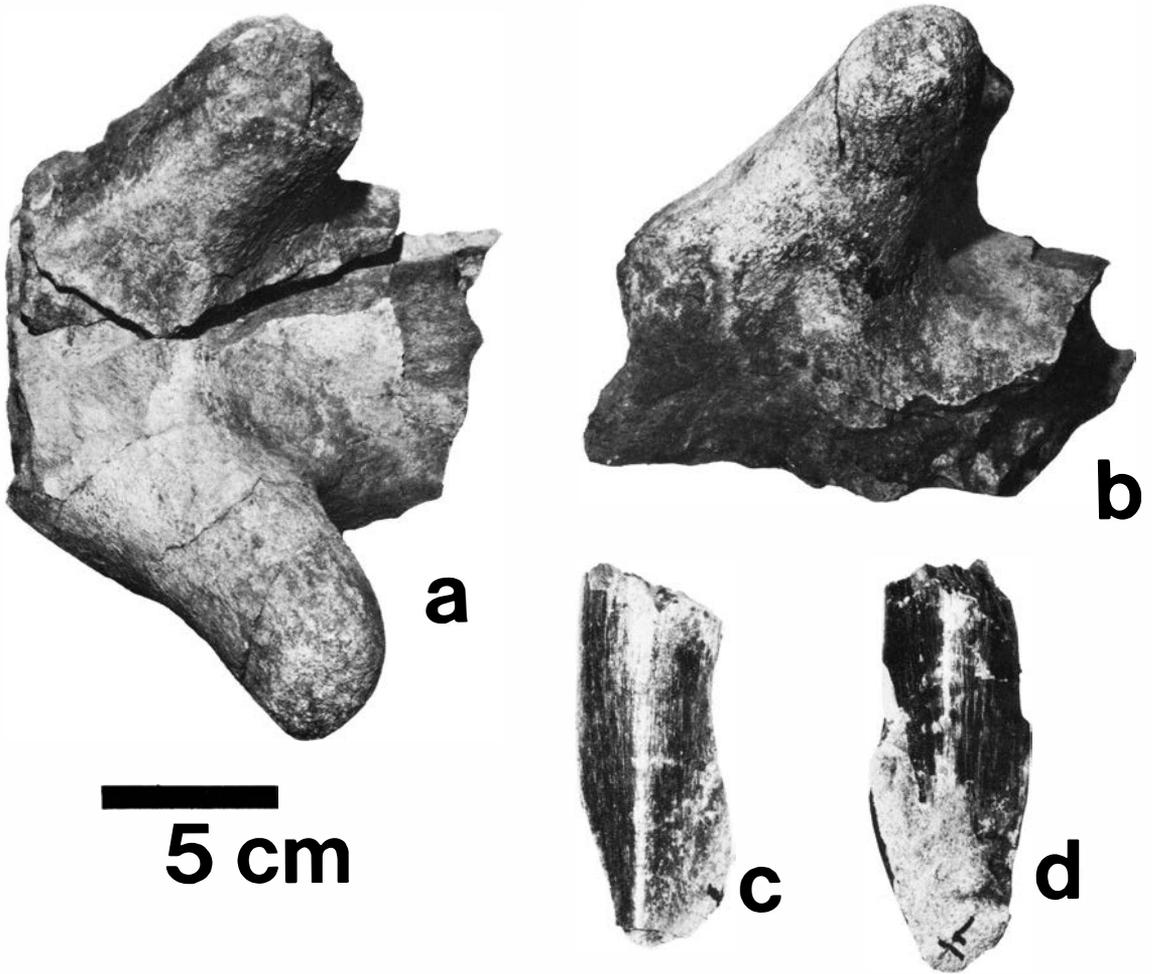


Fig. 5. Uncatalogued UCM partial skull and canines of *Uintatherium anceps* from the Uinta Formation, Piceance Creek Basin, northwestern Colorado. a, dorsal view of rostrum with two maxillary horns. b, right lateral view of rostrum. c, external view of left upper canine. d, external view of right upper canine with adhering matrix.

Appendix 2:

Description of measured stratigraphic section in Fig. 6. Uinta Formation ("Tu1" of Hail 1974):

Unit	Lithology	Thickness (m)
13	Paper shale, grey	5.00 +
12	Sandstone, buff, medium-grained, subarkosic, trough-crossbedded. ET 7-5, the locality which produced the uncatalogued UCM specimen, a partial	14.75

skull of *Uintatherium* sp.

(Fig. 5), is just above a channel scour base and is approximately 5 m below the top of the unit.

11	Sandstone, buff, fine-grained, massive.	2.25
10	Siltstone, brown, fossil leaves and plant fragments.	2.00
9	Sandstone, buff, medium- to coarse-grained, quartzose, trough-crossbedded in upper part, planar crossbeds in lower part, <i>Platanus</i> leaves at base of unit.	10.5
8	Sandstone, buff, fine-grained, massive, plant debris near base.	5.5

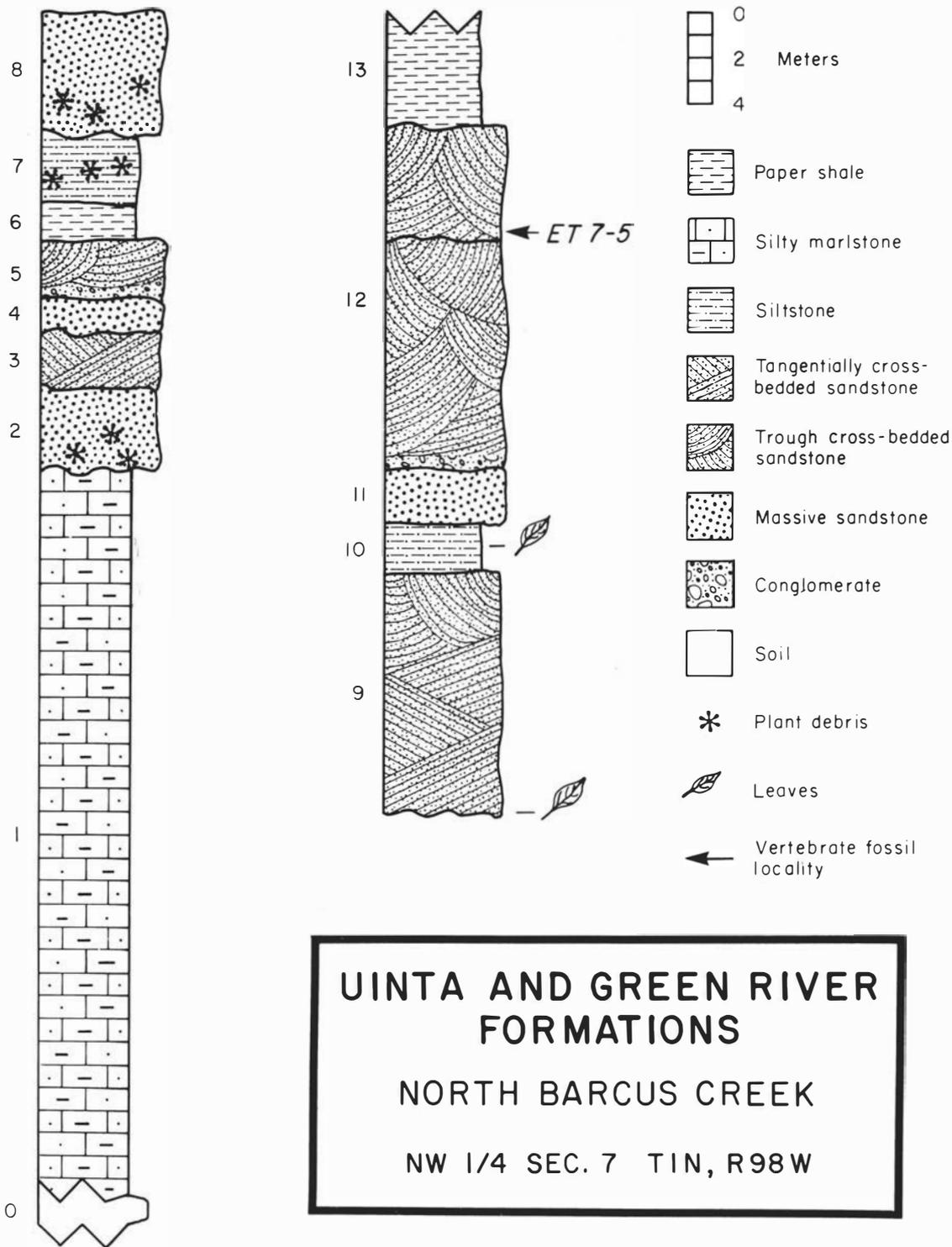


Fig. 6. Measured stratigraphic section of part of the Green River (unit 1) and Uinta (units 2–13) Formations on the north bank of North Barcus Creek, NW 1/4, Sec. 7, T. 1 N., R. 98 W., Rio Blanco County, Colorado, showing the stratigraphic position of ET 7–5, the locality at which a partial skull of *Uintatherium anceps* (Fig. 5), was collected.

7	Siltstone, brown, plant debris throughout unit.	3.0
6	Paper shale, grey, insect larvae.	1.5
5	Sandstone, buff, medium-grained, subarkosic, trough-crossbedded with massive conglomeratic layer at base.	2.5
4	Sandstone, buff, fine-grained, massive.	1.5
3	Sandstone, buff, medium- to coarse-grained, quartzose, planar crossbedded.	2.25
2	Sandstone, buff, fine-grained, massive, contains, plant debris near base.	3.75

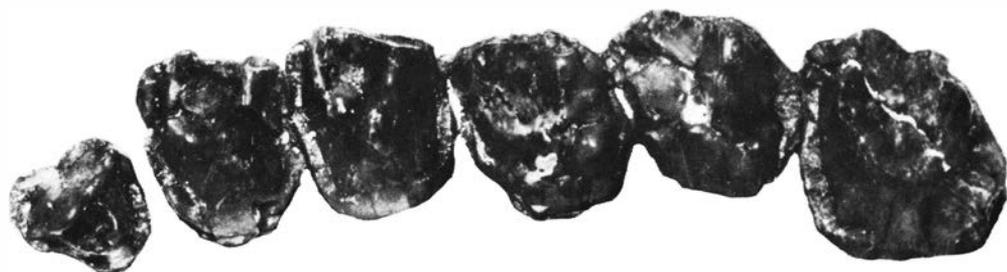
Green River Formation:

1	Marly siltstone, weathers light grey and yellow and forms a well-weathered slope overgrown by sage, juniper and pinyon. Some beds are more marly and more resistant. Hail (1974) included this unit in his unit "Tu1" but noted that it is "similar in lithology to Parachute Creek Member of Green River Formation and may merge elsewhere with Parachute Creek Member." On the basis of its lithology, we here assign unit 1 to the Green River Formation.	31.5+
0	Soil (covered), thickness not measured.	-----

PLATES

Plate 1

1. *Prodinoceras martyr*. AMNH 21714 (holotype), occlusal view of right P2/–M3/ (photograph reversed). × 1,3.
2. *Prodinoceras diconicus*. IVPP V4079 (holotype), occlusal view of right P2/–M3/ (photograph reversed). × 1,5.
3. “*Jiaoluootherium*” *turfanense*. IVPP V4082,2, occlusal view of left P2/–M3/. × 1,5.
4. “*Houyanotherium*” *primigenum*. IVPP V4080 (holotype), occlusal view of left P2/–M3/. × 1,5.
5. “*Phenaceras*” *lacustris*. IVPP V5058,1, occlusal view of left P2/–M3/. × 1,5.



1



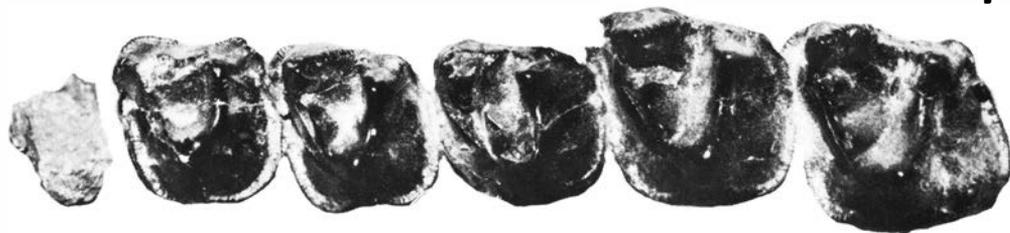
2



3



4



5

Plate 2

1. *Prodinoceras martyr*. AMNH 21714 (holotype), occlusal view of right M/3. $\times 1,5$.
2. “*Jiaoluootherium*” *turfanense*. IVPP V4082,3, occlusal view of left M/2–3. $\times 1,5$.
3. “*Houyanotherium*” *simplum*. IVPP V4082, occlusal view of left P/2–M/2. $\times 1,5$.
4. “*Jiaoluootherium*” *turfanense*. IVPP V4082,3, occlusal view of left C/1, P/3–M/3 and right C/1, P/2–M/1, $\times 1,3$.
5. “*Phenaceras*” *lacustris*. IVPP V5058,1, occlusal view of left P/2–M/3, $\times 1,5$.



1



2



3



4



5

Plate 3

"Jiaoluotherium turfanense"

1. IVPP V64022, dorsal view of right manus. $\times 1,0$.
2. IVPP V64022, dorsal view of right pes. $\times 1,0$.
3. IVPP V4082, dorsal view of left calcaneum, $\times 1,0$.
4. IVPP V4082, ventral view of left calcaneum. $\times 1,0$.
5. IVPP V4082, dorsal view of left astragalus. $\times 1,0$.
6. IVPP V4082, ventral view of left astragalus. $\times 1,0$.

